Commentationes Biologicae

38

The distribution and morphology of *Pontoporeia affinis* Lindström f. *brevicornis* (Crustacea Amphipoda) inhabiting North American lakes, with a description of a new aberrant male form from the area

Sven G. Segerstråle

Institute of Marine Research, Biological Division
Helsinki/Helsingfors

Societas Scientiarum Fennica
Helsinki—Helsingfors 1971

Abstract

SEGERSTRÅLE, SVEN G: *The distribution and morphology of Pontoporeia affinis Lindström f. brevicornis (Crustacea Amphipoda) inhabiting North American lakes, with a description of a new aberrant male form from the area.* Commentat. Biol. 38 (1971), 19 pp.

That aberrant form of the adult male of *Pontoporeia affinis* Lindström living in fresh waters of North America which the author described in 1937 as f. *brevicornis* was at that time known from only two lakes in the area. New material recently examined by the author shows that this form occurs at least in four additional lakes, including three of the Great Lakes. The distribution and morphology of f. *brevicornis* is surveyed on the basis of the original description and the new material, and the neotenic nature of the form and the history of its spread are discussed. Furthermore, a new aberrant neotenic male form, found in the collections from two North American lakes, is described.

Introduction

In recent years I have examined an extensive material of the amphipod *Pontoporeia affinis* from fresh waters of North America, where the species is, as well known, a widespread and highly important component of the bottom fauna; for instance, in the Great Lakes. The purpose of this work has been to gain deeper insight into the phenomenon of summer-breeding observed earlier in some North American lakes (survey in SEGERSTRÅLE 1967) — normally the amphipod, one of the glacial relicts of North America and Eurasia, reproduces in winter.[1]

The collections concerned, sent to me from various North American institutes or received in connection with a visit to laboratories in the Great Lakes region in 1966, proved to contain numerous specimens of that form of the adult male of *P. affinis* which was described in 1937 as f. *brevicornis* (SEGERSTRÅLE 1937). This description was based partly on the data given in a paper of 1928 by F. B. ADAMSTONE and referring to five specimens caught in L. Nipigon (north of L. Superior), partly on my own examination of the same number of specimens from the latter lake.

The main characteristic in which the *brevicornis* form differs from the normal adult male is the much shorter flagella of the antennae (Figs. 3, 5). ADAMSTONE assumed that this divergence was due to the males in question not having yet reached the final developmental stage. However, in the

[1] The new observations of summer-breeding in lakes of North America will, it is hoped, be published in the near future.

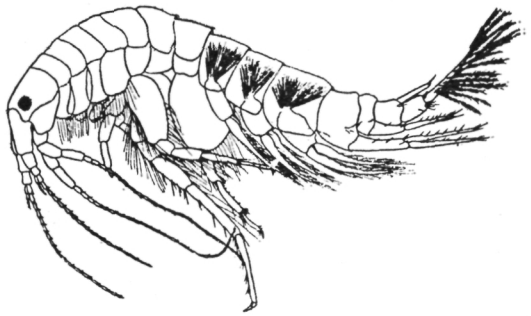


Fig. 1. Pontoporeia affinis, adult male of the type *brevicornis* from L. Nipigon, Canada. From ADAMSTONE's paper of 1928, where this form was assumed to be a younger stage of *P. filicornis* SMITH (cf. p. 5).

1937 paper, where details of the sexual differences and their development in *P. affinis* are described, I demonstrated that this view was wrong: the male form *brevicornis* is adult, but its morphology exhibits neotenic features, i.e., signs of inhibition of normal development. The most spectacular expression of this is the shortness of the antennae.

Examination of the new material of *P. affinis* received has considerably widened our knowledge of the distribution and morphology of f. *brevicornis*. Furthermore, collections from two lakes have proved to include an aberrant male form which has not been observed before. These new results are presented below, in the hope that they be of help to zoologists in North America, who have so far paid little attention to the *brevicornis* form, a fact that is probably due to the original description being included in a paper written in German and not easily available in America.

Before embarking upon a discussion of the subject of this paper, some comments are required which refer to the taxonomic status of the *Pontoporeia* inhabiting lakes of North America.

