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The taxonomic status and prehistory of
the glacial relict *Pontoporeia* (Crustacea Amphipoda)
living in North American lakes

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Abstract

SEGERSTRÅLE, SVEN G.: The taxonomic status and prehistory of the glacial relict *Pontoporeia* (Crustacea Amphipoda) living in North America lakes. *Commentat. Biol.* 89, 18 pp., 1977. — It is shown that the prevailing view that the *Pontoporeia* inhabiting North American freshwaters as a glacial relict is identical with the Eurasian relict species *P. affinis* should be abandoned. The form living in lakes of North America is a separate species and should be referred to as *P. hoyi*, under which name it was described by S. I. Smith in 1874. The characteristics of this species and its prehistory are discussed. It is concluded that the animal is derived from North American arctic populations of *P. femorata*, a circumpolar and marine species, whereas *P. affinis* has probably evolved from *femorata* populations inhabiting the sea off Siberia. In both cases the evolution would have been due to the special conditions of the Ice Age (dilution of sea water, isolations in proglacial lakes).

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Introduction

In my paper on the immigration of the glacial relicts of Northern Europe, published in 1957, attention is drawn to the possibility that the relict Eurasian amphipod *Pontoporeia affinis*, described by G. Lindström in 1855 on material from the Baltic Sea, may have invaded North America from ice-dammed waters in Siberia. This eastward movement would parallel the westward migration concluded to have occurred in the case of the relict *Pontoporeia* (and other relicts) of Northern Europe (for evidence of Pleistocene proglacial waters in Siberia, see also Segerstråle 1976 b). The idea of eastward migration to North America was suggested, on the one hand, by faunal indications that ice-dammed waters also existed in eastern Siberia, and on the other, by the belief current at the time of publication of my paper that the *Pontoporeia* living as a relict in lakes in North America was identical with the Eurasian *P. affinis*.

Today the above view on the origin of the North American freshwater *Pontoporeia* is no longer tenable. As will be shown below, recent studies have proved that this amphipod is a different species from *affinis* and should be referred to as *P. hoyi*, under which name it was described by S. I. Smith in 1874. This result is not merely of taxonomic interest, but also affects our theories of the prehistory of the *Pontoporeia* of North America. Accordingly, the present paper will deal with two subjects, the status of *P. hoyi* as a separate species and the provenance of this glacial relict.

In 1958 Dr. E. L. Bousfield of the National Museum of Natural Sciences in Ottawa, Canada, published a paper on the freshwater amphipods of the glaciated parts of North America. He concurred with the view then generally held that the *Pontoporeia* of that area was not specifically distinct from *P. affinis*, but considered that the evidence available might provide grounds for subspecific recognition of all the North America material as *P. affinis hoyi*. The matter was complicated by records from coastal North America of a rather large, morphologically and ecologically distinct *Pontoporeia*, possibly separable from Lindström's form, but Dr. Bousfield concluded that "until more extensive information on the taxonomy, distributional ecology, and physiology of the entire North American and European species complex becomes available, it seems advisable to refer all North American freshwater material simply to *P. affinis* Lindström". Dr. Bousfield has continued his work on the taxonomy of the *Pontoporeia* of North American lakes and, since these problems are of special interest to me, being closely connected with the prehistory of glacial relicts (cf. Segerstråle 1957, 1971 a, b, c, 1962, 1976 a, b), we have exchanged letters on the subject. Both of us have found several morphological differences between *P. affinis* and *P. hoyi* and have, hence, concluded that the two forms are not identical. For comparison, I sent Dr. Bousfield material from the Baltic Sea and from a Finnish lake, and in a letter of 1970 he wrote that he considers *hoyi* a clearly distinct species. For my own part, after having examined various morphological details of the North American fresh water *Pontoporeia* in slide mounts (the major part of the material was received from numerous lakes of the area in connection with earlier studies; cf. Segerstråle 1971 a, b) and compared it with the Baltic form, I have come to the same view as Dr. Bousfield. In a recent letter (November, 1976) he wrote that, in the course of his work on *Pontoporeia*, it has proved necessary to revise the whole group of described forms of this genus, including those inhabiting Eurasia. As this large-scale project will require much work and time, and the publication of the results can hardly be expected in the near future, I have decided to present a separate article on the special taxonomic problem of *P. hoyi* and the associated subject of its prehistory. I do so in the hope of making some contribution to the realization of Dr. Bousfield's large project. As my paper is concerned with matters on which both of us have worked, I have informed Dr. Bousfield of my intention to publish it, and he has replied that I am free to pursue my plan.

