M. le Docteur E. Leloup
avec ses meilleurs
voeux pour 1958
l'auteur

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From the Zoological Museum of the University and the Biological Laboratory of the Institute of Marine Research, Helsinki/Helsingfors

On the Immigration of the Glacial Relicts of Northern Europe, with Remarks on their Prehistory

By

SVEN G. SEGERSTRÅLE

Communicated September 16th, 1957

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To the Memory of

SVEN LOVÉN

Inaugurator of
Research on
Glacial Relicts

CONTENTS

I. FOREWORD.

The author's interest has long been attracted by the glacial relicts of Northern Europe, that remarkable element of the aquatic fauna of this area which was first reported, about a century ago, from the Swedish lakes Vänern and Vättern by SVEN LOVÉN and has since been the subject of a vast literature, dealing with involved problems of zoogeography, ecology, taxonomy, genetics, morphology, etc.

Particular interest attaches, of course, to the fundamental question of the immigration of relicts into the North-European lacustrine area, since most of the animals concerned are derived from forms which today inhabit the arctic marine waters of Eurasia. As a matter of fact, this problem has continued to be eagerly discussed up to the present day. Its main points are still subject to argument and a thorough scrutiny of the history of this invasion as a whole, based upon our present knowledge of relict distribution and modern geological views, has long been felt desirable.

The present account is an attempt to fill this gap. As a first step towards the elucidation of the immigration route of the relicts, the author, in 1956, published an account of their occurrence in Finland and the adjacent Russian areas, where a great number of new localities have been discovered in the last few decades, and some aspects of the immigration problem were discussed in two other papers (SEGERSTRÅLE 1954, 1957). In March 1955, the author paid a visit to Russia in order to secure recent literature and discuss problems, including those of Quaternary geology, with workers in that eastern area, which is of special importance with respect to the problem of relict invasion.

Finally, the present paper will also contain a discussion of some new suggestions on the prehistory of the glacial relicts which are based upon study of the immigration problem.

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II. BACKGROUND.

1. DATA ON THE LATE- AND POST-GLACIAL HISTORY OF NORTHERN EUROPE.

The (southern) extent of the last glaciation is seen from fig. 11 (p. 40). About 20 000 years ago the southern margin of the ice-sheet began to retreat from northern Germany. However, the main regression did not set in until the period known as Gotiglacial time, when the margin of the ice began to retreat from Scania and the Danish islands of Zealand and Langeland. Between this stage and the beginning of its recession from northern Germany the ice advanced several times, as is shown by the moraines left behind (fig. 11).

When the southern part of the Baltic basin ultimately became free of ice, the first stage of the Baltic came into existence, the depression being filled with fresh water. For a short time there seems to have existed a narrow connection between this region and the ocean, across western Scania. When this connection was cut, owing to the general crustal uplift, the *Baltic Ice-Lake* began to form (fig. 34, p. 80). This freshwater stage ended when the ice-sheet, about 10 000 years ago, reached a part of Central Sweden low enough to allow drainage of the lake down to the level of the ocean, and salt water entered the Baltic basin: the *Yoldia Sea* then came into existence (fig. 30, p. 72). The connection with the ocean was gradually cut again, however, as a result of land-upheaval, and the Baltic was converted into a new freshwater lake, the *Ancylus Lake* of the early post-glacial period; the lake drained westward through an outlet at the site of the previous sound, later through a southern outlet. Finally the last, salty stage in the history of the Baltic set in, owing to the penetration of salt water into the basin through the Danish sounds. In the *Littorina Sea* (fig. 35, p. 84), which now formed, the salinity of the Baltic reached values considerably higher than those of today. At that time, large areas along the coasts of the Baltic were again flooded.

2. SURVEY OF EARLIER VIEWS ON THE HISTORY AND IMMIGRATION OF THE RELICTS OF THE AREA.

The classical lecture given by LOVÉN before the Swedish Academy of Science on October 10, 1860, and printed in 1862, which initiated research on the glacial relicts, bore the modest title »Om några i Vettern och Venern funna Crustaceer» (On some crustaceans found in the lakes Vättern and Vänern). The crustaceans reported from the Swedish lakes concerned were *Mysis relicta*, *Mesidotea entomon*, *Pontoporeia affinis*, *Gammaracanthus lacustris* and *Pallasea quadrispinosa*[1]. Two of them, *Mesidotea* and *Pontoporeia*, were also known from the Baltic. LOVÉN stressed that most of these animals were known from the Arctic Sea in an identical or closely related form, whereas none had been found off the west coast of Scandinavia. *Pallasea quadrispinosa* held a special position, as it was of lacustrine origin and seemingly identical with a species known from Lake Baikal. In addition, a fish, *Myoxocephalus* (*Cottus*) *quadricornis*, was regarded by LOVÉN as belonging to the same unexpected faunal element of the Swedish lakes. He summed up as follows (p. 288, transl.): »Thus we have, enclosed in our lakes, a group of strange animals which from these lakes point towards the sea, and not towards that in the west, but, via the Baltic, across land, towards the Arctic Sea with its low salinity, and furthermore, one species connected with a lake of the Siberian mountains».

The explanation for the surprising facts thus revealed, LOVÉN sought in the geological past of Northern Europe. Already by that time it was generally assumed — LOVÉN reviewed the results of THORELL and earlier authors — (1) that this area had once been glaciated, (2) that wide areas of Central Sweden etc. had been flooded by the sea, and (3) that a connection between the Baltic and the White Sea had existed. LOVÉN suggested that the animals reported by him from Vänern and Vättern were remnants of that arctic fauna which could be assumed to have lived in the cold sea in front of the ice-cap. They had entered the Baltic area »from the east, from the present White Sea, the salinity of which, like that of the Arctic Sea on the whole, is low, but which, nevertheless, seems to harbour very high-arctic species» (p. 305). Later on, owing to crustal uplift, the Baltic was again barred from the Arctic Sea. As a consequence, most of the isolated species died out; only a few of them, being especially capable of adapting themselves to the new conditions, survived in the Baltic and

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[1] In this historical survey, the modern names (cf. p. 29) are used for the relicts even in cases where the original paper gives another name.

even in some of the largest lakes. This was Lovén's explanation, which laid the foundations of relict research. (The term »relict» was coined later on, by Peschel in 1875.) Lovén concluded by commenting on the presence of the ringed seal in several lakes, viz. Baikal and the neighbouring Oron (modern handbooks mention the animal from Lake Baikal only, under the name of *Phoca sibirica;* cf. Bobrinsky, 1944, p. 177), Onega (Bobrinsky does not mention this lake amongst those inhabited by the Ringed Seal), Ladoga and Saimaa; he assumes that these freshwater occurrences of the marine animal concerned are also due to past changes in the relations of land and sea.

In a subsequent paper of 1863, »Till frågan om Ishafsfaunans fordna utsträckning öfver en del af Nordens fastland» (On the question of how far the arctic marine fauna extended over a part of Northern Europe), Lovén published reports of new finds of relicts in numerous Swedish lakes, in some lakes of Finland, in Ladoga and Onega and in the Baltic. He stressed that the races of herring living in the Baltic and in the White Sea are morphologically identical and that the same applies to Baltic and arctic specimens of the fish *Liparis vulgaris*, as well as to the polychaetes *Harmothoë sarsi* and *Terebellides strömi*. On the other hand, in discussing the modifications of the relict forms of *Myoxocephalus*, *Mesidotea* and *Mysis*, he emphasized that these forms had proved to represent morphologically juvenile stages of the arctic ones.

In connection with a lecture on the Baltic, given before a meeting of Scandinavian scientists in 1863 and published in 1865, Lovén once more advanced the views surveyed above.

Lovén's view on the history of the Baltic herring and *Liparis vulgaris* was adopted by Malmgren in his account of the Finnish ichthyofauna of 1863, and applied to some other fishes of the Baltic, too.

Stimulated by Lovén's theory, Russian workers also soon began to search for glacial relicts, especially in the Karelian area through which the immigration from the White Sea was assumed to have taken place. In 1868, Kessler (and one of his collaborators) established the occurrence of relicts in Onega and the adjacent lakes; in Ladoga such animals had already been found by Finnish and Russian zoologists. The new records were included in Kessler's account of 1868 of the fauna of Lake Onega and its neighbourhood. There reference was made to Lovén's theory, but Kessler did not express any own view on the matter.

However, this theory found an advocate in the Russian zoologist Jarzhynsky who, in 1868 and 1869, carried out investigations of his own in Karelia, establishing new localities for relict animals. As a result of all these studies, relicts were proved to occur in many places along the strait assumed by LOVÉN to have existed between the Baltic and the White Sea, in that area where Ladoga and Onega lie to-day; and in an article (published in the popular journal »Znanye») JARZHYNSKY eagerly argued in favour of LOVÉN's hypothesis.

New localities were continually discovered in Karelia, and, on the basis of the comprehensive data gathered, an animated discussion arose between Russian workers, in the last quarter of the 19th century, concerning the origin and history of the relicts of the area. In the 70's and 80's, LOVÉN's theory was attacked by GRIMM, CHERNIAVSKY, POLJAKOV, and others; the last-mentioned author thought it possible that the relicts had spread to their present area through active migration.

Limnocalanus macrurus was included for the first time in the group of marine relicts of North-European lakes by NORDQVIST (1887) and CREDNER (1887), and their view has been generally accepted by later authors. It may also be noted that the latter author, in his comprehensive account of the relict lakes of the world, shares the unfavourable attitude towards the postulated immigration of arctic relicts from the east, stressing that up to that time no marine deposits had been found in the area between the Baltic and the White Sea.

In 1900, SAMTER and WELTNER reported on the first find of relicts in northern Germany: in Lake Madüsee in Pommern *Mysis relicta*, *Pallasea quadrispinosa* and *Pontoporeia affinis* had proved to occur. As regards their immigration, the authors rejected LOVÉN's assumption of a former connection between the Baltic and the White Sea on the basis of geological records, and concluded that the relicts of the Swedish lakes had come from the west, from the North Sea. In the case of Lake Madüsee the following hypothesis was advanced: When the ice-cap began to melt and its margin retreated across the area concerned, water was dammed up between the ice and the so-called Baltic terminal moraine, running south of Madüsee; as a consequence, the region was submerged. The freshwater basin so formed emptied, in the form of a wide strait along the coast of Jutland, into the North Sea. This area must have been brackish at that time and there *Mysis oculata* was modified and adapted to life in diluted water. From the North Sea the relicts invaded the strait which stretched towards the present coast of northern Germany and was fresh in its eastern part; finally, when the ice-dammed basin drained down to the Baltic and the lake was formed, a population of the relicts was isolated there.

In subsequent years, SAMTER and WELTNER found the three relicts in numerous other lakes of northern Germany (SAMTER 1901, SAMTER & Weltner 1902). As most of the localities were situated in an area which was thought not to have been submerged during the Glacial Age, the authors concluded that the interpretation of their invasion given for Madüsee was not applicable to these cases.

In 1902, WESENBERG-LUND reported the occurrence of *Mysis, Pontoporeia* and *Pallasea,* as well as some other remarkable animals, in a Danish lake, Furesö, in northeastern Zealand (Själland; *Pallasea* had already been caught in some other lakes of the island). WESENBERG-LUND quoted the view advanced by SARS (1867, 1895) and NORDQVIST (1885) that *Pallasea* could not be regarded as a relict in the same sense as *Mysis* and *Pontoporeia,* since no marine form is known from which it can be derived and since the genus seems to comprise lacustrine species only; furthermore, *Pallasea* tolerates comparatively warm water. Hence, WESENBERG-LUND believed it probable that the crustacean had immigrated into Furesö considerably later than the arctic *Mysis* and *Pontoporeia.* He stressed the difficulty of finding a plausible explanation to account for the presence of the marine forms in the lake and advanced the following hypothesis: The adaptation of *Mysis oculata* took place in the Ancylus Lake (this stage in the development of the Baltic had been postulated by MUNTHE in 1887); when, during the Littorina Period, the water of the Baltic again become salty, the Ancylus fauna sought refuge in the mouths of rivers. By active immigration upstream, the relicts also reached nearby lakes at this period. In this way Furesö, which had never been flooded by the sea, was also populated by relicts, either from the east, i.e. from the Sound (Öresund) with which Lake Furesö is connected by the River Mölleaa, or from the west, from Roskilde Fjord, along a former connection. A corresponding invasion had also resulted in the presence of the relict in the lakes of northern Germany.

In a paper of 1905, in which the whole distribution of *Mysis*, *Pallasea* and *Pontoporeia* in Northern Europe is surveyed, SAMTER returned to the problem of their immigration. He stressed the established absence of these relicts in lakes outside that part of Central and Northern Europe which had once been covered by the inland ice and concluded that their occurrence in the latter area must no doubt be due to events connected with the glaciation. As regards the path of invasion, his interpretation differs fundamentally from that advanced in the paper of 1900 by him and WELTNER. On the basis of results achieved in the 90's by Finnish and Swedish geologists (BERGHELL, DE GEER, SEDERHOLM, RAMSAY), SAMTER now accepted LOVÉN's idea of an eastern connection; however, he also assumed immigration from the west (Skagerrak), across that part of central Sweden which was suggested to have been flooded by the sea during the Yoldia Period. SAMTER reckoned with the possibility that *Mysis oculata* was transformed into *M. relicta* independently in different waters and that the relicts of northern Germany had invaded the lakes of the area from the Ancylus Lake, after becoming adapted there to fresh water.

In a paper of 1907, on the plankton of Lake Mälaren, SVEN EKMAN gave data on the occurrence and ecology of *Mysis relicta* and *Limnocalanus macrurus* in Swedish lakes. He concluded that they are mainly relicts of the Ancylus Lake, where the transformation and adaptation of *M. oculata* and *L. grimaldii* might have taken place, but also reckoned with the possibility of their independent development in other lakes.

In 1912, the Swedish zoologist JÄGERSKIÖLD gave a survey of all the known localities of glacial relicts in Northern Europe, and discussed the problems of morphology, ecology, etc., involved. As regards the origin of these animals, he quoted LOVÉN's theory and referred to the geological view prevailing at that time that the eastern connection with the Arctic Sea, postulated by LOVÉN, had really existed. JÄGERSKIÖLD noted the special position of *Pallasea*, pointed out by earlier authors, but stressed the similarity of the range of this crustacean and that of the other relicts. Like WESENBERG-LUND, JÄGERSKIÖLD suggested that the modification and adaptation of the original invaders took place both in the Ancylus Lake and in other isolated freshwater basins.

In the following year, 1913, an important new contribution to the discussion on the immigration of the relicts was given by VON HOFSTEN. He found LOVÉN's idea of an eastern invasion fully warranted, in view of the established presence of relicts (they are denoted as »arctic or marine glacial») in Onega and the adjacent eastern lakes. However, VON HOFSTEN opposed the concept prevailing at that time that the eastern path had been the only invasion route, and stressed the possibility of immigration from the west as well, across central Sweden, which was flooded during the Yoldia period. As a matter of fact, in 1910, the geologist MUNTHE had already expressed the view that all marine-glacial relicts had immigrated both from the east and the west — mainly from the latter direction — but had not given any facts in support of his theory. The argumentation of VON HOFSTEN is briefly as follows. The presence of *Mysis relicta* in Irish lakes and of *Pontoporeia affinis* in some lakes of southwestern Norway shows that both species must have lived along the Scandinavian coasts in late-glacial time; hence, they have without doubt invaded Northern Europe from the west, too. In the case of *Gammaracanthus,* no corresponding evidence is available but there is every reason to draw the same conclusion. The assumption of a western immigration is also the most natural explanation in the case of the Ringed Seal (subfossil find on the Swedish west coast). *Myoxocephalus* (*Cottus*) had probably come from the west, *Mesidotea* from the east. One might, to be sure, expect the western invaders to have survived in some of the deep, cold fjords of western Scandinavia; however, VON HOFSTEN regarded this objection as of no importance, since, according to him, some relict species must have lived off the coast concerned (cf. above). The main western invasion was assumed to have occurred at the time of the Yoldia Sea. Finally, VON HOFSTEN discussed the history of some other marine forms of Northern Europe which are not found in lakes but the occurrence of which in the Baltic and neighbouring marine waters was concluded to be due to the Ice Age (*Halicryptus spinulosus*, *Pontoporeia femorata*, etc.).

In 1913—1920 EKMAN published his well known series »Studien über die marinen Relikte der nordeuropäischen Binnengewässer» (I—VII) which meant a signal advance in our knowledge of the history, systematics, morphology and ecology of these animals. Below, a brief review is given of those of his results which have a special bearing on the problems discussed in the present paper:

EKMAN shared the opinion that the *Limnocalanus macrurus* living as a relict in lakes is derived from the arctic marine *L. grimaldii*. The following history is concluded for *Limnocalanus* in the Baltic basin: *L. grimaldii* lived in the Yoldia Sea; when the Ancylus Lake came into existence, this form was modified into *macrurus*, and re-transformed into *grimaldii* as the water became salty again. This may have been the case if the Ancylus Lake was entirely fresh; if some parts of it remained saline, *grimaldii* may have lived there continually. The lake populations of *Limnocalanus* (*macrurus*) exhibit a gradual series of morphological changes which mainly concern the form of the head, the front becoming increasingly high and steep when advancing from younger towards older lakes. (II, 1913.) The relict *Pontoporeia affinis* is not, as was assumed by JÄGERSKIÖLD et.al., derived from *P. femorata*, but from an identical form living in the Arctic Sea. (IV, 1918.) There is no doubt about the relict nature of *Pallasea quadrispinosa;* the best evidence is afforded by its distribution, which coincides with that of the other relicts. The absence of a marine form from which *quadrispinosa* could have been derived does not invalidate this conclusion, for the ancestor may have been a lacustrine one. The fact that the genus *Pallasea* is a pronouncedly Siberian one suggests that the species *quadrispinosa* was probably originally a native of lakes of Siberia. From there it may have migrated down rivers to coastal estuarine waters and, following the coast, arrived in the brackish waters of the late-glacial sea of Northern Europe, becoming a relict as the basins were isolated. For this reason *Pallasea quadrispinosa*, too, is to be regarded as a marine glacial relict. (V, 1918.) In the course of their life in fresh water, *Limnocalanus* and *Mesidotea* have undergone considerable modification, whereas *Mysis* and *Pontoporeia* do not exhibit any morphological changes; however, a reduced size is typical of the freshwater populations of most relicts. (VI, 1919.)

In a paper of 1917, on the origin of the peculiar arctic element of the Aralo-Caspian fauna, the Swedish geologist HÖGBOM put forward a hypothesis which for the first time gave a natural explanation of the occurrence of glacial relicts in Northern Europe at unexpectedly high levels; in the main, his view is still generally accepted. (Cf. fig. 23.)

As is well known, the North-European relicts *Phoca*, *Mesidotea*, *Mysis*, *Gammaracanthus*, *Pontoporeia affinis*, and *Limnocalanus* are also found in the Caspian Sea as identical or closely related forms. As an explanation of this feature, a number of hypotheses had been advanced before HÖGBOM's, none of them, however, being convincing. The chief stumbling block was the lack of geological evidence of a former connection between the Arctic Sea and the Aralo-Caspian basin. HÖGBOM suggested the following explanation (somewhat simplified here). When the ice-cap of the last glaciation, advancing from the north, reached the coast of northern Russia, ice-dammed waters must have accumulated in the valleys of the rivers draining northwards. As the ice-margin advanced, these ice-lakes, and with them animals from the Arctic Sea which had been cut off from the sea as the coastal waters were isolated and dammed up, finally reached the watershed in central Russia and drained down to the Caspian Sea; with the overflow, conceivably mainly along the River Volga, the arctic faunal element also reached the Aralo-Caspian basin. HÖGBOM thought his theory applicable also to those relict localities of Northern Europe which were never (during the last glaciation) connected with the sea, and were, therefore, difficult to understand, viz. Lake Kenozero east of Onega, several lakes of Northern Germany and Lake

Furesö in Denmark (cf. above). In the case of Germany and Denmark, Högbom attributed the presence of the relicts to the same glacial phase which brought them to the Caspian Sea, viz. to that regression of the ice-margin in the course of the final melting period which was followed by the Gotiglacial advance; in connection with this regression of the ice-margin, marine animals might have entered the Baltic basin. When the ice-cap once again moved forward, the coastal waters of the southern Baltic with their fauna were dammed up in front of the advancing ice and reached those levels where the lakes at present harbouring relicts are situated today. As an alternative, Högbom suggested that animals from the White Sea migrated from ice-dammed waters south of Ladoga towards the west, along the ice-margin (see fig. 23); however, he considered invasion by way of the Baltic more likely, especially in the case of the western relict localities. He concluded his paper by pointing out the probable applicability of a similar explanation to the occurrence of relicts in non-uplifted areas in North America and Ireland. (Cf. p. 100.)

In 1922, the information concerning the North-European relicts up to that date was summarized by Ekman in his classical account of the immigration history of the Scandinavian fauna. The passage on the invasion of these animals reads as follows (p. 289—90, transl.):

»There has been a fairly full discussion among Swedish relict investigators as to whether the relicts immigrated from the east or from the west. Lovén, and after him Jägerskiöld, fairly decidedly expressed the opinion that the immigration came from the east only, whereas N. v. Hofsten (1913) suggested that several species, at least, have also been able to invade from the west. The latter view must be correct. As, at the time of the Yoldia Sea, the Scandinavian Peninsula was surrounded by arctic seas on all sides, there is no good reason to deny that the euryhaline species were capable of reaching western Sweden, for instance, from the west. *Mysis* also lives as a relict in Irish lakes. Again, in the case of more stenohaline brackishwater species, they must have had access to ideal paths for spread in that imposing system of deeply intruding bays with greatly diluted water which during certain late-glacial periods extended from the White Sea across all the lower parts of Finland and Scandinavia; and there can be no doubt that this invasion path has been more used than the longer way around Norway. But even the latter would not have been totally impassable at the time concerned, when the melting of the ice-caps contributed to the dilution of the Norwegian fjords. The occurrence of *Pontoporeia* in Lake Orrevand in the region of Jaederen

[S. W. Norway] is possibly the result of such a migration, although the species may equally well have come from the east.» For *Pallasea*, Ekman reviewed the result arrived at in his paper of 1918 (cf. above, p. 13). Besides *Myoxocephalus quadricornis*, another fish, the smelt (*Osmerus eperlanus*) was now also included in the group of glacial-marine relicts. Furthermore, the vendace (*Coregonus albula*) and the whitefish (*Coregonus lavaretus*) were suggested to be glacial relicts in certain Swedish lakes.

In 1925, Verestshagin summarized the records of relicts from northern Russia, published or otherwise known by then. He stated that the relicts may be divided into two groups. The first group includes those forms which are found only below the highest shore-lines of the late-glacial sea; such a distribution is typical of *Myoxocephalus*, *Mesidotea*, *Gammaracanthus*, etc.[1] The second group, comprising the rest of the relicts, is characterized by occurrence at higher levels also. Most of the localities reported by Verestshagin referred to the latter group, whereas those harbouring members of the former group were few: L. Seliger (Valdai area), lakes near Vitebsk, etc. (cf. map fig. 12).

In the same year, 1925, Thienemann published a paper on the glacial relicts, especially *Mysis relicta*, of northern Germany. His main purpose was to find an explanation for the absence of *Mysis* from many of the deeper lakes of the region, in spite of the fact that the low temperature demanded by this relict is available there. A plausible answer to this question was found in the poor oxygen supply at greater depths in summer, combined with the warming of the upper strata. Thienemann suggested that in the past these lakes may well have offered *Mysis* tolerable conditions, before their eutrophization set in.

In the first section of the paper, Thienemann surveyed the distribution (localities given in map, see fig. 00 11 in the present paper) of the relicts of northern Germany and discussed their immigration. He subscribed to the sluicing-up theory of Högbom and examined in detail the relation of the lakes to the so-called »Baltic terminal moraine». Högbom had already assumed this terminal moraine to have been deposited as a result of that very advance of the ice-cap which had sluiced the relicts up to higher levels. Thienemann found good agreement between the position of the relict lakes and the moraine concerned, even in the case of Lake Schaalsee

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[1] Besides, *Limnocalanus* and *Eurytemora velox* are mentioned. However, the former relict copepod has since been found in some »too high» continental lakes (cf. below pp. 19 and 24) and thus belongs to the second group; for *Eurytemora*, cf. Ekman 1922 (p. 302—33).

(south of Lübeck), despite the fact that today this lake drains towards the Elbe (this conclusion had already been drawn by him in 1918, on the basis of ichthyofaunal observations).

As a possible explanation of the remarkable absence from northern Germany of a number of the glacial relicts of Fennoscandia, viz. *Myoxocephalus*, *Mesidotea* and *Gammaracanthus* (= the first group of VERESTSHAGIN, see above; for *Limnocalanus,* which was also mentioned by THIENEMANN among the relicts concerned, see p. 15, foot-note), even in lakes that would appear to offer them favourable conditions, THIENEMANN suggested that these animals were not present in the cold sea across which the ice-sheet proceeded at the time of the Baltic advance, but immigrated later on.

In 1927, DECKSBACH discussed some relict localities, disclosed since HÖGBOM published his paper, viz. Lake Wigry in Poland and Lake Seliger in N. Russia (Valdai region). DECKSBACH arrived at the same conclusions as did HÖGBOM, and later THIENEMANN, in the case of the lakes of northern Germany, viz. that there exists a clear relationship between the position of these localities and the so-called Baltic moraine, although, according to new Russian investigations, the eastern continuation of this moraine was to be drawn in a way different from that given by HÖGBOM. As regards Lake Seliger, which belongs to the drainage area of the Volga, DECKSBACH concluded that the *Pallasea* living there has had the same history as the relicts of neighbouring areas, i.e., that it is derived from the Baltic. Incidentally, the same conclusion of a Baltic origin had already been drawn by KESSLER in 1877, with regard to the occurrence of the fishes *Coregonus albula* and *Osmerus eperlanus* in the uppermost reaches of the River Volga (cf. BERG 1928, p. 110, foot-note 3). In addition, on the basis of ecological data, the author discussed the distribution of relicts in the lakes Ladoga, Vyg (East Karelia), and Seliger, as well as in some lakes near Vitebsk, stressing the agreement of his results, as regards the controlling ecological factors, with those obtained by THIENEMANN.

In 1928, THIENEMANN published a continuation of his paper of 1925, giving details of the occurrence of *Mysis*, *Pontoporeia*, and *Pallasea* in the lakes of northern Germany (excepting those of East Prussia), as related to temperature and oxygen supply; data on the presence of other benthic forms were included. Just as in the publication of 1925, the two ecological factors mentioned were shown to determine the distribution of the relicts concerned; the tolerance limits obtained were suggested to be of general application. A report on *Pontoporeia* and *Pallasea* had already appeared in 1926.

Furthermore, THIENEMANN subjected the immigration of the relicts to a new discussion. Some modifications of his concept of the Baltic terminal moraine had proved necessary, but he found that they did not affect the fundaments of the idea that the relicts had been sluiced up ahead of the advancing ice-sheet. As regards the existence of a preceding marine stage of the Baltic — according to THIENEMANN a condition of the hypothesis — he quoted WASMUND, who thought such a stage, in the form of the so-called Eem Sea, unquestionable.

In 1928 a paper was also published by BERG, on the origin of the northern element in the Caspian Sea, which is worthy of mention, since, among other things, the theory of HÖGBOM is discussed.

BERG quoted the results of the Russian geologist JAKOVLEV, who had found deposits of varved clay on the watershed north of the uppermost reaches of the River Volga; this indicated the former existence there of a large ice-lake, draining southwards. Evidence of the ice-dammed lakes postulated by HÖGBOM for this region had thus been obtained, and BERG subscribed to his idea that animals from the northern sea which inhabited these lakes had been passively transported southwards to the Caspian Sea with the overflow.

In 1930, a new contribution to the discussion of the relicts of northern Germany was made by EKMAN. The reason for the publishing of his paper was an attack directed in 1929 by GAMS against HÖGBOM's sluicing-up theory — which was at that time generally accepted — and its application by THIENEMANN. This author had assumed that the Eem Sea existed immediately before that advance of the ice which led to the deposition of the Baltic terminal moraine (cf. above). GAMS opposed this view, referring to geological evidence that the Eem Sea belonged to the last Interglacial and thus was much older than had been supposed by THIENEMANN. Gams suggested that the relicts of the area concerned had reached their present sites by active migration from the Yoldia Sea, thus in principle reviving views that had prevailed before HÖGBOM advanced his explanation.

EKMAN regarded the latter mode of immigration as most unlikely from a biologist's point of view. He admitted that the Eem Sea could not have been responsible for the sluicing-up of the relicts; furthermore, he was aware of the fact that the Baltic terminal moraine referred to by THIENEMANN did not indicate the maximal extension of the ice-cap of the last glaciation but represented only one of the so-called interstadial stages of the retreating phase. However, Ekman believed it theoretically possible that, regardless of the modified conception of the time of the Eem Sea, marine water had been present in the Baltic basin at the outset of the last glaciation; furthermore, he thought it possible that the relict had survived in ice-dammed waters south of the watershed of northern Germany, after having been transported across it in front of the ice in connection with its maximal advance. As a more probable alternative, Ekman suggested, on the basis of ecological data, that just before that advance of the ice which sluiced up the relicts, a marine fauna had penetrated into the Baltic basin across the region of Öresund (the Sound). Furthermore, Ekman, referring to Högbom, stressed the possibility of an eastern connection having existed between the Baltic and the ocean, perhaps by way of ice-dammed lakes. Finally, he pointed out the fact that geological investigations in North America and Ireland had proved to support the idea, advanced by Högbom, that the presence of relicts there in regions which had never been reached by the sea was also due to the sluicing-up effect of ice-dammed waters.

A popular article on the relicts of Sweden, published in 1931 by another Swedish zoologist, Nybelin, is noteworthy, since it included a new view on the immigration history of *Pallasea.*

After mentioning Ekman's hypothesis of immigration from Siberia (cf. p. 13), Nybelin continued (p. 740, transl.): »However, could one not equally well suppose that *Pallasea* already lived in Northern Europe before the great glaciation, during which it was pushed up the rivers of northern Germany — the animal is known to like running water — and, as the ice began to melt, followed the latter northwards again?» As regards the origin of the other Swedish relicts, Nybelin seemed to reckon with invasion from the west, along that connection between the Baltic basin and the Atlantic which existed across central Sweden during the Yoldia period.

In his account of the biological history of the North Sea and the Baltic, of 1932, Ekman expressed the following view on the history of the marine glacial relicts of Northern Europe (p. 38): »Es sind verschiedene Meinungen zu der Frage geäussert worden, ob die glazialmarinen Relikte von NO her (vom Weissen Meer) oder von W her (durch die mittelschwedische Meerenge) ins Baltische Meer gelangt sind. Nachdem die Geologen immer entschiedener zu der Ansicht übergegangen sind, dass während der *Yoldia*-Zeit keine Verbindung zwischen Weissem und Baltischem Meer bestanden hat (MUNTHE 1929), so ist eine Einwanderung von W her wahrscheinlicher.»

In 1937, BOWKIEVICZ reported on the first finds of *Limnocalanus macrurus* in continental waters west of Ladoga (with R. Neva). The relict copepod concerned had two years earlier been proved to occur in Lakes Strusto and Voloso, situated about 230 km southeast of Riga (cf. map fig. 12); the latter lies 132 m. above sea-level and has no outlet.[1] BOWKIEWICZ found the presence of the animal in the lakes understandable only as a result of past geological conditions and refers to the hypothesis of HÖGBOM as a plausible explanation. Accordingly, he reckoned with two alternatives: either the ancestors of the populations living in the two lakes were sluiced up there by the ice from the neighbouring Baltic coast, or they immigrated along ice-dammed waters, coming from the east, after having first been sluiced up from Ladoga.

MUNTHE's well known and comprehensive work »On the late-Quaternary development and the Stone Age settlement of Northern Europe, primarily the Baltic», published in 1940, also included discussions of the history of relicts.

This author regarded it as probable that, in the region of Öresund, there have existed early late-glacial connections between the ocean and the Baltic basin, allowing marine animals, including relicts, to enter the latter area; *Pontoporeia affinis* and *Pallasea quadrispinosa* are mentioned as such forms. The presence of relict animals in Lake Furesö in Denmark was considered difficult to explain, but MUNTHE admitted the possibility of HÖGBOM's sluicing-up hypothesis, which had later been supported by EKMAN in the case of this lake. MUNTHE's attitude towards the applicability of HÖGBOM's idea to the lakes of northern Germany was more sceptical, as he found geological evidence to be lacking. *Phoca*, *Myoxocephalus*, *Mesidotea* and *Gammaracanthus* are thought to have invaded the Baltic at a later stage, viz. when the sound across central Sweden came into existence. On account of new geological results, MUNTHE abandoned the idea of an eastern connection between the Baltic and the sea, and suggested that only the relicts of Onega had immigrated from the White Sea.

