

9. On Relics in the Swedish Fauna.

By

Greta Philip.

Introduction and History.

The following treatise is only meant to give a short summary of what is known about the relics in the fauna of Sweden. It is entirely founded on records in the Scandinavian geological and biological literature.

It is to be presumed that the preglacial fauna of Sweden had been destroyed by the ice, and that the fauna of to-day has been formed by contributions from different quarters since the recession and melting of the ice. During the postglacial epochs the fauna has varied in composition and character under the influence of variable climatic conditions, and owing to changes in the distribution of land and water. The new elements in the fauna that were thus spread over Scandinavia have not as a rule entirely supplanted the preceding forms, these having in most cases remained as relics in favourable localities.

The study of the relics must therefore be of great importance in seeking to obtain some knowledge both of the composition of the fauna during past epochs and of climatic and other geographical conditions.

The attention of scientists was first directed to the presence of relics in the fauna, when SVEN LOVÉN in 1860 read a paper before the Royal Swedish Academy of Science on »Some Crustacea found in the Lakes Vättern and Vänern» [20]. He told that in these lakes live some marine Crustacea, the only habitat of which was before considered to be the Arctic Ocean. He supposed that this marine fauna had immigrated from the east, since none of its forms had been found on the west coast of Sweden, but some of them in the Baltic as well as in some Finnish lakes and in the Ladoga. LOVÉN therefore concluded that the Baltic had once

been in communication with the Arctic Ocean through the White Sea. The Baltic which was supposed to have been an arctic inland sea, a supposition which was supported by the occurrence of arctic marine fossils in the shell beds, extended over great parts of Central Sweden. Afterwards, when the land began to rise and the sea retreated, many bays were transformed into lakes, where the fauna was enclosed. Some forms could survive in spite of the water being changed into fresh-water. LOVÉN considered the marine fauna found in the great lakes of Sweden as such remains adapted to the new conditions. Later on he found most of these relics and some other arctic forms also in the fauna of the Baltic (22). LOVÉN's explanation of the occurrence of relics thus corresponds, in principle, with the present day interpretation, although he was not aware of the fact that the Baltic had once been a fresh-water lake.

When LOVÉN had discovered this relic fauna, great interest was taken in the matter, and many investigations have since been made in those parts of the world, where the Quaternary conditions have been similar to those in Sweden, and where such a fauna could be expected to be found. Observations of this kind have now been procured from Norway, Denmark, Finland, North Russia, North Germany, and Ireland, as well as from North America. The term »relic» was gradually brought to embrace all fresh-water animals of marine origin, even the pelagic fauna in the lakes. In a monograph »Die Reliktenseen» of 1888, CREDNER (6) severely criticized the great number of so-called relic lakes and applied this term exclusively to such lakes as can be proved on geological grounds to have been parts of the sea. In connection with the geological and climatic researches which have been made by the Scandinavian geologists during the last decades, the question of the occurrence and importance of relics has of course been further discussed. A fairly extensive literature has been written on this subject and the term »relic» has been differently applied by different authors, e. g. JOHANSEN (16), WESENBERG-LUND (41, 42), ZSCHOKKE (43).

We generally understand by relics in the fauna such animals as are now found in isolated localities, out of their ordinary habitat, and the occurrence of which we can explain only as remains from a formerly more extended fauna. In this sense the word is going to be used in the following treatise. But there is always the possibility that some species which are now considered to be relics, on further investigations will prove to be the »advance-guard» of a beginning immigration. In every single case we must therefore find out that we are not dealing with such forms, but with real relics.

The study of the Swedish relics has chiefly been confined to the water fauna, above all the Crustacea. Lately some attention has also been paid to the occurrence of land-animals in sporadic localities, outside their proper habitat, and these too have been called relics. Otherwise it is of course always the case that the more active land-animals, with the excep-

tion of some groups, for instance the land-molluscs, can more easily than the water-animals accommodate their habitat after the external circumstances.

The Swedish relics — leaving for a while the above mentioned land-animals out of consideration — can, according to the epoch of the post-glacial development from which they are derived, suitably be divided into three groups, namely, 1) *relics from the late Glacial Sea*, 2) *relics from the Ancylus Lake*, and, 3) *relics from the Litorina Sea*. This classification will be used in the following, although it is sometimes rather difficult to decide to which of these groups a form ought to be properly referred.

The Development of the Fauna in the Baltic.

As the last inland ice retreated, the sea filled its place and covered great parts of Sweden and Finland. This sea had the character of an arctic sea with only slightly salt water, owing to the quantity of fresh-water from the melting inland ice and the rivers. This glacial sea, in the beginning probably communicated with the White Sea, which opinion as we know was already suggested by LOVÉN. This communication no longer existed when the land began to rise, and the connection between the Baltic part of the late Glacial Sea and the main ocean passed over Central Sweden. Fossil remains of the fauna in this sea are rare. The well known discovery of *Yoldia arctica* in glacial deposits in the valley of the Mälaren ought to be mentioned here. Just here a salt under-current entered from the North Sea, enabling this typical marine animal to live there, which of course it could not have done in the other parts of the Baltic, where the water was only slightly salt. This sea contained rather a poor fauna, probably somewhat similar to the one now living in the White Sea. It is also likely that this Baltic fauna had immigrated from the White Sea through the passage above mentioned. Most groups of sea animals were probably represented in the Baltic, as it is very likely that, besides the still remaining ones, several other species lived there, although they have not been found neither as relics nor as fossils. Among mammals from this time there are *Phoca fœtida* and *Phoca grœnlandica*, the latter found in arctic clay in Stockholm. Probably also *Halichærus grypus* arrived already during the time of the late Glacial Sea [25]. Furthermore there are some fish: *Cottus quadricornis* and *Liparis lineatus* and some Crustacea, among others *Idothea entomon*, *Mysis relicta*, *Gammaricanthus loricatus*, and *Pontoporeia affinis*, already observed by LOVÉN [20]. All these animals, except *Phoca grœnlandica* and *Gammaricanthus*, still live in the Baltic as relics. Besides, there was also a fauna of other animals: some worms, Rotatoria, and Protozoa etc. which have also left relics. Some of our fresh-water fish, which now live in lakes as