In 1874, S. I. SMITH described *Pontoporeia hoyi* on material from L. Superior and L. Michigan. This form was later generally regarded as conspecific with *P. affinis*, described in 1855 by G. LINDSTRÖM from specimens caught in the Baltic Sea (see, for instance, STEBBING 1906, EKMAN 1913, JUDAY and BIRGE 1927, BOUSFIELD 1958). However, the matter obviously needs reconsideration. This work has been started by Dr. E. L. BOUSFIELD of the National Museum of Natural History, Ottawa, Canada (pers. communic.). He is currently evaluating new morphological evidence that material of *Pontoporeia* from freshwater lakes of eastern North America is specifically distinct from material of *P. affinis* from the Baltic Sea and adjacent lakes (material from a Finnish lake). Resurrection of the name *hoyi* is a possible result of Dr. BOUSFIELD's study. In this context an ob-

servation made by me in connection with the present work deserves mention. Comparison of material from the two areas mentioned disclosed a fairly marked difference in the structure of pereipod 7 of the adult male, the *brevicornis* form included (the European material originates from the Baltic Sea and two adjacent lakes, L. Hiidenvesi in Finland and L. Madü-See in northern Germany; in the latter case the drawings given in EKMAN's paper of 1913 were used). As inspection of Figs. 12 A and 12 C will show, the North American adult male, in contrast to its counterpart from Northern Europe, exhibits a marked bend in the proximal part of the propodus, and the carpus is more or less club-shaped.[1]

The normal adult male of *P. affinis*, characterized by striking elongation of the antennae, will be referred to below as f. *filicornis*, under which name it was described as long ago as 1874 by SMITH (who accorded it specific status). In my paper of 1937 this form (and its European equivalent) was named f. *typica*.

A note on *P. kendalli*, described in 1909 from »Chamberlain Lake, Maine, river below the lock dam» by A. H. NORTON, should be added. NORTON regarded this form as a separate species. However, in my paper of 1937 I had already concluded that *P. kendalli* was identical with the normal male of the North American *P. affinis*. This view has been confirmed by examination of the type mount of *kendalli*, which was recently sent to me by Dr. BOUSFIELD. The structure of pereiopod 7 is the same as in *filicornis* (a correct drawing of this is given by NORTON, whereas SMITH obviously overlooked its marked modification), and the differences NORTON points to as regards the antennae and certain limbs have, on close examination of the mount, proved to be non-existent. For instance, the absence of dorsal bristles and calceoli on the flagella of the antennae stressed by NORTON does not fit with the facts, both being present. Also the locality of »*kendalli*» as given by NORTON, requires comment. Mr. M. J. DADSWELL, of the University of Carleton, Ottawa, who is working on the distribution of the glacial relict crustaceans in eastern North America, concludes, in a letter recently sent to me that the specimen treated by NORTON was not caught in Chamberlain Lake, as recent sampling there has not yielded any relicts. He assumes that the mount of »*kendalli*» was wrongly labelled and that NORTON's specimen may have been caught in L. Champlain (Vermont, south of Montreal), where *Pontoporeia* is known to live.

[1] Judging from the drawings of *P. affinis* ssp. *erythrophthalma*, described by K. D. WALDRON (1953) from L. Washington, the just-mentioned characteristics are also found in this form. (As a discussion of its taxonomic status will be included in BOUSFIELD's *Pontoporeia* paper, I shall confine myself to this comment.)

Distribution and morphology of the *brevicornis* male form of *Pontoporeia affinis*

Distribution

As will be remembered, the description of the *brevicornis* form of the adult male of *P. affinis* was based on material from L. Nipigon and L. Superior. Apart from these two lakes, *brevicornis* is only recorded from one other locality, viz. L. Cayuga, in the state of New York (GREEN 1965, 1968; det. by the present author; as regards HENSON's record of 1954, see p. 16). The new material of *P. affinis* from fresh waters of North America examined by me includes *brevicornis* males from the following four additional localities: Green Lake (west of L. Michigan), L. Michigan, L. Huron (including Georgian Bay), and L. Ontario (Fig. 2). As emerges from Table 1, in these lakes, *brevicornis* has been caught at all four seasons of the year. It is also seen that in most of the lakes concerned *brevicornis* lives side by side with the normal male form, f. *filicornis*, and that they may occur at the same season (cf. GREEN 1968). In some of the collections from L. Michigan the *brevicornis* form greatly outnumbers *filicornis;* the material of the former from this