In the same year, 1940, EKMAN surveyed the distribution of relicts in Sweden. As regards their immigration, he referred to MUNTHE's view

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[1] Later on *Mysis*, *Pontoporeia* and *Pallasea* were also found in L. Voloso, and *Pontoporeia* in L. Strusto (DRAKO 1954).

(cf. above) that, at that early late-glacial time when the ice-margin still ran across southermost Sweden, the Baltic basin was connected with the ocean and that the relicts may have come by this route.

In Spärck's account of the distribution and history of the Danish fauna (1942), the presence of relicts (including the smelt) in L. Furesö which was discussed earlier by Wesenberg-Lund and Ekman (cf. pp. 10 and 19) was explained as due to damming-up of the brackish water of the Sound. *Pallasea* is thought to have reached Denmark from arctic Eurasian waters by migrating along the coast of Northern Europe.

In 1949, Gerd summarized the records available up to that time of the relicts' distribution in East Karelia; discussions of general problems were included.

As regards the question of a late-glacial connection between the Baltic basin and the White Sea, the author referred to recent investigations by Russian geologists, according to which such a connection never existed (in 1934, Jakovlev had advanced the opposite view). Accordingly, Gerd suggested that only the lakes of the Ladoga area received their relicts from the Baltic side, whereas the rest of the East-Karelian lakes were invaded from the White Sea. As a biological circumstance supporting this view, he pointed to the fact that no relicts had been found in the wide area between Ladoga and Onega. Concerning the lakes of the Kenozero group, Gerd concluded, on the basis of results published in 1946 by the geologist Lavrova, that their relicts immigrated along the valley of the R. Onega in connection with a marine transgression (= the view of Högbom, p. 13 above).

Gerd also discussed the differences in the frequency of relict species in the East Karelian lakes and the reasons for the established variation. He concluded that high temperature is the main restricting factor and gave an ecological spectrum for *Pallasea*, *Pontoporeia*, *Mysis* and *Gammaracanthus* which showed their relation to depth, temperature, oxygen supply, and bottom conditions. He suggested that, since their isolation, the relicts of East Karelia have become, and are still becoming, sparser, on account of unfavourable changes in their ecological milieu (cf. Thienemann 1925, 1928 above). As an example, the *Gammaracanthus* of Lake Putkozero was mentioned: this relict, recorded from the locality 80 years earlier, had not been refound in 1947.

Finally, Gerd discussed the relationship between the age of the lakes and the morphology of the relicts inhabiting them. Among other things, he stressed the comparatively slightly pronounced modifications exhibited by the *Myoxocephalus* and *Limnocalanus* of Ladoga, a feature which is in good accordance with the late isolation of this lake.

A different attitude towards the problem of the White Sea — Baltic connection and the history of relicts was expressed in a publication of the same year (1949), by GORDEEV, on the relict crustaceans of Karelia (the paper summarized a thesis for a doctorate).

After having reviewed the history of the connection problem, GORDEEV continued (p. 6, transl.): »The latest investigations of the Russian geologist ZEMLJAKOV, POKROVSKAYA and SHESHUKOVA (1941) and the Finnish paleontologist MÖLDER (1944), carried out on the isthmus between Onega and Ladoga, have undoubtedly established that a connection would have been possible.»

»On the basis of his investigations into the distribution of relict crustaceans in the Karelian lakes, the present author supports the view of these workers.»

As regards those lakes of the area investigated which lie outside the region once flooded by the Baltic and the White Sea respectively, GORDEEV referred to the possibility of the relicts having reached them by active migration along rivers.

The paper contained, furthermore, discussions of the rôle of temperature, oxygen and other ecological factors in the distribution of relicts in the Karelian lakes. The conclusions arrived at purported to serve as the scientific basis for introduction of these species into lakes from which they are missing, in order to raise their production of fish food (cf. GORDEEV, 1951, 1952 and 1954; GERD 1952, 1954).

In THIENEMANN's thorough account of the history of the European lacustrine fauna (1950), considerable space was devoted, as would be expected, to the glacial relicts. For those relicts whose distribution is restricted to the Baltic region and understandable only if the geological development of this basin is considered, the term »Baltic animals» (»Baltikum-Tiere») was coined. In this group, besides the classical relicts, and *Osmerus eperlanus*, THIENEMANN included *Coregonus albula*, forms of the genus *Coregonus* s.s. (cf. EKMAN 1922), and a few other animals, and the immigration history of each member of the group is dealt with on the basis of earlier papers by the author himself, EKMAN, SPÄRCK, and others. As regards the invasion of northern Germany, THIENEMANN quoted a paper by the Swedish geologist WENNBERG (1943) in which the so-called Langeland advance of the ice-cap was made responsible for the sluicing-up of relicts in this area.

The lengthy account of the marine amphipods of USSR, published in 1951 by Gurjanova, gave the following views on the history of the relicts of the Baltic (p. 94 and map fig. 16): These animals originated from brackish waters off the coast of Siberia; from there their ancestors spread, in connection with the Ice Age, to the North Atlantic; the Baltic was reached from the west. Gurjanova thus presented a view contrasting with that of Lovén and those later authors, who, like him, suggested immigration from the White Sea.

A paper by Lomakina, of 1952, gave new data on the morphology and systematics of *Gammaracanthus loricatus* and *Pontoporeia affinis*, as well as on the distribution of these amphipods in Russian waters; the bearing of these on the question of a late-glacial connection between the White Sea and the Baltic was also discussed. What Lomakina found is briefly as follows:

Gammaracanthus loricatus is a species of circumpolar distribution and confined to habitats with a depth of at most 10—25 m. and a salinity not exceeding 25—30 $^0/_{00}$; forms living in estuaries (see below) and found also in the littoral zone tolerate dilution down to 5—10 $^0/_{00}$. One such form, var. *ostiorum*, occurs in the estuaries of rivers emptying on the arctic coast between the White Sea and the Kara Sea; it exhibits fairly strong individual variation, but is on the average characterized by reaching maturity earlier than the main form, and by having a characteristically curved rostrum and epimeral plates of the same shape as a form living in the estuaries of great Siberian rivers, from the Ob to the Lena, and the River Anadyr in the Far East, and described as a subspecies, *G. loricatus aestuariorum*. Its characteristics are: size smaller than in the main form, dorsal carina and projections less strongly developed, rostrum shorter and curved, second segment of peduncle of second antenna markedly turgid, owing to strong development of antennal gland (this is interpreted as an adaptation to life in diluted water), gnathopods and epimeral plates somewhat different from those of the main form, differences also in the setation of epimeral plates and pereiopods, etc. The *Gammaracanthus* of the Caspian Sea resembles both the main form and ssp. *aestuariorum*, but is distinctly smaller; Lomakina suggested that it may have gone through a freshwater stage before reaching the Caspian Sea.

As regards the relict *Gammaracanthus* of lakes, it was shown to represent extreme development of the characteristics of the estuarine forms. Lomakina considered the lacustrine form an independent species, not simply a variety (*G. lacustris;* cf. p. 34).

Lomakina proceeded to compare the morphology of the *Gammaracanthus* of Lake Ladoga with that of the population living in Onega and other Karelian lakes. Careful examination by her revealed that specimens from the former lake differ less from the main form than do those from Onega and the other Karelian lakes. It was suggested that this feature is due to historical factors, Ladoga having been connected with the Baltic as late as the Littorina period and thus subject to saltwater influence, whilst in Onega and the other Karelian lakes lacustrine life has been of much longer duration.

Corresponding studies on *Pontoporeia affinis* gave the following main results.

The subspecies *P. affinis gurjanovae*, described from the Kara Sea by Birula in 1937, has proved to occur in the estuaries of some northern Russian rivers, from Pechora to the Far East; the Baltic *affinis* is closely related to this form. On the other hand, the relict form, living in lakes, exhibits some minor, but fairly distinct, divergences: it is smaller, the telson tapers distally and is furnished with fewer setae; in addition, reduction of setation is also observable in the last uropods. This form is considered the typical one (for criticism, cf. p. 34). As in the case of *Gammaracanthus*, Lomakina found the *Pontoporeia* of Ladoga to be less different from the marine form than that of Onega and the Karelian lakes, and the same explanation of this feature was advanced.

Finally, Lomakina discussed the bearing of the results achieved on the question of the Baltic — White Sea connection. The history of this intricate problem was reviewed and the author stated that opinions amongst geologists still differed. As regards the results obtained, on comparing the *Gammaracanthus* and *Pontoporeia* of Ladoga with populations from Onega and other Karelian lakes, Lomakina suggested that, together with corresponding observations by earlier Russian biologists (Berg, Rylov, Gurjanova, Gerd) on other relicts (*Myoxocephalus*, *Limnocalanus*, *Mysis*, *Mesidotea*), they rather support the view that no late-glacial connection existed. In consequence, the invasion was concluded to have come from two directions independently: to Ladoga, from the west, via the Atlantic and the Baltic; to Onega and the Karelian lakes, from the diluted, estuarine waters of the Arctic Sea.

In a paper by Gerd, also published in 1952 and purporting to show the desirability and possibility of introducing crustaceans, especially relicts, into those fresh waters of northwestern Russia (Karelia and adjacent regions) where they do not occur, in order to raise their production of fish food, the author expressed the same view as LOMAKINA as regards the history of the relicts: the localities in Karelia and the Onega area were reached from the Arctic Sea; Ladoga and its neighbouring lakes, again, from the west, along the Atlantic — Baltic route.

In 1953, WIERZBICKA reported on the presence of *Limnocalanus macrurus* in several localities within a lake complex in northern Poland (see fig. 12). This was the second time that the crustacean had been found in continental lakes east of Ladoga-Onega. As regards the reason for its occurrence in the region, WIERZBICKA, like BOWKIEWICZ who had reported on the first continental localities (cf. p. 19), referred to HÖGBOM's theory as the most probable explanation.

In the second edition of the well known marine zoogeography by EKMAN, of 1953, the following view on the immigration of the relicts of Northern Europe was presented (p. 128):

»Some of the glacial relicts — — — apparently reached the highest inland lakes only with the help of this Ice Lake [the so-called Baltic Ice Lake is meant], and according to MUNTHE (1940) it is probable for other reasons that the Ice Lake incorporated a marine predecessor in the southwest and thus received a marine cold-water fauna which was, however, poor in species. With the continued retreat of the ice-margin, it was possible for seawater to enter into the Baltic basin and so the Yoldia Sea was formed. — — — The connection [of the Yoldia Sea] with the ocean went across what is now the central Swedish lowland; an earlier assumption of a connection with the White Sea across Ladoga and Onega is now considered by the geologists to be wrong.»

However, in another publication of the same year, on the fauna of the Bothnian Bay, EKMAN also seemed to reckon with an eastern immigration (1953 b, p. 186, transl.): »These animals are remnants, relicts, from that ancient arctic sea, the Yoldia Sea, which was the late-glacial predecessor of the Baltic and had open connections with the rest of the Arctic Sea both in the east and the west.»

In the early forties, MATHIESEN carried out a study on the biology and ecology of Norwegian glacial relicts; like some of the Russian investigations mentioned above, its purpose was mainly practical, viz. the provision of a scientific basis for the introduction of relicts as fish food into new Norwegian habitats. A paper on the results obtained was published in 1953; it includes a complete list of the Norwegian relict localities known up to that year, and the immigration problem is also briefly touched upon. The following view is given (p. 83):

»Whether these relict crustaceans migrated from the east or from the west is still an open question in some cases. Two of the relict crustaceans are unquestionably eastern immigrants, viz. *Pallasea quadrispinosa* and *Idothea entomon*. The last has not reached farther than to certain Swedish lakes, while *Mysis relicta* is found in the Irish lakes, Loch Neagh, Loch Erne, and Loch Corrib, and this form together with *Pontoporeia affinis* and *Limnocalanus macrurus* are found in several North American lakes. The transition from marine forms, which at one time were present in the ocean outside the respective coast lines to a fresh water form has thus independently taken place in many lakes.»

»Whether the Norwegian population of *Pontoporeia affinis* and *Mysis relicta* on Jaeren [Jaederen, southwestern Norway] are descendants of western immigrants or whether they once migrated along the coast of southern Norway in the brackish water cannot yet be decided. If they are descendants of western immigrants, one should expect to find relict crustaceans in several lakes along the west coast of Norway. No other populations of such animals are known here, but our knowledge of these lakes is very limited. It is to be expected that many of the deep, formerly submarine lakes in Tröndelag should give positive findings if an independent western relict formation has taken place. The existence here of *Salvelinus alpinus* has correctly been accepted as a relict population (Grieg 1908).»

An article of 1954 by the Finnish geologist Sauramo, on the late-glacial flora, included the following statement on the invasion of relicts (Sauramo 1954 a, p. 135, transl.):

»Owing to a marine transgression at the beginning of the Alleröd period, the White Sea was connected with the Baltic across Onega and Ladoga. The straits seem to have been comparatively narrow and short-lived, but, nevertheless, sufficient for the influx of salt water into the Baltic in the south and northeastern Finland in the north. At that time Onega, Ladoga and the Baltic received a number of animals from the White Sea, which still thrive there today as glacial relicts. Among them are the crustaceans *Mysis oculata relicta*, *Mesidothea entomon*, *Pontoporeia affinis* and *Pallasiella quadrispinosa*, and, among the fishes, *Cottus quadricornis*.»

In a report by Kudersky, of 1955, on the observation in 1954 of *Mysis relicta* in a lake on the isthmus between Ladoga and Onega (Kotkozero; in reality the locality was known earlier, cf. Segerstråle 1956 a, p. 24), it was stressed that most of those lakes of this area which had been investigated and found not to harbour glacial relicts could not be considered to offer a favourable habitat to such animals. Consequently, the absence there of such animals was no valid argument against the hypothesis of a former connection between the Baltic and the White Sea.

ZENKEVICH's account of the fauna and flora of the seas of USSR (1956) expressed a more favourable attitude towards the idea of immigration from the east than is found in most other recent publications: »As early as the sixties of the last century the theory was advanced (LOVÉN) that, during the Yoldia period, the Baltic had a direct and wide connection with the White Sea, across Ladoga and Onega, and that the fauna was identical in both seas. Although this hypothesis is looked upon with doubt at the present day — — — the existence even today of some features of similarity between the fauna of the White Sea and the Baltic is difficult to explain without assuming a direct connection in pre-Ancylus times» (p. 285, transl.).

For recent geological publications on the question of whether or not a connection between the White Sea and the Baltic did exist in late-glacial times, see pp. 56—57.

3. MAIN PROBLEMS OF THE IMMIGRATION HISTORY.

As is shown above, the history of the glacial relicts inhabiting the waters of Northern Europe has been a topic of discussion for almost a century. The item which has particularly caused argument is the question of eastern versus western immigration. As we have noted, there are still today those who subscribe to the view, advanced by LOVÉN, that the relicts have immigrated into the Baltic region from the Arctic Sea in the east, across the Onega-Ladoga area, whereas others deny this possibility and only reckon with invasion from the Atlantic in the west; finally, there are those who think that both paths were utilized. The attitude of most modern Russian workers seems to be against the hypothesis of an eastern route (GURJANOVA, GERD, LOMAKINA); of EKMAN's last two statements on the matter, one (1953 a) represents the same view, whilst the other (1953 b) also suggests immigration from the east; MATHIESEN (1953) likewise reckons with both alternatives; SAURAMO (1954), again, speaks of the eastern route alone.

Another problem which has given rise to eager discussion is the history of the relict populations inhabiting a number of continental lakes west of Onega-Ladoga, especially in northern Germany, where their occurrence in such lakes was first disclosed, somewhat more than half a century ago. To explain the presence of glacial relicts in the waters concerned, which are all situated above the level of the Baltic of late-glacial times, the sluicing-up theory of Högbom, advanced in 1917 is, as we have seen, practically unanimously accepted today. The conclusion that it was the so-called Langeland advance of the ice-cap that was responsible for the transportation of the relicts up to their present sites (Wennberg 1943) was a further step towards clearing up the matter.

On reviewing the earlier opinions regarding the history of the glacial relicts, the present author was struck by the fact that one essential point has been largely overlooked in the discussions.

In most cases, the invasion is thought to have occurred either by way of connections between the Baltic and the White Sea, which have been postulated by a number of geologists to have existed somewhat before the onset of the Yoldia period; or by way of a western strait which at the latter period opened a way from the Atlantic into the Baltic basin, across central Sweden.

However, in the case of those relicts which live in continental lakes (W. of Onega-Ladoga), i.e., *Mysis*, *Pontoporeia*, *Pallasea* and *Limnocalanus* (in the following called Group I), no such immigrations are required to explain the present existence of relicts in those parts of Northern Europe which were once covered by Baltic water, for the simple reason that the relicts concerned were brought into the Baltic basin (and subsequently spread with its water) when the continental ice-dammed lakes drained down into this basin. And, on the other hand, even if we assume immigration through the eastern or western connection mentioned above, this by no means explains how the relicts reached the continental lakes, an event which must be of a much earlier date.

As regards the invasion into these lakes, Högbom suggested, as will be remembered, that before they were sluiced up the slope of the continent by the ice-cap, the relicts had entered the Baltic or the Ladoga region by way of a connection between the White Sea and the Baltic which Högbom assumed to have existed at a certain phase of the regression of the inland ice. Some later authors (Ekman 1930, Munthe 1940) suggested the possibility of early invasion from the Atlantic side, but, on the whole, little has been written on this subject since Högbom published his paper of 1917.

For those relicts which do not live in lakes of the Continent, i.e., *Myoxocephalus*, *Mesidotea*, *Gammaracanthus*, and *Phoca*, (»Group II»), a different history must be postulated: they might have reached the Baltic later on, and in their case the above-mentioned connections with the western and eastern oceans must be taken into consideration as a possibility.

Thus against the background of our present knowledge, as surveyed in this section, one is faced with the following main questions: what is the history (1) of those relicts which were the first to immigrate into the ice-dammed lakes of the continent; (2) of the second group of relicts? But numerous minor problems also deserve closer scrutiny. These various items will be dealt with in later sections of the present paper.

However, before proceeding to this task, it is first necessary to discuss the relation of the ancestors of the relicts to salinity, and secondly, to survey our present knowledge of the occurrence of the relicts in different parts of Northern Europe, since any conclusion on the history of these animals must, of course, be based on their distribution today.

4. THE RELICTS TREATED. THE ANCESTORS OF THESE ANIMALS AND THEIR RELATION TO SALINITY.

a. *The relicts treated.*

The present account is confined to those glacial relicts of Northern Europe which occur in lakes (most of these forms are also found in the Baltic), because their history is of particular interest.[1] Within this group, again, the main stress is laid upon the »classical» relicts, i.e., those already mentioned by LOVÉN but including, in addition, *Limnocalanus*, a copepod which was also early realized to have had a similar history (cf. p. 9).

A note on the term »marine-glacial relict» may be inserted here (cf. SEGERSTRÅLE 1956 a, p. 1). This term, coined by EKMAN (1922, p. 280;

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[1] Besides the just-mentioned forms the relict group concerned includes the smelt (*Osmerus eperlanus*), the vendace (*Coregonus albula*) and, probably, the parasitic worm, *Echinorhynchus salmonis* O. F. M. (NYBELIN 1931). The author hopes to publish a special paper on the immigration of these fishes and of some other members of the ichthyofauna of Northern Europe which all seem to have had the same history as the relicts treated in the present paper.

For those glacial relicts of Northern Europe which are restricted to the sea, such as *Pontoporeia femorata*, *Mysis mixta*, and *Halicryptus spinulosus*, see, for instance, EKMAN 1953 a.

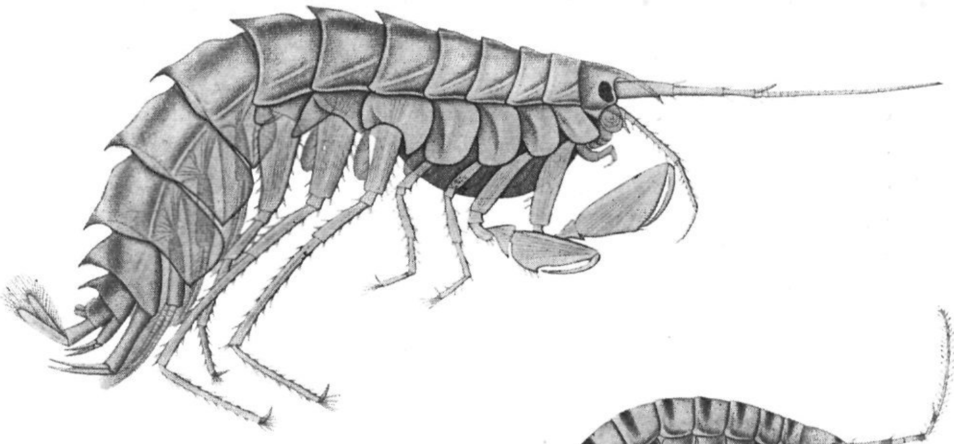
etc.) and generally adopted, was based on the conception that the animals concerned were isolated in the North-European lakes from the glacial sea, directly or via the Ancylus and Littorina stages of the Baltic basin. However, as will be shown in the present paper, this cannot have been the case: although, admittedly, most of the relicts under discussion were originally natives of the Arctic Sea, they seem to have reached the Baltic area by way of an interjacent ice-dammed freshwater lake where they lived for a long time. Hence, the usage of the term »marine-glacial» for these relicts is scarcely appropriate. This is especially so in the case of the lacustrine *Pallasea.* That this relict was included in the marine-glacial group was due to EKMAN's conception of its having come from Siberian fresh waters along a diluted marine path; however, today it appears probable that it adopted a purely lacustrine route (cf. p. 92 ff.). The inclusion of *Pallasea* in the group of marine-glacial relicts has led geologists, even in recent works, to overlook its different ecological requirements and to base discussions concerning the geological development of North-European regions on the false assumption that the animal may have invaded from the ocean in the west (cf. 19).

The list of the relicts to be discussed comprise one mammal, one fish and six crustaceans, as given below; the local forms described from the area under consideration for *Phoca* and *Myoxocephalus* (*Cottus*), by NORDQVIST 1899, SMIRNOV 1929, BERG 1916 a, BERG & POPOV 1932, LÖNNBERG 1932, 1934, 1939, are omitted.

MAMMALIA:	the Ringed Seal	*Phoca hispida* Schreber
PISCES:	the Fourhorned Bullhead	*Myoxocephalus* (*Cottus*) *quadricornis* (L.)
CRUSTACEA:	the amphipods	*Gammaracanthus lacustris* G.O.S.
		Pallasea quadrispinosa G.O.S.
		Pontoporeia affinis Lindstr.
	the isopod	*Mesidotea entomon* (L.)
	the mysidacean	*Mysis relicta* Lovén
	the copepod	*Limnocalanus grimaldii* (de Guerne) in the Baltic, *L. macrurus* G.O.S. in lakes.

The above list calls for some comments:

Myoxocephalus. In accordance with the usage in the Russian literature, the generic name *Myoxocephalus* has been substituted for *Cottus*, the name which has so far been generally used in western countries; the reason for this is the clear morphological divergence between the genera (in *Myoxocephalus* the opercular membranes of the two sides, 1



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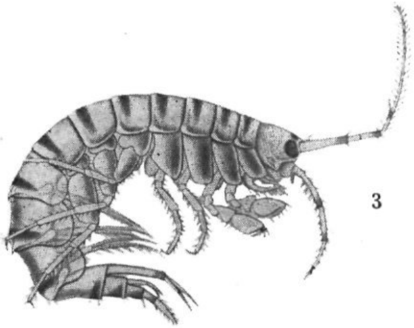

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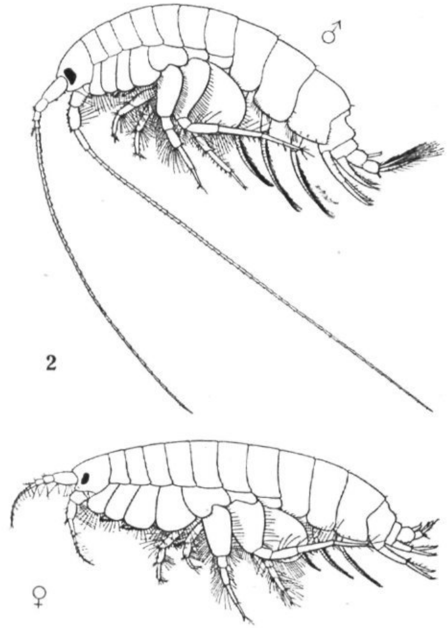

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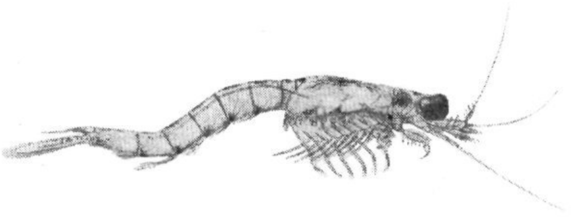

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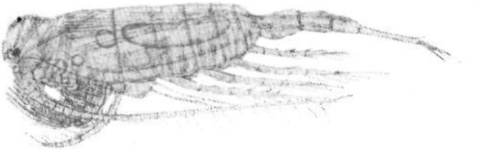

Figs. 1–5 and 6–7 (opposite page): the relicts treated (the Ringed Seal, *Phoca hispida*, omitted). — 1. *Gammaracanthus relictus* (ovigerous female from L. Vättern; Sars 1867). Size, up to nearly 4 cm. (female). — 2. *Pontoporeia affinis* (from the Baltic; Segerstråle 1937). Size, up to 14 mm. (relict form). — 3. *Pallasea quadrispinosa* (from Sars 1867). Size, up to nearly 30 mm. (male). — 4. *Mysis relicta* (male, from L. Mjösa, Norway; Sars 1879). Size, up to 20 cm. and more. — 5. *Limnocalanus macrurus* (from Sars 1903). Size, up to more than 2 mm. —

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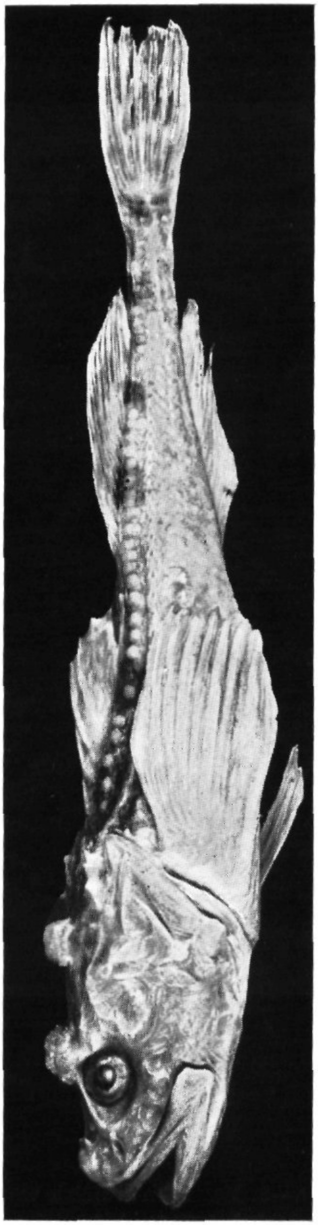

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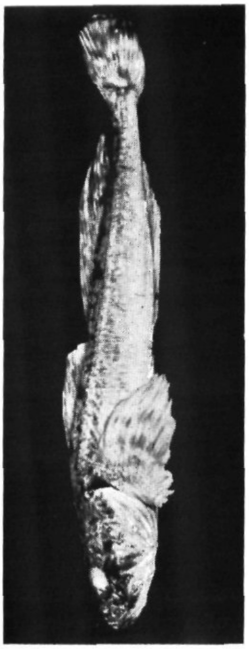

7 b

6. *Mesidotea entomon* (from Gulf of Bothnia, natural size; Hels. Zool. Mus., photo L. Koli). Maximum size in the Baltic about 9 cm. — 7 a—b. *Myoxocephalus quadricornis*. — *a*, from Gulf of Finland (3/4 natural size, Hels. Zool. Mus., photo L. Koli) maximum size in the Baltic, more than 30 cm. — *b*, from L. Suonteenselkä, Suonenjoki, Finland (3/4 natural size; Hels. Zool. Mus., photo L. Koli). Note the small size and the total absence of head tubercles.

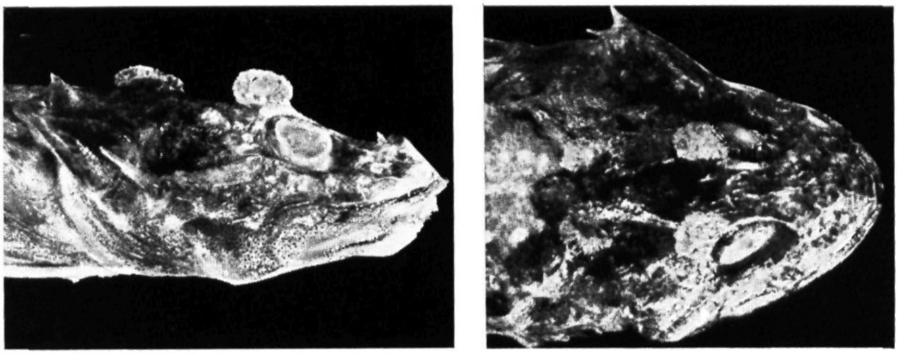

Fig. 8.

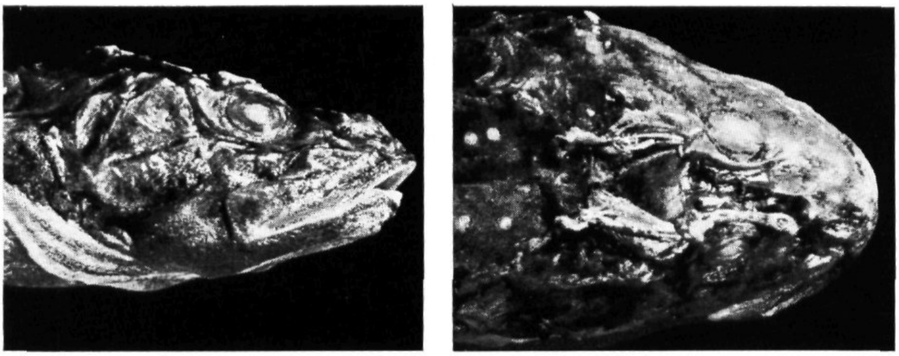

Fig. 9.

Figs. 8—9. Variation in Baltic waters of head tubercles in the Fourhorned Bullhead, *Myoxocephalus* (*Cottus*) *quadricornis*. Fig. 8: head of a specimen (length 200 mm.) with well developed tubercles, in lateral and dorsal view. Fig. 9: corresponding pictures of a specimen (length 260 mm.) with weakly developed tubercles. Both specimens (females) caught at Kiviniemi in the innermost part of the Gulf of Bothnia (Collections of Hels. Zool. Museum; photo L. Koli.) Discussion p. 33.

fusing ventrally, have a free margin there; in *Cottus*, the median part of the fused membranes has grown into the ventral surface of the head).

The Fourhorned Bullhead of the Baltic, *Myoxocephalus quadricornis* (L.), and that occurring in arctic waters, *M. q. labradoricus* (Girard), are considered by BERG & POPOV (1932) to be two different forms, the main divergences referring to the development of the four turbercles on the head. These are said to be »well developed, high, massive, spongy» in the Baltic form, but »feebly developed, usually in the form of elongated crests, feebly or not at all spongy» in *labradoricus*.

However, in both forms the tubercles concerned are subject to great variation. As regards *labradoricus*, ANDRIASHEV, in his recent handbook on the fishes of the arctic seas of USSR (1954), states (p. 388, translated): »Generally they [the tubercles] are considerably more weakly developed than in the typical form [of the Baltic] — — — but in many cases one observes vigorous growth and they may show an almost mushroom-like form.» Correspondingly, the Baltic form may exhibit feeble development of the tubercles, a feature which seems to have been overlooked in the literature to date. For instance, in a material of 30 specimens received in 1957 by the Zoological Museum of Helsinki from the innermost part of the Gulf of Bothnia, the »*labradoricus*» type, as depicted by BERG & POPOV (loc. cit., fig. 4) was actually predominant (see figs. 8—9; morphological analysis made by Mr. L. KOLI, M.A.). In view of this wide morphological range within both forms, it might be rewarding also to subject the variation of the other, minor characteristics to a closer scrutiny. As a matter of fact, it seems well within the bounds of possibility that the two forms of the Fourhorned Bullhead discussed lack truly distinctive characteristics, which would be not at all surprising, since the Baltic form is obviously derived from that living off the arctic coast of Eurasia (cf. p. 36).