Historical notes on the taxonomy of the *Pontoporeia* of North American lakes

The first record of a representative of the amphipod genus *Pontoporeia* in lakes of North America was published in a report by Professor S. I. Smith on the results of dredgings performed in Lake Superior in 1871 (Smith 1871). In a paper of 1874, on the crustaceans of the fresh waters of the United States, Smith said that the first examination of this *Pontoporeia* led him to the conclusion that the animal was identical with the *P. affinis* inhabiting Scandinavian lakes and the Baltic Sea; as mentioned above, it was from the Baltic that the species was described in 1855. However, later comparison by Smith of specimens from Lake Superior and the Swedish lake Vättern revealed some differences which seemed to be of specific value, and Smith named the new species *P. hoyi*, in honour of Dr. P. R. Hoy. The main differences between *hoyi* and *affinis* mentioned by him refer to the first gnathopods: in the propodus, the palmary margin is less oblique in *hoyi* than in *affinis* and *hoyi* has a couple of spines near the tip of the closed dactylus, whereas the European material has only setiform hairs. These characteristics seemed to be constant features in Smith's material from North America. The new species had been found to be common in the stomachs of whitefish living in Lake Superior and Lake Michigan. Dredgings in the latter lake had also yielded females carrying eggs, and with them males with the long antennae figured by Sars in his account of the freshwater malacostracan crustaceans of Norway (1867). Smith regarded these males as adults, a view that later proved erroneous (see below).

In his paper of 1874 Smith also described another new species of *Pontoporeia*, *P. filicornis*, on the basis of a single specimen, dredged with *P. hoyi* from Lake Michigan. Its main characteristics were the very elongated antennae; the flagella of the first pair nearly reached the tip of the abdomen and those of the second pair were even longer. However, in view of the very close agreement of *filicornis* with *affinis* and *hoyi* in all other parts of the body, Smith also suggested that the elongation of the antennae might be only a sexual characteristic of the old male, a conclusion that has been confirmed by later studies (Segerstråle 1937).

1895. G. O. Sars publishes his well-known account of the amphipods of Norway, which includes the Great Lakes of North America in the range of *Pontoporeia affinis*.

1907. In A. L. Weckel's paper "The fresh-water Amphipoda of North America" Smith's descriptions of *P. hoyi* and *P. filicornis* are repeated without comments.

1909. A. H. Norton describes a new species of *Pontoporeia*, *P. kendalli*, on the basis of a single specimen from a freshwater locality in Maine, USA, characterized by marked elongation of both pairs of antennae. In 1937 (see below) I suggested that the animal was merely a normal adult male of the *Pontoporeia* living in North American lakes, a conclusion that was confirmed by later examination of the type mount of the animal (cf. Segerstråle 1971 a).

1913. The Swedish zoologist S. Ekman describes two new European species of the genus *Pontoporeia*, *P. sinuata* and *P. weltneri*. As in the case of *P. filicornis*, the main feature of both forms was the marked elongation of the antennae. The material of *sinuata* originated from the Baltic, that of *weltneri* from the lake Madüsee in northern Germany. In my paper of 1937 it was conclusively demonstrated that *sinuata* and *weltneri* were simply the adult male stages of *P. femorata* and *P. affinis*, respectively (cf. the suspicion expressed by Smith in 1874). Ekman also gave his opinion of Smith's *P. filicornis*, having examined figures of Smith's specimen; he considered it a separate species, a view later proved wrong (see above). He also examined material of *hoji* from Green Lake, Wisconsin, and arrived at the conclusion that it was typical *affinis*.

1927. In the in paper "*Pontoporeia* and *Mysis* in Wisconsin lakes", Ch. Juday and E. A. Birge maintain that *P. hoji* and *P. affinis* are identical species. They refer to the Norwegian zoologist G. O. Sars, who had received material from Green Lake, Wisconsin, and pronounced it to be conspecific with the *Pontoporeia* of European lakes. This view of Sars, well-known as a carcinologist, has no doubt influenced later authors.