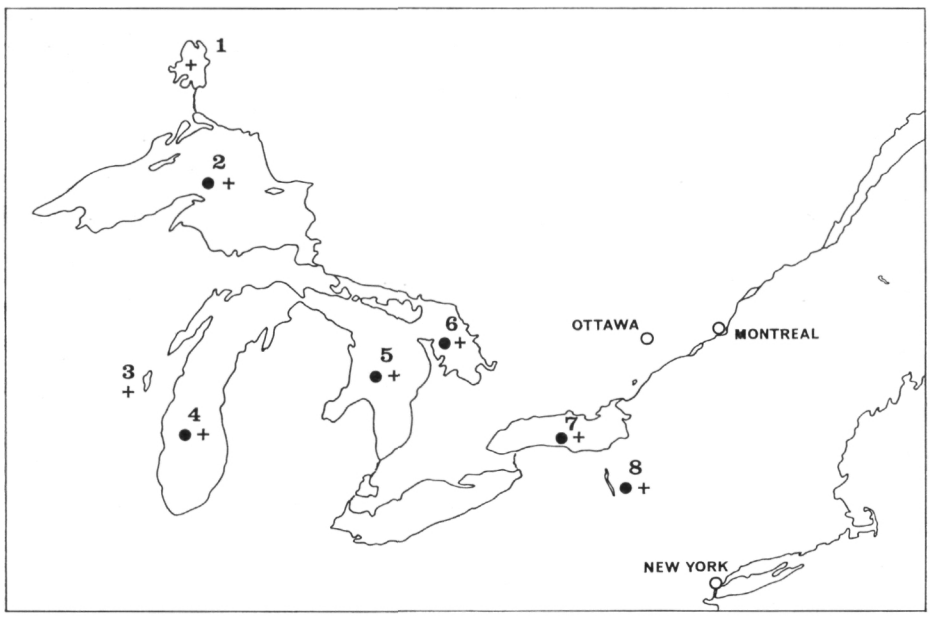


Fig. 2. Known distribution of the adult male form *brevicornis* (crosses) of *Pontoporeia affinis*. 1 L. Nipigon. 2 L. Superior. 3 Green Lake. 4 L. Michigan. 5 L. Huron. 6 Georgian Bay. 7 L. Ontario. 8 L. Cayuga. Dots: known presence of the normal male form, *filicornis*, in *brevicornis* lakes.

lake comprises about a hundred specimens. It seems likely that *brevicornis* may be frequent in other North American lakes, too. In many cases this form was caught with sledge or plankton nets, a fact that points to its having the same semi-pelagic nature as has earlier been found to be typical of the normal male of *P. affinis* (SEGERSTRÅLE 1937, MUNDIE 1959, WELLS 1960, 1969, MARZOLF 1965, MCNAUGHT and HASLER 1966).

Table 1. Observed occurrence and time of sampling of *Pontoporeia affinis* f. *brevicornis*. Occurrence of the normal male form, f. *filicornis*, in the same lakes also considered. Except for L. Nipigon, the data given are based on material examined by the author. + = f. *brevicornis*, ++ = f. *filicornis*.

Lake	Male form	Month	Remarks
Cayuga	+	VII, IX	Cf. also GREEN 1965, 1968
»	++	III, VIII, IX	
Green L.	+	VIII	
Huron	+	XII	
»	++	VI, XI	
» Georgian Bay	+	XI	
» » »	++	VI, VII	
Michigan	+	V–X	Cf. also SMITH 1874
»	++	V, IX	
Nipigon	+	»summer»	ADAMSTONE 1928
Ontario	+	II	
»	++	?	ADAMSTONE 1928
Superior	+	XII	Cf. also SEGERSTRÅLE 1937
»	++	VI, VII	

Morphology

As was already mentioned, the *brevicornis* male form of *Pontoporeia affinis* may be regarded as a neotenic form of the normal male, f. *filicornis*. Hence, for the understanding of the morphology of *brevicornis*, data on the development of the male of the species concerned are required. As elaborated in my 1937 paper on *P. affinis*, the strong modification of the adult male takes place in connection with the last moult. Figs. 3—4 and 6,7,12, which refer to North American material illustrate the main differences of the adult male of this species from the penultimate stage. The following comments should be made.

Antennae. Flagella: penultimate stage, length of second pair of antennae not surpassing about half the length of the body (Fig. 4); flagellar segments of two types, viz. long segments in the proximal part of the flagella and short ones distally; most of the long segments furnished with apical dorsal

bristles, whereas such bristles are generally lacking on the short segments and, if present, appear on a few alternating segments only (Figs. 7 B, C); in *filicornis*, flagella of the second pair of antennae surpassing posterior end of body (Fig. 3), flagellar segments gradually increasing in length toward tip of flagellum; dorsal bristles short and confined to alternating segments, lacking distally (Figs. 6 B, C); calceoli (ovate, semitransparent, stalked sense organs of amphipods, typical of the adult male) present on ventral side of flagellar segments. Peduncle: in *filiformis* strong reduction of setation, appearance of calceoli (Fig. 6 A).[1]

Pereiopod pair 7. In *filicornis*, over-all reduction of setation; instead, appearance of numerous short obtuse spines, peglets, along posterior margins of merus and carpus; propodus with marked proximal bend (Fig. 12 A); merus exhibiting particularly strong modification: striking reduction of setation, posterior edge with curved profile, pronounced postero-distal lobe, row of c. 15—20 peglets (Fig. 10 A).

Urosome segment 1. In *filicornis* this segment modified to form a deep dorsal depression (Fig. 11 A).

Uropod pair 3. In *filicornis*, rami and their apices furnished with numerous long feathery setae (length about 3/4 of ramus). Cf. Fig. 1.

Note on the development of the antennal flagella. For an understanding of the modification of the flagella, knowledge of the way in which their segments increase in number is essential. This process is elucidated in Fig. 15.