well as in the Bothnian Gulf, and most of which are also found in the White Sea, probably entered the Baltic already at the time of the late Glacial Sea, e. g. the salmon (*Salmo salar*), the gwyniad (*Coregonus lavaretus*), the vendace (*C. albula*) etc. We may presume that some molluscs were not missing, though we have no other remains than *Yoldia arctica*. At the same time a rich fauna of arctic marine animals seems to have lived off the west coast of Sweden, judging from the great number of fossils which have been preserved in shell-beds and arctic clay.

At the end of the melting-time of the inland ice, the Baltic was because of the rising of the land changed into the Ancylus Lake. With the formation of this lake the character and composition of the fauna must have altered considerably, though, as has already been mentioned, it was never typically marine. Some typical fresh-water animals which have been found in the strata of the Ancylus Lake bear evidence of this change. Most of these fossils are remains of molluscs, some of which are such typical fresh-water forms as *Ancylus fluviatilis* and several species of *Planorbis* and *Psidium*, and, further, *Limnæa ovata*, *Neritina fluviatilis* etc. In a clay deposit from this time at Skattmansö in Uppland NATHORST [30, 31] has found a great quantity of remains of the Ancylus-fauna: fresh-water molluscs, some insects, one ostracode, and a great number of skeletons of eel-pouts (*Lota lota*) and of the four-horned sting-fish (*Cottus quadricornis*). Besides, remains of *Phoca fœtida* and of *Halichærus grypus* (MUNTHE 29) were found. These important finds prove among other things that fresh-water fish lived in the Ancylus Lake, and very likely a great number of these fish immigrated during this time, namely those which, according to LUNDBERG [23], have come from the east and through the rivers spread to the great fresh-water lake. It is to be supposed that part of the arctic marine fauna died by the change, but several species succeeded in adapting themselves to the new conditions, especially as the change into fresh-water proceeded very slowly. We can say that these formed a group of original arctic animals, enclosed in the Ancylus Lake, i. e. a group of *arctic marine relics*. Many of these have already been mentioned in connection with the fauna of the late Glacial Sea, and their occurrence and habitual and biological characters will be more closely treated in the following. The Ancylus fauna existed of course also in the bays which were changed into lakes when the land rose, and therefore we find arctic relics in many of these lakes, relics which, with only a few exceptions, have adapted themselves to freshwater in the Ancylus Lake and not exactly in these lakes. The glacial relics have come to the lakes of West Sweden only in the case when these have been in communication with the »Vänerbay» the water of which is supposed to have been almost fresh.

The subsequent sinking of the land in the southern part of the country resulted in those straits which there connected the Baltic with the main Ocean and transformed the Ancylus Lake to the Litorina Sea. The salinity of the Litorina Sea was considerably greater than that of the Baltic nowadays

[MUNTHE 28]. The water in the northernmost part of the Bothnian Gulf contained about the same percentage of salt as the water does now just west of Bornholm — owing to the fact that the salt current which still comes from the Ocean was then able to flow more richly. This had a great influence on the composition of the Baltic fauna. Many fresh-water animals died out, and new marine species immigrated. A milder climate than ours was prevailing during at least a part of the Litorina time; this had some influence on the marine fauna, although not such a great one as on the flora and the land-fauna. The fauna in the shell-beds and shell-containing clays is a typical marine. The mollusc-shells found on the west coast of Sweden are often about twice as large as those on the east coast. Among new forms in the Baltic we observe *Cardium edule*, *Tellina baltica*, *Mytilus edulis*, *Litorina litorea* etc. Also some other marine fossils from the Litorina Sea have been found on the Baltic coast. In 1860 LILLJEBORG [18] described the skeleton of a now extinct whale-species, which was found in Gräsön in the archipelago of Uppland and which is supposed to originate from the Litorina time. Remains of seals and fish have also been found. A great number of other marine animals, which have now retreated, probably lived at that time also in the northern parts of the Baltic. Of the Ancyclus fresh-water fauna, which could not as a rule live in salt water, a few species, however, still remained, among others *Neritina fluviatilis*, which is regarded as a relic from the Ancyclus Lake. By the continuing rising of the land the Baltic assumed its present dimensions, and the percentage of salt again diminished. The marine fauna of the Litorina Sea had to retreat, leaving, however, some relic forms. We explain as such relics, among others, some ostracodes.

Under the influence of various factors the fauna of the Baltic has, thus, got its present composition. The real marine animals have adopted themselves to the comparatively small salinity, and some fresh-water forms have immigrated from lakes and rivers to the innermost parts of the archipelago.

Glacial Relics.