Quite apart from the taxonomic question just discussed, there is no doubt that the form with strongly developed head tubercles is much commoner in the Baltic than in arctic waters. In seeking the reason for this, we must remember that the Baltic is by far the warmest area within the range of *Myoxocephalus quadricornis* s.l. This fact suggests that it is the comparatively high temperature, combined with favourable salinity conditions, that is responsible for the excellent morphological development of the Fourhorned Bullhead in the Baltic (as is well known, the fish also attains a remarkable size in this area; for instance, in the collections of the Helsinki Museum there is a specimen from Finnish coastal waters

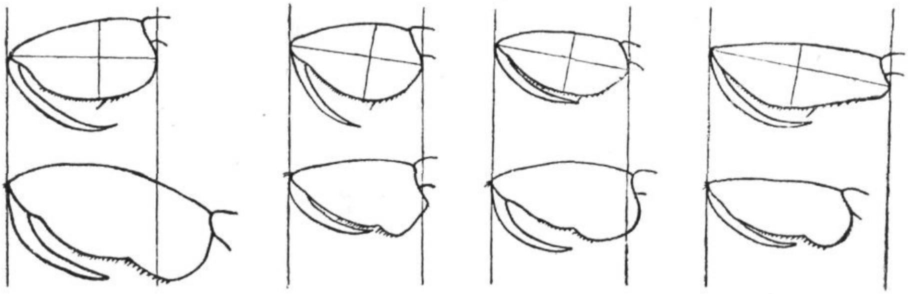

Fig. 10. Gnathopods of *Gammaracanthus* showing the gradual transition from the marine type to the lacustrine one. Upper row: gnathopod I. From the left: *G. loricatus loricatus*, *G. loricatus caspius*, *G. loricatus aestuariorum*, *G. lacustris*. After Lomakina 1952. Cf. p. 22.

which has a length of not less than 35 cm). This conclusion on the temperature factor gains some support from the provenience of the Baltic material of »*labradoricus*» type discussed above, caught as it was in the northernmost, coldest part of the Baltic basin.

Gammaracanthus. Instead of the status of variety only (*Gammaracanthus loricatus* (Sabine) var. *lacustris* G. O. SARS; see, for instance, EKMAN 1940 and THIENEMANN 1950), LOMAKINA, in 1952, proposed that the relict form should be considered an independent species, thus reviving the view advanced by SARS in 1895. The present author follows LOMAKINA, even though it appears difficult to decide the correct taxonomic status of the various forms of *Gammaracanthus* described today (cf. fig. 10 and p. 22 and GURJANOVA 1951) since they were all no doubt derived in comparatively recent time from the same marine ancestor, the typical *G. loricatus*.

Pontoporeia affinis. The following may be quoted from a recent paper by the author (1956 a, pp. 3—4): »LOMAKINA (1952, p. 119—123) reports some minor differences between the form living in the lakes of East Karelia and that from the Kara Sea (and the Baltic); these differences refer mainly to the body size and the telson; the lacustrine form is considerably smaller, and its telson generally cone-shaped and furnished with fewer setae. For this reason, LOMAKINA separates this form from that described from theKara Sea, 1937, by BIRULA under the name *P. affinis gurjanovae* and regarded by LOMAKINA as practically identical with the Baltic *P. affinis*. The lacustrine form is by her given the status of a subspecies of its own, *P. affinis affinis*. Quite apart from the question of whether the differences found are of subspecific value, it must be emphasized that the original description of the species *P. affinis*, by LINDSTRÖM in 1855, was based on material from the Baltic, whence this form cannot but be the typical one.»

The following may be added. By the courtesy of Prof. E. GURJANOVA (Leningrad), the author has had the opportunity to compare specimens of *P. affinis* from Baltic waters and from the Kara Sea. The result was the same as that arrived at by LOMAKINA, viz. that there is no appreciable difference between the two forms. The Baltic and the Siberian coastal waters are thus inhabited by the same *affinis*, described by LINDSTRÖM. As regards the form living in lakes, the author doubts whether those of its characteristics, referred to by LOMAKINA, are sufficiently pronounced to justify subspecific status (a tendency towards a cone-shaped telson is also found in Baltic populations) and proposes that it should be regarded only as a variety of the main form, var. *lacustris* nom.nov. Accordingly, the forms of *Pontoporeia* discussed in the present paper should be: *P. affinis* in the Baltic and eastern arctic waters, and *P. affinis* var. *lacustris* in lakes of Northern Russia (and, conceivably, other lakes of Northern Europe).

b. *The ancestors of the relicts and their relation to salinity.*

The prevailing view on the origin of the relicts and the ecological requirements of the ancestral forms as regards salinity emerges below (cf. EKMAN 1914, 1922, 1953 a; *Phoca* omitted):

Relict	*Ancestor*	*Relation to salinity of the ancestor*
Myoxocephalus quadricornis	*M. quadricornis*	Marine form
Gammaracanthus lacustris	*G. loricatus*	» »
Pallasea quadrispinosa	Unknown	Freshwater form
Pontoporeia affinis	*P. affinis*	Brackishwater form
Mesidotea entomon	*M. entomon*	» »
Mysis relicta	*M. oculata*	Marine form
Limnocalanus macrurus (*L. grimaldii* in the Baltic)	*L. grimaldii*	Brackishwater form

As is seem from the above list, three of the seven relicts concerned are regarded as originally marine, three as derived from brackishwater forms, and one as of lacustrine origin. However, the present study has led the author to the conclusion that even those relicts whose ancestors have so far been considered marine, viz. *Myoxocephalus quadricornis*, *Gammaracanthus lacustris* and *Mysis relicta*, are, in fact, descendants of brackish-water forms. The arguments for this view are given below.

Myoxocephalus. The Fourhorned Bullhead, living as a relict in the Baltic and named *Cottus quadricornis* by LINNAEUS in 1746, as well as those more or less dwarfed forms of it which are found in surrounding lakes (including Karelian ones), is no doubt derived from that circumpolar form which is known today as *Myoxocephalus quadricornis labradoricus*, and was described by GIRARD in 1850 (under the name *Acanthocottus labradoricus*). On its distribution in Eurasian coastal waters, BERG & POPOV (1932, p. 156) give the following data: In the Murman area only in the Kola Bay, common in the White Sea, enters river mouths: Tuloma, Dvina, Pechora, Ob, Yenissei, Khatanga, Lena, Yana, Kolyma.

In order to obtain more information about the relation of the fish to salinity, the present author approached Prof. A. N. SVETOVIDOV (Leningrad, Zool. Inst. of the Acad. of Science) on the matter. Prof. SVETOVIDOV kindly referred to an account by Prof. ANDRIASHEV of the fishes of the northern seas (1954, see below). For his own part, Prof. SVETOVIDOW added (transl.): »Judging from what is known about the fish from other publications, it lives mainly in brackish regions, although also found in marine water. Characteristically enough, in areas off the mouths of rivers, mostly young specimens are found; and it is no less characteristic that in the southern part of the Kara Sea, reproduction takes place in the lower reaches or estuaries of rivers (POKROVSKAYA 1951).»

The above-mentioned work by ANDRIASHEV included the following statement (p. 390, transl.):

»Occurs in the coastal zone (rarely at depths exceeding 15—20 m.) in brackish and considerably diluted marine waters. Penetrates into areas off the mouths of rivers and into estuaries, where the young (of the 0- and 1-year group), especially are often found. Remains near the coast for the whole year, does not perform any considerable migrations.»

In a later letter, Prof. SVETOVIDOV, after discussions with Prof. ANDRIASHEV, added that, according to the latter, *M.q. labradoricus* does not, as a rule, occur at salinities above 24 $^0/_{00}$.

Summing up, our present knowledge of the ecological nature of the ancestor of the relict *Myoxocephalus* of Northern Europe clearly indicates that is it not, as stated in the earlier literature on relicts, properly marine, but in the main confined to brackish waters, and it even seems probable that for reproduction it requires a rather low salinity.[1]

Gammaracanthus. According to LOMAKINA (1952; cf. above p. 22), *G. loricatus* is confined to marine areas of lowered salinity, at most 25—30 $^0/_{00}$. In addition to the typical form, LOMAKINA, as will be remembered, describes two forms living in greatly diluted water: var. *ostiorum* in the estuaries of rivers between the White Sea and the Kara Sea, and subsp. *aestuariorum*, in the estuaries of several rivers of northern Asia. In view of the fact that the ancestors of most of the relicts of North Europe seem to have come from the White Sea and since, further, var. *ostiorum* represents a transitional stage between the typical form and *G. lacustris*, it is justifiable to suggest that this form has been derived from *ostiorum*, through extreme development of its characteristics (form of rostrum and epimeral plates; cf. LOMAKINA). As regards the distribution of var. *ostiorum* in the White Sea region, it has so far been caught in the mouths of the R. Gridina and the R. Ponoi, respectively situated on the west coast and at the outlet of the basin concerned.

Mysis. In the early days of relict research it was not known that *Mysis relicta* also lives in the sea. However, in the last few decades its occurrence has been established in quite a number of marine localities off the arctic coast of northern Russia and Siberia; they are all pronouncedly brackish. The following localities may be mentioned: the White Sea, in the estuary of the R. Dvina (DERJUGIN 1925, etc.; see footnote), the estuary of the R. Pesha, in almost fresh water (GURJANOVA 1929), the estuary of the R. Pechora (DERZHAVIN 1923, acc. GURJANOVA 1929), the estuary of the R. Ob (POPOV & MOSEVICH 1926, acc. GURJANOVA 1929), Bay of the R. Yenissei (GURJANOVA 1929), the estuary of the R. Lena (PIROZHNIKOV 1955), the estuary of the R. Yana (GURJANOVA 1929), the R. Anadyr (STAMMER 1936).

Considering the common occurrence of *M. relicta* in diluted waters

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[1] It may be noted in this connection that, according to recent investigations (K. J. PURASJOKI 1957, unpubl.), the main range of the Baltic *Myoxocephalus quadricornis* seems to be confined to areas with a salinity below c. 6 $^0/_{00}$. However, it must be remembered that this relict form seems twice to have undergone a freshwater stage (cf. p. 98) as a result of which its salinity tolerance may be less pronounced than that of the ancestral form.

off the arctic coast of Eurasia, there seem to be good grounds for abandoning the prevailing view that the ancestor of the relict *Mysis* was a purely marine form and to consider *relicta* as derived from the brackishwater *M. relicta*, which without morphological changes has adapted itself to life in fresh water. In other words, we seem to have to do with a parallel to another relict, viz. *Pontoporeia affinis*, which, as EKMAN (1918) showed, is derived from an identical marine form, confined to diluted arctic waters.

If we accept the suggested view on the origin of the relict *Mysis*, the following two striking features are plausibly explained:

(1) The occurrence of typical *relicta* in the brackish Baltic, a phenomenon which is otherwise not easily understood (cf. EKMAN 1919, p. 491: »Dass die Tiere des Ostseebeckens so vollständig mit *Mysis oculata relicta* übereinstimmen würden, was von vornherein nicht zu vermuten, eher wäre eine wirkliche Zwischenstellung wahrscheinlich gewesen, da der Saltzgehalt des Ostseebeckens bekanntlich gering ist»).

(2) The absence of *relicta* in the uplifted lakes of western Scandinavia. If the crustacean is confined to greatly diluted water, this is easily understood, since the marine path to the area concerned was no doubt impassable (cf. p. 52).

As regards North America, where *M. relicta* also lives as a glacial relict in many lakes, no marine localities in the neighbouring coastal waters are known. However, the marine fauna of this region is, on the whole, little known as yet. The case of *Pontoporeia affinis* is illustrative in this connection: it occurs as a relict in a number of the fresh waters of North America (for instance in the Great Lakes) where it has no doubt come from the adjacent arctic coast, conceivably through glacial sluicing-up; at the same time, however, as far as this area is concerned, the marine *affinis* was, until recently, known from one locality only (Collinson Point, Alaska, SHOEMAKER 1920; in 1954 the species was, in addition, reported by DUNBAR from Ungava Bay, N. Labrador).

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[1] In one of his papers of 1956 (a, p. 27), the present author erroneously stated that *Mysis relicta* is absent from the White Sea; the reason for this was a map in LOMAKINA's publication of 1952 (p. 115) where only *M. oculata* is given for this area. In his answer to a letter from the present author, Prof. S. V. GERD (Leningrad) confirms the presence of *relicta* in the estuary of the R. Dvina and suggests that it also occurs in other estuaries of the White Sea. (The crustacean was reported from this area as long ago as 1870, by JARZHYNSKY.)

The occurrence of *Mysis relicta* in some lakes of Ireland and England also deserves mention, as it may, at first sight, seem difficult to explain this fact, if one assumes that the salinity of the ocean prevented the crustacean from invading the coastal waters of Scandinavia (cf. point 2 above). Must one not, at least in this case, reckon with a marine ancestor? These questions will be elaborated in connection with a discussion of the history of *Pallasea quadrispinosa* (Section III: 10); it may be anticipated that the seemingly odd Irish-British occurrences may plausibly be explained even if *Mysis relicta* is assumed to be the ancestor of the relict form.

The taxonomic relations between *M. oculata* and *M. relicta* which have been dealt with in earlier papers by a number of authors (LOVÉN 1862, SARS 1867, 1879, EKMAN 1913, 1919, OLOFSSON 1918) will not be discussed in the present paper, as this problem has been specifically studied for some years by the Swedish zoologist CHARLOTTE HOLMQUIST (Lund University). But it may be noted in passing that, according to this author, the specimens from Spitsbergen, referred to by OLOFSSON as *M. relicta*, in reality belong to *M. oculata* (HOLMQUIST 1949).

Concluding remarks. It has been suggested above that those forms of *Myoxocephalus*, *Gammaracanthus* and *Mysis* which live as relicts in Northern Europe are typical inhabitants of Eurasian estuaries. This means that with respect to salinity they seem to be of just the same nature as those relicts which were earlier regarded as typical brackishwater forms: *Pontoporeia affinis*, *Mesidotea entomon* and *Limnocalanus grimaldii*, all common in arctic estuaries (cf. for instance, EKMAN 1914, 1918 a, DERZHAVIN 1923, PIROZHNIKOV 1955; as regards the reasons for the occurrence there of all these forms, see p. 103).

As is well known, estuaries are characterized by great salinity fluctuations, and seasonally the waters off arctic rivers must be extremely diluted. One indication of this is the recording of *Pontoporeia affinis* in the estuary of the Yenissei at a salinity of 3.3 $^0/_{00}$ (Vega Expedition, cf. EKMAN 1918 a, p. 328). And still more, most of the relicts have been caught in purely fresh water in arctic Eurasian rivers (DERZHAVIN 1923, Pirozhnikov 1931; cf. p. 106). It is easily understood that these animals must have been especially fitted for changing into freshwater forms (cf. EKMAN 1914, p. 509). Since we may conclude that those relicts which were earlier thought to originate from marine ancestors, were also in reality derived from brackishwater forms, just like *Pontoporeia*, *Mesidotea* and *Limnocalanus*,

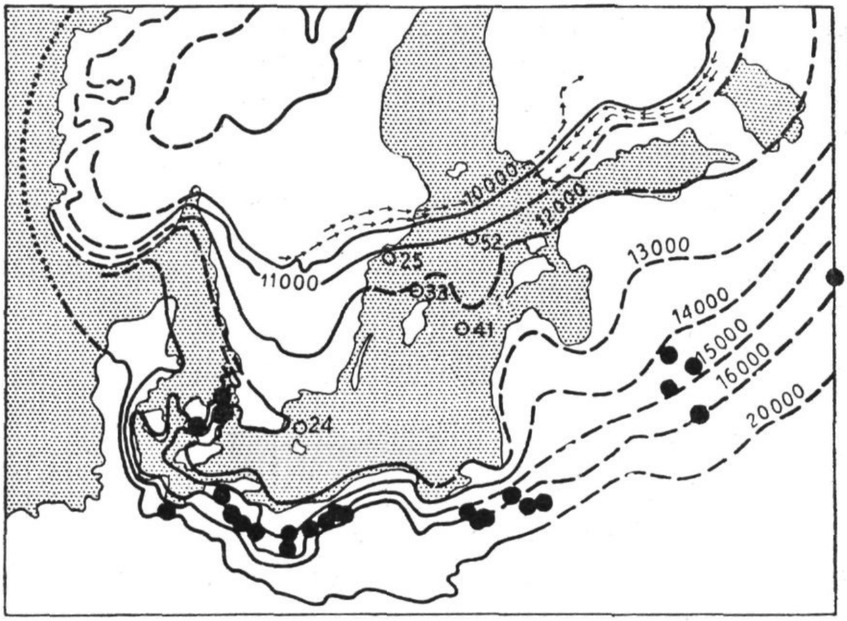

Fig. 11. Millenial ice-margins (before present; after De Geer 1954) and position of relict localities in the continental area, including Denmark. For details of location, see figs. 12 and 25 in the present paper and Thienemann 1925, Spärck 1942.

this means a welcome simplification of the problem of the ecological adaptation involved in the history of the glacial marine relicts.

As will be shown in a later section (p. 102 ff.), the brackishwater ancestors of these animals seem in the past to have lived, and perhaps even developed, in a Siberian ice-lake of an earlier glaciation; this renders the present existence of the relicts in the lakes of Northern Europe so much the more understandable from an ecological point of view.

5. DISTRIBUTION OF THE RELICTS.

The close relationship between the distribution of relicts, taken as a whole, and the extent of the last glaciation emerges from the maps figs. 11 and 13, in which the peripheral continental localities are given. The occurrence of the animals concerned within the area will be briefly commented upon below.

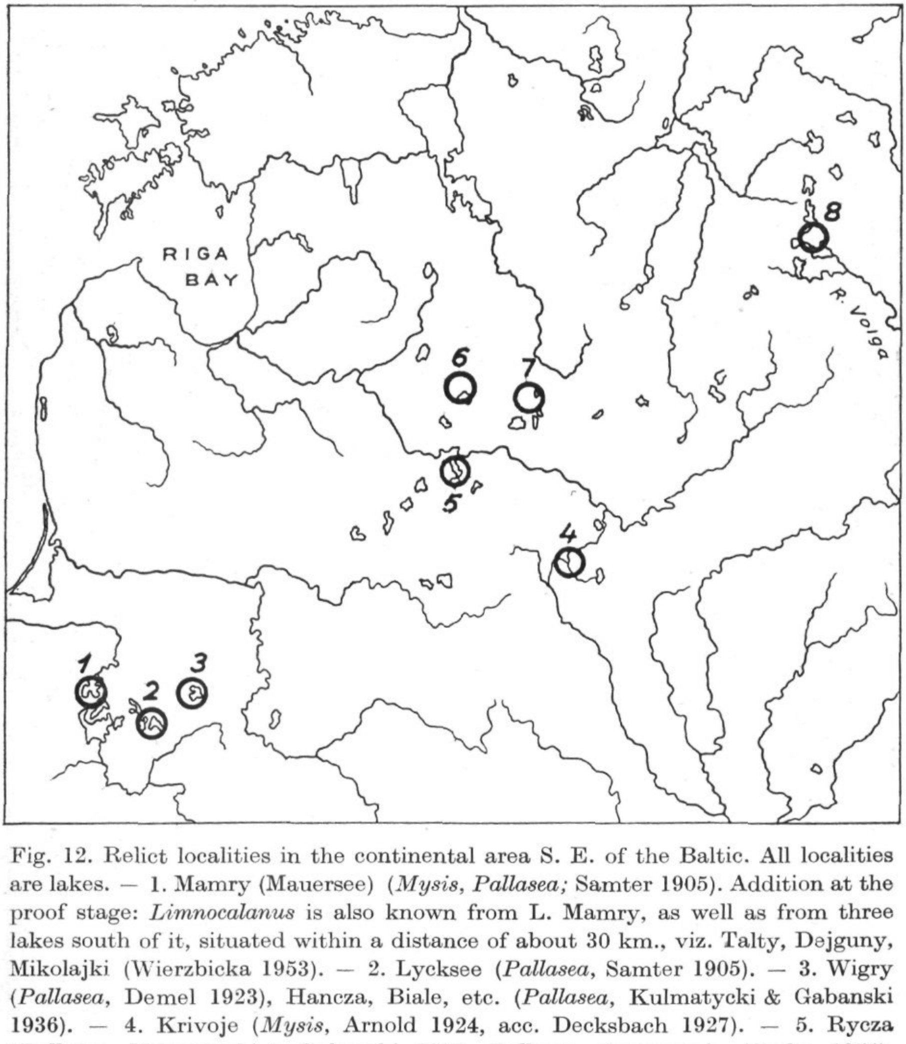

Fig. 12. Relict localities in the continental area S. E. of the Baltic. All localities are lakes. — 1. Mamry (Mauersee) (*Mysis*, *Pallasea;* Samter 1905). Addition at the proof stage: *Limnocalanus* is also known from L. Mamry, as well as from three lakes south of it, situated within a distance of about 30 km., viz. Talty, Dejguny, Mikolajki (Wierzbicka 1953). — 2. Lycksee (*Pallasea*, Samter 1905). — 3. Wigry (*Pallasea*, Demel 1923), Hancza, Biale, etc. (*Pallasea*, Kulmatycki & Gabanski 1936). — 4. Krivoje (*Mysis*, Arnold 1924, acc. Decksbach 1927). — 5. Rycza (*Pallasea*, Kulmatycki & Gabanski 1936; *Pallasea*, *Pontoporeia*, Drako 1954), Strusto (*Limnocalanus*, Bowkiewicz 1937; *Pontoporeia*, Drako 1954), Voloso (*Limnocalanus*, Bowkiewicz 1937; *Limnocalanus*, *Pontoporeia*, *Pallasea*, *Mysis* Drako 1954). — 6. Ilsa (*Mysis*, Arnold 1924, acc. Decksbach 1927). — 7. Jassji (*Mysis*, Arnold 1924, acc. Decksbach 1927). — 8. Seliger (*Pallasea*, Behning 1924).

As was already mentioned in the foregoing section, the Danish lakes and those continental ones which are situated west of Onega-Ladoga, harbour only relicts of Group I (*Mysis*, *Pallasea*, *Pontoporeia*, *Limno-*

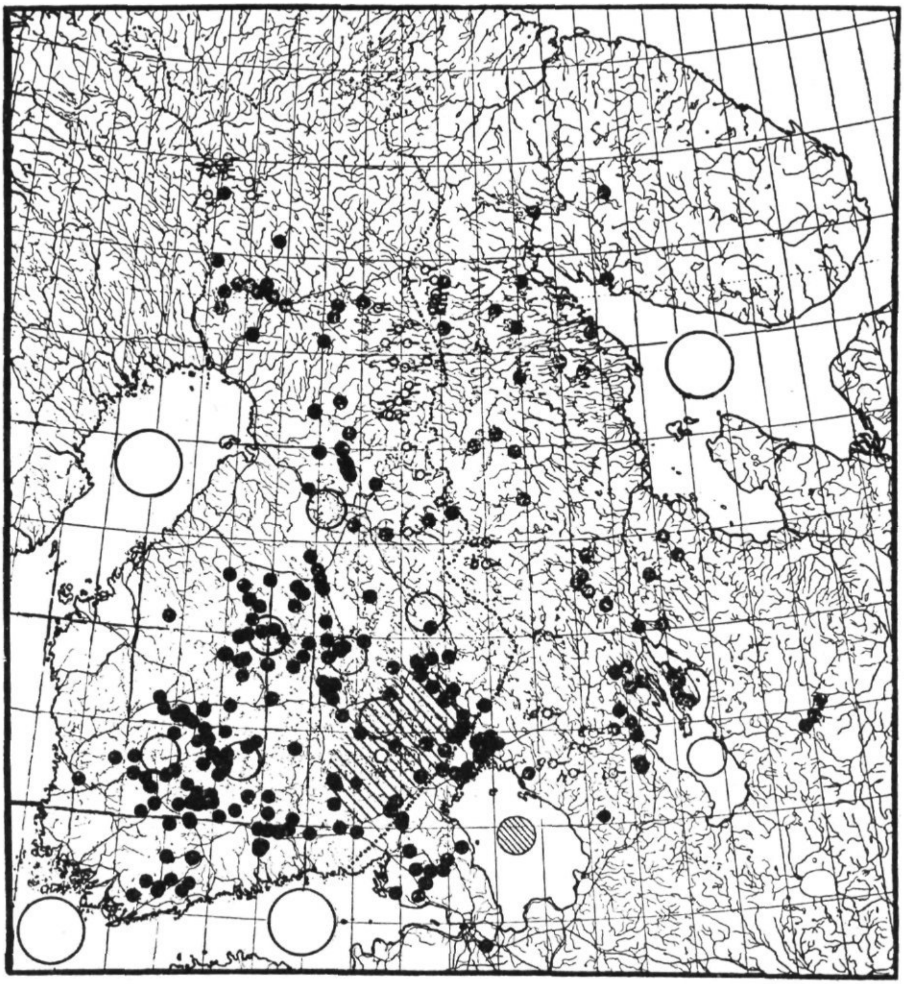

Fig. 13. Distribution of relicts in Finland and adjacent parts of Russia (for position of locality Kubenskoye Ozero, outside the map, see fig. 24). Black dots and big open rings in the inland area: freshwater localities, the rings indicate larger lakes; the other big rings indicate marine occurrence. Small rings with minus symbol: localities in North Finland and East Karelia with probable absence of relicts.

Hatched: occurrence of the Ringed Seal (*Phoca hispida*) in lakes. After Segerstråle 1956 a, with additions (Segerstråle 1956 b, Haverinen 1956, Hels. Zool. Museum).

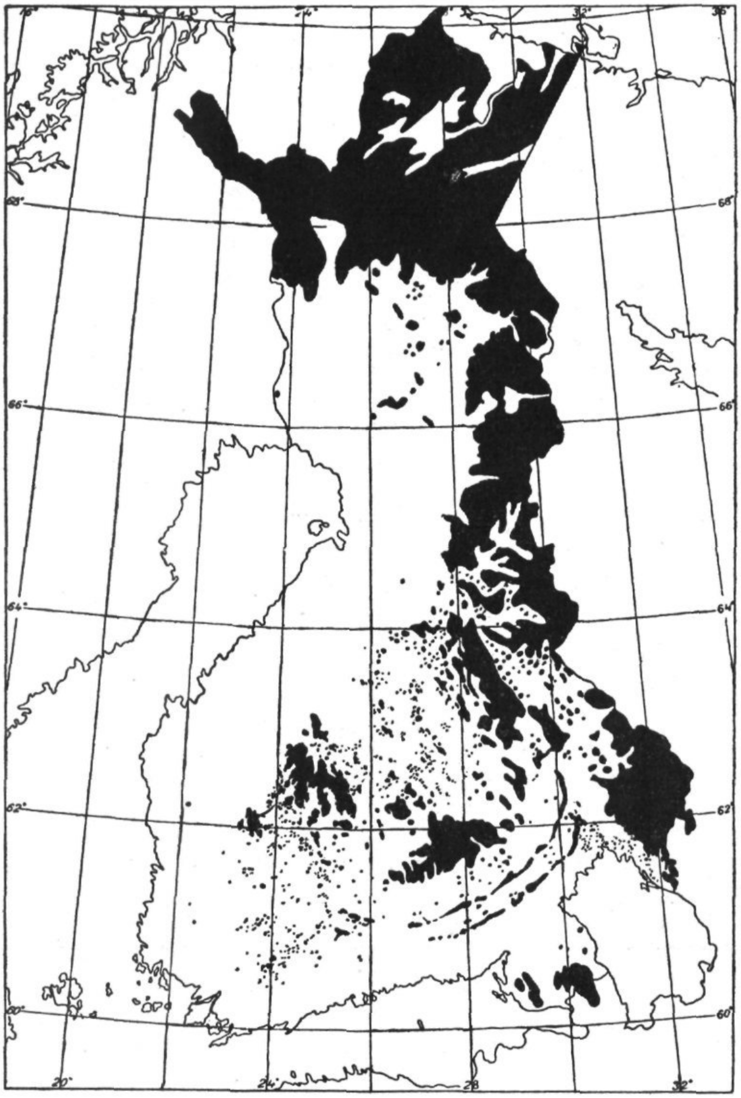

Fig. 14. Shaded areas indicate those parts of Finland (and some eastern areas today belonging to Russia) which were not flooded in late- or post-glacial times. After Sauramo 1940. The question of the highest shorelines in the eastern and north-eastern regions is still under discussion.

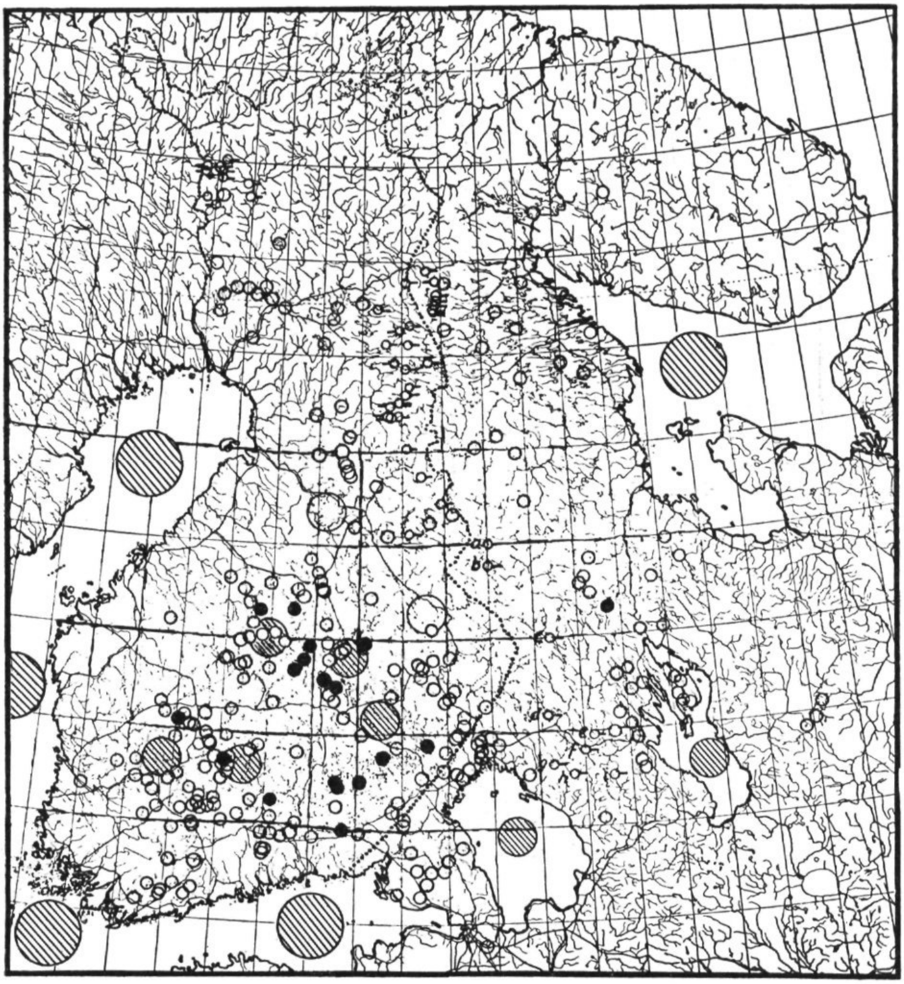

Fig. 15. Distribution of *Myoxocephalus* (*Cottus*) in Finland and neighbouring parts of Russia (dots and hatched rings). After Segerstråle 1956 a, with additions (Segerstråle 1956 b; Molekyyli 1957; collections of Hels. Zool. Mus.: Sorsavesi in Leppävirta, Isojärvi in Längelmäki).

calanus). By far the most widespread in these waters is *Pallasea*, followed by *Mysis*, *Pontoporeia* and *Limnocalanus*. In those lakes of northern Germany which were treated by THIENEMANN in 1925, *Pallasea* was found in 18 lakes against 10 for *Mysis* and 3 for *Pontoporeia*. (Cf. map fig. 12.)