1928. A new contribution to the question of the taxonomy of the *Pontoporeia* inhabiting North American lakes is made by F. B. Adamstone. In 1922, in Lake Ontario, he had obtained the head of a specimen bearing the long antennae (partly broken off) mentioned in Smith's description 1874 of *P. filicornis*. In the following summer, five other specimens (males) with long antennae were dredged from Lake Nipigon (north of L. Superior). However, these specimens differed from the type in several respects; in particular, the antennae were clearly shorter, the second pair reaching only somewhat beyond the middle of the body. In spite of this, Adamstone did not doubt that they were Smith's *filicornis*, assuming that the males caught in Lake Nipigon had not yet reached the final developmental stage. As emerges from my paper of 1937 (see below), this view was wrong: Adamstone's specimens were adult males, although exhibiting signs of neoteny, i.e., inhibition of the normal full development. The most marked feature of this was the shortness of the antennae. This conclusion was based on examination of material from Lake Superior, received by me from the collections of the U. S. Natural Museum in Washington.

1937. In my paper "Zur Morphologie und Biologie des Amphipoden *Pontoporeia affinis*, nebst einer Revision der *Pontoporeia*-Systematik", I maintain that *P. hoji* is identical with *P. affinis*, referring to the earlier views of Ekman and Sars. Studies of the development of the amphipod (material from the Baltic) revealed that during the last moult the male undergoes a striking modification, especially clearly visible in the strong elongation of the antennae. It was this drastic change of the male that had led Ekman to give his "*P. weltneri*" and "*P. sinuata*" (see above) specific status. The paper includes a description of the neotenic male form, for which the name f. *brevicornis* was proposed.

1951. In her account of the amphipods inhabiting the seas of the USSR, the Soviet zoologist E. Gurjanova regards *P. boyi* as synonymous with *P. affinis* and, hence, includes the relict lakes of North America in the range of *affinis*. In a paper of 1952 on the origin of the glacial relict amphipods, her colleague N. B. Lomakina also refers to the *Pontoporeia* living in lakes of North America as conspecific with *P. affinis*.

1953. K. D. Waldron describes (in a mimeographed paper, University of Washington) the *Pontoporeia* living in Lake Washington as *P. affinis* subspecies *erythrophthalma* on account of the red colour of the eyes. The paper is commented upon below, pp. 9—10.

1954. E. B. Henson reports a male specimen of *P. affinis* from Lake Cayuga (N. Y.). The specimen was sent to me and determined as an adult male belonging to the form *brevicornis*.

1957. As was mentioned in the Introduction, in my paper of this year on the immigration of the glacial relicts of North Europe, the *Pontoporeia* of North American lakes was referred to as *P. affinis*, according to the view held at that time.

1958. For the paper by Bousfield of this year, see above, p. 4.

1959. In his paper on the origin of the relicts *Mysis* and *Pontoporeia* living in lakes of North America, K. E. Ricker writes of the latter crustacean under the name *P. affinis*.

1962. In her account of the Amphipoda Gammaridea of the northern part of the Pacific, Gurjanova repeats the view of 1951 that the range of *Pontoporeia affinis* includes the relict lakes of North America.

1971. On the basis of extensive material of *Pontoporeia* from North American lakes, I give additional data on the morphology and distribution of the *brevicornis* form of the adult male, described in my paper of 1937 and characterized by neotenic features. In the paper of 1971 the normal adult male is referred to as f. *filicornis*, under which name it was described in 1874 by Smith, who, as we have seen, accorded it specific status. The new study of *brevicornis* reveals that this male form has a wide distribution in North America; the material of it originated from 8 lakes, including most of the Great Lakes. In many of the lakes *brevicornis* lives side by side with *filicornis* (see map in Fig. 2 in Segerstråle 1971 a). In the collection from Lake Michigan, comprising more than a hundred specimens of *brevicornis*, this form clearly outnumbers *filicornis*. *Brevicornis* proved to be somewhat smaller than *filicornis* (average length from tip of rostrum to base of telson c. 6.5 and c. 7.5 mm, respectively).

In the paper of 1971 a third form of the adult *Pontoporeia* male, found in the material from Lake Cayuga and Great Bear Lake, is described as f. *intermedia*. As is indicated by the name, this form shows morphological features which are intermediate between *filicornis* and *brevicornis*. It may be mentioned that these two male forms were also present in the material from Lake Cayuga.

Although the *Pontoporeia* living in lakes of North America is referred to as *P. affinis* in the paper of 1971, my correspondence with Dr. Bousfield, mentioned in the Introduction, leads me to stress the need for reconsidering its taxonomic status.