In the original description of *brevicornis* it was already pointed out that the antennae of this male form of *Pontoporeia affinis* essentially resemble the penultimate stage of the normal male and that this also applies to some details of the mouthparts. With respect to the dorsal depression of the first urosome segment, again, it was found that *brevicornis* occupies an intermediate position between the penultimate and final stages of the normal male. In addition, there is a third category of *brevicornis* characteristics, viz. such practically identical with the corresponding morphological features of the normal adult male. This applies, for example, to pereiopod pair 7 and uropod pair 3. Below, these various structural details of *brevicornis* are surveyed.

Antennae. As emerges from Figs. 7, 8, and 9, in *brevicornis* these appendages are very similar to the penultimate stage of the normal *affinis* male. The following differences may be noted: in peduncle segment 3 in both

[1] Some of the characteristics of the adult male, for instance, the elongation of the antennae and the appearance of long feathery setae on the third pair of uropods, are clear adaptations to its semi-pelagic mode of life which facilitates finding of the female (cf. SEGERSTRÅLE 1937).

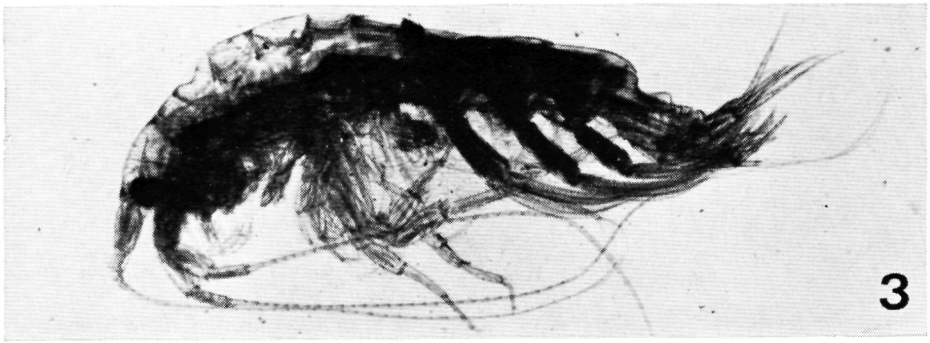
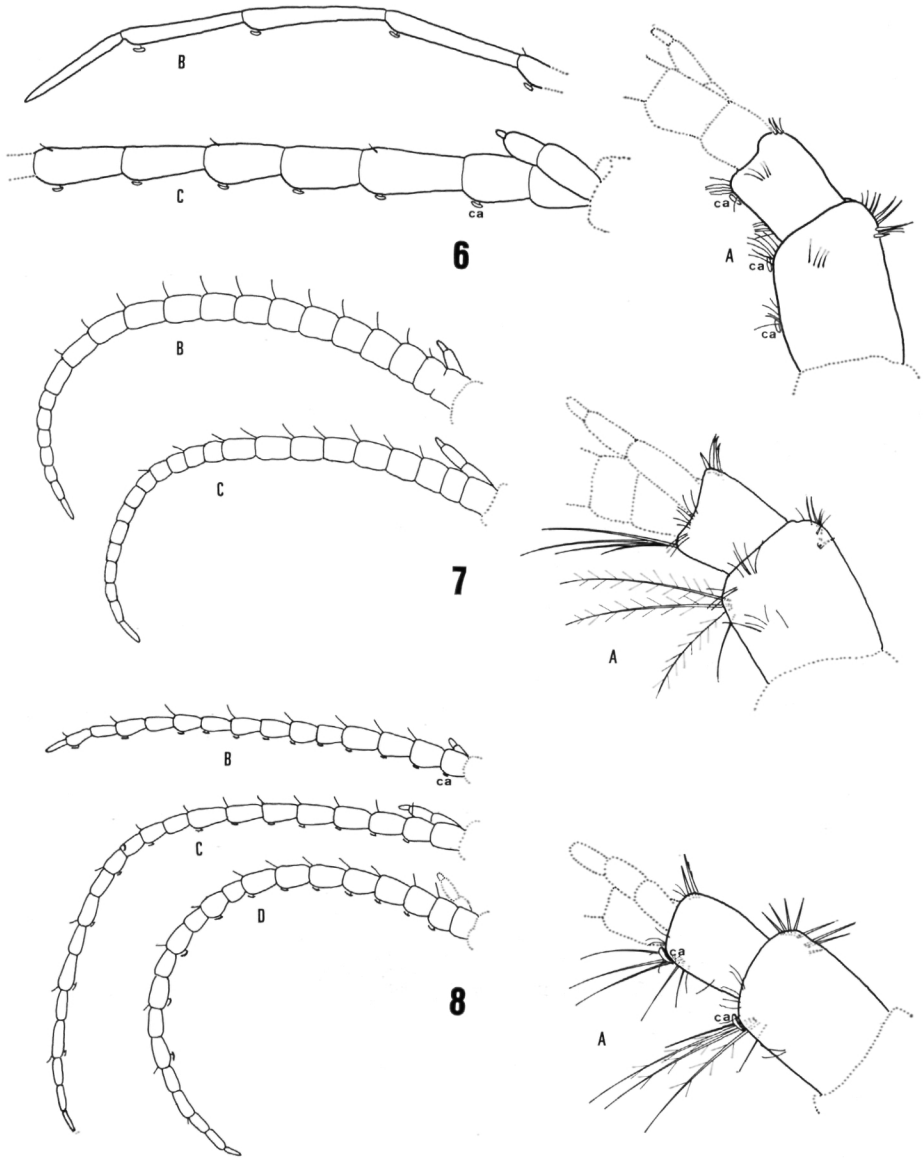