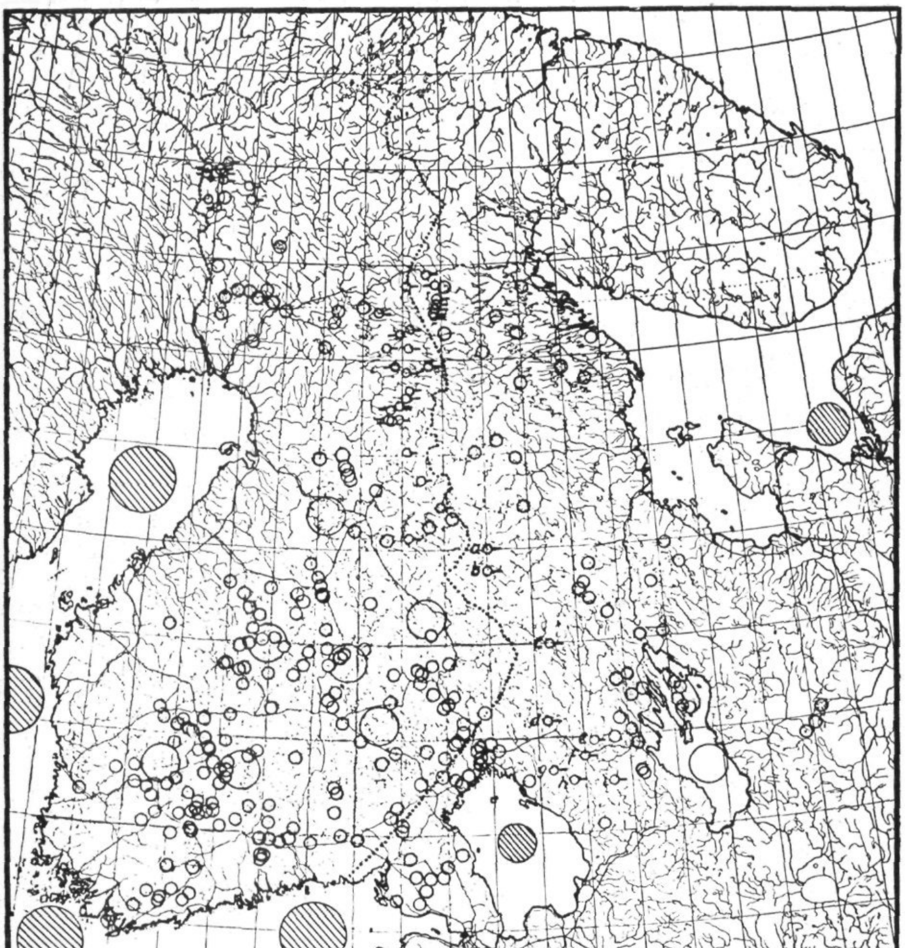

Fig. 16. *Mesidotea* is not recorded from Finnish lakes, but occurs in adjacent waters: the Baltic, L. Ladoga, and the White Sea (hatched rings). After Segerstråle, 1956 a.

The four relicts just mentioned are also the main forms of Fennoscandia and the adjacent eastern area. On the Russian side, the sequence of importance is *Pontoporeia*, *Pallasea*, *Mysis* and *Limnocalanus*, in Finland the order of frequency of the three first-mentioned forms is reversed: *Mysis*, *Pallasea* and *Pontoporeia* (for details, see SEGERSTRÅLE 1956 a, p. 11—12). Likewise, in Sweden and Norway the relicts of Group I are

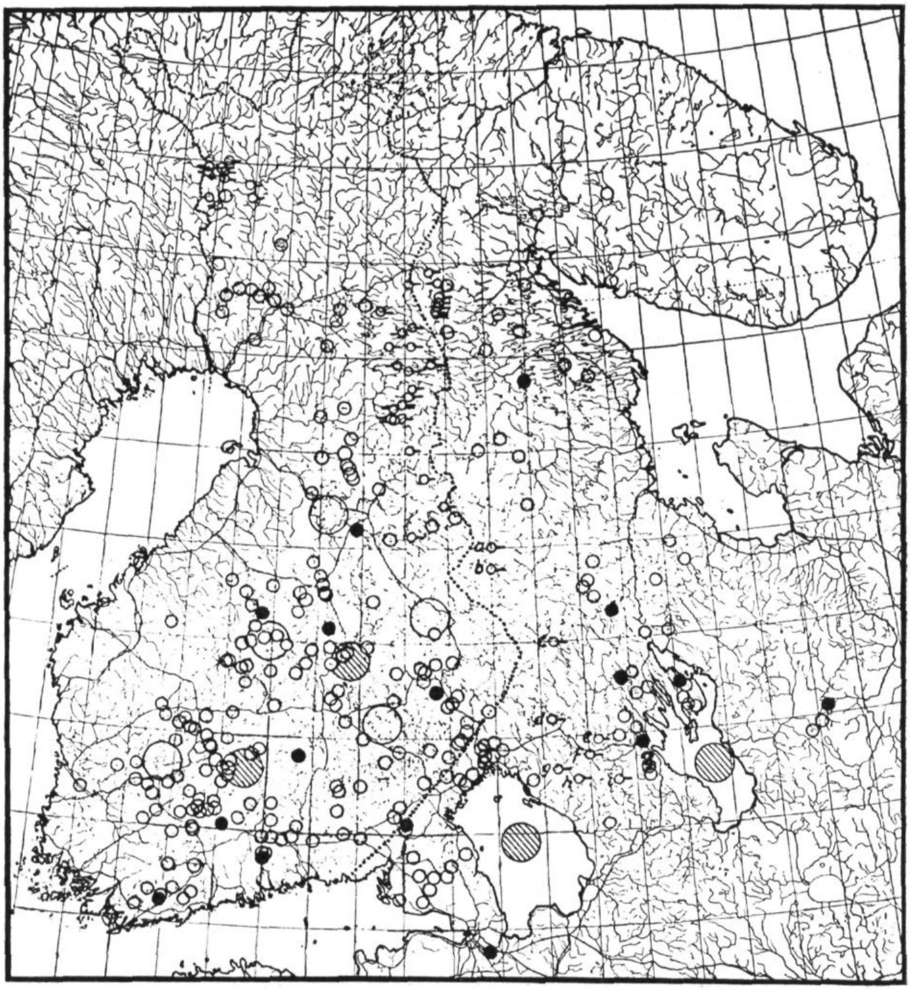

Fig. 17. Distribution of *Gammaracanthus* in Finland and adjacent Russian areas (dots and hatched rings). After Segerstråle 1956 a, with addition from Segerstråle 1956 b.

by far the commonest ones. In Norway, *Limnocalanus* is known from many localities; in other areas this small pelagic crustacean is, on account of the collecting technique, no doubt grossly underrepresented in the material (cf. SEGERSTRÅLE 1956 a, p. 13).

The relicts of Group II, i.e. *Myoxocephalus*, *Mesidotea*, *Gammar-*

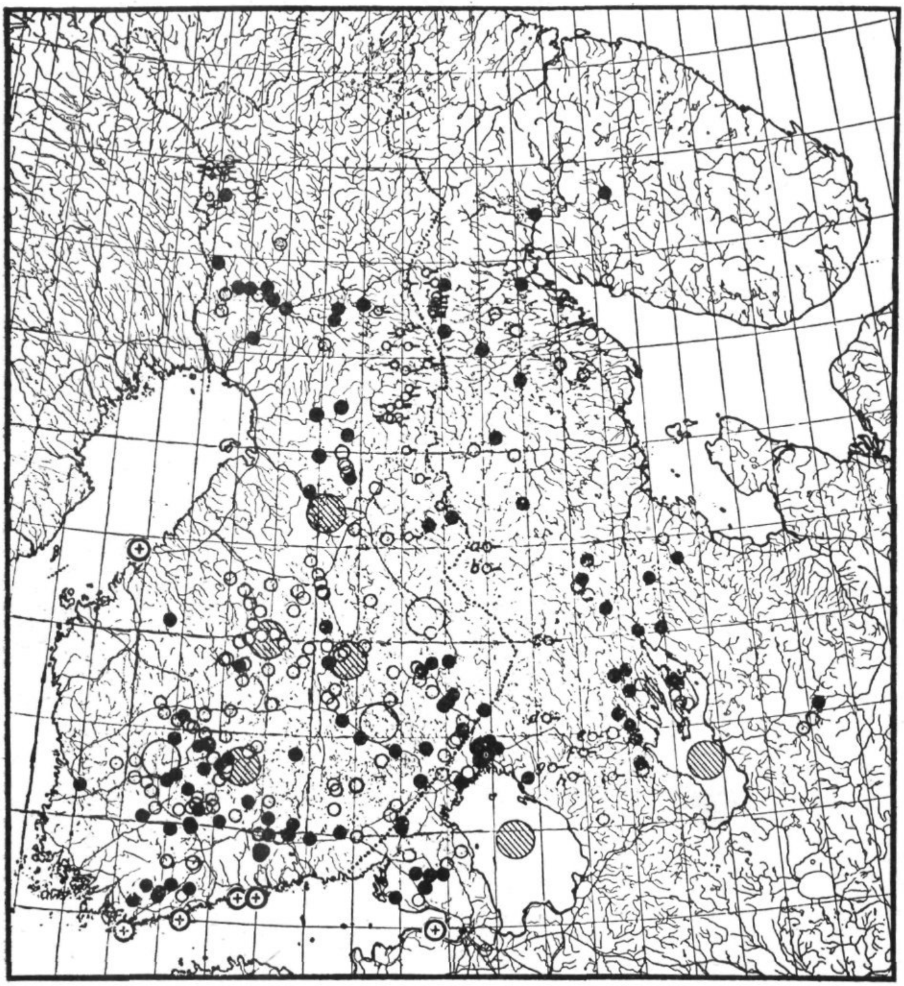

Fig. 18. Distribution of *Pallasea* in Finland and adjacent Russian areas (dots and hatched rings; crosses in rings: marine localities). After Segerstråle 1956 a, with additions (Segerstråle 1956 b; Haverinen 1956; Hels. Zool. Museum: R. Oulujoki, near Lamminaho).

acanthus and *Phoca,* which are totally absent from the Danish and continental lakes (west of Onega-Ladoga), are comparatively rare in the Fennoscandian and neighbouring Russian areas (cf. maps figs. 13, 15—17, 20; for *Phoca*, see SEGERSTRÅLE 1956 a). *Mesidotea* has never been recorded from Finnish or Norwegian lakes, and is known only from Ladoga as well

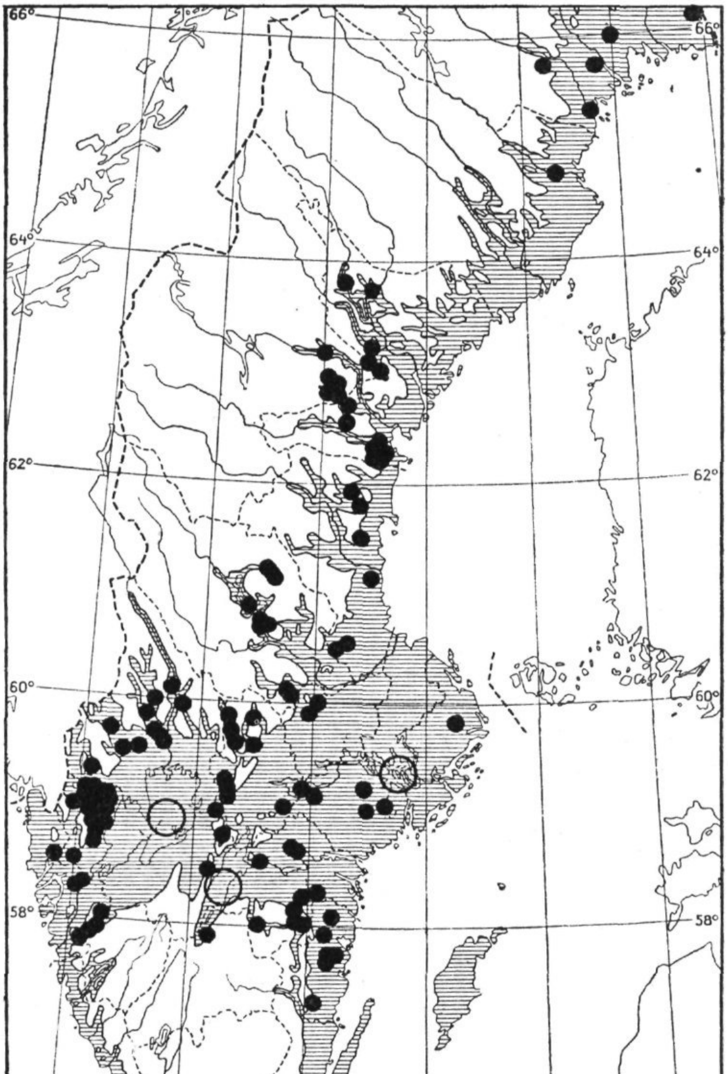

Fig. 19. Relict localities in Sweden. Combined from maps in Ekman 1940, with additions (Nybelin 1953, Jacobson 1954, Ekdahl 1957). Hatched; areas flooded in glacial times (after same maps; for modern views on the submersion of southern Sweden, see p. 66 and figs. 27—29).

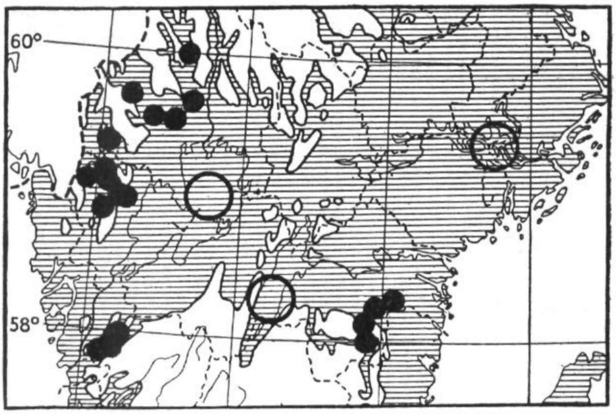

Fig. 20. Distribution in Sweden of relicts of Group II (*Myoxocephalus* [*Cottus*], *Gammaracanthus, Mesidotea*). Combined from maps in Ekman 1940, with additions (Nybelin 1953, Jacobson 1954, Ekdahl 1957). For details, see fig. 30.

as Vättern, Vänern and a few other lakes in Sweden (map fig. 20); *Phoca* is confined to the Saimaa district in Finland, and Ladoga (map fig. 13).[1] *Myoxocephalus* and *Gammaracanthus* are wide-spread but comparatively rare (maps figs. 15, 17, 20) and restricted to deeper lakes; in Norway the above-mentioned fish is lacking.

The relict lake *par excellence* is Ladoga, the only one harbouring all 8 relicts treated in the present paper. Next to it come Vättern and Vänern with 7 relicts (*Phoca* missing); lakes with 6 relicts are: in Russia: Onega, Segozero; in Finland: Kallavesi, Päijänne; in Sweden: Mälaren. No Norwegian lake is inhabited by more than four relicts; this maximum is found in Mjösa and Öyeren.

In the Baltic, and especially in its inner parts, all relicts, with two exceptions, are common; *Pontoporeia*, *Mesidotea*, *Mysis*, and *Limnocalanus* are even among the characteristic forms of the benthic and pelagic fauna of this area. The striking abundance of relicts in the waters of the inner Baltic is obviously due to their low salinity, which offers favourable conditions to brackishwater forms, and to the low winter temperature

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[1] According to a brief note in an official report on economic conditions in Finland in the 18th century (RUDENSCHÖLD 1738, p. 2), the Ringed Seal seems also to have lived at one time in L. Päijänne in southern Finland (reference kindly given by Dr. A. PYNNÖNEN).

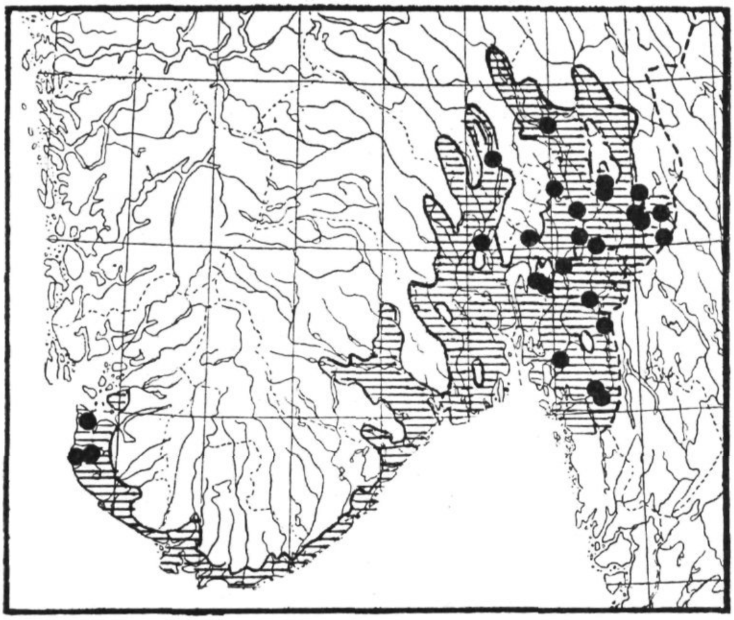

Fig. 21. Relict localities of Norway, according to data given in Mathiesen 1953. Flooded areas (after Nybelin 1931) hatched.

(like most other arctic forms, the relicts reproduce exclusively or mainly in the cold season).

One of the two exceptions is *Pallasea*, which, being a freshwater form, occurs only rarely even in the inner Baltic waters, and always near the coast (map fig. 18). The other exception is *Gammaracanthus*, which has never been recorded from Baltic waters.

As regards the location of the relict localities in relation to the level of the Baltic in late-glacial times, it will be remembered from the historical survey given in Section 2 that the Danish and continental lakes (west of Onega-Ladoga) inhabited by relicts without exception lie above that level. The German relict lakes are situated up to as much as 177 m. above sea-level (Wennberg 1943, p. 13) and Lake Seliger even lies at 205 m. In this connection mention should also be made of Lake Kenozero, east of Onega, and some adjacent lakes, which lie considerably (60—106 m.) above the level of the White Sea. As will be remembered, a quite separate history, including »sluicing-up» with ice-dammed waters, was postulated by HÖGBOM for the relict population of such »too high» lakes (cf. p. 13).

By contrast, practically all other relict lakes of the area treated have once been reached by Baltic water in late-glacial time when the earth-crust subsided under the weight of the ice and wide areas were flooded (cf. figs. 14, 19, 20); in Finland, the question of the highest shore-lines in the eastern and northeastern regions is not solved conclusively as yet. Also in Norway and East Karelia practically all localities are situated below the shore-lines of the adjacent late-glacial ocean (fig. 21). Owing to the crustal uplift since the glaciation, many of the lakes which were at one time or another isolated from the Baltic basin today lie high above its level (maximum elevation 280 m., west of the central part of the Gulf of Bothnia); the highest lake known to harbour relicts (those with *Pallasea* alone not considered; for reason, see below) is Alasjön in Jämtland (N. Sweden), situated at 213 m. above sea-level (EKMAN 1940).

Some exceptions or doubtful cases are to be noted. In one area, Jämtland in Sweden, *Pallasea* is thought recently to have migrated above the highest late-glacial shore-lines (NYBELIN 1944); also a few other Swedish localities above these lines are known for the crustacean (EKMAN 1940, p. 54). In Norway, the relation of some localities to the level concerned has not been cleared up so far (cf. p. 75).

In conclusion, it may be stressed that all Finnish lakes inhabited by such forms as *Mysis*, *Pontoporeia* and *Limnocalanus* have without doubt at some time been isolated directly from the Baltic basin.

III. IMMIGRATION.

1. ARE THE RELICTS DESCENDANTS OF WESTERN OR EASTERN IMMIGRANTS?

At the time that LOVÉN advanced his theory of relict immigration from the east, along a strait connecting the White Sea with the Baltic, nothing was known concerning the occurrence of these animals in continental lakes (apart from the Onega-Ladoga region), in areas above the level of the late-glacial Baltic. However, as was pointed out previously (p. 27), the immigration of the relicts into these waters no doubt represented the first phase in their conquest of Northern Europe. Hence, our first task must be an attempt to solve the question of how the relicts reached the continental waters.

There seems to be no reason to doubt the prevailing view that their existence today in the localities concerned is due to sluicing-up in front of the ice-cap, as suggested by HÖGBOM in 1917 (cf. pp. 13, 55). But what about their history before being sluiced up?

The view advanced by HÖGBOM may first be recalled. In his paper of 1917, which was, properly speaking, devoted to the problem of the history of the arctic element in the Aralo-Caspian fauna, this author also touches briefly upon the immigration of relicts into the German lakes and the Danish L. Furesö, the only continental lakes outside the Onega-Ladoga area which were at that time known to harbour relicts. HÖGBOM suggested that when the ice-cap retreated prior to the Gotiglacial advance (which he believed to have been responsible for the sluicing-up of the relicts into the continental area), animals from the White Sea were enabled to invade the region between this sea and Ladoga, which region he assumed to have been flooded by marine water. When the ice-margin began to advance across the area, animals from the White Sea were isolated and transported up the continental slope in ice-dammed waters; subsequently, they may have migrated westwards along the ice-margin. An alternative which HÖGBOM thought even more likely, especially with regard to western relict localities, is that bays of the southern Baltic were transformed by the advancing ice into lakes by way of which the animals were directly sluiced up to higher levels in the neighbouring inland area. As regards the question of how they reached the Baltic, nothing was expressly said, but HÖGBOM no doubt reckoned with invasion from the White Sea in this case, too (cf. the last lines on p. 254 of his paper).

As mentioned previously (p. 18), EKMAN, in 1930 (cf. also EKMAN 1940), expressed the view that, before the sluicing-up phase, relicts had entered the Baltic from the west, across the region of Öresund; however, he also refers to HÖGBOM's view of their having reached northern Germany from the east. As will be remembered (p. 19), later on (1940) MUNTHE, like EKMAN, assumed invasion to have taken place across the Öresund region, but regarded the sluicing-up theory as less firmly grounded.

When today we have to determine our stand on the question of eastern versus western invasion, there cannot be the least doubt that the eastern route has been the only one utilized by the relicts, *Phoca* possibly excepted (cf. p. 74).

For western immigration would have entailed that, on leaving their original sites in the arctic waters of western Eurasia, the animals con-

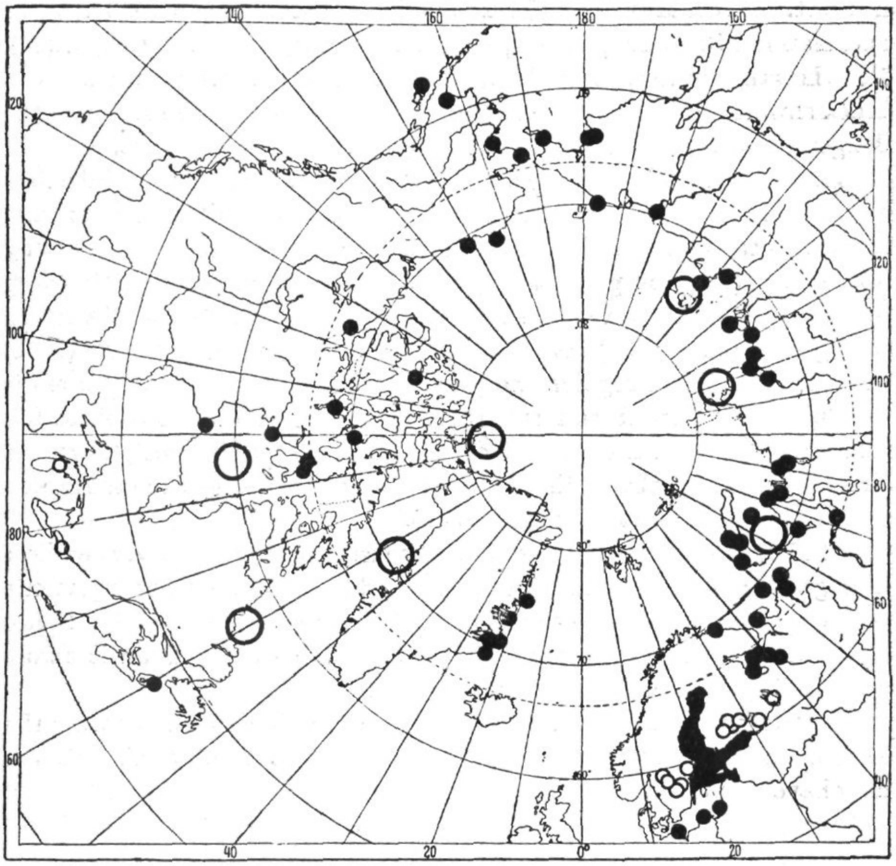

Fig. 22. General distribution of *Myoxocephalus* (*Cottus*) *quadricornis*. The large circles mark finds not precisely indicated, the small open circles finds in inland lakes (more recent Finnish finds lacking; cf. fig. 15). After Ekman 1953 a. Note the total absence of the fish in lakes on the west coast of Scandinavia, a feature which it shares with the other relicts treated in the present paper.

cerned circumnavigated the Scandinavian Peninsula down to the Danish region, and such a migration must be concluded to have been impossible. The case of *Pallasea* seems to afford an especially strong argument against such a theory. On the one hand, the distribution of this species in Northern Europe, which is in principle the same as that of the other relicts, suggests that it had the same immigration history; on the other hand, it is a lacustrine form which even in the inner Baltic is only rarely met with in coastal waters (for Finland, cf. SEGERSTRÅLE 1956 a, p. 27 and map fig. 18 in the present paper; for Sweden, EKMAN 1918 b, p. 334). But the other relicts, too, which, as we have found, are all pronounced brackishwater forms (cf. p. 39), cannot be expected to have survived the dangers involved in the marine passage around Scandinavia.

The above view is strongly supported by the fact that no glacial relicts are known from the numberless uplifted lakes along the western and northern coasts of Scandinavia, a feature which was also referred to by MATHIESEN (1953, cf. p. 25 above) as an indication that the relicts living in the lakes of southwestern Norway are not descendants of western immigrants (cf. fig. 22). It is also to be noted that ZENKEVICH (1956) expresses doubts as regards the passability of the western route: »It is difficult to see how these forms [the relicts], which do not tolerate full salinity, have been able to invade the Baltic from the west, from the North Sea. More probably they entered this basin — — — from the north-east, from the Arctic» (p. 288, transl.).[1]

Although the question now under discussion concerns the very earliest immigration of relicts, it may be anticipated that the foregoing arguments will also prevent us from assuming that such animals entered the Baltic along the strait which connected this basin with the Atlantic across central Sweden during the Yoldia Period.

We thus arrive at the conclusion that the first invasion came from the east. Our next task will be to examine the question of how this invasion may have occurred.

2. THE INITIAL IMMIGRATION FROM THE WHITE SEA REGION.

a. *The problem and extent of present geological knowledge.*

As will be remembered, HÖGBOM assumed that, before the Gotiglacial advance of the ice-sheet, the ancestors of the relicts had reached the region between the White Sea and Ladoga (and also the Baltic), which he supposed to have been flooded by that sea; the animals were thought to have

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[1] To be sure, MATHIESEN pointed out that the lakes of western Norway have not been much studied so far. However, it seems very unlikely that a fish such as *Myoxocephalus* would never have been recorded from these waters, if really present. It may, further, be recalled that MATHIESEN suggested that the lakes of the Trondheim region were especially suitable for population by relicts. However, on carrying out fishery investigations in 23 lakes on the islands of Hitra and Smöla off Trondheim, SIVERTSEN (1947) was unable to find any relicts.

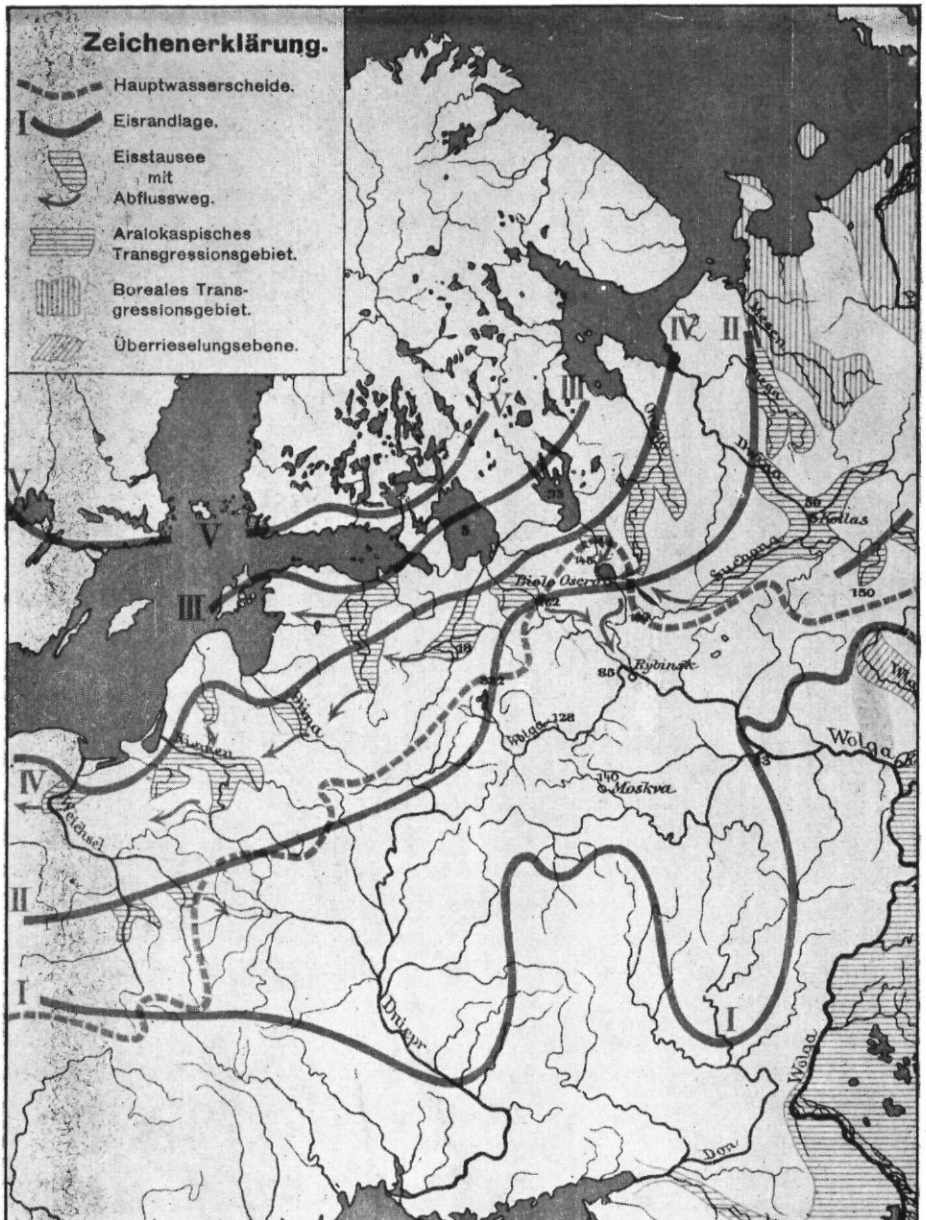

Fig. 23. Part of the map given in Högbom 1917, to illustrate his »sluicing-up» theory. The lines I—V indicate suggested successive positions of the ice-margin. After having retreated from II to III, the ice-cap is suggested to have advanced again to line IV. It is this forward move that Högbom considered responsible for the sluicing-up of animals native to the White Sea from the Baltic which they had reached at the time when the ice-margin had retreated to line III. Horizontally hatched areas: postulated ice-dammed waters; broken lines: main watersheds.

subsequently arrived in their present western continental area by migration combined with sluicing-up by the ice (fig. 23).

HÖGBOM based his idea of the flooding of the White Sea-Ladoga area upon the existence, near Petrozavodsk, on the western shore of Onega, of deposits including marine molluscs. These strata had previously been interpreted, by RAMSAY, as belonging to the last Interglacial, but HÖGBOM was inclined rather to attribute them to last glaciation, viz. that phase of it which preceded the Gotiglacial advance.

However, HÖGBOM's view cannot be upheld, since the deposits near Petrozavodsk — like other marine sediments in Karelia, found later on in the area between the White Sea and the Baltic, viz. near Leningrad (R. Mga), near Povenetz on the northern shore of Onega, on the watershed between Onega and the White Sea, etc. — seem, in fact, to be of interglacial age (cf. for instance, ZANS 1936, GERASIMOV & MARKOV 1939, pp. 135—137). As will soon emerge, this negative result does not, however, represent any real drawback to the biologist trying to reconstruct the process of relict immigration into Northern Europe.

The same is true of the still unsolved question of whether or not a connection existed between the White Sea and the Baltic at a later phase, at the time of the final withdrawal of the ice-cap. As was stressed earlier (p. 27), this question has no real bearing on the problem of how the relicts of Group I first reached the Baltic area, because, even if such a connection did exist, this would not explain their presence in the continental localities west of Onega — Ladoga; furthermore, as will be shown, the conception of a late connection is not necessary for understanding even the invasion of the relicts of Group II, which seem to have had the same initial immigration history as those of Group I. To the members of the former Group, the White Sea — Baltic connection would merely have meant a new, later possibility for invasion. To illustrate the still controversial opinions among geologists as regards the late White Sea — Baltic connection under discussion, two recent papers may be briefly reviewed.