1974. M. J. Dadswell's paper on the distribution, ecology, and postglacial dispersal of certain crustaceans and fishes in eastern North America includes the following comment on the taxonomic status of the *Pontoporeia* of the area (p. 5): "Bousfield (personal communication) now believes the North American freshwater populations to be a different species from at least the Baltic '*affinis*'. At the present time, however, the species concepts are not yet clear, and until they become so, it is better to maintain, with reservation, *P. affinis* for the eastern North American freshwater populations".

1976. In my paper on the role of proglacial lakes in the dispersal of glacial relicts, the *Pontoporeia* inhabiting North American lakes is still referred to as *P. affinis*, but attention is once more drawn to the need for revising its taxonomic status.

The characteristics of *P. boyi*

In the papers reviewed above, the *Pontoporeia* living in North American lakes and described in 1874 under the name *P. boyi* was referred to as *P. affinis* Lindström 1855, a species described on material from the Baltic Sea. The same name has been used in practically all other publications; see, for instance, Larkin 1948, Pennak 1953, Rawson 1953, Dunbar 1954, Segerstråle 1959, Teter 1960, Wilson 1960, Cooper 1962, Segerstråle 1962, Frey (edit.) 1963, Marzolf 1963, 1965 a, b, Green 1965, 1968, Henson 1966, 1970, McNaught and Hasler 1966, Robertson and Alley 1966, Wells 1968, Alley 1968, Hiltunen 1969 a, b, Kidd 1970, Hamilton 1971, Rains 1971, Segerstråle 1971 b, c, Johnson 1975. The only exception found by me in the literature is in the papers by Eggleton of 1936 and 1937, where he uses the species name *boyi* Smith for the *Pontoporeia* of Lake Michigan. However, as was mentioned in the Introduction, both Dr. Bousfield and myself have arrived at the conclusion that *P. boyi* should be re-established as a separate species and the designation *P. affinis* should be abandoned in the case of the *Pontoporeia* living in lakes of North America. Of the characteristics found by us, those listed below would suffice to justify this view.

Gnathopods of pair I. In his description of *P. boyi*, Smith attributed special importance to the structure of this pair of legs (immature specimens examined). In the propodus, *boyi* has a less oblique palmary margin than *affinis* and couple of stout spines near the tip of the flexed dactylus. Smith found that the different palmary margin and its armature of spines was a constant feature of the North American form. Bousfield (in letter) pointed to the same differences, characterizing the propodus of the Baltic form as long-ovate and that living in lakes

of North America as deep-ovate. Examination by me of material from both areas has given the same result. (Fig. 1).

Pereiopods of pair VII. As was demonstrated earlier by me (1971 a), the adult males of all three forms recorded from North American lakes, viz. *filicornis*, *intermedia* and *brevicornis*, exhibit the following features totally absent in adult males from the Baltic (and a Finnish lake, Hiidenvesi, from which material was available): the carpus widens towards its distal end, appearing club-like; in addition the proximal part of the propodus shows a conspicuous bend (Fig. 3 A).

Telson. As found by Bousfield and me, the telson of adult males is more rectangular and more deeply cleft in *P. hoyi* than in *P. affinis*; in the latter the tapering lobes result in a comparatively open cleft (Fig. 2).

Note on the Pontoporeia of Lake Washington. As was mentioned earlier, this lake harbours a form of *Pontoporeia* described in 1953 by Waldron as *P. affinis* ssp. *erythrophthalma* on account of the red colour of the eyes. Waldron gave a detailed description of the crustacean and compared it with the European *P. affinis*, on the basis of material from Finland (apparently marine localities) and published data, mainly those given in my paper of 1937 (the life history of the *Pontoporeia* inhabiting Lake Washington is also discussed). Surprisingly enough, there is practically no comparison with the *Pontoporeia* living in other lakes of North America; of Waldron's 54 figures, 51 refer to the Washington form and 3 to the Finnish material.

Comparison by me of the Washington *Pontoporeia*, as described by Waldron, with material from other North American lakes has led me to the conclusion that the two forms are so similar that they should be regarded as conspecific (for the question of giving the Washington *Pontoporeia* subspecific status, see below). Inter alia, the characteristics of *P. hoyi* listed above are also observed in the Washington form (for gnathopod, I, see Waldron's Fig 20; for pereiopod VII, Fig. 31 and text, p. 25; for telson, Fig 43). The only noteworthy differences found by me are those in the number of segments in the flagella of the antennae and the number of peglets on the posterior margin of the merus of pereiopod VII. The ranges of these numbers in Waldron's material and my material of *hoyi* are as follows: Flagellar segments: first pair of antennae — Waldron 32—51, Segerstråle 19—40; second pair — Waldron 45—72, Segerstråle 45—63 (Segerstråle 1971 a; *hoyi* referred to as *affinis* in this paper). Peglets: Waldron 19—35, Segerstråle 13—21. Even if the trend towards lower numbers emerging from my *hoyi* material is confirmed in future studies, it can hardly be considered more than an indication of the existence of local races within the species. As shown by the number of flagellar segment, the adult male of the Washington *Pontoporeia* belongs to the form *filicornis*.