The greater part of the Swedish relic fauna as yet known consists of glacial relics. These are found in the Baltic and the Bothnian Gulf as well as in a great number of lakes in Central Sweden. Among the glacial relics there are specimens of most groups of water-animals. Among these the most important and best known will now be more closely described.

Phoca fætida MÜLL. occurs in the Baltic from Öresund to the northern parts of the Bothnian Gulf, rarely in the south and more frequently towards the north [LOVÉN 20, 22]. It is also met with in the innermost parts of the bays and in the almost fresh water at the mouths of the rivers [14]. Like most glacial relics, it is not found at the west coast of Sweden,

whereas it lives in the Arctic Ocean and the White Sea. Further it is found in several lakes between the Finlandian Gulf and the White Sea: the Saima, the Ladoga, and the Onega. As mentioned before, *Phoca fœtida* has also been found in the Ancylus-strata at Skattmansö [30], a clear evidence that this marine animal has been able to survive the Ancylus time.

Among relic mammals is also to be counted *Phoca grænelandica* MÜLL., though it no longer belongs to our fauna. It is an arctic form, remains of which have lately been found in Litorina-clay near Sundsvall [ADLERZ 1] and also in Gotland in a deposit from the same time.

Cottus quadricornis L. is probably the glacial relic, the peculiar distribution of which was first known [LOVÉN 20, 22, LUNDBERG 23, LILLJEBORG 19]. It has its proper habitat in the Arctic Ocean, where it has been found in various parts and it is a typical arctic species. It is quite common in the Bothnian and Finlandian Gulfs and in the northern parts of the Baltic proper, but less frequent south of Gotland, and it is missing altogether of the west coast of Sweden. As to our lakes it is found in the Vänern and the Vättern, and according to an old statement, which has now proved correct, also in the Fryken in Värmland. Likewise a hitherto doubtful information as to its occurrence in the Mälaren has nowadays proved to be true [LÖNNBERG 27]. By adding to these localities those in the Ladoga and the White Sea, the relic character of *Cottus quadricornis* in Scandinavia becomes obvious as well as the direction from which it has immigrated. Most likely it is also to be found in the Baikal.

It is interesting to observe the habitual variations of the fresh-water form of the *Cottus* compared to the marine one [LOVÉN 21]. The *Cottus* of the Vättern is distinguished from that of the Baltic by a paler hue, smaller size and somewhat different proportions. The most visible difference lies in the four bone bumps on the head, which are much less developed in the fresh-water form. The *Cottus* of the Ladoga resembles that of the Vättern, and the one of the White Sea is more like that of the Baltic. *Cottus quadricornis* of the Mälaren, on the other hand, is to be placed between the fresh-water and the marine forms [LÖNNBERG 27]. This is especially interesting as the Mälaren was once a bay of the Litorina Sea and the fauna therein has thus during a much shorter time than the fauna of the Vättern been isolated from the sea. The finds of *Cottus* skeletons in the Ancylus clay at Skattmansö [30] has already been mentioned. These discoveries are of special importance in that the skeletons prove to have belonged to the form now living in the Vättern, *Cottus quadricornis* var. *relicta*, as it is also sometimes called. It has thus arisen as an adaptation to the fresh-water of the Ancylus Lake. As to the present Baltic form we must suppose that it again got its original character, when the water in the Baltic became more salt.

Another fish, *Liparis lineatus* LEP., was already by LOVÉN [22] grouped among the glacial relics. It is found on the west coast of Sweden as well as in the Baltic, though not to the south of Gotland, but it has its proper habitat in the Arctic Ocean. It has been found in the White Sea at the Spitzbergen and Greenland.

In the Baltic both *Phoca fætida* and *Cottus quadricornis* feed mostly upon *Idothea entomon* L., also a relic which, besides, is to be found in the Vättern and the Mälaren [LOVÉN 20, 21, 22]. It is rare in the southern parts of the Baltic, and is missing altogether on the west coast of Sweden. The only fossil specimen in Sweden was found in a postglacial clay in Uppsala. This was exactly like the now living animal. *Idothea entomon* lives, besides, in the Arctic Ocean, e. g. along the northern coast of Norway and Sibiria; it is also to be found at Kamtschatka and in the Sea of Ochotsk. It is very unlikely that it lives in the Ladoga and the Onega, as has been supposed before [NORDQVIST 33]. The relic forms agree with the arctic type, except in the size, which varies in accordance with the size of the water in which they live. In the Baltic, *Idothea entomon* can reach 72 mm. in length, but in the Vättern only 45 mm.

The best known and most often mentioned of the glacial relics is probably *Mysis relicta* LOV. [LOVÉN 20, 21, 22, EKMAN 7, NORDQVIST 32, 34]. It lives in the Bothnian Gulf and in a great number of our lakes: the Vänern, the Vättern, and the Mälaren, several lakes in Dalsland and Värmland and as far north as in the Siljan in Dalarna. It is also met with in the Mjösen in Norway [SARS 38] and, lastly, in the Ladoga and the Onega and in a number of other Finnish lakes as well. All these lakes lie below the highest level of the Glacial Sea. Thus, the occurrence of *Mysis relicta* needs not here be ascribed to a later immigration. The places, where it is found in Sweden, all lie below the highest shore-line of the Ancylus Lake — excepting, of course, those which belong to the Väner-district — a clear evidence that *Mysis* already in the Baltic Lake had adapted itself to fresh-water.