In 1955, the Russian geologists BISKE and LAK published a paper on the late-glacial marine deposits of East Karelia; it constituted a critical survey of the recent literature, by EPSTEIN, LOMAKINA, POKROVSKAYA, SHESHUKOVA, MÖLDER, LAVROVA, APUHTIN, GORETSKY, etc., as well as previous work, and also presented the results of the authors' own recent investigations. The main conclusions arrived at are as follows:

Marine deposits unquestionably belonging to the last glaciation are found only in northern Karelia, near the head of Kandalaksha Bay and west of this bay, down to the Louhi area in the south. South of this area, the diatom material, collected in a number of localities, contains freshwater species for the most part. Where, locally, marine diatoms occur, they probably originate from interglacial strata. This interpretation is also applied to the local occurrence of marine diatoms in samples from the watershed between Onega and the White Sea, which was suggested by some earlier workers to indicate the existence of a late-glacial connection between this sea and Onega. On account of new investigations, an unfavourable attitude is also held towards MÖLDER's idea, based on diatoms samples from the isthmus between Onega and Ladoga, of a connection between the White Sea and the Baltic (MÖLDER 1944). BISKE and LAK attribute special significance to the fact that in a number of inland localities west of the White Sea deposits with exclusively lacustrine diatoms were found directly upon moraine or the rock crust. As the most likely explanation of the absence of late-glacial marine indications from central and southern Karelia, the authors suggest that during the Yoldia Period the White Sea was still filled with ice and thus cut off from the Arctic. The marine influence in northern Karelia is thought to have been due to influx from the Arctic in the north, along a narrow strait which in late-glacial times temporarily separated the Kola Peninsula from Fennoscandia (cf. LAVROVA 1947).

One year later, in 1956, the Russian geologist APUHTIN published a brief paper where views are advanced which are very different from those of BISKE and LAK (whose results are not, on the whole, mentioned by APUHTIN): the theory of a late-glacial connection between the White Sea and the Baltic is once more revived, viz. in the form of the so-called Karelian Ice Sea, postulated and named by HYYPPÄ (1943): and APUHTIN believes this connection to have been simultaneous with the deposition of the marine sediments found at high levels in northern East Karelia (cf. above). He thus opines that, at the time concerned, there existed not only a southern connection between the White Sea and the Baltic, across the Onega-Ladoga region, but also northern straits, west of Kandalaksha Bay (cf. SAURAMO 1954 and other authors, too, mentioned on p. 81 in the present paper).

b. *The suggested mode of immigration.*

East of L. Onega there lies, at a considerable altitude and in an area which has not been uplifted since the glacial epoch, a group of lakes where relict animals have been found. The lakes and their relict fauna are as follows (for position, see map fig. 24; »A.» = altitude; data from GERD, 1949 and letter, SEGERSTRÅLE 1956 a):

Terehovo Ozero	A. 67 m.	*Limnocalanus*, *Mysis*
Potshozero	A. 65 m.	*Limnocalanus*
Kenozero	A. 60–61 m.	*Gammaracanthus*, *Limnocalanus*, *Mysis*, *Pallasea*
Latsha Ozero	A. 106 m.	*Mysis*

Note. Parts of Kenozero have special names: Dolgoe Ozero, Glubokoe Ozero, Svinoe Ozero.

As far as Kenozero is concerned, the problem of relict immigration had already been touched upon by HÖGBOM — *Mysis* had been recorded from the lake in 1882 (by CZERNIAVSKY). HÖGBOM thought that animals of the White Sea had been sluiced up the valley of the R. Onega, situated east of Kenozero and receiving the outflow from this lake (cf. fig. 23): »Im Drainierungsgebiet des Onegaflusses lebt noch (im Kenosee) *Mysis relicta*, deren Auftreten dort, oberhalb der spätglacialen höchsten marinen Grenze, eine ungezwungene Erklärung durch Transport mit dem in diesem Flusstal vorgeschobenen, durch Absperrung des Mündungsbuchtes des Onegaflusses gebildeten Eissee bekommt» (p. 253). In support of this view, HÖGBOM referred to RAMSAY, who had found evidence of corresponding damming-up of the R. Pinega, a tributary of the neighbouring R. Dvina. HÖGBOM, whose main purpose was to explain the presence in the Aralo-Caspian basin of arctic animals, suggested that the ice-lake in the valley of the R. Onega, as well as similar adjacent waters »bei dem Vorrücken des Eises sich verschoben, bis sie ihre Abflüsse über die Wasserscheide gegen das Wolgagebiet bekamen» (p. 253).

It now seems highly probable, in the light of present geological knowledge, that the ice-lake of the R. Onega also represented the first step in the conquest of Northern Europe by the relicts.

However, before elaborating this point, some geological data obtained since HÖGBOM published his paper may be referred to.

HÖGBOM's conclusion of the ice-cap having dammed up water in the valleys of rivers running down the slope of northern Russia was purely theoretical, and not founded on observations in the field: »Die Eisseen sind freilich betreffs ihrer Details ganz hypothetisch, insofern keine direkte auf diese Eisseebildungen gerichtete Beobachtungen in der Natur zu Grunde für die Karte liegen — — —» (p. 251). Later work, however, has amply verified this idea. As shown in fig. 24, geologists have found wide

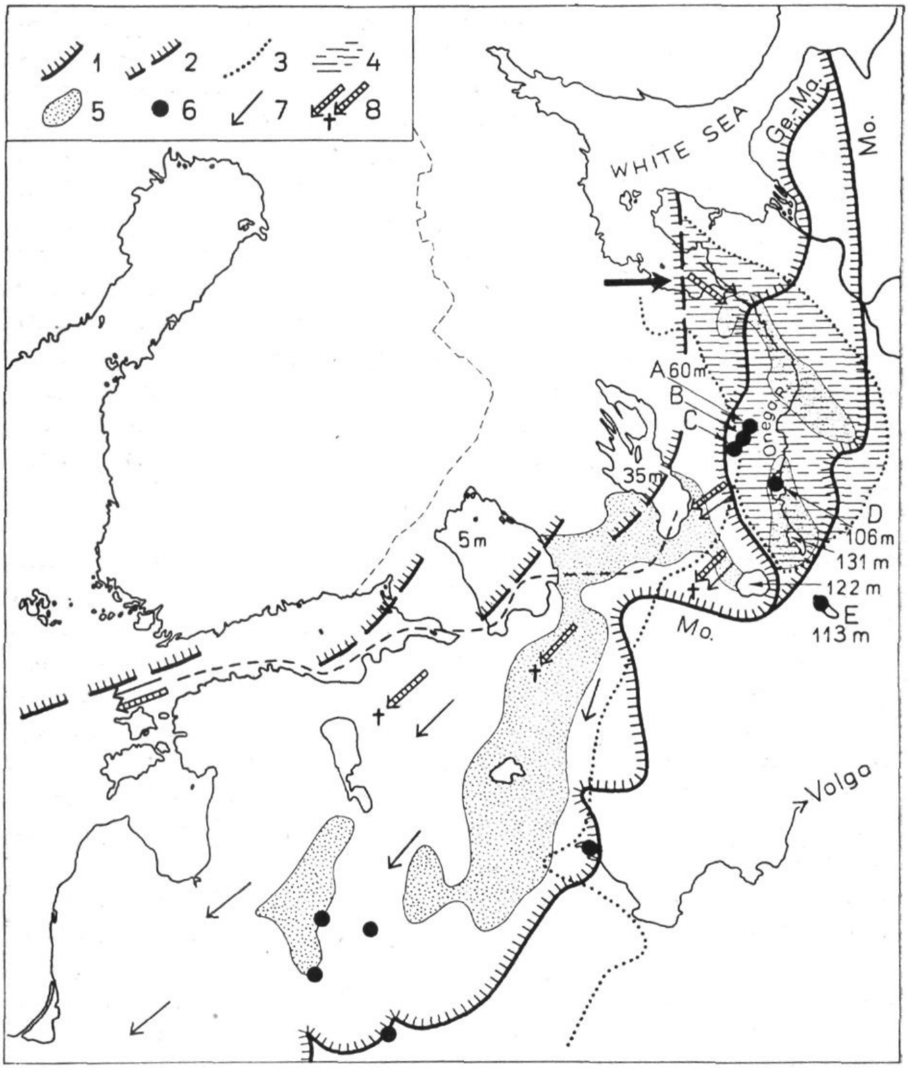

Fig. 24. The Onega Ice Lake and its rôle in the spread of relicts. — 1. Extent of ice-cap (in the north, two versions given, as advanced by Moskvitin 1952 and by Gerasimovich & Markov 1954 respectively. — 2. Tentative position of ice-cap. — 3. Watershed. — 4. Onega Ice Lake (successive stages combined). — 5. Sediments deposited in ice-lakes (after Moskvitin 1952). — 6. Relict localities (figures give height, in metres, above sea-level): A Kenozero, B Potshozero, C Terehovo Ozero, D Latsha Ozero, E Kubenskoye Ozero; for other localities, see fig. 12). — 7. Migration of relicts of Group I. — 8. Migration of relicts of Group II; cross: spread impossible for ecological reasons. Discussion pp. 60—61.

stretches within the once glaciated area to be covered with lacustrine sediments, deposited in front of the ice during its phase of retreat. To the south, such deposits have been disclosed as far as the Valdai region. JAKOVLEV (1928) reported the occurrence of varved clay on the watershed between the drainage basins of the R. Onega and the Volga, at a level of 130 m., and even south of the watershed such glacial deposits were found. Taken in conjunction with biological data, such as the occurrence of *Pallasea* in L. Seliger (Valdai region), *Mysis* in L. Kubenskoye Ozero (c. 200 km. S.E. of L. Onega), and the fishes *Coregonus albula* and *Osmerus eperlanus* — also glacial relicts (cf. p. 21) — in the upper reaches of the Volga (BERG 1928), these observations afford conclusive evidence of animals having been sluiced far southwards, as suggested by HÖGBOM.

Let us now return to the question of the ice-lake which was formed in the valley of the R. Onega and its rôle in the immigration history of the relicts.

As will be seen from fig. 24, the advancing ice-cap no doubt moved across the valley but seems to have stopped before reaching its uppermost part. Russian geologists are not quite unanimous as regards the position of the extreme limit; therefore, the figure gives two versions, advanced by well known workers (MOSKVITIN 1952 and GERASIMOV & MARKOV 1954). However, as emerges from the map, both alternatives permit the conclusion that, during the last glaciation, there existed a permanent ice-dammed lake in the uppermost part of the Onega valley.

Now, the author suggests that it was from this water that the conquest of Northern Europe by the relicts started. The question of their presence in the lake will be discussed farther below.

As suggested by HÖGBOM, in explanation of the occurrence of relicts in L. Kenozero (cf. p. 13), the bay off the mouth of the R. Onega must have been cut off by the advancing ice. The animals living there were gradually sluiced up the valley of the river with the water, and as the flow coming down the valley mixed with the seawater, the dammed basin was transformed into a freshwater lake. Those animals which had survived the change through adaptation to lacustrine conditions, were able to live in that part of the lake which remained beyond the ice-margin. When the ice began to retreat and wide stretches of dammed waters were formed along its margin as a consequence of melting and inflow of water along rivers running northwards, a large lake came into existence in the upper part of the valley of the R. Onega; direct evidence of this exists in the form of lacustrine deposits there (cf. fig. 24). In the course of the recession of the ice-margin, relicts of this lake also invaded western areas, conceivably by passive transportation, across the watershed between the drainage basins of the R. Onega and L. Onega. That this did actually occur is indicated by the presence of relicts in the lakes on the watershed in question (cf. p. 58 above and fig. 24). As a matter of fact, these lakes lie much lower, at 60—67 m, than the upper part of the valley of the R. Onega, the uppermost lake of which is at a level of 131 m. It is of importance to note in this connection, that, according to the position given by Prof. S. V. GERD (Leningrad) on a map sent to the present author, one of the lakes of the Kenozero group, Terehovo Ozero, lies west of the watershed (cf. fig. 24).

The crossing of this watershed seems thus to have been an event of great importance, which brought the relict faunal element into the Baltic basin and enabled its subsequent wide spread over Northern Europe.

One may ask why HÖGBOM did not suggest the mode of invasion proposed above. One reason might have been that he did not know enough about the local topography of the area concerned. Furthermore, the route now assumed was of no special interest to HÖGBOM, who, as we know, believed the relicts to have immigrated by way of marine waters between the White Sea and Ladoga.

It may be added that LAVROVA (1946, acc. GERD 1949, p. 130) also suggests that the relicts of the Kenozero group immigrated from the north, along the valley of the R. Onega.

An essential question remains to be discussed, viz. whether ancestors of the relicts may be concluded to have been present in the White Sea before the ice-cap of the last glaciation advanced across the basin.

In this respect, the history of the present fauna of the White Sea first calls for comment.

It goes without saying that the present fauna of this sea need not necessarily be identical with the original one, since the former immigrated later on when this became possible through the melting of the ice which had filled the basin in question. The new immigration may have come from two sources: on the one hand, from neighbouring marine waters and, on the other, from the ice-lake in the valley of the R. Onega as it finally drained down to the White Sea.

However, it must, of course, be expected in both cases that the relict species, in identical or closely related forms, will today be found in the

White Sea, if the immigration has come from this area. This is in fact the case, as far as relicts of marine origin are concerned. Details are given below.

In relict waters	*In the White Sea*	*Source of information (White Sea)*
Phoca hispida s.l.	*Phoca hispida* s.l.	Bobrinsky 1944
Myoxocephalus quadricornis s.l.	*M. quadricornis* s.l.	Andriashev 1954
Gammaracanthus lacustris	*G. loricatus*, *G. l. ostiorum*	Lomakina 1952 (cf.p.)
Pontoporeia affinis	*P. affinis*	Lomakina 1952 (cf. Segerstråle 1956 a, p. 27)
Mesidotea entomon	*M. entomon*	Lomakina 1952
Mysis relicta	*M. relicta*	Jarzhynsky 1870 (cf. p. 38)
Limnocalanus macrurus (*L. grimaldii*)	*L. macrurus*	(in the estuary of R. Dvina; Lomakina 1952, cf. Segerstråle 1956 a, p. 27)

An alternative to the idea, discussed above, that the ice-lake of the Onega valley received its brackishwater inhabitants from the White Sea is given below.

The lacustrine *Pallasea quadrispinosa* is not known from the White Sea; an old statement claiming its presence there, by Jarzhynsky (1870, pp. 315—16), is obviously incorrect (cf. Segerstråle 1956 a, p. 27). However, the species might have lived in fresh waters within the drainage area of the R. Onega when the last glaciation began and have been included in the ice-lake of the valley concerned as it was formed. Without this assumption it seems impossible to explain the fact, referred to previously, that *Pallasea* has, in principle, exactly the same range in Northern Europe as the other relicts, which suggests a similar history.

The reason for the presence of *Pallasea* in the fresh waters of the White Sea region before the last glaciation will be elaborated later (Section III: 10). It may be anticipated that this relict would have come from Siberia in connection with the maximum glaciation, prior to the last one, migrating in the ice-dammed waters along the margin of the ice-cap.

In connection with this immigration problem, it will also be shown that the same westward invasion from Siberia is also to be reckoned with respect to the relicts of brackishwater type, discussed above. The possibility that these animals likewise lived in lakes south of the White Sea when the last glaciation set in seems, however, considerably smaller than in the case of *Pallasea*, which tolerates comparatively high temperatures and was thus more fitted to survive warm interglacial phases (cf. p. 66). Hence the alternative suggestion that these animals survived in estuaries and were sluiced up the Onega valley from such areas of the White Sea appears more likely.

3. FURTHER CONTINENTAL SPREAD. INVASION OF NORTHERN GERMANY AND DENMARK.

Once the relict species had crossed the watershed separating them from the catchment area of the Baltic, in the way just proposed, further dispersion westward became possible by way of those waters which were dammed up along the ice-margin and which, for topographical reasons, flowed in this direction (cf. fig. 00 and HAUSEN 1913, p. 72). It is no doubt as a result of this flow, together with active migration, and conceivably also southward sluicing-up in connection with temporary advances of the ice, that the relicts are today found in L. Seliger and in lakes farther to the west (map fig. 12). This history has, as a matter of fact, already been outlined by DECKSBACH and BOWKIEWICZ (cf. pp. 16, 19).

As regards northern Germany, some historical data may first be recalled. HÖGBOM suggested that the relicts of northern Germany had been sluiced up from coastal waters of the southern Baltic, which they had reached from the White Sea across the Onega-Ladoga area. As an alternative, he proposed migration along the ice-margin from dammed-up waters south of Ladoga; the latter explanation was regarded as much less probable, especially in the case of western localities. THIENEMANN (1925, 1928, 1950) subscribed to and elaborated HÖGBOM's theory. EKMAN (1930) was also an adherent to it, whereas MUNTHE (1940) was more sceptical.

As was mentioned before, there can be no doubt that HÖGBOM's idea of the damming-up effect of the ice-cap offers the correct explanation of the occurrence of relicts in the lakes of northern Germany. In fig. 26, an attempt is made to visualize the immigration, taking into consideration both alternatives advanced by HÖGBOM. That involving sluicing-up directly from the Baltic is no doubt preferable as an explanation of how the more western areas (especially Denmark, see below) were invaded. As most of the relict lakes of northern Germany are situated near and south of that moraine line which is attributed to the so-called Langeland advance, the reconstruction given in the figure is based upon this assumption (cf. EKMAN 1930, fig. 1; WENNBERG 1943, fig. 4 and p. 15).

Fig. 25. Position of relict localities in relation to the moraines of the Langeland advance (F) and to those of the preceding and subsequent stages (E and G). After Wennberg 1943; Danish localities added.

How did the relicts reach the Baltic from the eastern dammed-up waters? It seems probable that the invasion took place across the area southeast of the present Baltic, not via the Gulf of Finland. To be sure, we do not know how far to the north the ice-margin retreated before the Langeland advance, but the history of the relicts of Group II, as outlined in a later section (III: 5), points to the mouth of the Gulf of Finland having been continually blocked by ice up to a later phase.

Also the presence of relicts in Danish lakes (see fig. 25) seems to find a natural explanation in terms of the sluicing-up of waters in connection with the Langeland advance, or, in the case of some lakes (Furesö, Farum Sö), by a subsequent one; as an alternative, the latter localities might have been invaded by way of ice-lakes following the ice, as its margin retreated from the Langeland position. At any rate, invasion from the nearby ocean (an alternative suggested by Spärck 1942, cf. p. 20 above)

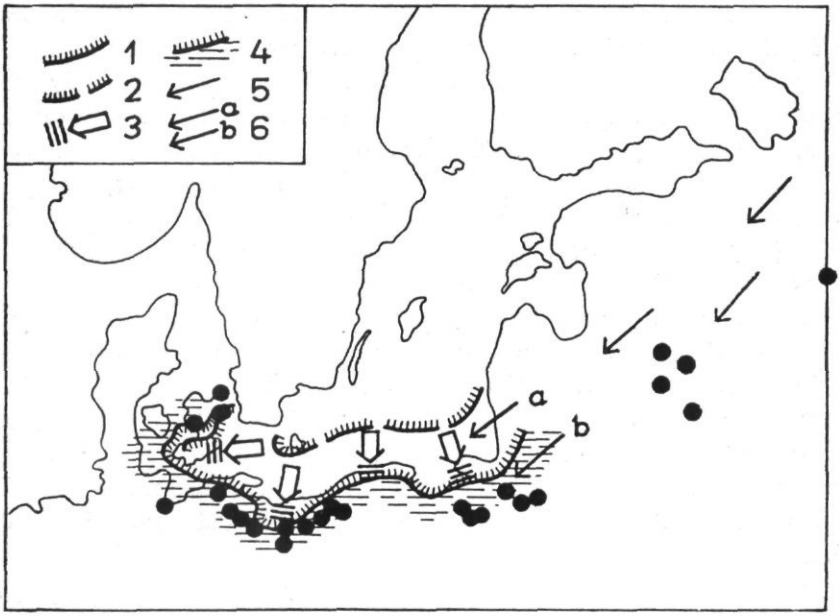

Fig. 26. The relicts spread westward from the Onega Ice-Lake and are sluiced up from the Baltic. — 1. Langeland advance (after De Geer 1954; for Zealand, the subsequent stage is also given). — 2. A tentative stage of the ice-cap prior to the Langeland advance. — 3. Damming up of water in front of the moving ice. — 4. Dammed waters. — 5—6. Migration of relicts; *a*, by way of the Baltic, *b*, along the ice-margin. Discussion p. 64 ff.

cannot be taken into account. For an understanding of the immigration into Denmark, it is essential to recall that that area is assumed to have lain above sea-level in late-glacial times.

In the case of L. Furesö, sluicing-up of the relicts was postulated by Ekman as long ago as 1930 (cf. also Segerstråle 1954, p. 31).

As will be remembered (cf. pp. 27, 41), the continental waters discussed above harbour only some of the relicts, viz. *Mysis*, *Pallasea*, *Pontoporeia* and *Limnocalanus* (Group I). The explanation for this seems to be that the western path was in an ecological respect impassable to the other species (Group II). This matter will be elaborated in a subsequent section (III: 5). But even within Group I, ecological factors must be considered, if we are to understand the present distribution in the area concerned. As was previously mentioned, in the continental waters (those of Denmark included) *Pallasea* is by far the most frequent species; it is followed by *Mysis*; *Pontoporeia* and *Limnocalanus* are rare.[1]

No doubt the relicts in question were originally considerably more frequent in the area, but died out in the course of time in many of the lakes, as the eutrophization of these set in and rendered the deeper layers poor in oxygen, so that the relicts, which cannot endure high temperatures, were prevented from living in the lower layers with their colder water (cf. THIENEMANN 1925, 1928); in this connection the influence of the warm postglacial phases must especially be taken into account. Against this background, the striking preponderance of *Pallasea* is by no means surprising, for, compared to the other relicts, this crustacean is markedly eurythermic (cf. THIENEMANN 1928, DECKSBACH 1927, GERD 1949). As an example, L. Seliger may be mentioned. There, the only one of the relicts to occur is *Pallasea*, and even it is restricted to the littoral-sublittoral zone. Decksbach explains this as a consequence of unfavourable oxygen conditions in the deeper waters, due to the eutrophization of the lake.

4. FINAL SPREAD INTO THE BALTIC BASIN. INVASION OF SOUTHERN SWEDEN.

When the ice-dammed lakes of northern Germany, inhabited by relict animals, finally drained down to the Baltic basin, this meant a milestone in the history of their invasion of Northern Europe. From then on they become permanent inhabitants of the Baltic and, further, were enabled to spread into the surrounding areas as these were freed from ice and flooded by Baltic water.

For the understanding of the invasion of southern Sweden, it is necessary to consider the new results regarding the late-glacial history of this region published in 1953 by the Swedish geologist E. NILSSON. In that paper, detailed maps are given of the areas flooded by the early outlets of the Baltic Ice Lake across Scania (Skåne) which were only sketched in previous papers (cf. for instance, MUNTHE 1940). Furthermore, it is suggested that farther north, too, up to the Vättern region, wide areas were successively submerged, as the ice-margin retreated, by the outflow from the Baltic Ice Lake and from large ice-lakes connected with it. Some of NILSSON's maps are given in figs. 27—29.

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[1] In the case of *Limnocalanus*, the paucity of records might be due in part to reasons of sampling technique (cf. p. 46).

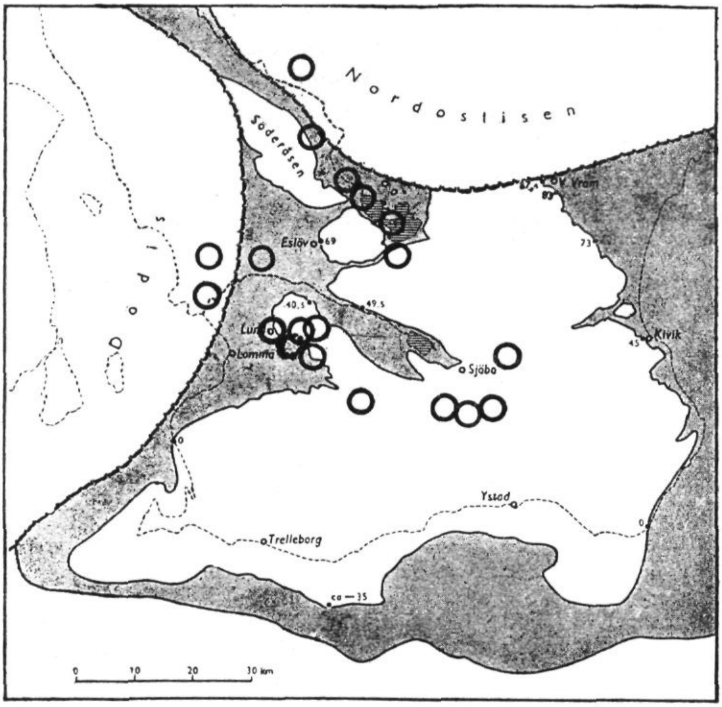
As shown by the present author in a foregoing paper (SEGERSTRÅLE 1954), in the case of *Gammarus pulex*, the first Scandinavian area reached by the former inhabitants of the ice-lakes of Northern Germany was Scania in southermost Sweden. The occurrence of *Pallasea* in L. Ringsjön of this area (see fig. 19) can be plausibly explained as due to this migration (cf. SEGERSTRÅLE 1954, p. 31) (MUNTHE 1940, p. 29, and NILSSON 1953, p. 163, assume the crustacean concerned to have come from neighbouring oceanic waters).

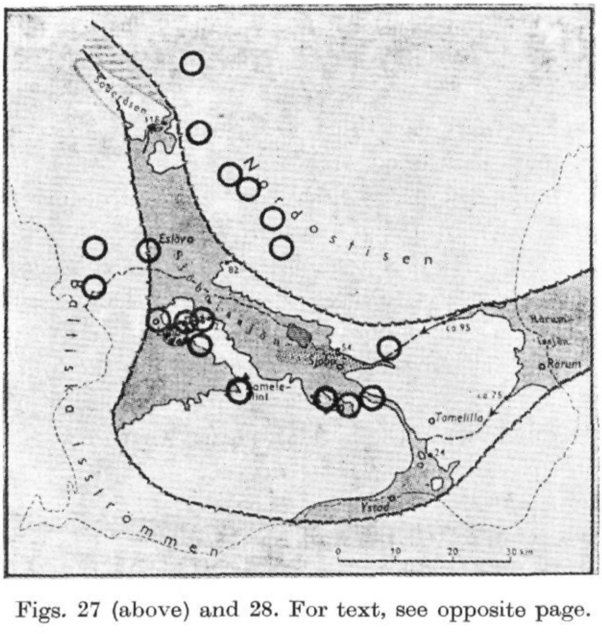
As regards the hydrographic possibilities for a lacustrine animal such as *Pallasea* to cross the early Baltic, it has been postulated (SEGERSTRÅLE 1954, p. 16) that at that time the water there was practically fresh, at least in the upper strata; and the presence in L. Ringsjön of *Gammarus pulex*, which is very sensitive to salt water, suggests that even at that somewhat later phase when the Ringsjön area was connected with the ocean (cf. fig. 27), the saltwater influence must have been negligible in shallow water, apparently owing to the immense outflow of melt-water around Scania.

The occurrence of *Pallasea* and other relicts (*Mysis*, *Pontoporeia*, *Limnocalanus*) in L. Ivösjön in northeastern Scania would be due to somewhat later invasion from the Baltic (EKMAN 1930, p. 237, suggests immigration from the ocean via the Baltic Ice Lake).

As was mentioned in the literature survey (p. 18), NYBELIN in 1931 had already touched upon the possibility that *Pallasea* existed, before the last glaciation, in waters of northern Germany and from there spread northwards.

A glance at the map, fig. 19 (p. 48), shows that, apart from the two Scanian lakes just mentioned and some localities in the coastal area northwest of Öland, there are no records of the occurrence of relicts from southern Sweden up to L. Vättern. This absence is difficult to reconcile with the fact that this area, which includes the highland of Småland, is thought by NILSSON to have been largely flooded by Baltic water (cf. fig. 29 in the present paper). The present author has touched upon the problem in an earlier paper (1954), from which the following may be quoted (p. 36—37): »It is natural to ask why there are no records of the classical Arctic relicts from the highland of southern Sweden. One would expect them to live there as well as do the vendace (*Coregonus albula*), and other aquatic animals, such as gastropods, which were above concluded to have immigrated by way of the Baltic Ice Lake. Ecological factors can hardly be thought of, as the relicts concerned are common in





Figs. 27 (above) and 28. For text, see opposite page.

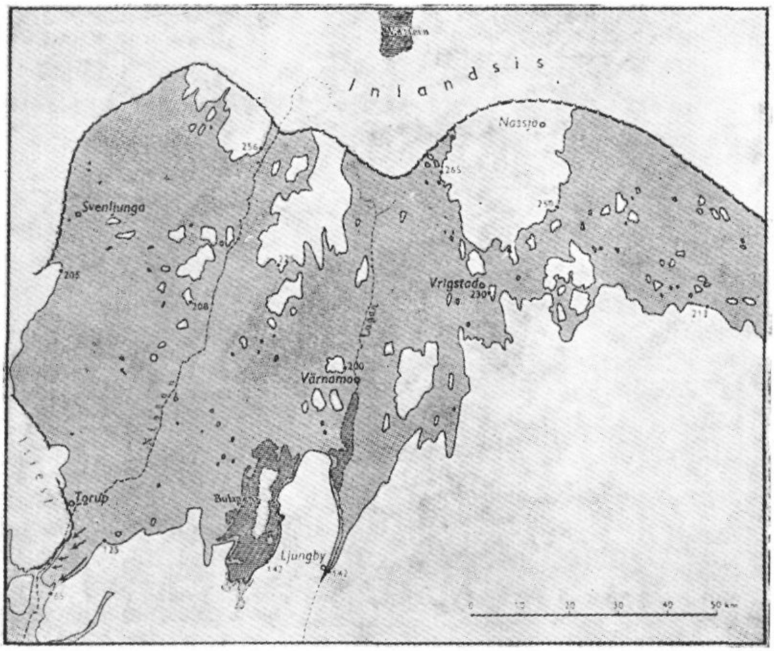


Fig. 29. A subsequent phase of late-glacial flooding in southern Sweden. Swedish west coast in the lower left corner, southern end of L. Vättern at the top. From E. Nilsson 1953.

Figs. 27 and 28 (opposite page). Submergence of southernmost Sweden (present coast-line dotted) during the waning phase of the ice-cap, according to E. Nilsson 1953. Flooded areas coloured grey. Nordostisen = the Northeastern ice-stream, Baltiska isströmmen = the Baltic ice-stream, Södis = dead-ice.

Below: a very early stage. At about that time, communications between the fresh waters off the Scania coast and the ice-dammed lakes of northern Germany seem to have opened up, enabling aquatic animals inhabiting the lakes — including glacial relicts — to reach Scania. The rings indicate localities of another animal, viz. the amphipod *Gammarus pulex*, which would have immigrated along the same path (after Segerstråle 1954).

Above: a somewhat later stage. It is at that time that L. Ringsjön (a little N. E. of centre, hatched) might have been invaded by *Pallasea* (and *G. pulex*).

Finnish lakes which are of much the same ecological type as those of Småland. Prof. SVEN EKMAN, with whom the author has discussed the matter, thinks it possible that the lack of records from the highland of southern Sweden is simply due to this area having been comparatively little investigated by hydrobiologists.»

5. APPEARANCE IN THE BALTIC OF THE RELICTS OF GROUP II.

As has been pointed out previously, *Myoxocephalus*, *Gammaracanthus* and *Mesidotea* have not been recorded from the lakes of northern Germany or adjacent areas, including Denmark.[1] Before embarking upon a discussion of the reasons for this feature, earlier views may be recalled.

THIENEMANN (1925, p. 399) stated: »Vielleicht ist das Fehlen der übrigen, in Fennoskandien verbreiteten Relikten in Norddeutschland (*Cottus quadricornis*, *Chiridotea entomon*, *Gammaracanthus loricatus*, *Limnocalanus macrurus* [regarding the last-mentioned, see p. 15] so zu deuten, dass diese — im Gegensatz zu *Mysis*, *Pallasea* und *Pontoporeia* das Eismeer, über das der Gletscher der baltischen Eiszeit vorstiess, *nicht* bewohnten, sondern dass sie erst in das postglaziale Yoldiameer einwanderten. Nehmen wir das an, so wird ihre Existenz in Fennoskandia, ihr Fehlen in den Seen Norddeutschlands, die ihnen meines Erachtens ebenfalls günstige Lebensbedingungen bieten, verständlich.» The same view is expressed in THIENEMANN's account of the immigration history of the freshwater fauna of Europe (1950, p. 499): »Ich halte diese Theorie auch jetzt noch aufrecht, denn sie scheint mir die einzige Erklärungsmöglichkeit für diesen Unterschied in der Verbreitung der beiden Gruppen der glazialmarinen Relikte zu bieten. Soviel ich sehe, ist auch von keiner Seite eine andere Erklärung gegeben worden.»