As regards the red colour of the eyes of the Washington *Pontoporeia*, given subspecies status by Waldron, the following should be mentioned. The only earlier reference to the eye colour of the freshwater *Pontoporeia* of North America seems

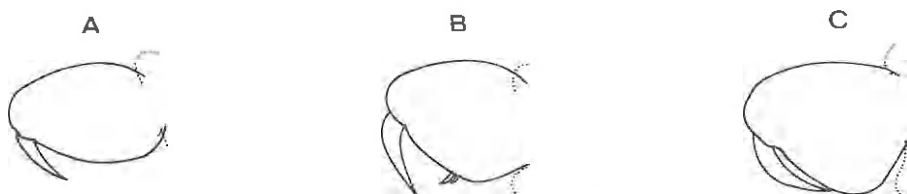


Fig. 1. Gnathopod of pair I, distal part (propodus and dactylus) (immature males). Setae omitted, only spines shown. A, *Pontoporeia affinis*, length from tip of rostrum to base of telson 7 mm, Baltic Sea; B, *P. hoyi*, 7 mm, Great Slave Lake, Canada; C, *P. femorata*, 10 mm, Baltic Sea. Figures drawn by the author.

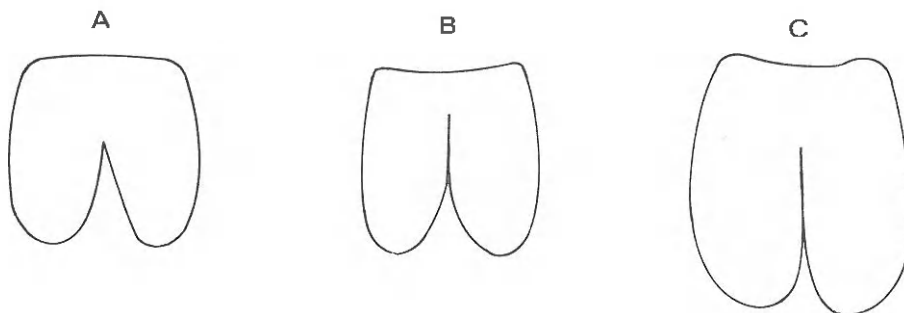
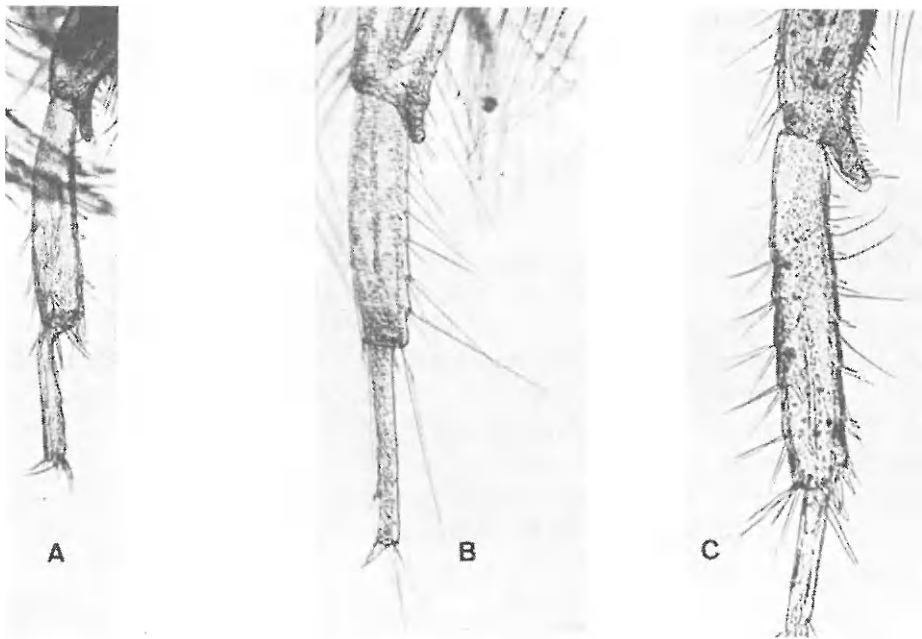


Fig. 2. Telson in adult male (spines omitted) of: A, *P. affinis*, 6.8 mm, Baltic Sea; B, *P. hoyi*, 7.7 mm, Lake Cayuga, N. Y., USA; C, *P. femorata*, 8.5 mm, Baltic Sea. Figures drawn by the author.