Fig. 3. Pontoporeia affinis, adult male of the normal type, *filicornis*: right antenna of the first pair removed (Charleston Lake, Canada).

Fig. 4. P. affinis, penultimate stage of the normal male (Devil Lake, Canada).

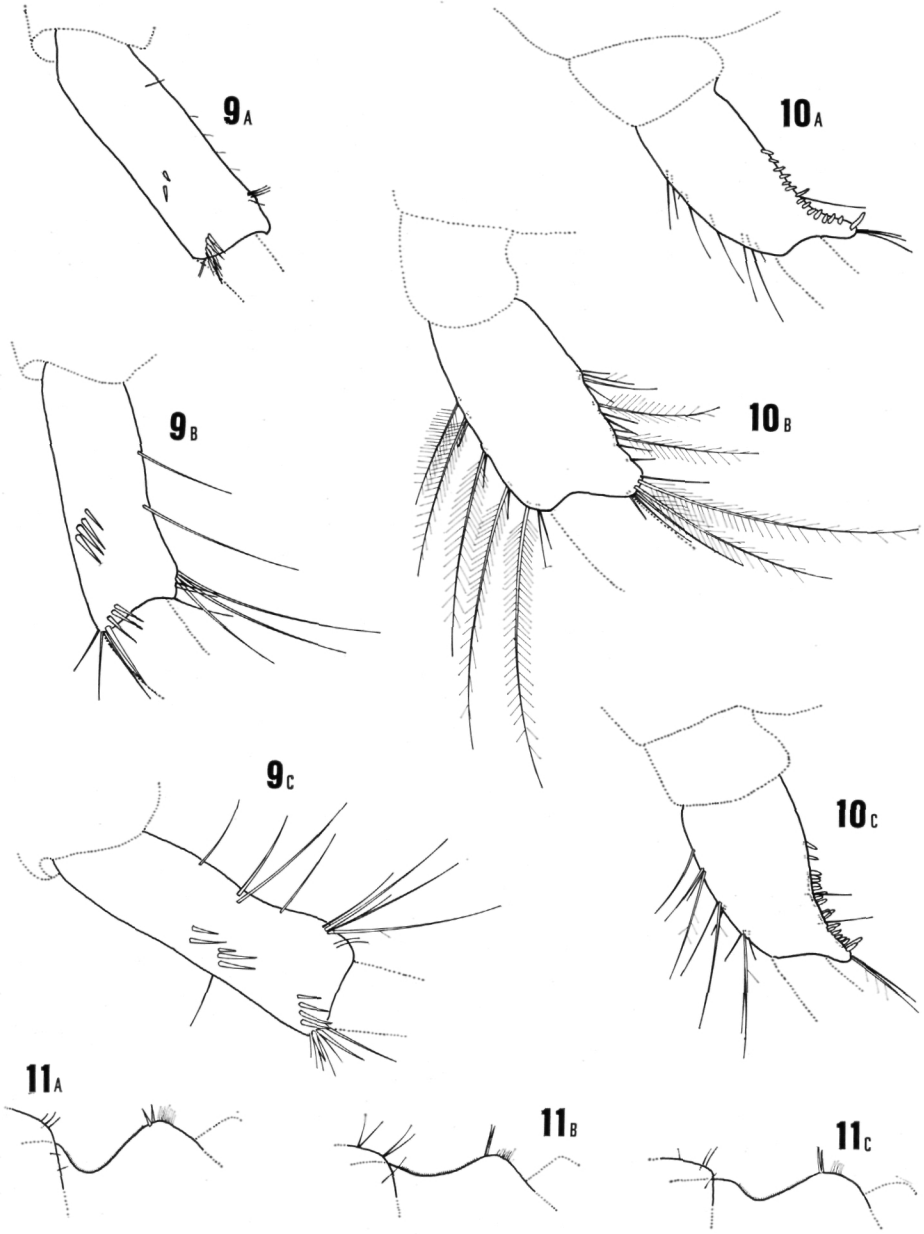
Fig. 5. P. affinis, adult male of the type *brevicornis* (last pereiopod deformed; L. Michigan).