The original form of *Mysis relicta* is *Mysis oculata* FABR. This is according to S. O. SARS [38] an arctic form, which has been observed in various places in the Arctic Ocean on the northern coast of Europe as well as of that of North America. One single specimen has also been found in Öresund (see p. 139). *M. relicta* differs from *M. oculata* in many respects, especially as to the structure of the telson. The former is in the lakes smaller, never exceeding 18 mm., whereas the arctic form measures 25 mm. As to the fresh-water form, it is, according to SAMTER and WELTNER [36], larger in lakes which are specially cold. The relic is, as a rule, like younger forms of the arctic species. A biological peculiarity which shows the arctic origin of *Mysis relicta* is its preferring water of comparatively low temperature, never exceeding about 14° C. In the summer it is consequently found in the cold depth of the lakes, in the winter it also spreads to the surface. During the wintermonths the pro-

pagation takes place. The size of the Baltic *Mysis relicta* considerably exceeds that of the lake form.

Mysis relicta has also been found in some lakes in North Germany [SAMTER 37] and in the Furesö in Seeland [WESENBERG-LUND 41, 42], but as all these lakes are situated above the highest level of the glacial sea, it is to be supposed that *Mysis* and several other arctic forms living in some of them have immigrated thither through the rivers. Probably it is the forms, which were first accommodated to the Ancylus Lake, that have thus spread, as they are only found in those German lakes, into which we may suppose they had come from the Baltic. Therefore *Mysis* is here a relic in another sense than in the Swedish lakes.

Already LOVÉN [20] proved that *Gammaracanthus loricatus* SAB. was an arctic relic. It occurs in a number of lakes together with *Mysis relicta* but not in the Vänern, which seems strange, as it is found in several lakes in Värmland, which once were parts of the »Väner-bay». It is also missing in the Baltic. *Gammaracanthus* has also been found in some Finnish lakes and in the Ladoga [NORDQVIST 32, 33], generally in rather deep water near the bottom of the lakes. The proper abode of this crustacean is the Arctic Ocean, where it has been found at different places e. g. near the Spitzbergen, at Greenland and the north coast of America. The relic form of *Gammaracanthus* presents some slight differences to the arctic form, as it is smaller, and the size diminishes with the size of the water in which it lives. In the Polar regions it is said to attain the length of 50 mm., in the Ladoga and the Finnish lakes it measures 36 mm. at the most, in the Vättern 33 mm., in the lakes of Värmland only 28 mm. etc. We can say that the fresh-water form of *Gammaracanthus* also shows a greater likeness to the younger forms of the arctic one.

Two other Amphipoda, which have also been considered as glacial relics, are *Pallasiella quadrispinosa* SARS and *Pontoporeia affinis* LINDSTR. However, several scientists e. g. NORDQVIST [32], WESENBERG-LUND [41, 42], doubt about the former being a relic. It has the same distribution in Sweden as *Mysis*, it is true, but it is not as most other relic crustacea a typical deep-water animal especially seeking cold water, but it lives in water with comparatively high temperature near the surface. Its propagation does not either take place only during the winter, although it produces more eggs in this season, which has been observed by SAMTER and WELTNER [36], who consider *Pallasiella* a relic. Neither did SARS [38] agree with LOVÉN's conception of *Pallasiella* being a relic,¹ and he pointed out as the chief reason for his opinion that no arctic marine form was known, from which it might descend. Out of Sweden *Pallasiella* has been found in several lakes in Finland [32] and Norway [38] as well as in the Ladoga [33] and in a number of small shallow lakes in Denmark [41, 42] and North Germany [37].

¹ LOVÉN counted it under the name of *Gammarus cancelloides* GERSTF. among the arctic crustaceans in the Vättern and the Vänern [20].

Pontoporeia affinis LINDSTR., on the other hand, is certainly a relic. This form has about the same distribution in Sweden and Finland [LOVÉN 20, 21, NORDQVIST 32] as *Mysis*; besides, it is found in some Norwegian [SARS 38, 39], Danish [WESENBERG-LUND 41, 42], and North German lakes [SAMTER 36]. The original arctic form is *Pontoporeia femorata* KRÖYER, which is common in the Arctic Ocean; it is also to be found along the west coast of Norway, in the Skagerack, the Kattegatt and the Belts, and even in the south-western parts of the Baltic [41]. These two species are closely related to each other. *P. affinis* is a deep-water animal, though not so much as *Mysis*; it lives in cold water and therefore every spring and autumn wanders from more shallow to deeper water and vice versa. The propagation of this animal also is limited to the winter.

The copepod *Limnocalanus macrurus* SARS seems to be a typical glacial relic on account of its distribution and habits [EKMAN 7]. It forms an important part of the pelagic fauna in the deep water of the Bothnian and Finlandian Gulfs [NORDQVIST 34] and lives also in the cold depths of a great number of those Swedish lakes, which have been part of the late Glacial Sea, i. e. in the Vättern, the Vänern, and the Mälaren as well as in most other lakes where *Mysis relicta* lives, and besides in several others in different parts of the country from Skåne to Dalarne. In the Oresjön in Dalarne the history of the immigration of *Limnocalanus* does not agree with that of most other glacial relics; it must have come directly from the late Glacial Sea, as the Oresjön is situated above the bore-line of the Ancylus Lake. *Limnocalanus* must therefore have adapted itself to the fresh-water of this lake independently of the adaptation in the great Baltic Lake. The same is the case in a lake in Västergötland, which has not either been in communication with the Ancylus Lake. The occurrence of *Limnocalanus* in the Nömmen in Småland, a lake situated even above the highest level of the Glacial Sea, is more difficult to explain. It is possible [EKMAN 7, »Nachtrag»], that the ice-dammed lake, which, at the end of the ice age, comprised the present Vättern, might also have extended over the Nömmen. In this case *Limnocalanus* seems to have spread from the late Glacial Sea to the ice lake and also to the Nömmen.