Figs. 3—4. (see opposite page). Fig. 3 (top). Distal part of pereopod VII in: A, adult male of *P. hoyi* f. *brevicornis*, Lake Ontario; B, penultimate stage of male of *P. hoyi*, Devil Lake, Canada; C, adult male of *P. affinis*, Baltic Sea. After Segerstråle 1971 a; *P. hoyi* there referred to as *P. affinis*. Fig. 4. Pereopod VII (proximal part omitted) in: A, adult male of *P. femorata*, 10 mm, Baltic Sea; B, merus of same specimen, more strongly magnified, to show in detail, besides the setae, the row of short, stout spines, or peglets, along the posterior margin (the peglets are characteristic of the adult males of all forms of *Pontoporeia*); C, part of the figure of pereopod VII given by Ekman in his description of "*Pontoporeia sinuata*" = adult male of *P. femorata* (Ekman 1913, Pl. 1, Fig. 5); as will be seen, the peglets have been overlooked.



Figs. 3 and 4. For explanation, see opposite page.



to be the statement in Smith's description of *P. filicornis* that the eyes are black (only one specimen available). This colour is characteristic of the North European *P. affinis* (observations by me on live specimens; cf. also Sars 1895 and Stephensen 1929). However, it should be noted that Smith's description of *filicornis* was based on a preserved specimen; the original colour may thus have changed. My conclusions regarding the prehistory of *P. hoyi* (p. 13 onwards) made me suspect that the red colour of the eyes is not restricted to the *Pontoporeia* of Lake Washington but may possibly be a normal characteristic of *P. hoyi*. Accordingly, I wrote to Dr. Dadswell, who had kept live specimens of the crustacean in aquaria, and asked for information on the matter. He replied as follows: "As I recall and this is hazy, some or most had black eyes; however, a few populations had reddish ones — I cannot remember which ones. — I am sorry I cannot be of more aid to you concerning eye color but I have not kept *Pontoporeia* in the lab now for more than four years nor did I write down eye color observations when I had them". Thus it is not only the Washington *Pontoporeia* that has red eyes and I venture to guess that future studies by North American workers will show that the red eye colour is a characteristic of *P. hoyi*.

According to Waldron, the eyes of Lake Washington specimens, immediately after they have been brought to the surface, have a whitish appearance (the material seems to have been dredged at about 60 m depth). This is said to be due to the fact that the pigment of the ommatidia is retracted; exposure to light results in the expansion of the red pigment, causing the red colour to become clearly visible. It is of interest that studies carried out on *P. affinis* from Baltic localities by the Finnish physiologist Donner (1971) have shown that in this species, which has black eyes, light also seems to cause migration of the pigment: after prolonged dark-adaptation (2—3 weeks) the eyes appeared more or less white. Donner also refers to other studies on the eye of amphipods that demonstrate photo-mechanical movements in these organs.

Lake Washington holds a unique position among the freshwater localities of *Pontoporeia* in North America, being the only one situated *west* of the Cordilleran ranges. The case has been commented upon by Ricker (1959), myself (1971 c), and Holmquist (1975). Ricker and Holmquist suggest that the crustacean reached this region from the sea, whereas I consider it more probable that immigration occurred from the east, along the River Fraser, by which route a number of fishes are assumed to have crossed the Cordillerans during the Ice Age, coming from the proglacial lake known as the Mississippi refuge (McPhail and Lindsey 1970). The apparent identity of the Washington *Pontoporeia* with *P. hoyi* seems to speak in favour of the latter view. Sluicing up in ice-dammed waters probably formed part of the final stage of the journey of *Pontoporeia* to Lake Washington (cf. Segerstråle 1976 b).