Figs. 6 A—C. Antenna 1 of *Pontoporeia affinis* f. *filicornis*. *A*, peduncle segments 2 and 3 of left antenna (L. Michigan). *B*, proximal part of of right flagellum (L. Michigan). *C*, distal flagellar segments (L. Cayuga). ca = calceolus.

Fig. 7 A—C. Antenna 1 of *P. affinis* f. *filicornis*, penultimate stage. *A*, peduncle segments 2 and 3 of right antenna (Cayuga Lake). *B*, left flagellum (Georgian Bay). *C*, same (Cayuga Lake).

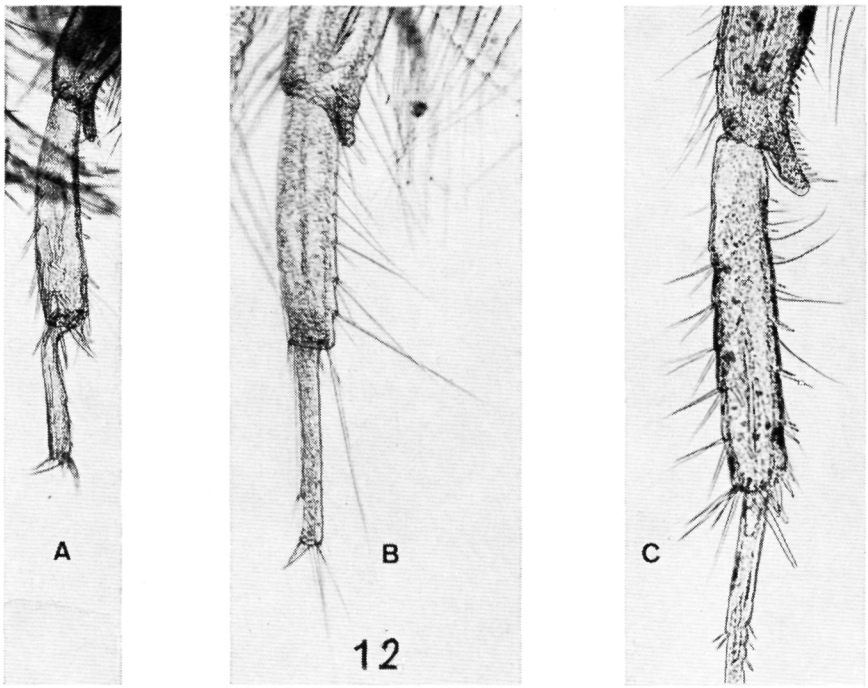
Figs 8 A—D. Antenna 1 of *P. affinis* f. *brevicornis*. *A*, peduncle segments 2 and 3 of right antenna (L. Michigan). *B*, left flagellum (L. Ontario). *C*, same (L. Michigan). *D*, same (L. Michigan).



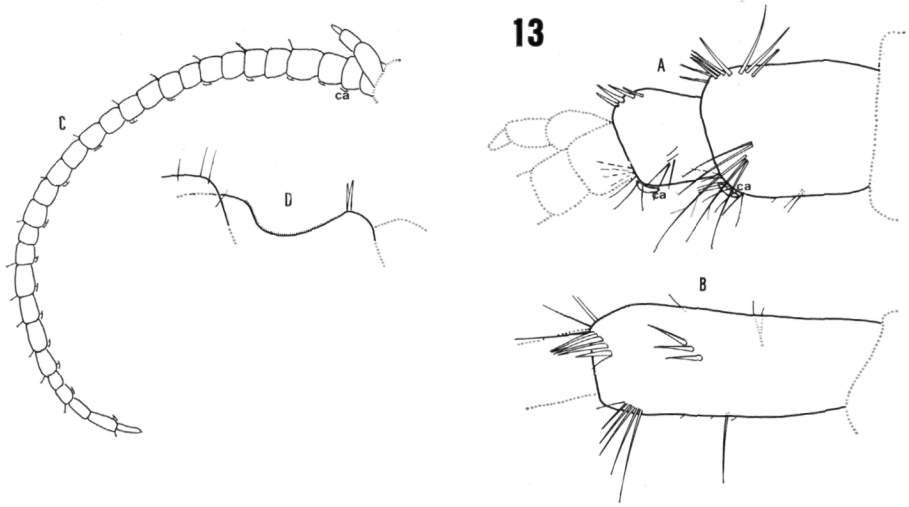
Figs. 9 A—C. Peduncle segment 3 of left antenna 2. *A*, *P. affinis* f. *filicornis* (L. Michigan). *B*, penultimate stage of *filicornis* (L. Michigan). *C*, *P. affinis* f. *brevicornis* (L. Michigan). In *A* and *C*, calceoli present on opposite (inner) side of segment.