Limnocalanus shows the same inclination for water of low temperature as *Mysis*, but contrary to this it never rises to the surface of the water. *Limnocalanus macrurus* is supposed to descend from *Limnocalanus grimaldi* or some other species closely related to the latter. *L. grimaldi* lives in the Arctic Ocean. — *L. macrurus* also lives in the pelagic region of the Ladoga [NORDQVIST 33].

Also among animals belonging to other lower groups we have found glacial relics. LOVÉN [21, 22] interpreted as such some Annelida: *Terebellides Strömi* SARS and *Antinoe Sarsi* KINB. The former lives round our coasts and the latter only in the Baltic, but they are both northern species found at the Spitzbergen, among other places. There the *Antinoe* is larger than in the Baltic. A similar distribution has *Halicryptus*

spinulosus STEB., which is very frequently found in the Baltic and the Polar regions, but is missing at the west coast of Sweden.

Finally LEVANDER [19] has drawn the attention to the possible occurrence of relic Rotatoria and Protozoa in the northern parts of the Baltic. Of Rotatorians he mentions *Anuraea Eichwaldi* LEV., which lives in the Bothnian and Finlandian Gulfs, but is missing in the southern parts of the Baltic. A form decidedly related to it has been found on the Norwegian coast. Of Protozoans he mentions *Tintinnus bottnicus* NORDQV. the distribution of which is said to comprise the Finlandian Gulf, the Karajakfjord in Greenland, and Davis Sound.

Planaria alpina DANA, living in Central Europe, where it is considered as a relic, has also been found by v. HOFSTEN in the mountains of North Sweden [10]. Contrary to ZSCHOKKE [43] he does not consider it as a relic here, since it lives in the same conditions as in other arctic regions.

Besides the glacial relics before mentioned also some fresh water fish occur as relics in our country [LUNDBERG 23]. In connection with the immigration of the fauna we have already mentioned that several fish as early as during the late glacial epoch arrived to the Baltic. Such are the four horned sting-fish (*Cottus quadricornis*), the salmon (*Salmo salar*), the trout (*S. trutta*), the gwyniad (*Coregonus lavaretus*), the vendace (*C. albula*), the sticklebacks (*Gastrosteus*), the smelt (*Osmerus eperlanus*), and the lamprey (*Petromyzon fluviatilis*). When the land rose, these fish were isolated in some lakes, which are situated near the highest level of the glacial sea, and where they are still living and may be considered as relics. Some of them have probably spread to neighbouring waters. They still live in the Baltic. The distribution of the charr (*Salmo alpinus*) is difficult to explain. It lives in Sweden within a vast, strictly limited mountainous region stretching from the furthest north along the boundary between Sweden and Norway to north Dalarna. It is also to be found in the Vättern and in some other localities in the central and southern parts of the country. It does not occur in the Baltic, which perhaps depends on its being a typical arctic fish, which likes the cold, clear water of the mountain-lakes. In Finland [NORDQVIST 35] it lives in the lakes, which are connected with the White Sea and in some other lakes, belonging to the Saima-system. The charr is also to be found in the Ladoga, the Onega, and the White Sea [NORDQVIST 35]. This distribution shows that the charr probably lived in the late Glacial Sea, from which it has come into all these lakes where it is now living as a relic. It has also been considered as a relic in some lakes in the south of Norway [GRIEG 9]. LUNDBERG [23] considers that the occurrence of the charr can be explained by presuming that it migrated from the west into the large ice-dammed lakes which at the end of the glacial age were situated between the mountains and the ice-border. But HÖGBOM [14] points out that, on account of the many steep falls, it could not have gone up the rivers

which were outlets for the ice-dammed lakes. We cannot therefore tell which way the charr has immigrated.

Finally, we have to mention that LÖNNBERG [24], when investigating the fauna of Öresund, found that part of it has a decidedly northern character. Some purely arctic specimens are to be found there, e. g. *Mysis oculata* FABR., which find has been mentioned before, and also some arctic types belonging to the Echinodermata and the Molluscs. LÖNNBERG supposes that these arctic animals have lived in the Sound ever since the late glacial time. During the Ancylus time, they, however, moved a little towards the north, but when the Litorina Sea was formed they returned to their former abode. The slight salinity and the generally low temperature of the water in the Sound, as well as other favourable conditions, have helped them to stand in the struggle against southern and more typically marine forms.

Relics from the Ancylus Lake.

Compared to the glacial relics the Ancylus ones constitute a group which is little known and few in number. In a special sense those relic arctic animals might be considered as Ancylus relics, which, had once adapted themselves to the fresh-water of the Baltic lake, where, on the other hand, they were remains from the fauna of the Glacial Sea.