The prehistory of *Pontoporeia hoyi*

In his paper of 1959 Ricker considered the origin of the relicts *Mysis* and *Pontoporeia* in North America in relation to the Pleistocene glaciation and presented two alternatives. These relict crustaceans may have immigrated from Siberian ice-dammed waters, as suggested in my paper of 1957 on the prehistory of the glacial relicts of North Europe, or their ancestors may have lived in arctic coastal waters of North America. Both theories involved sluicing up in proglacial waters to their present inland localities. In his paper of 1974, Dadswell shares Ricker's view that the ancestors of the relicts lived in waters trapped by the advancing ice-caps along the coast of North America (Hudson Bay and James Bay are mentioned) and were transported southwards in proglacial lakes. The conclusion reached in the present study that *Pontoporeia hoyi* described from North American fresh waters is not identical with *P. affinis*, but must be regarded as a separate species, supports Ricker's and Dadswell's idea of the independent origin of this crustacean.

As regards the ancestor of *P. hoyi*, it seems likely that this species is derived from *P. femorata*, which, having a circumpolar distribution, also lives in the arctic waters off the coast of North America. This suggestion is based on the fact that the characteristics of *P. hoyi* described above show clear affinity with *P. femorata*; see Figs 1—4. If future studies show that *hoyi* has normally red eyes (cf. above), this will be additional evidence pointing to *femorata*, which has red eyes (observations by me on live specimens; cf. also Sars 1895 and Stephensen 1929).

The spines on the propodus of the first pair of gnathopods in females and immatures of *hoyi* are lacking in *femorata*, but the replacement of setae by spines is apparently a common feature in amphipods. For instance, this is observed in connection with the last moult of the male of *Pontoporeia*, which produces the adult stage (see Fig. 3 and Segerstråle 1937, Pls. XIII and XIV). Hence, such a modification during the evolution from *femorata* to *hoyi* would not be surprising.

The idea of *femorata* being the ancestor of *hoyi* is supported by the existence, in arctic North American waters, of a yet undescribed form of *Pontoporeia* which exhibits many close affinities to *femorata* (Bousfield's paper of 1958 and commun. in letter). Furthermore, this conclusion is in accordance with the view of the Soviet zoologist Lomakina, who suggested (1952; cf. also Gurjanova 1962 and Zenkevich 1963) that *P. femorata* is the ancestor of all the other forms of the genus. Her conclusion is based on the existence of forms that are transitional with respect to the main diagnostic characteristic of *femorata*, viz. the dorsal bifurcate process on urosomal segment I. The *femorata* living in the brackish Baltic Sea and the form described from the freshened gulfs of the Sea of Japan, *P. ekmani* Bulycheva 1936, referred to as *P. femorata ekmani* by Lomakina 1952 and Gurjanova 1962, exhibit a more or less marked reduction of the bifurcate process; in the Caspian *P. affinis microphthalmus* Ekman 1916 the process is represented by a small hump only, furnished with two spinelike projections, and in *P. affinis* from Eurasian brackish

waters and lakes the reduction is practically total (for morphological variation in the latter type of localities, see Lomakina, pp. 120—123 and Segerstråle 1957, pp. 34—35). (As was mentioned above, Lomakina regards the freshwater *Pontoporeia* of North America as conspecific with *P. affinis*.)

Besides occurring in lakes of Eurasia, *P. affinis* lives in the Baltic and in diluted waters off the coast of northern Russia and Siberia (cf. Gurjanova 1962). A parallel to the latter distribution can be expected to exist in North America, where a *Pontoporeia*, referred to as *P. affinis*, is reported from strongly diluted waters off the coast (see, for instance, Johnson 1964). Future examination of this form will probably show that it is identical with *P. boyi*, which, carried by proglacial lakes in the wake of the melting ice-caps of the Pleistocene, finally reached the coast and survive there in sea water of very low salinities.

A remark on the Eurasian *P. affinis* should be inserted here. Comparison of specimens from the Baltic and from a Finnish lake with material from Siberian coastal waters (Lomakina 1952, Segerstråle 1957, Gurjanova 1962) has shown that there are no appreciable differences between the forms living in the two areas. The Baltic with neighbouring lakes and the brackish waters off Siberia are thus inhabited by the same *P. affinis*, and this distribution is in good accordance with the view that the North European populations of this species have immigrated from Siberian ice-dammed waters (Segerstråle 1957, 1976 a).