MUNTHE's geological work of 1940 also (p. 92) reckoned with earlier invasion on the part of the relicts of Group I; he based this conclusion on the occurrence of these animals at levels higher than that of the Yoldia Sea. They were suggested to have immigrated from the Baltic Ice Lake, which the relicts had reached, according to MUNTHE's hypothesis (cf. p. 19), via southwestern connections with the ocean. Like THIENEMANN, MUNTHE believed the relicts of Group II to have entered the Baltic during Yoldia times.

The conclusion that Groups I and II immigrated at two different

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[1] For *Phoca*, see below p. 74.

phases, seems, in fact, unavoidable. For if we assume simultaneous immigration, this would imply that the relicts of Group II died out later on in the lakes of Germany and adjacent areas. To be sure, these relicts are ecologically comparatively exigent, but it seems, nevertheless, difficult to explain their total absence from the region on an ecological basis. The environmental factors of special importance to the animals concerned are no doubt low temperature and good oxygen supply (as regards *Myoxocephalus*, cf. LÖNNBERG 1932; *Gammaracanthus:* VALLE 1929, GERD 1949, LOMAKINA 1952). Now there are in northern Germany a number of lakes with depths of more than 50 m. which have proved cold in their deeper layers and well aerated down to the bottom (THIENEMANN 1925, 1928). In the first of the quotations given above, THIENEMANN himself concluded that the lakes concerned offered favourable living conditions for the relicts of Group II.

Their distribution in Sweden gives some additional support to the idea that they immigrated later than those of Group I. As emerges from a glance at fig. 19, none of the former relicts is recorded in Sweden south of about 58° N., although, as was mentioned earlier, wide southern areas are supposed to have been submerged by Baltic water. To be sure, relicts are not, on the whole, known from there (cf. p. 67), but it is hard to believe that a fish such as *Myoxocephalus* would have escaped observation by the fishermen of the area, which is very rich in lakes, if it had been present. Hence, it seems more likely that southern Sweden had already been lifted above the level of the Baltic when the basin was reached by the relicts of Group II.

How, then, is the postulated difference in the time of invasion of the relicts to be explained?

First, one must rule out the possibility that the relicts of Group II came along the western connection between the Atlantic and the Baltic, which existed across central Sweden during the Yoldia Period; the reasons for this attitude towards a hypothesis advanced by a number of earlier workers have been given previously (p. 55). Again, as regards direct immigration from the White Sea at the stage of the Baltic Ice Lake, present geological opinion seems very divided about this idea (p. 56). And even if this late immigration from the east were geologically acceptable, the question arises of why the relicts of group II did not join those of Group I in their initial conquest of the Continental area.

In this case, likewise, the suggested ice-dammed lake in the valley of

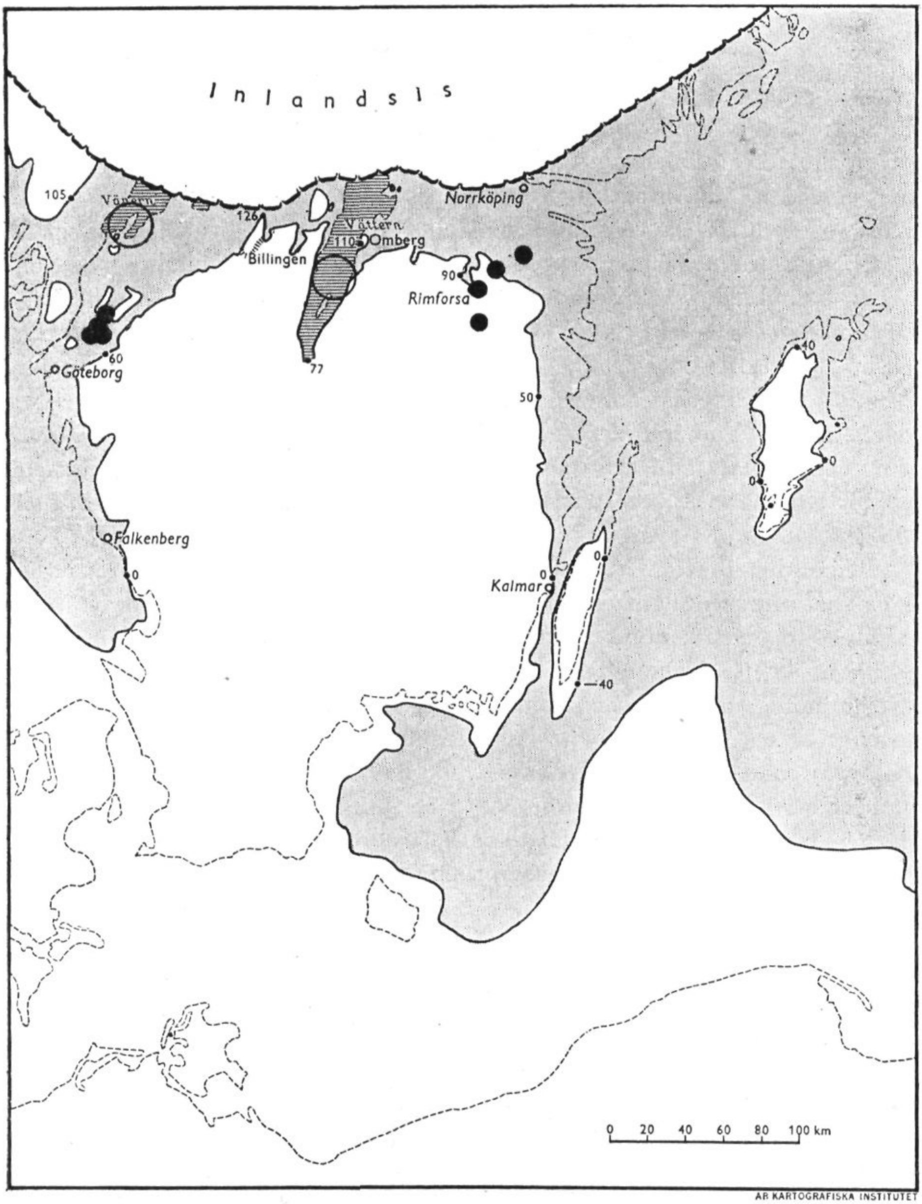

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Fig. 30. The Scandinavian localities (indicated by dots and rings) first reached by the relicts of Group II. The grey area is the Yoldia Sea, at its very first stage (according to Nilsson 1953). Representation of Group II in the lakes concerned: the four lakes in the southwest (Sävelången, Färgen, Mjörn, Anten) are inhabited by *Mesidotea*; Vänern and Vättern, by *Mesidotea*, *Gammaracanthus* and *Myoxocephalus*; the eastern lakes, by *Myoxocephalus* (the lakes and their altitude, from the south: Åsunden 85 m., Åländern 92 m., Örn 78 m., Borken 60 m.). After Ekman 1940, Ekdahl 1957. Cf. p. 73.

the R. Onega seems to afford a plausible solution of the problem (see fig. 24).

First, it is of importance to state that *Gammaracanthus* is known from L. Kenozero on the western border of the valley concerned (fig. 24). Hence, it may be concluded that this exigent relict, and hence conceivably also *Myoxocephalus* and *Mesidotea*, lived in the Onega Ice Lake. The subsequent history of these animals is postulated by the present author to have been as follows:

Owing to the restricted ecological valence of the relicts belonging to Group II, they were unable to spread from the ice-lake concerned to the southwestern continental area reached by Group I. It is to be remembered in this connection that the route there from the ice-lake crosses regions characterized by very even relief; hence the waters which were once dammed up there along the margin of the ice-cap must have been shallow and thus easily warmed. Especially during those climatic phases of the late-glacial period which caused the retreat of the ice-margin, it seems readily conceivable that the temperature of the dammed lakes exceeded the comparatively low tolerance limit of the animals in question.

By contrast, the nearby and deep L. Onega was no doubt much more easily reached and populated by the relicts of Group II, when the ice-margin had retreated far enough to render this possible, and subsequent further spread to Ladoga and the Gulf of Finland, across the intervening flooded isthmuses, might also have been possible. It goes without saying that this westward route from the initial ice-lake must also have been utilized by the relicts of Group I. At first, all these animals were isolated in the Gulf of Finland, but as soon as the mouth of the Gulf opened behind the retreating ice-margin, they were enabled to enter the rest of the Baltic basin which, as we have found, had already at an earlier date been populated by the relicts of Group I from the continental ice-dammed waters.

This theory by which the relicts of Group II have had the same initial history as those of Group I but, for topographically conditioned ecological reasons, were long prevented from invading the Baltic, seems to offer the most natural explanation of their different distribution.

As regards the time of arrival of the relicts of Group II off the coast of Scandinavia, after crossing the Baltic, fig. 30 is instructive. This figure, after NILSSON (1953), gives the shore-lines of the Yoldia Sea at its earliest phase, and the level above the present sea of those localities of the relicts concerned which were at that time free from ice and thus open to invasion.

As will be seen, at least one of the *Myoxocephalus* localities east of Vättern, viz. L. Åländern, could have been reached already from the Baltic Ice Lake, since it lies about 4 metres above the highest Yoldia shore of the region in question.[1] Conceivably the relict of Group II invaded Scandinavia by way of the very latest stage of the Baltic Ice Lake; according to recent paleobotanical investigations by Cleve-Euler (1955), the mouth of the Gulf of Finland was not freed from ice until the so-called Salpausselkä stage I, which is attributed to that time when the ice-margin lay at the northern end of Mount Billingen west of Vättern (cf. Sauramo 1952, fig. 11), just before the Baltic Ice Lake drained down to the level of the sea (onset of the Yoldia Period).

The Ringed Seal deserves some special comments. It seems likely that it also lived in the ice-lake of the Onega valley. We have to remember that the animal no doubt reached the Caspian Sea through sluicing-up of ice-lakes, and there are even direct observations, referred to already by Högbom, of seals having lived in an ice-dammed basin (on the coast of West Greenland; H. Rink, acc. Credner 1887, p. 67). Whether *Phoca* originally also immigrated into the southwestern continental waters remains an open question; if so, the animal probably soon died out for ecological reasons and on account of hunting. In contrast to the other relicts, it may also have been ecologically possible for *Phoca* to circumnavigate Scandinavia and enter the Baltic across central Sweden during the Yoldia period, but its present distribution and the lack of fossil evidence in the far west (no finds known west of Uppland; Ekman 1922, p. 384) points towards invasion from the east.

6. INVASION OF CENTRAL SWEDEN AND SOUTHERN NORWAY.

When the Yoldia Period set in and the Baltic Ice Lake drained down to the level of the ocean, this represented the beginning of a new phase in the spread of the relicts. The flooding of the lowlands of central Sweden, which followed the continual retreat of the ice-margin, allowed invasion of this area and the adjacent region west and northwest of Vänern, as well as of southeastern Norway, and even more western Norwegian areas were reached.[2]

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[1] It may be noted that, in the region concerned, the highes shores of the Ancylus Lake lie below those of the Yoldia Sea (cf. maps in Sauramo 1952, Nilsson 1953).

[2] An earlier westward connection south of Mount Billingen (cf. Munthe 1940, and Nilsson 1953) must have been impassable on account of too high a salinity west of the strait.

The invasion at that time of those parts of central Sweden which lay beyond the limits of the Baltic is easily understandable from a hydrological point of view, because even in late Yoldia times the water which covered the region must have been practically fresh in the upper layers. This feature, which has been discussed by the author in a previous paper (SEGERSTRÅLE 1954, p. 17 and 21), would have been due to the immense outflow of Baltic water and the nature of the straits which connected the Vänern basin with the ocean and which are today thought to have been considerably narrower than was assumed earlier.

As regards Norway, the relicts have seemingly used the same paths for their immigration as those postulated by HUITFELDT-KAAS for Baltic fishes (1923). This author assigned special importance to that route which runs from the Vänern area in a northwestern direction, over Kongsvinger to Österdalen in nearby Norway (fig. 31). The water must have been greatly diluted in this strait, especially in the late Yoldia time.[1] This is indicated by the fact that southeastern Norway was invaded by many pronouncedly lacustrine fishes, for instance, the vendace (*Coregonus albula*), the bream (*Abramis brama*), and the roach (*Leuciscus rutilus*). Very likely the Kongsvinger route was also the main immigration path of the relicts, the Norwegian localities of which are concentrated in the nearby southeasternmost corner of the country.

MATHIESEN (1953, p. 84) drew attention to the doubt expressed by some Norwegian geologists that the larger lakes of southeastern Norway have never been connected with the sea; in the case of the large Mjösa, it has been assumed that a glacier occupied the area and only melted away after the land had risen sufficiently to break the connection with the sea. An opposite interpretation was advanced, in 1924, by the geologist HOLTEDAHL, and MATHIESEN considered this view more likely from the biologist's standpoint. He referred to the presence in Mjösa of the relict planktonic copepod *Limnocalanus macrurus*, which cannot easily be thought to have entered the swift-flowing outlet from the lake. The present author fully subscribes to MATHIESEN's view and would apply it also to the semipelagic *Mysis relicta*, another of the relicts of Mjösa, because in this case, too, there is no evidence to support such an active mode of invasion.

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[1] HUITFELDT-KAAS attributed the immigration of fishes from the Baltic to the Ancylus Period, but at that time the connection with Norway would already have been broken (cf. MUNTHE 1940, plate X; SAURAMO 1952, fig. 12).

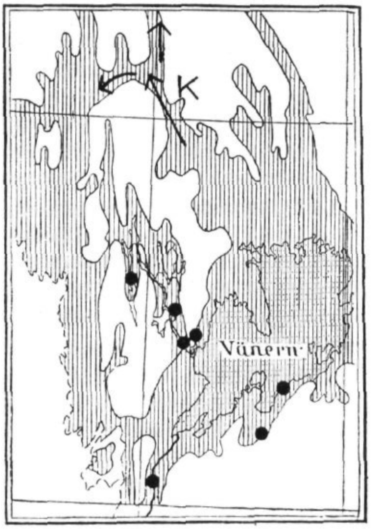

Fig. 31. The invasion route into Norway via the Kongsvinger area (K = Kongsvinger strait) in late Yoldia time (chart mainly after De Geer 1896). The localities of *Gammarus pulex* (dots, from Segerstråle 1954) indicate that the water was practically fresh in the region concerned.

The presence of relicts in the area near the Oslo Fjord (fig. 21) suggests that the water was greatly diluted there also. As a matter of fact, the enormous influx from the Baltic across Sweden and the large rivers of southeastern Norway, in late Yoldia times when large glaciers were still melting, must have caused a very marked lowering of the salinity in the regions concerned; this conclusion was drawn already by DE GEER (1896).

The great dilution of the coastal waters would also have been responsible for the peculiar isolated occurrence of relicts in the areas of Jaeren (Jaederen) in southwestern Norway, where such animals are recorded from three lakes: *Pontoporeia* from Orrevann and Fröylandsvann, *Mysis* from Stokkelandsvann (fig. 32); the first-named two lakes are inhabited by the vendace (*Coregonus albula*), too (RUSTAD 1949, p. 325).[1]

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[1] Mr. H. HOLGERSEN, Director of the Zoological Section of Stavanger Museum, Norway, has kindly given the following data on the occurrence of the vendace in the Jaeren area (in litt. 25. 9. 57): The fish was first recorded in 1937 (A. BERNHOFT-

Fig. 32. Distribution of the perch (*Perca fluviatilis*) (right) and the whitefish (*Coregonus lavaretus*) in Norway (and neighbouring areas of Sweden). After Huitfeldt-Kaas 1923. Occurrence of relict crustaceans (*Mysis, Pontoporeia*) in the Jaeren area indicated by black dots in the latter chart.

The immigration of relicts to these waters was touched upon by EKMAN and MATHIESEN (cf. pp. 14 and 25). The former author suggested invasion from the ocean and from the Baltic to have been equally possible, while the latter did not take any definite stand on the question. The conclusion drawn by the present author that the relict populations of the Jaeren lakes have had the same origin as those of southeastern Norway requires some words of argumentation.

According to HUITFELD-KAAS, numerous lakes of the Jaeren area are inhabited by the whitefish (*Coregonus lavaretus*) and he regarded it as quite conceivable that these populations, like those of the freshwater fishes of southeastern Norway, are descended from Baltic immigrants. This idea to which SÖMME has recently subscribed (1949, p. 109) is, in fact, strongly supported by the occurrence of the whitefish in several freshwater localities between southeastern Norway and Jaeren (fig. 32); and also the distribution of other lacustrine fishes, for instance the perch (*Perca fluviatilis*) (fig. 32), suggests that the spread of such forms far westwards along the south coast of Norway was once possible. Furthermore, hydrological considerations are in harmony with the idea that the relict crustaceans of Jaeren came from the east. As was stressed by EKMAN (1922, p. 461), and HUITFELDT-KAAS (1923, p. 269) the diluting

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OSA, in Stavanger Museums årshefte 46, 1935—36); it is known from the lakes Orrevann, Fröylandsvann, and Horpestadvann, situated at 4—24 m. above sealevel. There seems to be no doubt about the identity of the species.

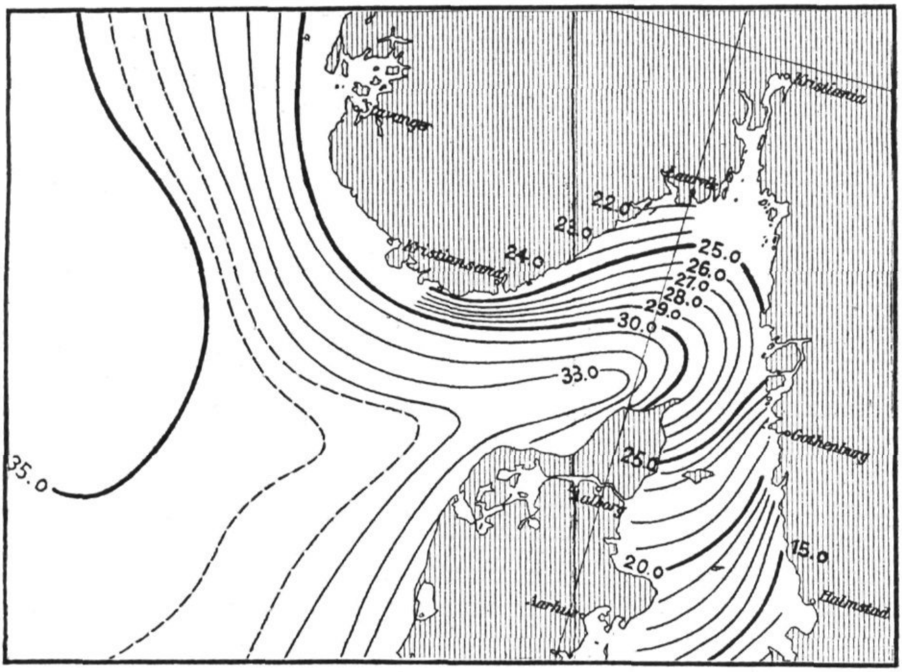

Fig. 33. Salinity conditions (mean values, in $^0/_{00}$, at surface, for May) in the Kattegat, the Skagerrak, and the adjacent North Sea. After Deutsche Seewarte's Atlas, 1927.

effect of the water coming from the Baltic and from melting Norwegian glaciers, must have been felt far to the west along the south coast of Norway. It is to be remembered that the current of diluted water must, as at the present day, have been pressed close to the coast owing to rotation of the earth (Coriolis effect). Our knowledge of present hydrological conditions off this coast is instructive in this respect (fig. 33). In spring, average salinity values of not more than 25 $^0/_{00}$ are observed there, and occasionally the dilution must, of course, be considerably greater. As an example, on June 10, 1933, only 22.21 $^0/_{00}$ was recorded at Oksöy, near Kristiansand in southernmost Norway (STRÖM 1936, p. 43). At the time of the relict invasion, much lower values were no doubt reached; as a matter of fact, the occurrence of the pronouncedly lacustrine fish *Coregonus albula* in the Jaeren area points to the water having had, at times, a salinity of only a few parts per thousand even so far west.

A further problem connected with the immigration to Norway is finally worthy of mention, viz. the poor representation of the relicts of Group II in that country. Not only *Phoca*, but also *Myoxocephalus* and *Mesidotea* are totally absent, and *Gammaracanthus* is known from 3 out of 26 localities only.

This poverty contrasts with the conditions in nearby areas of Sweden, where the three latter relicts live in Vänern, *Myoxocephalus* and *Gammaracanthus* in addition in about 10 other lakes, situated west and northwest of Vänern (NYBELIN 1953, LUNDBERG 1957).

The above-mentioned scarcity of the relicts of Group II in Norway warrants two conclusions in support of the views held in the present paper: first, that the immigration of relicts into Northern Europe came from the east: second, that the relicts of Group II are not easily dispersed (cf. p. 73.)

7. SPREAD OVER THE INNER BALTIC AREAS.

The conquest of the inner Baltic regions by the relicts may be reconstructed from geological maps.

It should first be stated that southern Finland, with the areas around L. Ladoga, was already freed from ice and thus opened to invasion at the time of the Baltic Ice Lake which, in its latest stages, is assumed to have reached up to southern Savo (Savolax) and Häme (Tavastland). The immigration of the Ringed Seal into those districts which are today occupied by the large lake Saimaa and where, after the isolation of the lake, this animal became a lacustrine relicts (for Päijänne, cf. p. 49) would thus appear to have taken place from the Baltic Ice Lake.

However, eastern and northeastern regions were also invaded at an early stage. Owing to the retreat of the ice-margin from the watershed between the basins of the Baltic and the White Sea and to the topography of the land which was freed from ice, water from the Baltic was enabled to penetrate far towards the north along a narrow bay which came into existence in front of the ice-cap, east of the watershed concerned (fig. **34**). The invasion of relicts along this path deserves some comments.

It has been concluded that the early Baltic Ice Lake was connected with the north, along the eastern route just mentioned, up to the Salla region (fig. 34). According to this view, corresponding early invasion of the area by the relicts inhabiting the Baltic Ice Lake would be expected. However, relict distribution does not support such a view.

According to HYYPPÄ (1936, p. 445), the first stage of the Baltic Ice

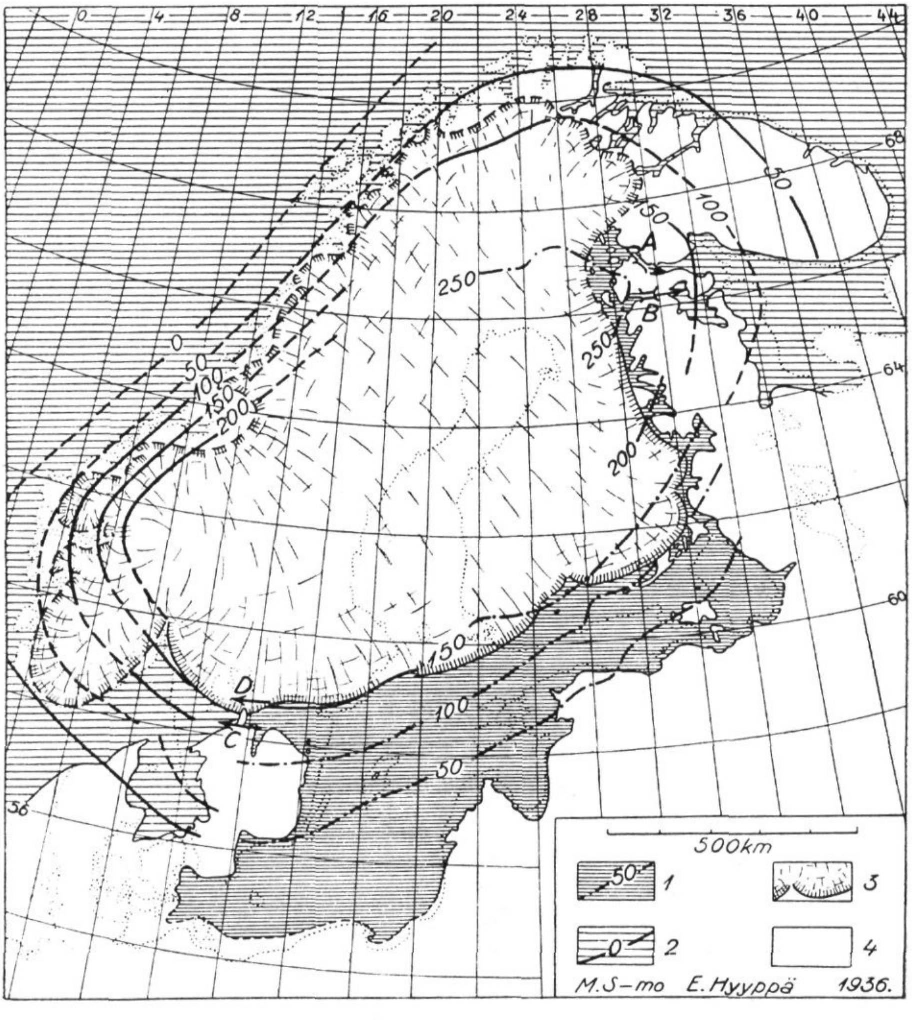

Fig. 34 The. Baltic Ice Lake, stage B III. — 1. Isobases of B III. — 2. Isobases of contemporary ocean. — 3. Ice-margin. — 4. Land. After Hyyppä 1936.

Lake to reach Salla and the adjacent Kuusamo, viz. the stage called B II, covered the land up to the level of 270—282 m. above the present level of the ocean ,and even at the stage B V, the water is concluded to have flooded the area up to abaut 250 m. (Hyyppä 1936; Sauramo 1940, fig. 71). Now, the sole religt locality in Salla, L. Vuorijärvi (175.5 m above sea-level), has probably been reached from the east (cf. p. 89), and in the adjacent, more southern, region of Kuusamo, Suomussalmi and Taivalkoski, relicts have not on the whole been found. It is to be noted that in this comparatively high area quite a number of lakes, situated below 250 m. down to about 200 m. (Kiantajärvi in Suomussalmi, 198 m), and apparently offering favourable habitats to the relicts, have been investigated without such animals being found (SEGERSTRÅLE 1956 a). By contrast, in the nearby lower region toward the south (Hyrynsalmi, Puolanka, Utajärvi, Kuhmo, Sotkamo) several localities are known (cf. fig. 13). The highest of them is L. Rauvanjärvi in Kuhmo (near the Russian frontier), situated at c. 199 m. above sea-level (commun. by Dr. K. VIRKKALA) and inhabited by *Pallasea.* As the Yoldia Sea would not have reached higher than c. 160 m. in the region concerned (cf. SAURAMO 1940, fig. 74), one may conclude that the relict arrived there at a late stage of the Baltic Ice-Lake; however, conceivably not later than B V, when the Rauvanjärvi region would have been flooded up to about 200 m. (cf. SAURAMO l. c., fig. 71). The above-mentioned seemingly total absence of relicts in the adjacent northern areas, even in the nearby Suomussalmi, suggests that the path there from the south was at that time still ice-blocked, or, alternatively, that the basins of the lakes concerned were occupied for a long period by ice; in the former case, the high shore-lines found in Salla and the adjacent areas would not belong to a Baltic stage.

According to BISKE and LAK (1955), in the Tolvand region west of Kandalaksha Bay, marine deposits are found up to an altitude of 235 m. As the threshold of the neighbouring Aapajärvi valley on the watershed between the catchment areas of the Baltic and the White Sea lies at an altitude of only 211 m. (HYYPPÄ 1936, p. 409), it would have been possible, from a topographical point of view, for the water of the White Sea basin to penetrate across this threshold in a westward direction, in early late-glacial time; this conclusion has also been drawn by botanists (cf. for instance, KOTILAINEN 1954, CLEVE-EULER 1955). However, in the case of the relict animals, there is no evidence of immigration along this route or other, more southern, early straits across the present watershed (cf. VIRKKALA 1948, 1954, KANERVA 1956). This feature seems explainable, if we assume that the flooding of areas in northern Karelia by salt water refers to a very early phase, before the final withdrawal of the ice-cap had begun, and that it was due to influx from the ocean in the north (cf. BISKE and LAK 1955, p. 57 of the present paper).

During the period of the Yoldia Sea which followed that of the Baltic Ice Lake, invasion of even more northern areas became possible along the eastern route, owing to early melting of the ice-cap in the north (fig. 36).

It was at that time that the northernmost relict localities of Finland, L. Unarinjärvi southwest of Sodankylä (*Mysis*) and the R. Äkäsjoki in Kolari (*Pallasea*), were reached; and now the relicts also spread to most of the other localities of Finland which had not been populated previously (cf. fig. 36).[1] The salinity of the Baltic in Yoldia time seems to have been too low to offer any obstacle to the spread of the relicts.[2]

When that transition stage between the Yoldia Sea and the Ancylus Lake, which is today (cf. SAURAMO, 1954 b) called the Echineis Sea, set in, only a few of the present relict localities of Finland were still covered by ice; among them was the large L. Oulujärvi (Ule träsk).

In northern Sweden comparatively small areas became open to invasion as the ice-margin withdrew, owing to the topography of the land and the effect of the crustal uplift, which was especially marked in this region (cf. fig. 19). As emerges from a glance at fig. 36, the localities west of the inner end of the Gulf of Bothnia were the last ones to be populated; this invasion took place from the Ancylus Lake.

The spread to the above-mentioned area marked the end of the immigration of the relicts within the Baltic region, a process which had been going on since these animals, coming from the ice-lake of the valley of the R. Onega, entered the Baltic catchment area across the watershed separating it from the valley concerned. As this crossing may have occurred 15 000—20 000 years ago (cf. fig. 11) and the invasion of the area last reached something like 7 000 years ago (computed from SAURAMO 1940, fig. 37), the whole spread of relicts over the Baltic drainage area seems to have taken some 8 000—13 000 or roughly 10 000 years.

With respect to the immigration history roughly outlined above, it must be born in mind that the time that has elapsed since the isolation of a lake, and its fauna, from any of the Baltic stages may differ widely, even within the same area, according to divergences in altitude. For instance,

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[1] As regards the Äkäsjoki locality, where *Pallasea* has been found at an altitude of not less than 212 m., one must reckon with the possibility that the crustacean reached it later on by upward migration from lower reaches of the river (cf. p. 51).

[2] LINDBERG (1910, 1916) did not, on the whole, find any signs of saline influence in samples of subfossil diatoms from the Yoldia deposits of Finland; on the basis of corresponding investigations, HYYPPÄ (1936) concludes the salinity of the Gulf of Finland to have been very low, and for western Finland (southern Ostrobothnia) MÖLDER (1946) gives a range of 3—10 $^0/_{00}$ (the present author's note: the higher values within this range would refer to deeper water levels).

a lake situated at a high level near the southern end of L. Päijänne, may have been isolated already from the Baltic Ice-Lake, whereas Päijänne itself was still connected with the Baltic basin in Ancylus time.

8. THE LITTORINA CATASTROPHE.

Up to and including the Ancylus period the water of the Baltic basin, being continually fresh or at most slightly brackish in its upper layers, offered favourable habitats for the glacial relicts which had lived under lacustrine conditions in the Onega Ice-Lake. However, with the onset of the Littorina period, about 7 500 years ago, the hydro-ecological situation changed fundamentally.[1]

As will be remembered (cf. p. 6), at that time oceanic water was enabled to penetrate into the Baltic between Jutland and southern Sweden. As a consequence, the Baltic became a diluted marine area, a hydrological status which has continued up to the present day. To the relicts inhabiting the basin this change implied a severe deterioration of the living conditions and in one case even led to total extinction.

The extent of the Littorina Sea may be seen from fig. 35. North of a line crossing the southernmost part of the Gulf of Bothnia, the transgression characterizing the Littorina period was compensated or outweighed by the land uplift; by contrast, south of the line, coastal areas which had already become dry land were again flooded to some extent. For instance, the submergence of eastern central Sweden extended again.

As is well known, at its maximum the salinity of the Littorina Sea was considerably higher than that of the present Baltic. According to MUNTHE, the isohalines for 8—10 $^0/_{00}$ at the surface, which today run across the westernmost Baltic, where the water of the basin is saltiest, moved high up into the Gulf of Bothnia, into an area which today has a salinity of 2—3 $^0/_{00}$ only (fig. 35); and comparable conditions must have prevailed in the Gulf of Finland.

How did this new milieu affect the relict animals? To answer this question, some data on their present distribution in the Baltic are necessary.