In EKMAN'S treatise [7] on crustacean plancton and marine relics, already referred to, the copepod *Eurytemora lacustris* POPPE is classified as an Ancylus relic. Besides in the Vänern and the Vättern, it lives also in a great number of minor lakes in Småland, Halland, Dalsland, Värmland, and Dalarna. Outside Sweden it has been found in a lake in Norway near the Swedish boundary, in Finland, in North Germany, and in one place in Jutland, but it is not known from anywhere else in the world. The other species belonging to the genus *Eurytemora* are marine types, we should, thus, here have a form especially adapted to fresh-water, which in all probability had arisen at the time when the Baltic was a fresh-water lake. The fact that it is missing in the Baltic to-day shows that this adaptation had been so complete that the new fresh-water form had not been able to stand the salt water of the Litorina Sea. The original form of *Eurytemora lacustris* has been supposed to be *E. affinis*, a variation of which, *E. affinis* var. *raboti* RICH., has been found in brackish water at the Spitzbergen. The arctic *Eurytemora*, from which the fresh-water form derives its origin, must have lived in the late Glacial Sea. Concerning the Swedish lakes, in which *E. lacustris* has been found, those in Småland are situated above the highest level of the sea, which shows the impossibility of their being isolated directly from the Ancylus Lake. *E. lacustris* must therefore have come to these lakes by means of passive spreading. As has been mentioned before, when speaking about the distri-

bution of *Mysis relicta*, the »Väner-bay» was in close communication with the Ancylus Lake, which discharged its water there. We may thus presume that the direct spreading of *E. lacustris* into the lakes in Värmland met with no obstacle.

EKMAN [7] mentions the possibility that *Bosmina obtusirostris* SARS var. *maritima* MÜLL. in the Baltic is a relic from the Ancylus time. It is a fresh-water animal, which constitutes a rather important part of the Baltic plancton. It may be supposed that it has through the rivers spread to the Ancylus Lake from lakes in the neighbourhood and since then has survived in spite of the salinity of the Litorina Sea. On the other hand it may be supposed to have come to the Baltic in later times, when the reduced percentage of salt presented more favourable conditions to the fresh-water forms.

Also *Neritina fluviatilis* L. belongs to this group. Elsewhere it lives as a fresh-water animal, but is met with rather frequently in the Baltic, where it may be considered as a remain from the Ancylus-fauna [DE GEER 8].

The Ancylus Lake has played an important part in helping to spread a great number of our fresh-water fish. In the treatise on the distribution of Swedish fresh-water fish LUNDBERG [23] says that most of the Baltic fresh-water fish have probably lived in the Baltic ever since their postglacial immigration without being influenced to any large extent by the salinity of the Litorina Sea. Among immigrated fresh-water fish from the Ancylus time we may mention the pike-perch (*Stizostedium lucioperca*), the distribution of which in Sweden is limited chiefly to the region once covered by the Ancylus Lake. But, curiously enough, it is missing in the Baltic. The salt water cannot have had a repellent effect, as the pike-perch is frequently met with in lakes which were once covered by the Litorina Sea. During the milder climate which was prevailing at the beginning of the Litorina time it spread rather far up in Norrland, where it still lives in various localities, where it may be considered as a relic, the pike-perch having as a rule retreated southwards [LUNDBERG 23, HÖGBOM 14].

Relics from the Litorina Sea.

Such relics were first discovered by J. G. ANDERSSON [5], who investigated the fauna of the deepest parts of the Baltic, the limited deep holes north-east of Bornholm and east of Gotland. In these holes, which are 30—300 m. deeper than the surroundings, the percentage of oxygen is very small and the water colder and saltier, as it never or rarely becomes changed by the bottom-current of the sea. Besides other animals also living in other parts of the Baltic, there were found in these holes three ostracodes, not known before in the Baltic fauna, viz. *Bythocythere simplex*

NORM., *Cythere limicola* NORM., and *Cythere tuberculata* SARS, which also live at the west coast of Sweden. Their occurrence in the Baltic might be explained by presuming that they have belonged to the fauna of the Litorina Sea, and when this retreated, they were left in these holes, where the relatively high salinity and the constant conditions of the water made it possible for them to live. All three are arctic forms, it is true, but they cannot be considered as arctic relics, as they could not have survived the fresh-water time of the Baltic.

To this group EKMAN [7] also refers *Eurytemora velox* LILLJ., which besides in the large lakes Vänern and Mälaren, lives in a great number of minor lakes in Uppland, Södermanland, Skåne, and Blekinge. It is otherwise a marine form, whose proper abode is the warmer seas in the south, a fact which excludes the possibility of its being an arctic marine relic. It is also found in the Baltic. All the lakes where it is found within the Baltic basin lie below the highest level of the sea as well as below the shore-line of the Litorina Sea.

Land-animal Relics.

As is already mentioned, there are in the Swedish fauna also some land-animals which live in scattered localities isolated from their real habitat. But while we can say that most of the before mentioned water-animals are rather so called »transgression relics» than real climatic ones, these land-animals have been considered as belonging to the latter category and are thus comparable to the relics in the flora. The position of these relics is more disputed than that of the water-animal relics, for the opinions about the postglacial changes in the climate are still very different, as is well known. The occurrence of these land-animals might be due also to other than climatic conditions, viz. the influence of man and the competition between the different species.