Figs. 10 A—C. Merus of left pereiopod 7. *A*, *P. affinis* f. *filicornis* (L. Michigan). *B*, penultimate stage of *filicornis* (L. Michigan). *C*, *P. affinis* f. *brevicornis* (L. Michigan).

Figs. 11 A—C. Dorsal contour of urosome segment 1. *A*, *P. affinis* f. *filicornis* (L. Michigan). *B*, penultimate stage of *filicornis* (Devil Lake, Canada). *C*, *P. affinis* f. *brevicornis* (L. Michigan).



Figs. 12 A—C. Distal part of left pereiopod 7. *A*, *Pontoporeia affinis* f. *brevicornis* (L. Ontario). *B*, *P. affinis*, penultimate stage (Devil Lake, Canada). *C*, *P. affinis*, adult male (Baltic Sea).



Figs. 13 A—D. P. affinis f. *intermedia* n.f. from Great Bear Lake, Canada. *A*, left antenna 1, peduncle segments 2 and 3. *B*, peduncle segment 3 of left antenna 2; calceoli present on opposite (inner) side. *C*, flagellum of right antenna 1 (note the failure of segment splitting in 4 consecutive segments in the distal part of the flagellum: these segments are comparatively long and each furnished with dorsal bristles; cf. legend to Fig. 15). *D*, dorsal contour of urosome segment 1.

Fig. 14. Peduncle segment 3 of left antenna 2 of the male from Cauyga Lake which is considered identical with f. *intermedia* of *P. affinis*.

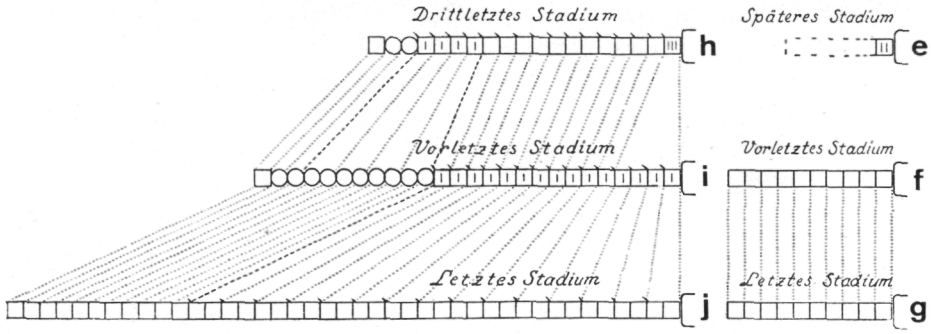


Fig. 15. Diagram showing the way in which the segments of the antennal flagella of *Pontoporeia affinis* increase in number. Female to the right, male to the left. After SEGERSTRÅLE 1937.

The initial, and in the female the only, mode of segment augmentation is the formation of new segments at the base of the flagellum (male: a, b, h; female: c—e). In the male, division of segments into two shorter ones sets in later on, beginning at the distal end of the flagellum (h; short segments indicated by rings). At the following moults this process affects an increasing number of segments (i—j). As a consequence, at the penultimate stage of the male (i) a considerable distal proportion of the flagellum consists of short segments. (Of the two segments resulting from the splitting of a long one, the distal segment is normally somewhat longer and wider than the proximal one. Partial failure of the splitting process is sometimes observed, as indicated by the presence of long segments between short ones; cf. Fig. 13 C. It may also happen that the right and left flagellum of a pair of antennae exhibit a somewhat different number of short and long segments, a feature which may result in a different total segment number. In connection with the last moult of the male the splitting process reaches the very base of the flagellum (j), causing a sudden increase in the segment number. (Another factor accounting for the striking elongation of the flagellum of the adult male is the marked stretching of the individual segments, especially distally; cf. Fig. 6 B.)

The splitting process also affects the setation pattern of the flagella of the male. Each of the original segments (exceptions: first segment in antennae 1 and, at times, segments 1—2 in antennae 2, as well as the last long segment, cf. Fig. 7 B) also bear dorsal bristles. When the splitting commences, these bristles disappear or are confined to the proximal part of the series of short segments (cf. Figs. 7 B, C). By contrast, at the last moult of the male the dorsal bristles of all the remaining long segments then split are retained, but appear on alternating segments only, the bristles concerned being taken over by the distal segments in the pairs of divided ones (if at earlier stages dorsal bristles occur on short segments, the same alternation is observed; cf. Fig. 7 C). Another characteristic of the dorsal bristles of the adult male is their shortness (cf. Fig. 6 C).

pairs of antennae, apical setae on under side somewhat shorter in *brevicornis;* flagella, alternating dorsal bristles in this form more numerous, at times reaching tip of flagellum; presence of calceoli in *brevicornis.*

Range of flagellar segments observed in *brevicornis*: first antennae, 13—26; second antennae, 18—30. For *filicornis*, in the material examined, the corresponding figures are 29—40 and 45—63, respectively. If one applies to *brevicornis* the same calculation of the final numbers of flagellar segments on the basis of the numbers of long and short segments present as applied to the penultimate stage of the normal *affinis* male (each of the long segments corresponding to two future ones, cf. Fig. 15), it emerges that *brevicornis* is a stunted equivalent of the penultimate stage of the former, the sum of »potential» segments being clearly lower: in the examined material of *brevicornis* this sum amounted to not more than 21—32 for the first pair of antennae and 25—37 for the second. The proportion of long to short segments may vary considerably in *brevicornis*, the extremes observed in the second pair of antennae being 2 long + 21 short segments and 13 long + 10 short ones, respectively.