Pontoporeia and *Mesidotea* penetrate farthest oceanwards, their out-

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[1] KULLENBERG (1954 and paper read before the Meeting of Baltic Hydrographers held in Helsinki, March 1957) suggests that the deeper strata of the Baltic basin contained salt water throughout the late- and post-glacial period.

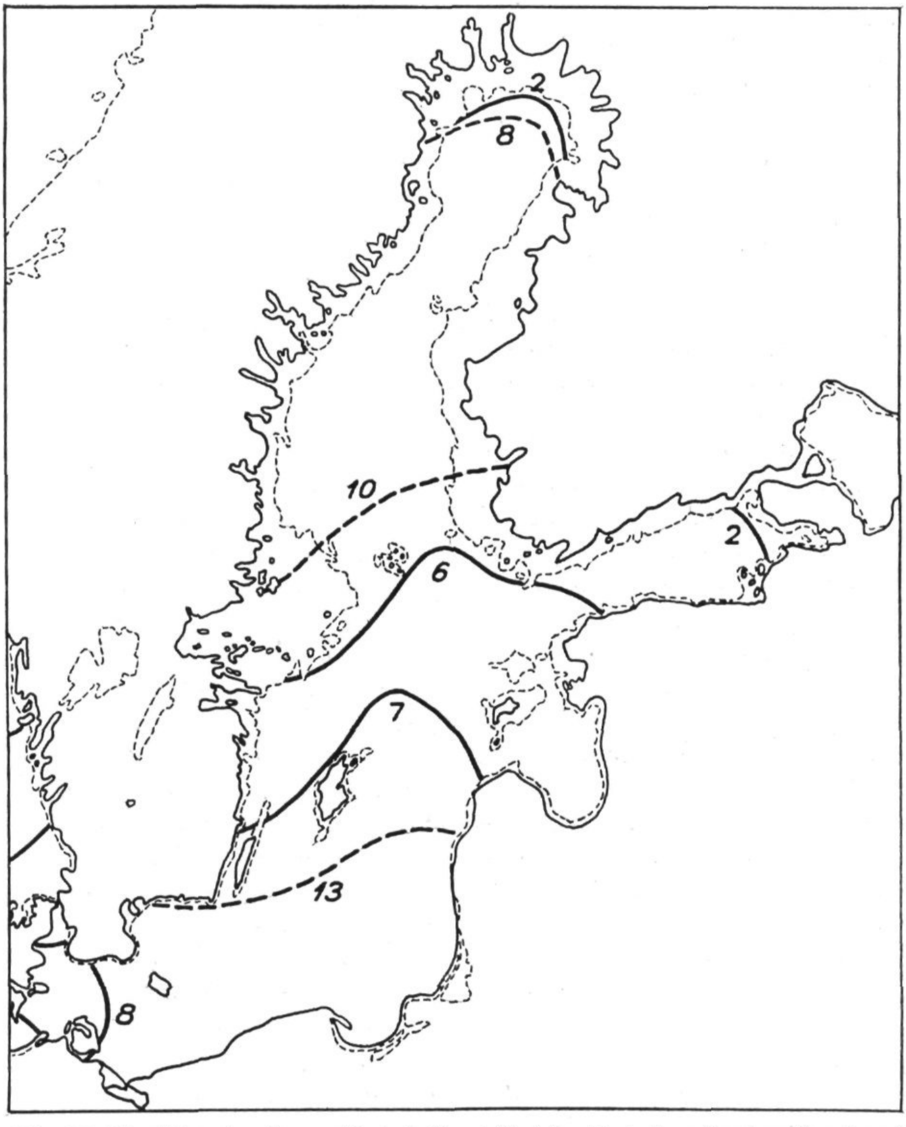

Fig. 35. The Littorina Sea, with isohalines ($^0/_{00}$) for that time (broken lines) and for the present Baltic (continuous lines). After Munthe 1940 (redrawn).

posts being found near the outlets of the Baltic (Ekman 1919, Bruun 1924), where the salinity, as was stated above, averages 8—10 $^0/_{00}$ at the surface. *Mysis*, *Limnocalanus* and *Myoxocephalus*, less tolerant of salt water, do not normally occur south of the central Baltic, their range being limited by the isohaline for 6—7 $^0/_{00}$ at the surface (EKMAN 1914, 1932; for *Myoxocephalus,* see also foot-note p. 37). *Pallasea* only rarely occurs in the coastal waters of the inner Baltic (about 15 localities, most of them situated in the two Gulfs; two only outside, viz. in the archipelago S. W. of Stockholm and in the mouth of the bay of Bråviken south of that region; EKMAN 1918, SEGERSTRÅLE 1956 a). The maximum salinity at these localities is about 6 $^0/_{00}$ at the surface (Tvärminne, on the southwest coast of Finland). (*Gammaracanthus* is absent from the present Baltic; see below.)

Considering their present distribution, as outlined above, one may conclude that at the climax of the Littorina period all the relicts concerned died out in the Baltic, except the restricted coastal waters with considerable local dilution and, further, in the innermost parts of the two Gulfs (cf. EKMAN 1913, p. 362; 1914, p. 507). From these refuges a new spread over the lost areas started as the salinity of the Littorina Sea gradually decreased; however, except in the cases of *Mesidotea* and *Pontoporeia,* reconquest of the whole Baltic was not possible but new limits were established farther inwards according to the salinity tolerance of each relict.

However, even this modest resumption of the earlier range was not achieved by one of the relicts, viz. *Gammaracanthus;* as is well known, this relict is totally lacking in the present Baltic. Its extinction in the Littorina Sea has been difficult to explain so far on the basis of its suggested purely marine origin (EKMAN, 1940, p. 53, speaks of »der launenhafte *Gammaracanthus*»; THIENEMANN, 1950, p. 507: »In der heutigen Otsee lebt *Gammaracanthus* nicht; den Grund dafür kennen wir nicht»). Since we may now conclude that the ancestor was confined to diluted water, the case appears to be less enigmatic and the following interpretation seems plausible.

The *Gammaracanthus* of the Baltic had a comparatively low salinity tolerance — perhaps of the same order as *Mysis* and *Limnocalanus.* Hence, the relict, like other relicts, was wiped out in the greater part of the Baltic. In contrast to them, however, it was unable to survive even in the remaining greatly diluted localities because of the fatal effect of another ecological factor, viz. temperature. As is well known, *Gammaracanthus* lives only in deep lakes where the temperature is constantly low. As its upper tolerance limit LOMAKINA (1952) gives 6—8^6 C. Since the deeper colder layers of the Baltic had too high a salinity for it to thrive, only shallower areas were accessible to it on this account, but there the water was seasonally too warm, even at the bottom.

In order to check the validity of this hypothesis, the author has surveyed the data collected and published by the Institute of Marine Research of Finland for the northernmost hydrographical station in the Gulf of Bothnia, from where temperature recordings from deeper layers are available, viz. Nahkiainen (64° 38′ N.). During the 20-year period 1930—1949, the three highest temperature values observed at the bottom, at 25 m. depth, were 13.5, 13.8 and 15.6° C; they refer to the months of August and September.

Considering these data, as well as the fact that in the Littorina Period the climate was considerably warmer than it is at present, it seems plausible to suppose that the temperature of those shallow Baltic localities where the salinity allowed *Gammaracanthus* to thrive, was at some seasons too warm for the relict.

This conclusion gains support from the fact that no finds of *Gammaracanthus* have been recorded from the innermost part of the Gulf of Finland, off the mouth of the R. Neva. As the animal is common in Ladoga, continual occasional transportation from there along the Neva would be expected; as a matter of fact, it is recorded from the river (BERG 1928, p. 108). There seems to be little doubt that it is the seasonal warming of the innermost part of the Gulf of Finland that prevents the relict from establishing itself in these waters, where the depth over a distance of more than 30 km from the Neva mouth outwards does not exceed 10 m. The same thermal obstacle is also to be reckoned with in other cases where restocking of the Baltic from nearby lakes inhabited by *Gammaracanthus* would be expected.

NYBELIN (1931) drew attention to the absence of the crustacean in all those lakes of central Sweden which are situated east of L. Vättern, even in L. Mälaren, which harbours all the other relicts (excepting *Phoca*) and he attributed this feature to the salinity of the Littorina Sea which once covered the region concerned (cf. fig. 35). This interpretation is no doubt justified. In the case of another amphipod, *Gammarus pulex*, a freshwater species, the present author has been led to the same conclusion that the stock inhabiting areas flooded by the Littorina Sea must have leen killed; for instance, in the very region referred to by NYBELIN (SEGERSTRÅLE 1954). In the case of *Gammarus pulex*, partial reconquest of the lost areas from nearby waters has apparently taken place, a fact which is not surprising since the species has a wider temperature range than *Gammaracanthus*.

It would, of course, be still easier to account for the extermination of *Gammaracanthus* in the Littorina Sea by the assumption that, during the period passed in the Onega Ice Lake (and perhaps earlier fresh waters, cf. p. 98) the relict was converted into a purely lacustrine form which was wholly unable to tolerate saline water. Such adaptation is, theoretically, readily conceivable and has, as a matter of fact, been concluded for another crustacean connected with the late-glacial history of the Baltic, viz. the copepod, *Eurytemora lacustris*. This species is found in many lakes within the region concerned but is totally lacking in the basin itself. In explanation of this phenomenon, EKMAN (1907) has suggested that the crustacean is descended from a closely related marine (probably brackishwater) form which was transformed, in the Ancylus Lake, into the lacustrine *E. lacustris* with no tolerance of saline water; as a result, this species was exterminated in the Baltic in Littorina time.[1]

The fact that the present author finds it difficult to interpret the disappearance of *Gammaracanthus* from the Baltic in the same way and suggests that the animal has retained some saltwater tolerance even after its adaptation to lacustrine conditions, is due to results obtained from studies on the relicts of Ladoga.

As was mentioned in a previous section (p. 22), LOMAKINA, in 1952, published a paper giving, among other information, the results of studies on the morphology of *Gammaracanthus* in various waters, Ladoga included. It was shown that the form living in this lake represents an intermediate type between that found in arctic estuarine water, on the one hand, and the Onega type, on the other. For instance, in specimens from Ladoga the dorsal carina is less reduced than in those from Onega, and the elongation of the palm of the gnathopods, another characteristic of the Onega type, is less marked. These morphological divergences were ascribed by LOMAKINA to differences in the geological history of the two lakes. Her interpretation is as follows. Unlike Onega, Ladoga was connected with the Baltic in Littorina time. As a consequence, characteristics of the marine ancestor, such as a well developed carina and short gnathopod palms, were re-established to some extent, and the time that has elapsed since the Littorina Period has been too short to allow the Ladoga population to return to the morphological stage resulting from its former lacustrine period. Corresponding results were arrived at by LOMAKINA as regards another relict, viz. *Pontoporeia:* in this case, also, the Ladoga

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[1] As is well known, the same evolutionary process is exemplified, on a large scale, by the lacustrine fauna as a whole: in spite of being descended from marine ancestors, most of its members have become so specialized for the new environment that they are unable to tolerate salt water, even in great dilution.

form proved morphologically closer to the marine form than to that living in Onega (and lakes of East Karelia and Kola; cf. p. 23). In discussing these results, LOMAKINA refers to similar earlier observations of a comparatively »marine» morphology in other relicts of Ladoga, viz. *Myoxocephalus* (BERG 1916 b), *Limnocalanus* (RYLOV, acc. GERD 1949), *Mesidotea* (size; EKMAN 1919, GURJANOVA 1946), *Mysis* (size; GERD 1949).

LOMAKINA's interpretation seems sound and is also, in principle, in good accordance, for instance, with the results of the classical studies of EKMAN in 1913 on the relict *Limnocalanus*, which showed a remarkable correlation between the morphology of this relict and the time elapsed since the isolation of the lake inhabited (cf. p. 12).

However, the attitude of most workers towards the idea of salt water having penetrated into L. Ladoga in Littorina time seems to be unfavourable (AILIO 1915, p. 41; LINDBERG 1916, p. 25; HYYPPÄ 1937, p. 138—39; and other authors, quoted by the latter); and in the case of the Yoldia Sea, evidence of saline influx is lacking (LINDBERG loc. cit; HYYPPÄ 1942, p. 155). However, like BERG, who discussed this controversy at an earlier date (1916 b, p. 1358) with reference to *Myoxocephalus quadricornis*, the present author, for the reasons mentioned above, finds it difficult to avoid the conclusion that Ladoga received salt water during some phase of the late-glacial period.

The »marine» morphology spoken of above refers especially, as far as *Myoxocephalus* is concerned, to the four tubercles on the head which are well developed in the arctic brackishwater form, and especially in that living in the Baltic today. It is an interesting feature that these tubercles must have re-appeared after the Ancylus period, when the Baltic population was again subjected to saline water; as is well known, subfossil remnants of the fish, found in deposits of the Ancylus Lake, exhibit very small tubercles, if any (NATHORST 1893; cf. BERG 1916 b, p. 1359, EKMAN 1922, p. 291). A comparable re-establishment of characteristics after the onset of the Littorina period has been suggested for *Limnocalanus* (EKMAN 1913). For a further discussion of the feature of »marine conservatism», cf. pp. 98—99.

9. INVASION OF EAST KARELIA AND ADJACENT AREAS.

Our survey of the immigration of the glacial relicts within the greater part of the Baltic catchment area, and their invasion of southern Norway having now been concluded, some comments may be made on the question of their spread to those eastern districts which drain towards the White Sea. In this discussion the easternmost part of the Baltic area will also be included, viz. that comprising the catchment area of L. Onega which along the R. Svir, L. Ladoga and the R. Neva, empties into the Gulf of Finland.

Some features of the process have already been touched upon. It was concluded that L. Kenozero east of Onega and two other neighbouring relict lakes, Potshozero and Latsha Ozero, all of which belong to the drainage system of the R. Onega, were populated from the ice-lake which occupied the valley of this river (pp. 60—61); for L. Kubenskoe, cf. p. 60. However, the question of how the relicts invaded the many other lakes of the eastern area concerned remains to be discussed.

If we glance at the map in fig. 13, it is seen that quite a number of relict lakes are found within the drainage area of L. Onega, the rest being scattered over more northern regions, up to Kandalaksha Bay and adjacent areas of the Kola Peninsula. The highest of these lakes, as far as the author is aware (cf. SEGERSTRÅLE 1956 a), are as follows (listed from south to north):

Draining towards the Baltic:

Matkozero (N. of Onega)	89 m.
Lososinskoe Ozero (W. of Onega)	186 m.

Draining towards the White Sea:

Segozero (N.W. of Onega)	114 m.
Paanajärvi (W. of Kandalaksha Bay)	134 m.
Vuorijärvi (W. of Kandalaksha, Salla area) (TANNER, cf. HYYPPÄ 1936, p. 412)	175.5 m.
Umbozero (Kola Peninsula)	152 m.

The occurrence of relicts in the area of L. Onega seems, in general, not to pose any special problems. The lakes concerned are no doubt remnants from the time when the margin of the ice-cap retreated across the region and the basin of L. Onega was filled with melt-water. The level of L. Lososinskoe, 186 m. (GERD 1949), however, appears unexpectedly high (due to local damming up in front of the ice?).

The spread farther northwards would have started with the overflow from the waterfilled basin of L. Onega. The concept of this northward migration is much facilitated, if, with BISKE and LAK, we assume that the lowlands west of the White Sea were for a long time occupied by a freshwater lake (cf. p. 57). Otherwise, it is, in fact, difficult to understand how immigration into the north was possible, especially as regards the relict localities of the Kola Peninsula, viz. the lakes Imandra, Umbozero and Vyptshozero. Besides *Limnocalanus*, *Mysis* and *Pontoporeia*, Imandra and Umbozero also harbour *Pallasea*, which can tolerate only a decidedly low salinity; on the other hand, at present the open part of Kandalaksha Bay exhibits an annual salinity range of as much as 21—28 $^0/_{00}$ at the surface (ZENKEVICH 1956, p. 260). Hence, it seems highly unlikely that *Pallasea* was able to immigrate northwards from the Onega area even in coastal waters, if the White Sea had an open connection with the Arctic Sea; this is so, even if we reckon with the diluting effect of the water coming from the melting ice-caps of nearby areas.

To be sure, BISKE and LAK also conclude that the Kandalaksha region has experienced salt-water influence, along a long narrow depression crossing the base of the Kola Peninsula, a depression which seems to have been flooded in late-glacial time. However, this saline influence was conceivably not very marked; besides, *Pallasea* and the other relicts may have immigrated since the disappearance of the saline strait (according to LAVROVA, 1947, it was of short duration).

As will be remembered, for the lakes of northern Germany, THIENEMANN concluded that many of them may earlier have harboured a richer relict fauna than that found today, when, owing to the process of eutrophization, the waters concerned no longer offer a favourable habitat for these animals (cf. p. 15). GERD (1952) advanced similar views as regards the East Karelian lakes. For instance, he suggested that, before their isolation from the basin of L. Onega, many lakes of the Onega region were inhabited by forms which are not found there today, owing to the depth having been too reduced. There is also tangible evidence of the disappearance of relicts. Two examples may be mentioned: L. Putkozero (near northern Onega): *Gammaracanthus* recorded in 1870 by JARZHYNSKY, not refound by GORDEEV in 1947 (GERD 1949, p. 132); L. Palezero. (N. W. of L. Onega): *Gammaracanthus*, *Pallasea* and *Pontoporeia* mentioned by JARZHYNSKY, today all forms absent (GERD, in letter of June, 1956). According to GERD (same letter) strong dystrophization, caused by increased inflow of humous compounds from bogs, is also to be reckoned with as a factor leading to extermination in such cases.

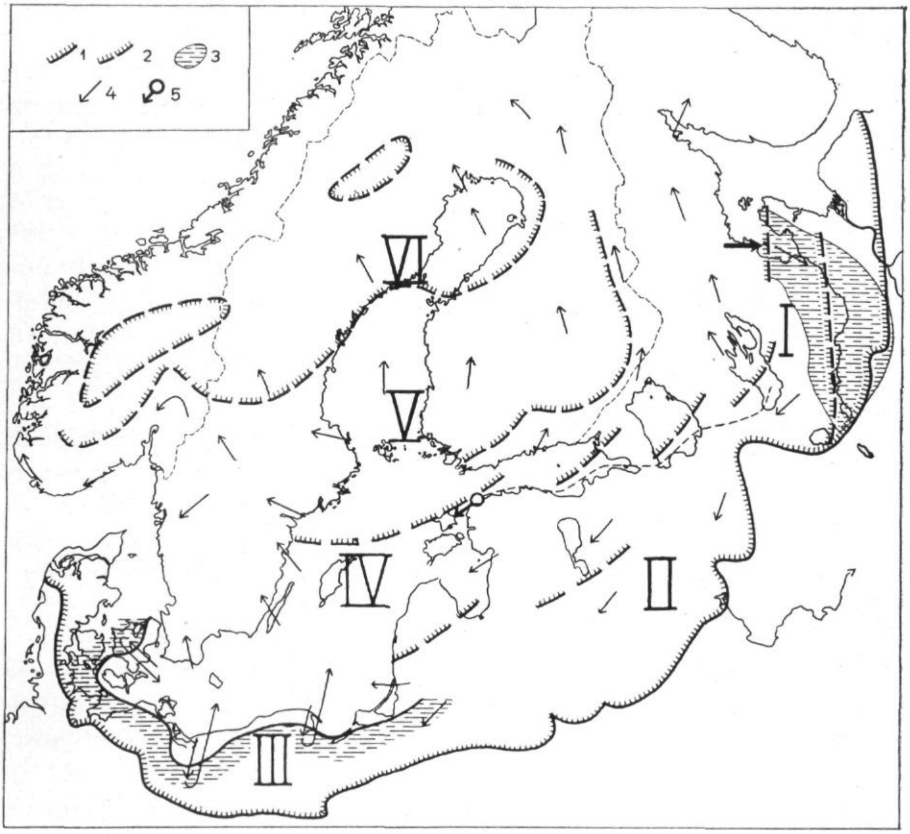

Fig. 36. Survey of the immigration of relicts into North Europe in connection with the last glaciation. — 1. Maximum extent of the ice-cap. — 2. Tentative positions of the ice-margin during the melting phase. — 3. Onega Ice Lake. — 4. Spread of the relicts of Group I. — 5. Arrival of the relicts of Group II in the open Baltic.

I. Sluicing up of water and animals from the White Sea, in front of the advancing ice-cap; formation of the Onega Ice Lake (which was also invaded by the lacustrine *Pallasea*, and possibly by other relicts from neighbouring fresh waters); spread westwards, during the waning phase of the ice-cap, along dammed waters; spread northwards, up to the Kola Peninsula, from L. Onega.

II. Continued westward spread of the relicts of Group I.

III. Sluicing-up of relicts with Baltic water in connection with the Langeland advance; subsequent return of relicts to the Baltic as the ice-margin retreated again.

IV. Invasion of southern Sweden; arrival of the relicts of Group II in the open Baltic.

V. Spread over Finland and across central Sweden, in late Yoldia times, to southern Norway; northward spread in the Baltic.

VI. Final spread, in Ancylus times, to the northernmost part of the Gulf of Bothnia and adjacent areas.

10. HOW DID *PALLASEA QUADRISPINOSA* REACH EUROPE? APPLICATION TO OTHER RELICTS. A RELATED INVASION PROBLEM: THE HISTORY OF THE IRISH-BRITISH RELICTS.

It has been concluded earlier in the present paper that *Pallasea* also entered, from adjacent fresh waters, that ice-dammed lake which once occupied the valley of the R. Onega and which harboured the marine relicts sluiced up from the White Sea. An attempt will now be made to explain the presence of this lacustrine crustacean in the fresh waters of the White Sea region.

As will be remembered, LOVÉN was already aware of the connection between *Pallasea quadrispinosa* and the Baikal area (cf. p. 7); and later EKMAN concurred with the view that this relict was a native of the fresh waters of Siberia (cf. p. 13).

As a matter of fact, this conclusion cannot be avoided. L. Baikal has long been known as the centre of the genus *Pallasea*; according to a letter to the present author from Prof. M. KOZHOV of Irkutsk University, today more than 15 species are recorded from the lake. On the other hand, outside it only 2 species are known, viz. *P. laevis*, described in 1923 from a lake of Novaya Semlya, and *P. quadrispinosa*.[1] No marine representatives of the genus are known.

The following data from Prof. KOZHOV's letter may be added. A number of the Baikal species are also found in the R. Angara, flowing out from the lake and joining the Yenissei; these species are *Pallasea cancellus*, *P. cancelloides*, *P. viridis*, *P. kessleri*, and perhaps one or two others (cf. also KOZHOV 1931). *P. kessleri* has also been recorded from the Yenissei and from the estuarine Yenissei Bay, as well as from lakes along the Siberian coast. This species is closely related to *quadrispinosa;* in fact the *Pallasea* of Ladoga was considered by DYBOVSKY in 1874 to be only a subspecies of *kessleri*. Prof. KOZHOV thinks it probable that *quadrispinosa* has been derived from this species (EKMAN 1918, p. 333, mentions *P. cancelloides* as a possible ancestor).

As regards the path utilized by *P. quadrispinosa* for its invasion of Northern Europe, EKMAN concludes as follows (1918 b, p. 334): »Aus den ursprünglich bewohnten nordasiatischen Binnengewässern hat sich die

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[1] *Pallasea quadrispinosa* does not occur in L. Baikal; cf. BERG 1933—35, p. 459: »Die sehr verbreitete, auch von SOVINSKI (1915) wiederholte Ansicht, dass *P. quadrispinosa* im südlichen Teil des Baikalsees vorkomme, wo sie von DYBOWSKI aufgefunden sei, beruht auf einem Irrtum.» For *P. laevis*, see p. 97.

Art durch Wanderungen flussabwärts ins Brackwasser der Flussmündungen verbreitet, ist weiterhin, der Eismeerküste folgend, ins brackige Wasser des spätglazialen noreuropäischen Meeres gekommen, um von dort aus in den durch die Landhebung abgesperrten ehemaligen Buchten relikt zu werden.» However, this view cannot be upheld today.

Firstly, during the four decades since the above-quoted statement was made, no finds of the species have been recorded from the coastal waters of Siberia and northern Russia, from where the crustacean was assumed to have migrated westward (BERG 1933—1935, p. 459; KOZHOV, commun. in the letter mentioned). As has also been stressed by BERG, such a migration therefore seems improbable. Ecological considerations lead to the same conclusion, for the long route along the arctic coast would hardly, even under glacial conditions, have been passable to an animal as intolerant of salt water as is *Pallasea quadrispinosa.*

On the other hand, present biological and geological evidence suggest that the relict reached Europe along another, purely lacustrine path. As a background to this new view, a brief digression into a related migration problem is necessary.

As will be remembered, the Caspian Sea harbours a peculiar northern element, consisting of most of the glacial relicts of Northern Europe, in identical or closely related forms, viz. *Limnocalanus*, *Mesidotea*, *Pontoporeia*, *Gammaracanthus*, *Mysis* and *Phoca;* in addition, the fish *Stenodus leucichthys* and two species of the amphipod genus *Pseudalibrotus*. It may also be recalled that HÖGBOM explained the presence of this northern faunal element as due to a forward move of the land-ice damming up water in the north and causing an overflow of Baltic water toward the Caspian basin — a theory which later gained tangible geological support (cf. p. 60).

On the other hand, it was pointed out by SARS, in 1927, that the Baltic-Caspian connection could not have been the sole route of migration, since the above-mentioned two species of *Pseudalibrotus* living in the Caspian Sea as well as *Stenodus leucichthys* are missing in the Baltic region. In 1933, on the basis of a comparative morphological study, GURJANOVA shoved that the Caspian and the Siberian *Mesidotea entomon*, including that of the lower reaches of the Yenissei, belong to the subspecies *glacialis*, while the form inhabiting the Baltic, the Ladoga and the White Sea belong to the subspecies *entomon;* likewise, similar studies on *Pseudalibrotus* indicated close faunal connection between the Caspian

Sea and marine Siberian waters. GURJANOVA concludes that the northern element in the Caspian fauna is due to immigration from the latter area.

In 1937, this idea was further elaborated by PIROZHNIKOV. On the basis of extensive hydrobiological studies in northern and western Siberia, he presented new facts in favour of it and also attempted to visualize the mode of immigration into the Caspian Sea. He refers to the established presence of many of those arctic forms, which live in the Caspian Sea, in the lower reaches and the mouth of R. Yenissei and R. Pjasina; some of these forms, viz. *Pontoporeia*, *Gammaracanthus* and *Mysis*, occur in the Yenissei at a considerable distance from the mouth (up to at least 59° 18′ N; cf. PIROZHNIKOV 1931). Furthermore, *Mysis* had been found in Lake Nalimye, situated in central Siberia, between R. Yenissei and R. Tas (see map, fig. 37) (cf. PIROZHNIKOV 1933). On the basis of these and other biological data, as well as results obtained by Russian geologists, PIROZHNIKOV suggests that the northern Caspian element immigrated by way of a large ice-dammed lake in western Siberia. The following details of this theory may be given:

During the glacial Epoch — to the present author obviously at the time of the maximum (third) glaciation (cf. FLINT 1947, p. 362) — a glacier, coming from the Taimyr Peninsula and moving S. W. and W., coalesced with the glacier of the northern Urals, thus cutting off a shallow marine area of northwestern Siberia which was transformed into an enormous ice-dammed basin. Owing to the inflow of water from the Ob, Yenissei, and other rivers, the salinity gradually decreased and the level of the basin rose. Because of this and the advance of the ice-margin, the southern watershed was finally reached and the lake began to drain southwards, along a spillway at the head of the R. Tobol (cf. map fig. 37). It was along this route that the northern element of the Caspian fauna is suggested by PIROZHNIKOV to have been carried into the Aralo-Caspian basin (the route assumed by HÖGBOM is thought to have possibly functioned as a parallel path to invasion).

Now, what bearing has this theory on the subject of the present section, i.e. the immigration of *Pallasea* into Northern Europe? The answer is that it seems probable that the ice-lake in western Siberia not only functioned as an intermediate stage in the migration of animals from the Arctic Sea to the Caspian, but also enabled lacustrine Siberian forms, *Pallasea* included, to reach adjacent areas of Europe. The arguments for this conclusion are as follows:

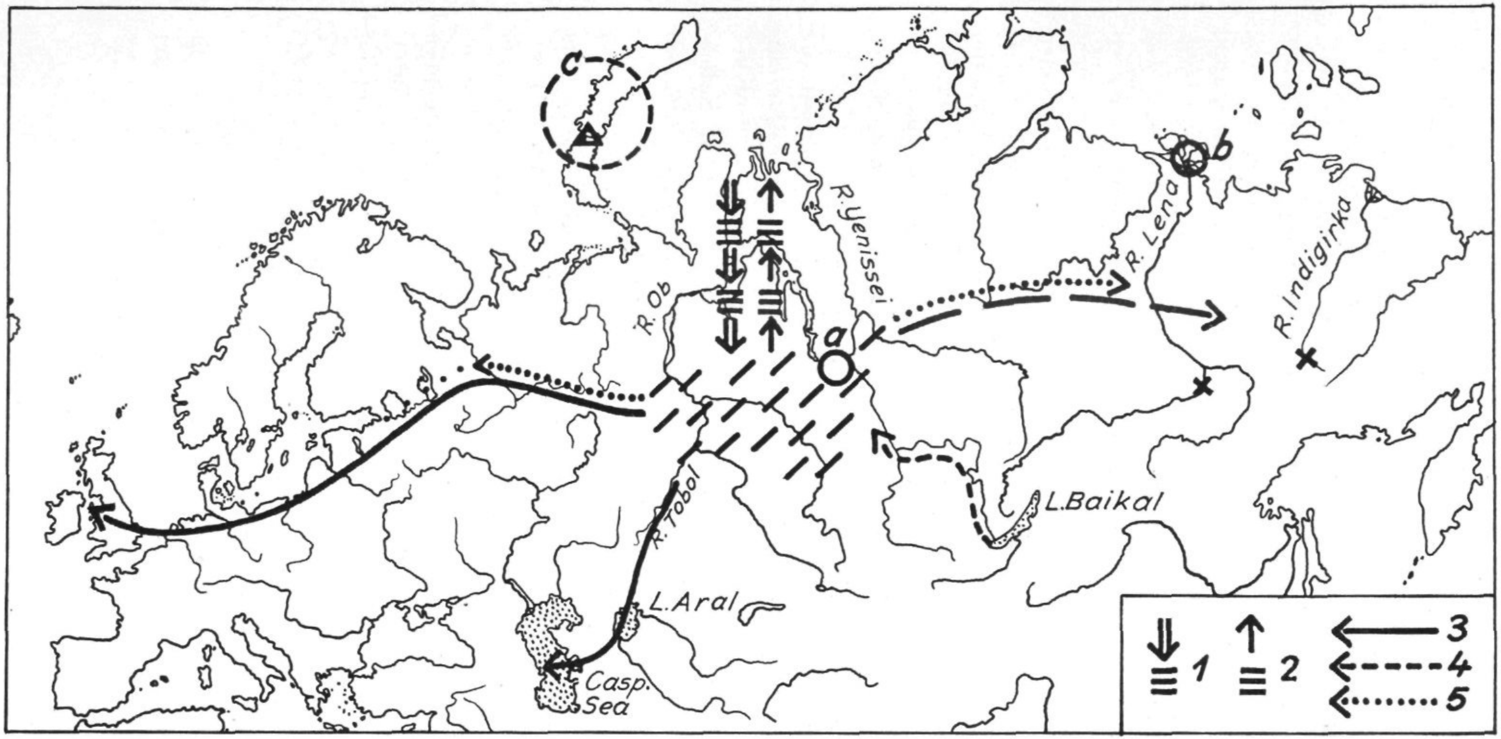

Fig. 37. The suggested role of the Siberian ice-lake of the maximum glaciation in the development and spread of glacial relicts. The extent of the lake at its highest level tentatively hatched.

1. Marine animals are sluiced up from the sea in front of the advancing ice-cap. — 2. Following the melting ice-margin, they return to the sea, having lost their ability to tolerate water of full salinity and, in some cases, having undergone morphological modification. — 3. Migration of these, originally marine, forms into Europe, the Caspian Sea, and the east. — 4. The ancestor of *Pallasea quadrispinosa,* conceivably *P. kessleri,* coming from Baikal, enters the ice-lake and gives rise to the former species; 5, this migrates westwards and eastwards.

Rings indicate localities of *Pallasea quadrispinosa* (range in Europe omitted): *a.* L. Nalimye, *b.* delta of R. Lena, *c.* Novaya Semlya (L. Bychkovodje, position not known to the author). Triangle: locality of *P. laevis* (apparently derived from *P. quadrispinosa*). Crosses: inland localities of *Mesidotea entomon* in eastern Siberia.