Some butterflies and some molluscs have been considered as relics belonging to land-animal relics. Already 1886 some Lappland butterflies of the genus *Oeneis* were found in Ingarön in the archipelago of Stockholm (HOLMGREN 11). The geological consequences of this discovery have been discussed more closely by WAHLGREN [40] in a paper of 1909. He holds forth as his opinion that among the butterflies there occur glacial relics as well as pseudo-relics or pseudo-glacial relics, as the latter have also been called. To the first group he counts especially two: *Colias palæno* LIN. and *Argynnis pales* W. V. The proper habitat of these in Sweden is the mountain region, but they are both found also in scattered localities in the south and central parts of the country, especially on fens where the latter occur in the relic form *arsilache* ESP. These two species live also in the Alps, but are generally missing in the lowlands of central Europe. Probably they immigrated from the south, and in their

isolated localities south of the mountain region, they seem to be relics from the glacial time. WAHLGREN considers the above mentioned butterflies in Ingarön and some other species to be pseudo-glacial relics. These are: *Oeneis norma* THBG, *Oeneis jutta* HÜBN., *Argynnis freja* THBG, and *Argynnis apherape* HÜBN. var. *ossianus*. They are generally typical northern forms, living in the northern parts of Scandinavia. The species of the genus *Oeneis* are as relics found in the archipelago of Stockholm, as mentioned above, and the two belonging to the genus *Argynnis* in the Kolmården, and *Argynnis apherape* var. *ossianus* also on a fen in Uppland. All these species have outside Scandinavia a decidedly easterly distribution; they occur in Russia and in Central Asia, but not in Central Europe or in the Alps. According to WAHLGREN their immigration to Scandinavia must, thus, be considered as having taken place from the north-east and not from the south. Especially this circumstance and also the fact that in Sweden they occur in localities, which up to a relatively late time were situated below the level of the sea, speak against the probability of their being glacial relics. WAHLGREN therefore believes that they are relics from a later deterioration in climate during which they were spread further south than nowadays, and he considers them to be comparable to the northern *Salix* species occurring in north Uppland, and which by SERNANDER are called »subatlantic glacial relics». But, perhaps, these butterflies might just as well be interpreted as »advance guards» of a beginning spreading.

The question of relic molluscs and the conclusions about the post-glacial changes of climate that may be drawn from their occurrences and from the finds of fossil molluscs have been treated by HÄGG [12] in 1908. He has given informations about the present and the former distribution of a great number of molluscs, chiefly land-gasteropodes. He is of the opinion that several southern species, which during former epochs were spread much further north than now, have left relics from this former distribution, now isolated from their proper habitat. He comes to the conclusion that the spreading of these molluscs towards the north must have taken place during a time when the climate was warmer than now. In accordance with the postglacial climatic periods of BLYTT-SERNANDER, HÄGG distinguishes southern relics from all the three periods during which the climate was supposed to have been warmer than now, viz. »boreal», »atlantic» and »subboreal» relics. Most of the localities where these relics are found are in Jämtland, but some also occur in other provinces. The present northern boundary of these molluscs is generally in south or central Sweden. According to A. C. JOHANSEN [15] it is only the summer temperature that influences the distribution of the molluscs. As a further proof of a higher summer temperature during the times when these molluscs had their greater distribution, HÄGG states that their present northern boundary in Europe and Sibiria shows a decided displacement towards north-east, or, in other words, follows rather closely the July isotherm.

The relic character of these molluscs in their northern localities has been doubted, and it has been supposed that some of these occurrences perhaps ought to be interpreted sooner as sporadic than as relic ones and, further, that the mollusc-fauna is a yet comparatively little known, so that several species seem to occur more scattered than what is really the case.

Quite recently HÄGG [13] has reported that northern molluscs have been found in the southern parts of Sweden, and these molluscs he interprets as northern relics.

The occurrence of relics has — as we know — been considered to have its greatest importance through the connection which it has had with the Quaternary changes of climate, a connection which has perhaps often been to strongly accentuated. Several scientists have in later times called the attention to the necessity of a more careful use of the term of »relics». Especially there can be supposed that the areas of distribution of the animals, as well as of the plants, are dependent of many other factors than the climate, and that the isolated occurrences outside the more continuous areas occupied by many species are more conditioned by edaphic factors and concurrence than by the direct climatic influence. If this is true, it will also be evident that the changes of climate cannot be measured with any accuracy by changes in the distribution of one or another species. As has been called attention to by GUNNAR ANDERSSON [4] and others, a rich material, gained from various species living under different conditions, must be at disposal to enable us to draw valuable conclusions regarding changes of climate.

Literature

referred to in this paper.

1. G. ADLERZ. *Phoca groenlandica* i Litorina-aflagring. Geol. Fören. Förh. Bd 28. 1906.
2. G. ANDERSSON. Den centraljämtska issjön. Ymer 1897.
3. ——. Rudolf Lundberg: Om svenska insjöfiskarnas utbredning. Ymer 1900.
4. ——. The Climate of Sweden in the Late-Quaternary Period. Sveriges Geol. Undersöknings Årsbok 1909 N:o 1.
5. J. G. ANDERSSON. Ett bidrag till Östersjöns djurgeografi. Ymer 1901.
6. R. CREDNER. Die Reliktenseen. Ergänzungsh. N:o 86 zu Petermanns Mitteilungen. 1887—1888
7. SVEN EKMAN. Über das Crustaceenplankton des Ekoln (Mälaren) und über verschiedene Kategorien von marinen Relikten in schwedischen Binnenseen. Zoologiska Studier tillägnade prof. T. Tullberg. Uppsala 1907.