The theory that the prehistory of *Pontoporeia boyi* (and *P. affinis*) involves evolution from *P. femorata* gains additional support from the study by Lomakina on another relict amphipod, viz. *Gammaracanthus relictus*. As shown in her paper of 1952, this form is obviously derived from the marine *G. loricatus* and two transitional forms exist, living in brackish coastal waters, viz. *aestuariorum* (in estuaries from the White Sea to the Kara Sea) and *ostiorum* (in the estuaries of R. Ob and R. Lena, and of R. Anadyr in the Far East). It seems likely that the form of *Pontoporeia* recorded from arctic waters off the coast of North America, which Bousfield (cf. above) characterizes as a rather large, morphologically and ecologically distinct form, offers a parallel to the intermediate brackish forms of *Gammaracanthus*. According to letters from Dr. Bousfield, the *Pontoporeia* concerned tolerates salinities as high as 30‰ and, as was mentioned earlier, is in many respects closer to *P. femorata* than the *Pontoporeia* of North American fresh waters.

The following comments may be added on the morphological differences between, on the one hand, *Pontoporeia boyi/affinis* and *Gammaracanthus lacustris* and, on the other, their suggested ancestors. In both cases the relict form is smaller and exhibits reduction of the chitinous armature, via transitional forms: in *P. boyi* and *P. affinis* the dorsal projections on urosomal segment I has disappeared; in *Gammaracanthus relictus* the rostrum is less strongly built than in *G. loricatus* and the dorsal projections are much less conspicuous on the four first pereon segments (Sars 1895, Lomakina 1952). Lomakina concludes that in both

cases the reduction is connected with a decrease in the salinity of the environment.

It is interesting to note that a tendency towards reduction of the armature is also found within the lacustrine amphipod genus *Pallasea*, one species of which, *P. quadrispinosa*, belongs to the group of glacial relicts and is confined to once glaciated areas in Eurasia (not recorded from North America). This crustacean normally bears two strong spines on each of the two first pleon segments, and lateral processes on the head and pereaeon. In some localities the spines and processes may be weakly developed or even totally lacking (see Segerstråle 1958). As the apparent ancestor of *P. quadrispinosa*, *P. kessleri*, has an even more strongly developed armature than the former species, we are here faced with a clearcut trend towards morphological reduction in the relict form.

The following earlier views on the relationship between *P. femorata* and *P. affinis* may be mentioned here. In his description of *affinis* (1855) Lindström suggests that the new species might perhaps be only a variety of *femorata*. Jägerskiöld (1912) considers that the relict *affinis* may be derived from *femorata*. Ekman (1918) disagrees with this view, his main argument against it being the fact that both species live side by side in the Baltic Sea. According to Ekman, *affinis* is an arctic brackishwater species, also living unchanged as a relict in fresh water. (Ekman 1919). I suggest the following plausible explanation of the co-existence of *femorata* and *affinis* in the Baltic Sea today: the species *affinis* evolved in the Siberian region and subsequently reached the Baltic basin (Segerstråle 1957, 1976 a), where it lives today, together with the euryhaline marine species *femorata*, which has immigrated from the direction of the Atlantic. Commenting on Lomakina's view on the prehistory of *Gammaracanthus relictus*, Holmquist (1966) also touches upon the prehistory of *Pontoporeia affinis*. As regards *Gammaracanthus*, she accepts only the species *G. loricatus*, characterized by her as variable and euryhaline, and includes in it *relictus* and those forms exhibiting transitional morphological features. Writing of *Pontoporeia*, she continues (p. 313): "Das gleiche ist höchstwahrscheinlich der Fall mit *Pontoporeia affinis*, die eine von *P. femorata* Kröyer 1842-43 getrennte Art ist-. Man kann nicht sagen, welche Art von der anderen stammt, nur dass beide sehr wahrscheinlich dieselben Vorfahren haben." Her view therefore differs from that advanced in the present paper.

Summing up, it seems likely that the arctic and circumpolar *Pontoporeia femorata* evolved two somewhat different forms in the Siberian and North American regions, *P. affinis* and *P. boyi*, of which the latter shows closer affinity to the ancestor. This evolution no doubt took place in connection with the Ice Age, when the dilution of the sea water as the ice-caps melted favoured gradual adaptation to a freshwater environment (cf. for instance, Gurjanova 1938); alternatively, the adaptation occurred in proglacial lakes originally containing coastal water (Segerstråle 1957). At any rate, sluicing up in proglacial waters has obviously played a paramount role in the dispersal history of the *Pontoporeia* living today in lakes of North America (Ricker 1959, Dadswell 1974, Segerstråle 1976 b).

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