(1) In L. Nalimye (cf. above) not only *Mysis* but also *Pallasea quadrispinosa* was found and must, hence, be assumed to have lived in the West-Siberian ice-lake; incidentally, this was the first time that the latter species had even been recorded outside the once-glaciated area of Northern Europe; for an earlier, unpublished find, viz. from Novaya Semlya, see below, point 3.[1] Nalimye proved also to harbour some typical Baikal animals, viz. the amphipod *Brandtia* (*Gmelinoides*) *fasciata* and two species of the gastropod genus *Valvata;* this indicates that the ice-lake was connected with the drainage area of the Yenissei where the suggested ancestor of *Pallasea quadrispinosa* lives today (cf. above p. 92).[2]

(2) Westward migration across the Ural mountains in ice-dammed waters seems possible, for the following reasons: (a) The ridge, fairly low even today, is suggested to have been still lower at the time of maximum glaciation (SACHS 1947, p. 21). (b) HÖGBOM (1917, p. 249—50) postulated the former existence of ice-dammed lakes in the central Urals, near the uppermost reaches of the R. Vishera (N. of Perm): »In seiner grossen petrographischen Arbeit *l'Oural du Nord* — — — beschreibt und abbildet L. DUPARC aus dem Quellengebiet des Wischeraflusses — — — grossenartige Terrassensysteme und horizontal verlaufende, ins feste Gestein eingeschnittene Linien, welche für jedermann, der in Gebieten früherer Eisseen gearbeitet hat, ganz ungezwungen den Gedanken auf Eisseeterrassen und Uferlinien führen. Auch werden tiefe Erosionsschluchten erwähnt, in welchen man die Abflussrinnen der Eisseen vermuten kann.» (c) During his visit to the USSR in 1955, the present author discussed the question of migration across the Urals in glacial time with two leading Russian Quarternary geologists (Academian J. P. GERASIMOV and Prof. K. K. MARKOV), and both thought this to have been possible, from a geological point of view.

(3) *Pallasea quadrispinosa* is recorded from a lake in Novaya Semlya (Ozero Bytshkovodje, coll. Moltshanova in 1907; noted by the author on going through collections in the Zoological Institute of the Academy of

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[1] Recently *Pallasea quadrispinosa* has also been caught in the delta of the R. LENA, under practically lacustrine conditions (PIROZHNIKOV 1955).

[2] It may be noted in this connection that elements of the Baikal fauna have later been found also in lakes belonging to the catchment area of the river Ghida (west of the Yenissei), as well as in L. Taimyr (in the central part of the Taimyr Peninsula) and that this feature is suggested to be due to the existence of earlier connections between these areas and the Yenissei (KOZHOV 1956).

Science, Leningrad).[1] The spread of the species to Novaya Zemlya suggests that wide stretches of water were dammed up in front of the ice during the waning phase of the maximum glaciation, in the region between Siberia and Europe (cf. map fig. 39). In this connection mention should also be made of the presence in a lake of Novaya Zemlya (Lomvand, N. of Matotshkin Strait, 52 m. above sea-level) of that form of *Pallasea* which was described by EKMAN in 1923 under the name of *P. laevis* and which has no doubt evolved from *quadrispinosa* since this species immigrated into Novaya Zemlya.[2]

(4) It is to be observed that those ice-lakes suggested to have existed in the central Urals were believed to be situated in the immediate neighbourhood of the head of the R. Vytshegda, tributary of the R. Dvina (see map fig. 37). Following the retreating ice-margin in dammed waters, *Pallasea* might thus easily have immigrated into the lower reaches of the Dvina and the nearby valley of the R. Onega, i.e. into that region where, in connection with the last glaciation, the Onega Ice-Lake came into existence, inhabited by marine forms which had probably been sluiced up there from the White Sea. Living in the fresh waters of the Onega valley since the maximum glaciation, i.e. for some 200 000 years, *Pallasea* entered the lake and, in the course of the waning phase of the last glaciation, experienced the same spread as those forms which were of marine origin.

(5) The history of the Irish-British glacial relicts points to westward dispersal of aquatic animals from the Siberian ice-lake (cf. pp. 99—102).

One may perhaps ask why there are no signs of *Pallasea* having reached more western continental regions as a result of the suggested migration from Siberia along the ice-margin during the maximum glaciation; it will be recalled that all the relict localities of this area seem to be due to

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[1] At the request of the author, Dr. N. B. LOMAKINA, of the just-mentioned Institute, has kindly given additional data on the sample in question. In her letter it is stated that the determination was made by the late Prof. VERESTSHAGIN and that the sample contains one young specimen only, 3.8 mm in length; the dorsal spines are not yet developed, being represented by small projections only. As is well known, this feature is typical of young *Pallasea quadrispinosa*.

[2] *Pallasea laevis* is characterized mainly by the absence of any projections from the body and thus differs from all other members of the genus. A very similar form was found some years ago in a large spring in southern Finland, where it has obviously developed from *quadrispinosa* by strong morphological reduction. The author intends to publish a special report on this subject and also to discuss its bearing on the probable history of *P. laevis*.

invasion from the Onega ice-lake of the last glaciation. The explanation of its absence there might be that the temperature of the last interglacial grew too high for the Siberian species in question (for literature on the interglacial climate, see SEGERSTRÅLE 1954, p. 67); only in colder regions, such as that of the White Sea, was survival possible. According to this view, *Pallasea* might also be expected in other fresh waters of cold Northeastern Europe than those located within the area of the last glaciation. The author ventures to hope that the species and other relicts will be searched for in the area concerned, as establishment of their presence there would mean further support of the view presented above.

It may be recalled that NYBELIN has already hinted at the possibility of *Pallasea* having lived in Europe before the last glaciation (cf. p. 18).

For the reasons given below (pp. 99 ff.), it seems probable that other relicts also reached Europe from the West-Siberian ice-lake along the same path as did *Pallasea* and may thus, like it, have entered the White Sea region, where later the ice-lake in the valley of the R. Onega came into existence in connection with the last glaciation. However, as was mentioned previously (pp. 62—63), it seems not very likely that they survived there until this glaciation.

The occurrence of the relict forms in the estuaries of the Dvina, the Pechora and other rivers of northern Russia is in harmony with this interpretation, as this occurrence is explainable as due (1) to westward migration along the path utilized by *Pallasea*, and (2) to subsequent transportation towards the coast in connection with the draining of the ice-dammed waters.

As regards the lack of records of relicts from western Siberia, i.e. the site of the ice-lake, it may be noted that PIROZHNIKOV (1937, p. 523) believes the lakes of this area — for reasons of depth and chemical composition of the water — to have offered unfavourable living conditions to the marine forms which inhabited the ice-lake.

According to the views advanced above, the ancestors of the relicts of Northern Europe seem to have passed through two freshwater stages, viz. the first in the Siberian Ice Lake and the second in the ice-lake of the Onega valley.

Against this background the question arises: is the ability of the estuarine forms of arctic Eurasia, as well as of the Baltic relicts, to thrive and even flourish in saline water, a trait surviving from the marine past or have we to do with a re-acquired characteristic? The former alternative seems clearly preferable, not least in view of the conservatism of the original morphological characteristics exhibited by the *Myoxocephalus* living today in the Baltic. In this form the four tubercles of the head, typical of the arctic form, are very well developed in spite of their disappearance during the foregoing lacustrine Ancylus Period (cf. p. 88); and we may even assume that they have also disappeared earlier in the history of the Baltic form, viz. in the Siberian ice-lake and the ice-lake of the Onega valley. As the former lake was suggested to have existed during the maximum glaciation, which ended about 180 000 years ago (cf. THIENEMANN 1950, table p. 301), the re-appearance of the tubercles suggests a strikingly high degree of morphological conservatism. Hence, a corresponding feature with respect to physiological characteristics, such as the relation to salinity, is not surprising. Incidentally, the inability of most typical lacustrine animals to tolerate salt water is explainable as a consequence of their marine ancestors having been exposed to fresh water for a very long time.

In this connection, the following observations made on *Artemia salina* may be recalled. GAYEVSKAYA (1916, acc. BERG 1916 b, p. 1355) found that this crustacean very easily adapts itself to variations in salinity and that these adaptations are accompanied by morphological modifications. These modifications are repeated in the following generations as long as conditions remain unaltered. If, however, the salinity is changed, *Artemia* very soon, after 2—3 generations, loses the acquired modifications and returns to its original form.

The history of the Irish-British relicts. Quite isolated from the relict area around the Baltic, there exist, in Ireland, southern Scotland and northern England, a number of localities inhabited by *Mysis relicta* and *Limnocalanus macrurus*, as well as by a fish which is also to be considered a glacial relict, viz. the vendace, *Coregonus albula* s.l. (cf. p. 15 and THIENEMEANN 1950, p. 481—83); the forms from the waters concerned, which are closely related to the main form, are described under the names *C. vandesius*, *C. vandesius gracilior*, and *C. pollan* (cf. SMITT 1895, BERG 1933).[1] The details of their distribution are given below (cf. map fig. 38).

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[1] An old tradition claims the Scotch occurrence of the vendace to be due to introduction from the Continent; however, this is no doubt incorrect (cf., for instance, MAXWELL 1904, p. 284).

	Mysis	*Limnocalanus*	*Coregonus*	Source of information
S. Scotland				
Castle and Mill Lochs (at Lochmaben in Dumfriesshire)			+	Berg 1933
N. England				
Ennerdale Water	+	+		Scourfield 1941, Gurney 1923, 1928
Windermere			+	Maxwell 1904
Derwentwater			+	Maxwell 1904
Bassenthwaite Water			+	Maxwell 1904
R. Greta (tributary of R. Tees)			+	Maxwell 1904
Ireland				
Lough Neagh	+		+	Samter 1905, Smitt 1895
Lough Erne	+		+	Samter 1905, Smitt 1895
Lough Corrib	+		+	Samter 1905, Smitt 1895
Lough Ree	+			Stammer 1936
Lough Derg	+		+	Thienemann 1950, Smitt 1895
R. Shannon	+			Stammer 1936

To explain the presence of *Mysis* in Irish lakes, Högbom (1917) tentatively proposed the same sluicing-up theory as he had applied to other cases, and his idea was later supported by Charlesworth (1928).

However, the present author finds it impossible to concur with the view that the relicts concerned have been carried up to their present sites from the neighbouring sea. The reasons for this unfavourable attitude are ecological and identical with those advanced against the hypothesis of western immigration of the North-European relicts; just as was especially concluded for one of these forms, viz. the lacustrine *Pallasea*, no possibility would have existed for the vendace to migrate to the British Isles from the east along a marine route (*Coregonus albula* s.l. is confined to Northern Europe and Siberia), as it is extremely sensitive to salt water (even in the diluted coastal waters of Finland the fish is confined to the inner parts of the Gulfs, with a salinity of at most c. 4—5 $^{0}/_{00}$). The marine path would also have been impassable to *Mysis* and *Limnocalanus* in view of their suggested nature as pronounced brackishwater forms (cf. pp. 35 ff.).

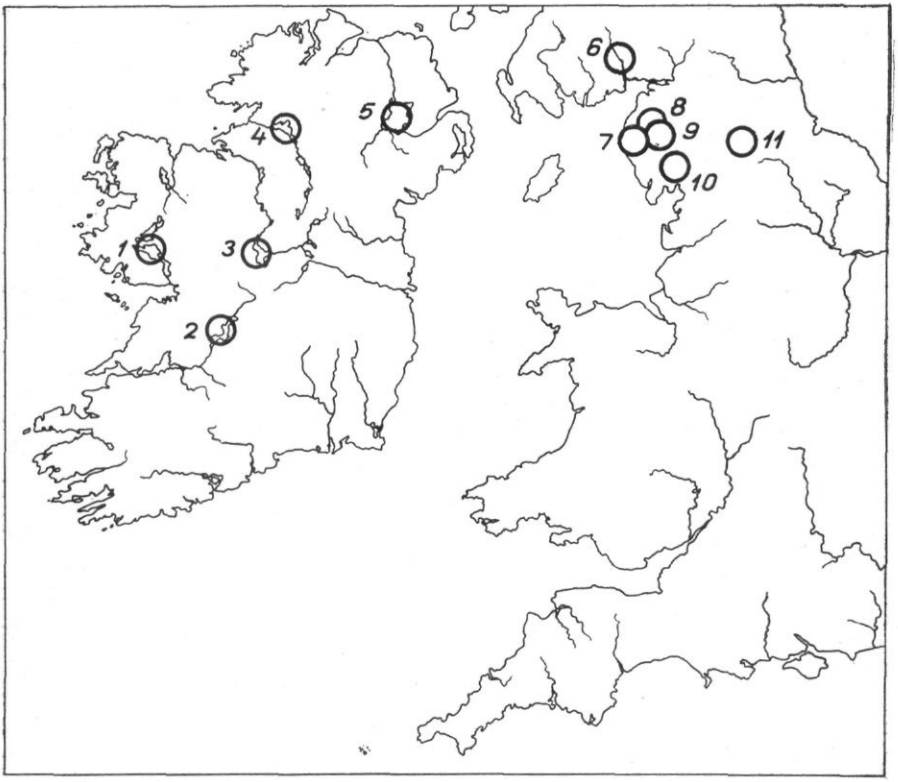

Fig. 38. The relict localities of the Irish-British area. — 1. Lough Corrib. — 2. Lough Derg. — 3. Lough Ree. — 4. Lough Erne. — 5. Lough Neagh. — 6. Lakes Castle and Mill Lochs. — 7. Ennerdale Water. — 8. Bassenthwaite Water. — 9. Derwentwater. — 10. L. Windermere. — 11. R. Greta. A further locality is R. Shannon, coming from Lough Derg and flowing through Lough Ree. Cf. table, p. 100.

The sole natural explanation seems to be that the Irish-British relicts immigrated along the margin of the ice-cap of the maximum glaciation, in ice-dammed waters. As the ice-masses of that glaciation are thought to have formed a continuous front up to and across the British Isles, such a migration would not have been impossible. The position of the Irish and British localities (map fig. 38) suggests that, during the withdrawal of the ice — the conceivable time of the spread in question — the northern part of that basin which is today the Irish Sea, and the adjacent area, were occupied by a freshwater lake from which the present relict localities are derived.

In this connection the following quotation from Gurney (1923, p. 433) is of interest, as it shows that the existence of such a lake has already been postulated earlier, likewise for zoogeographic reasons, and that the glacial relicts of Ireland and England have been thought to have immigrated from there (it is of no importance in this respect that Gurney, according to the views then prevailing, suggests the prehistory of the relict forms of *Limnocalanus* and *Mysis* to have been different from that postulated in the present paper): »Dr. Scharff has assumed the existence of a great lake occupying the trough of the Irish Sea to explain the present distribution of the genus *Coregonus* in Britain and Ireland, and if such a lake could have originated by freshening of a glacial sea, not only might *Limnocalanus grimaldii* have been therein isolated and transformed, but also *Mysis oculata* could in this way have been changed into *M. relicta* and have reached its present station in Lough Neagh.»

From where, then, did the eastern immigrants ultimately come? Did they exist in Northern Europe before the maximum glaciation and could they, thus, start their invasion from this area?

The answer to this question must be negative. As is well known, the maximum glaciation, extending from the north, reached beyond the watershed running across the European Continent in a west-east direction, excepting for a minor area in the extreme west. The topographical prerequisites for reaching the British Isles from the Continent seem thus to have been lacking at that time. Hence, we must conclude that the Irish-British relicts have had the same history as *Pallasea:* like this species, they came from the Siberian ice-lake of the maximum glaciation, migrating along the ice-margin, but reached much farther to the west. As in the case of *Pallasea*, there is nothing pointing to their having survived in other areas passed through during the long migration; and the reasons for this were conceivably the same as were concluded for *Pallasea* (cf. p. 98).

IV. REMARKS ON THE PREHISTORY OF THE GLACIAL RELICTS.

Pallasea quadrispinosa, apart from its wide distribution in that part of Northern Europe which was glaciated during the last glaciation, is known only from lakes of Central Siberia and Novaya Zemlya, and from the mouth of the R. Lena, a fact which strongly suggests that the species developed in the ice-lake of Siberia. It seems probable, furthermore, that it has been derived from *P. kessleri*, not only for morphological reasons but also because the latter species, apart from its main site in L. Baikal, is also found in the R. Angara-Yenissei (cf. above, p. 92), a fact suggesting that it lived in the ice-lake there. This interpretation requires that at some phase water from this lake also reached the river system of the Lena; for evidence of this, see below p. 106.

In connection with the problem of the prehistory of *Pallasea quadrispinosa*, the author has been led to make a further suggestion, viz. that the other relicts of brackishwater type have also possibly come into existence in the Siberian ice-lake, in other words, that that ancient freshened arctic area which GURJANOVA (cf., for instance, 1933—35) and ZENKEVICH (1934; cf. GURJANOVA l.c.) concluded to have been responsible for the evolution of these forms was identical with the ice-lake in question.

As a matter of fact, GURJANOVA has earlier expressed the view that it was under the special conditions of the glacial epoch that the transformation of the arctic marine animals into brackishwater forms took place: »The Siberian high-arctic amphipod fauna developed from brackishwater species and subspecies under the influence of alternating brackishwater and saline phases which occurred in the peripheral areas of the Arctic basin throughout the course of the glacial epoch» (GURJANOVA 1951, p. 95, transl.; cf. also GURJANOVA 1939). As arguments for the idea that the Siberian ice-lake represented the site of the transformation, the following points may be mentioned:

Pontoporeia affinis is thought by LOMAKINA (1952), on the basis of studies on comparative morphology, to have been derived from the marine *P. femorata*. This interpretation is based on the existence of a series of forms that are transitional with regard to the main distinctive characteristic, viz. the existence in *femorata* on urosome segment I of a dorsal bifurcate process which is absent in *affinis*. The *femorata* population living in the diluted Baltic and brackish waters of Siberia and Japan exhibits a more or less pronounced reduction of the bifurcate process; in the Caspian *P. affinis microphthalma* this is represented by a small hump only, furnished with two spinelike projections; in the *P. affinis* from northern brackish areas and lakes, the reduction is practically total (low dorsal elevation with two bristles and a tuft of minute hairs).

Now, it was concluded above that the Caspian *Pontoporeia*, together with other relicts, reached this area from the Siberian ice-lake. Since, moreover, this form, with the greatly reduced bifurcate process, is not

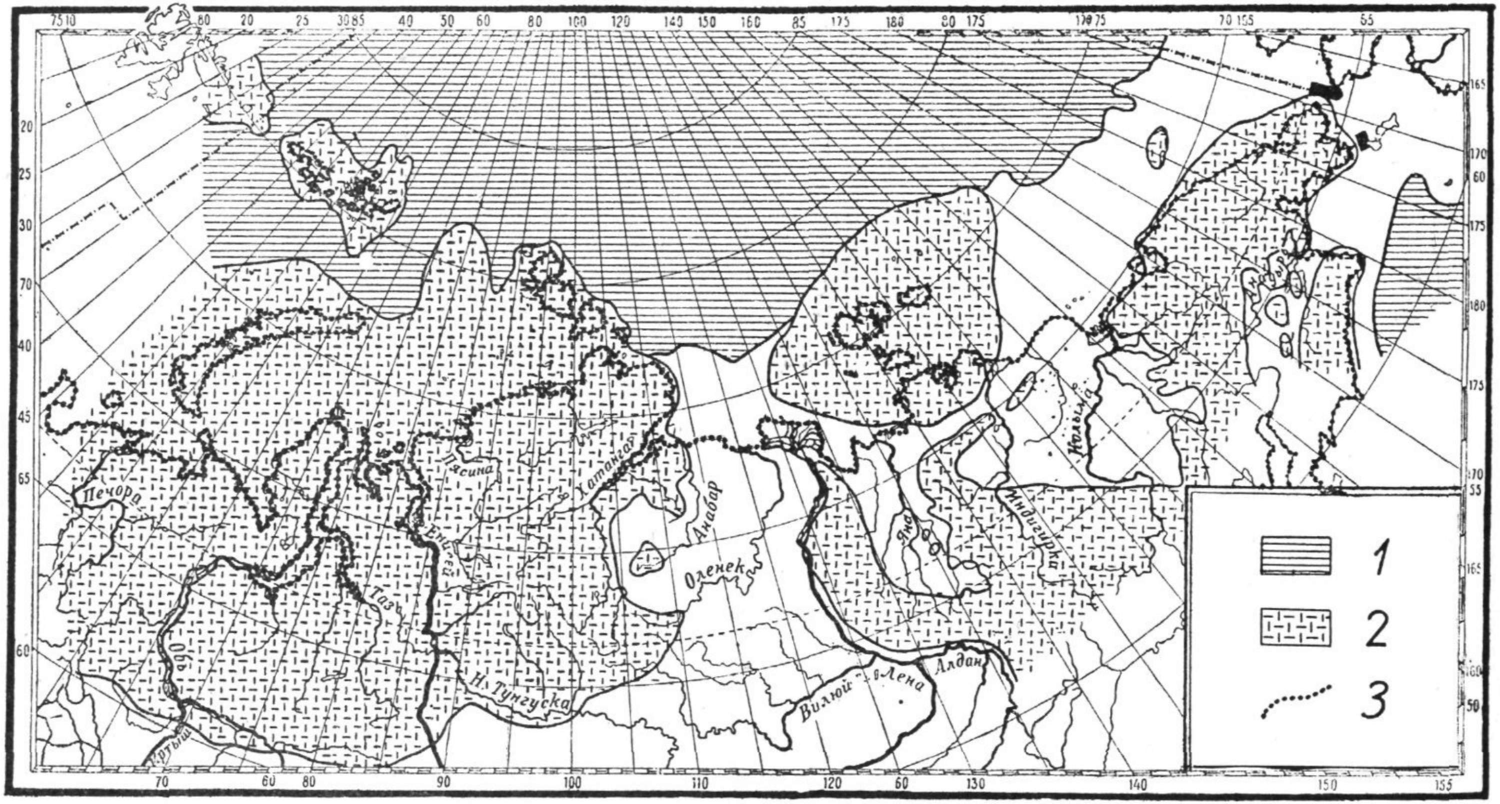

Fig. 39. Paleogeography of Siberia during the maximum (third) glaciation. After Sachs 1947 (partly redrawn). — 1. Sea. — 2. Ice-cap. — 3. Present coast-line.

known elsewhere, it seems probable that it developed from a population of *femorata* which was included in the Siberian ice-lake. The reason for the absence of the Caspian type of *affinis* from the coastal waters of Siberia (and other areas) to which the ice-lake finally drained down, might have been as follows: after the overflow from the ice-lake which brought one part of the population into the Caspian area, the modification of femorata continued in the lake and finally resulted in the typical *affinis*.

A similar conclusion seems natural in the case of another relict amphipod, *Gammaracanthus*, on the basis of data which have also been given by LOMAKINA (cf. also EKMAN 1916). The Caspian form, *G. loricatus caspius*, is in some respects closely related to the subspecies *aestuariorum*, described by LOMAKINA and living in estuarine waters of Siberia, in others there is more affinity to the marine form, *G. l. typicus;* for instance, the dorsal carina, so characteristic of *typicus*, is also absent in the first pereion segments of *aestuariorum*, but in *caspius* these segments are furnished with a carina in the form of rounded projections. The same interpretation as in the case of *Pontoporeia* seems plausible: *aestuariorum* and *caspius* are both derived from a population of the marine form which was isolated in the Siberian ice-lake, but, for the reasons mentioned above, that part of the population which immigrated into the Caspian Sea was subjected to the lacustrine influence for a shorter time.

The theory discussed above seems to imply that the Siberian ice-lake was connected with other, conceivably ice-dammed, waters far to the east; otherwise the occurrence of the same glacial relicts in American waters is difficult to explain, as it would imply that identical forms had developed there through convergent modification, an idea which seems highly unlikely, for instance, in the case of such a form as *Pontoporeia affinis*. It is to be noted in this connection that GURJANOVA (1933—35, p. 565) also assumes that that basin in which she believes the brackish-water forms of the Siberian estuaries to have developed, included the northern part of America.

Concerning the actual northward extension of the ice-caps of North America very little is known, except that the whole of the Arctic archipelago has been glaciated (cf. FLINT 1947, Plate 3). For instance, there is no exact knowledge of the northern limit of the glaciation in the northwestern marine area where this limit lies below the level of the present sea (FLINT loc. cit., pp. 231, 240). However, it is noteworthy that there seem to have been no marine areas separating Asia from America at the time of maximal glaciation (cf. fig. 39). Furthermore, there is even now evidence of the Siberian ice-lake having reached far eastward in Siberia: *Mesidotea entomon* is recorded from Jakutsk, more than 1 200 km. upriver from the mouth of the Lena (BIRULA, acc. BERG 1928, p. 109) and even farther east, viz. from the upper reaches of the R. Indigirka (EKMAN 1935, fig. 139).

The prehistory of the arctic brackishwater forms, as well as the abundance of brackishwater forms which came into existence in the ancient Sarmatic Inland Sea, suggests that isolation of a diluted or freshened marine area would have greatly favoured the development of brackishwater animals in general; perhaps being cut off from the sea constituted the very condition for the development of at least the majority of them. Furthermore, the past history of the arctic brackishwater animals offers an instructive example of how a disjunct range — that well known and often enigmatic characteristic of animals confined to diluted waters — may be explained as a consequence of a former wide distribution. Cf. GURJANOVA 1933—35, p. 565: »Wir begegnen also in der Arktis einer ebensolchen Erscheinung des Überlebens der Relikte des ausgesüssten arktischen Beckens in den Mündungen der sibirischen Flüsse, wie das Überleben der sarmatischen Relikte in den Limanen des Schwarzen und Asovschen Meeres.»

V. CONCLUSION.

On looking back on the immigration history of the glacial relicts of Northern Europe, as discussed in the preceding pages, a picture of a highly complicated, not to say kaleidoscopic, process presents itself. However, at the same time it is seen how quite a series of events and circumstances have, as it were, interacted with each other and led to the surprisingly wide distribution of the animals concerned. Amongst these factors, the following may be recapitulated:

(1) The existence, at the onset of the last glaciation, of the ancestors of the relicts in the White Sea region.

(2) The formation of an ice-dammed lake in the valley of the R. Onega which harboured the animals concerned, after their sluicing-up from the sea (or immigration from neighbouring lakes); as was concluded, it was from that ice-lake that the relicts were enabled to enter the drainage area of the Baltic and could thus spread over extensive North-European regions.

(3) A similar sluicing-up effect of the advancing ice-cap in the case of northern Germany and the adjacent Continental area, which process permitted the relicts to reach localities high above the shore-lines of the ancient Baltic lakes.

(4) The subsidence of the earth's crust under the weight of the ice and the subsequent land upheaval which also resulted in spread over wide areas and the present occurrence of the relicts at high levels. In this spread, the existence of the large Baltic basin played a paramount rôle, accentuated by the existence of favourable hydrological conditions (without high salinities) for thousands of years.

(5) The topography of Central Sweden which, in conjunction with this favourable hydrological factor, even made possible the conquest of southern Norway.

If we widen the perspective so as also to include the Siberian ice-lake of the maximum glaciation and its peculiar history, as well as its suggested rôle as an intermediator of the relict invasion of Europe and its significance in the morphological and ecological transformation of the ancestors of the relicts, the impression of a highly exceptional chain of events favouring the evolution and spread of the glacial relicts is strengthened. This is true not least of *Pallasea quadrispinosa* which, derived from the drainage area of the Yenissei, and utilizing the temporary routes offered by two successive glaciations, finally even reached the extreme western border of the Eurasian Continent, viz. Norway.

Taken as a whole, the history of the spread of the glacial relicts no doubt constitutes one of the most remarkable chapters in the annals of zoogeography.

The author expresses the hope that the new suggestions briefly outlined in the present paper will be checked and elaborated by colleagues in the countries involved, not least in USSR, whose territory has been so closely linked with the history of the animals discussed.

VI. SUMMARY.

The present paper deals with the immigration history of the following glacial relicts, occurring in the fresh waters of Northern Europe (most of them also in the Baltic): *Phoca hispida*, *Myoxocephalus* (*Cottus*) *quadricornis*, *Gammaracanthus lacustris*, *Pallasea quadrispinosa*, *Pontoporeia*

affinis, *Mesidotea entomon*, *Mysis relicta*, *Limnocalanus macrurus* (*L. grimaldii* in the Baltic).

The main conclusions arrived at are as follows:

1. Amongst these animals not only, as was assumed earlier, are *Pontoporeia*, *Mesidotea*, and *Limnocalanus* natives of brackish water (arctic estuaries), but this applies also to *Myoxocephalus*, *Gammaracanthus*, and *Mysis*. All the relicts treated have thus been especially fitted for adaptation to life in fresh water.

2. The restriction of the forms concerned, in the arctic area, to diluted water seems to be due to isolation of their marine ancestors, during the third (maximum) glaciation, in an enormous ice-dammed water-system in Eurasia (and N. America). Under the lacustrine conditions thus created, in some cases morphological modification of the original marine forms also took place, resulting in the afore-mentioned forms of *Pontoporeia*, *Mesidothea* and *Mysis*. When the ice-dammed waters drained down to the arctic Sea, their fauna also reached the sea but found tolerable living conditions only in the estuaries, i.e. the present arctic habitats of the relict species.

3. *Pallasea* also lived in the ice-dammed waters concerned, viz. in western Siberia, where the former existence of a large ice-lake has been postulated by geologists and biologists. However, its prehistory was different. The relict is of lacustrine origin and probably derived from *P. kessleri*, one of the many species of the genus inhabiting L. Baikal and also found in the R. Angara and R. Yenissei; from these rivers *P. kessleri* might have entered the ice-lake.

4. *Pallasea*, and probably also other relicts, reached Europe from the Siberian ice-lake, migrating across the continent along waters which had been dammed up in front of the ice-cap of the maximum glaciation; in this way, too, the region south of the White Sea was invaded (fig. 37). The occurrence of relicts in fresh waters of Ireland, southern Scotland and northern England was another results of this westward migration.

5. The wide present distribution of the relicts in northern Europe is due to immigration from the east in connection with the last glaciation. The main phases of this process are suggested to have been as follows (fig. 36).

6. The starting point, and the very condition, of the invasion was an ice-dammed lake in the uppermost part of the valley of the R. Onega, emptying into the White Sea from the south. This lake harboured the relict species which had been sluiced up there from the White Sea by the

advancing ice-cap; *Pallasea* entered the lake from adjacent fresh waters where the crustacean had lived since the foregoing maximum glaciation (cf. point 4). (Fig. 24).

7. The high position of the Onega Ice Lake enabled the relicts to cross the watershed towards the Baltic basin and, as a consequence, to spread over wide areas of Northern Europe (fig. 24).

8. The continental area west of Onega-Ladoga, up to Denmark, was invaded very early, during the waning phase of the ice-cap, in connection with advances of this, as suggested by Högbom (fig. 26). For ecological reasons, however, only some of the relicts, viz. *Pallasea*, *Pontoporeia*, *Mysis*, and *Limnocalanus* (and *Phoca?*) were capable of taking part in the westward spread (fig. 24).

9. When the continental ice-dammed waters drained down to the Baltic basin, the just-mentioned relicts also reached this and could utilize the excellent opportunity for dispersal offered by subsequent Baltic stages, up to the Littorina period (cf. below point 14).

10. In Scandinavia, southern Sweden was first invaded.

11. When the ice-margin retreated from the mouth of the Gulf of Finland, the rest of the relicts, viz. *Phoca*, *Myoxocephalus*, *Mesidotea*, and *Gammaracanthus* also entered the Baltic, after having immigrated into the Gulf from the Onega Ice-lake, via L. Onega and L. Ladoga (fig. 24).

12. The spread of relicts to southern Norway, even to the south-western localities, was a result of the outflow from the Baltic across central Sweden in late Yoldia times.

13. The spread over inner Baltic areas took place at the same time, as well as during the Ancylus Period, when the localities near the end of the Gulf of Bothnia were finally invaded. This marked the end of the spread of the relicts which had gone on since the emigration from thea Onega Ice Lake, for some 10 000 years.

14. The salt Littorina Period represented a catastrophe to the relicts, which could survive in local diluted coastal waters only, as well as in the innermost parts of the Gulf of Finland and the Gulf of Bothnia. When the salinity decreased and reached present values, the lost area was re-conquered to a corresponding degree. However, this picture does not apply to *Gammaracanthus*, which died out in the Littorina Sea, apparently on account of a combination of too high a salinity and too high a temperature of the Baltic water.

15. The migration of relicts into East Karelia and the Kola Peninsula started from L. Onega along a route with greatly diluted or fresh waters.

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