8. G. DE GEER. Om Skandinaviens geografiska utveckling efter istiden. Stockholm 1896.
9. J. A. GRIEG. Naar indvandrede röien i indsjøerne i det sydlige Norge? Naturen 1908.
10. N. VON HOFSTEN. Planaria alpina im nordschwedischen Hochgebirge. Arkiv för zoologi. Bd 4. Stockholm 1908.
11. E. HOLMGREN. Lepidopterologiska iakttagelser i Stockholms omgifningar. Entomol. Tidskr. 1886.
12. R. HÄGG. Über relikte und fossile Binnenmollusken in Schweden als Beweise für wärmeres Klima während der Quatärzeit. Bull. of Geol. Instit. of Upsala, Vol. 8. 1908.
13. ——. Über relikte und fossile Binnenmollusken in Schweden. Bull. of Geol. Instit. of Upsala. Vol. 9. 1910.
14. A. G. HÖGBOM. Norrland, naturbeskrifning. Uppsala 1906.
15. A. C. JOHANSEN. Om den fossile kvartäre Molluskfauna i Danmark og dens Relationer til Forandringer i Klimatet. Diss. Köbenhavn 1904.
16. ——. Om brugen af Betegnelsen »Relikt» i Naturhistorien. Medd. fra Dansk. geol. For. N:o 14. 1908.
17. K. M. LEVANDER. Om några möjligen relikta organismer i Finska och Bottniska viken. Medd. af Soc. pro fauna et flora Fennica. Häft 24. 1897—98 (1900).
18. W. LILLJEBORG. Om hvalben funna i jorden på Gräsön i Roslagen i Sverige. Forh. ved de Skand. Naturforskarnes 8:e möde i Köbenhavn 1860. Köbenhavn 1861.
19. ——. Sveriges och Norges fiskar. Stockholm 1891.
20. S. LOVÉN. Om några i Wettern och Wenern funna Crustaceer. K. Svenska Vet. Akad. Förh. Öfversikt, Vol. 18. 1861.
21. ——. Till frågan om Ishafsfaunans fordna utsträckning öfver en del af Nordens fastland. Ibid. Vol. 19. 1862.
22. ——. Om Östersjön. Förh. vid de Skand. naturforskarnes 9:e möte i Stockholm 1863. Stockholm 1865.
23. R. LUNDBERG. Om Svenska insjöfiskarnas utbredning. Medd. från K. Landtbruksstyrelsen. N:o 10 för år 1899 (N:o 58).
24. E. LÖNNBERG. Undersökningar rörande Öresunds djurlif. Medd. från K. Landtbruksstyrelsen. N:o 1 för år 1898 (N:o 43).
25. ——. Om de i Östersjön förekommande själhundarterna och deras kännetecken. Sv. Fiskeri Tidskr. Arg. 7. Stockholm 1898.
26. ——. Bidrag till kännedomen om hafsdjurens utbredning uppåt Bottenhafvet. Ibid. Årg. 11. Stockholm 1903.
27. ——. Hornsimpa i Mälaren. Ibid. Årg. 12. Stockholm 1903.
28. H. MUNTHE. Preliminary report on the Physical Geography of the Litorina-Sea. Bull. of Geol. Instit. of Upsala. Vol. 2. 1904.
29. ——. Om fyndet af gräsäl i Ancylusleran vid Skattmansö i Uppland. Geol. Fören. i Stockholm Förh. Bd 17. 1895.
30. A. G. NATHORST. Om en fossilförande lerafslagring vid Skattmansö i Uppland. Ibid. Bd 15. 1893.
31. ——. Nya fynd i ancylusleran vid Skattmansö i Uppland. Ibid. Bd 17. 1895.
32. O. NORDQVIST. Om förekomsten af Ishafscrustaceer i mellersta Finlands sjöar. Medd. af Soc. pro Fauna et Flora Fennica. Häft 11. 1884.
33. ——. Bidrag till kännedomen om Ladoga sjös crustacefauna. Ibid. Häft 14. 1886.
34. ——. Bidrag till kännedomen om Bottniska vikens och norra Östersjöns evertebratfauna. Ibid. Häft 17. 1890.
35. ——. Some biological reasons for the present distribution of fresh-water fish in Finland. Fennia, Vol. 20. 1908.
36. M. SAMTER und W. WELTNER. Biologische Eigentümlichkeiten der Mysis relicta, Pallasiella quadrispinosa und Pontoporeia affinis, erklärt aus ihrer eiszeitlichen Entstehung. Zool. Anzeiger, 27. 1904.

37. M. SAMTER. Die geographische Verbreitung von *Mysis relicta*, *Pallasiella quadrispinosa*, *Pontoporeia affinis* in Deutschland als Erklärungsversuch ihrer Herkunft. Anh. zu d. Abhand. K. Preuss. Akad. Wiss. 1905.
38. G. O. SARS. Histoire naturelle des Crustacés d'eau douce de Norvège. 1:re livraison. Les Malacostracés. Christiania 1867.
39. ——. An account of the Crustacea of Norway. 1895—1902.
40. E. WAHLGREN. Glaciala relikter och pseudorelikter bland våra dagfjärilar. Fauna och Flora, 1909.
41. C. WESEBERG-LUND. Sur l'existence d'une faune relicte dans le lac de Furesö. Overs. K. Danske Vidensk. Selsk. Forh. 1902.
42. ——. Om en nulevende i vore Søer indelukket arktisk Istidsfauna. Geogr. Tidsskr. 17 Bind. København 1904.
43. F. ZSCHOKKE. Die Beziehungen der mitteleuropäischen Tierwelt zur Eiszeit. Verh. d. Deutsch. Zool. Gesellsch. 1908. Leipzig 1908.