Mouthparts. In *brevicornis*, as in the penultimate stage of the normal *P. affinis* male, the incisor process of the mandible is comparatively strongly developed. Palp: among the setae along the inner side of the last segment, some are of the comb-like type; in *filiformis* such setae are lacking.[1]

Pereiopod pair 7. In the main, *brevicornis* exhibits the same modification as *filiformis.* In the merus (Fig. 10 C), the differences are practically confined to less pronounced shortening of setae in *brevicornis* and retention of the feathery structure of some of them.

Urosome segment 1. In the deepness of the dorsal depression, *brevicornis* occupies an intermediate position between the penultimate stage of the normal *affinis* male and its final stage, f. *filiformis*, where this characteristic is strongly developed; the neighbouring setae also are also of intermediate length in *brevicornis* (Figs. 11 A—C).

Uropod pair 3. The *brevicornis* male exhibits the same conspicuous modification as the *filiformis* type (appearance of numerous long feathery setae).

Size. In the collections examined in connection with the present study, the males of the *brevicornis* type are clearly smaller than the *filicornis* males, the body length (measured from tip of rostrum to base of telson) averaging c. 6.5 mm in *brevicornis* against c. 7.5 in *filicornis*; observed range: 5—8.5 mm in *brevicornis*, 6—9 in *filicornis.*

---

[1] As I have already pointed out (SEGERSTRÅLE 1937), the description of the mouthparts given by ADAMSTONE for his »*filicornis*» (= *brevicornis*) is not correct.

A new aberrant male form of *Pontoporeia affinis* from North American lakes

The material of *P. affinis* examined includes a collection from Great Bear Lake in northern Canada, sampled in 1963—1965 by the Arctic Biological Station, Fisheries Board of Canada, Montreal. Among the 32 vials concerned, one proved to contain an adult male of the species which differs from both the *filicornis* and the *brevicornis* type. The most striking feature of the specimen, which has a body length of 8 mm and was caught on August 17, 1965, at 30 m depth, relates to the antennae. These appendages are clearly longer than in *brevicornis*, the second pair reaching about 2/3 of the body length. On the other hand, they are unexpectedly short in comparison with *filicornis*, as the number of flagellar segments fall within the range of this form: the first pair of antennae contain 29 and the second pair about 50 such segments (the distal parts of the latter antennae were lost in connection with the mounting work, before exact counting). The lesser length of the flagella is thus caused by the shortness of their segments as compared with *filicornis*; in this respect they resemble *brevicornis*. The male under discussion is clearly adult (calceoli present on the antennae, typical modification of pereiopod pair 7 and uropod pair 3). Below, details of its morphology are given.

Antennae. Peduncles (Figs. 13 A, B): length of setae on under side of segments 2 and 3 of first antennae and segment 3 of second intermediate between *brevicornis* and *filicornis*; in their feathery structure some setae on segment 2 of the first pair of antennae resemble those of the former type of male. Flagella (Fig. 13 C): as in *brevicornis*, both pairs of antennae exhibit long (not divided) and short segments; however, the number of segments of the former type is low (4 in both pairs of antennae). As in *brevicornis*, alternating dorsal bristles on short segments, reaching the very tip of the flagella.

Pereiopod pair 7. Merus of the same modified type as in *brevicornis* and *filicornis;* peglets along posterior edge comparatively few (15). Proximal part of propodus bent as in both above-mentioned forms.

Urosome segment 1. Dorsal depression of the *brevicornis* type (Fig. 13 D).

Uropod pair 3. Presence of long feathery setae as in *filicornis* and *brevicornis*.

As emerges from the above data, the male from Great Bear Lake differs from the *brevicornis* type described on the foregoing pages in having clearly longer antennae, a much higher number of flagellar segments and a setation on the peduncles of both pairs of antennae which is intermediate between that of *brevicornis* and *filicornis*. Hence, I find it best to regard it as a

form of its own. As a name for the new form f. *intermedia* is proposed. As will be seen below, it seems not to be restricted to Great Bear Lake.

In 1954, E. B. HENSON reported a male specimen of *P. affinis* from L. Cayuga which had 29 segments in the flagella of the first pair of antennae and 43—45 on those of the second pair. In spite of these large numbers of segments, the second pair of antennae did not reach more than about 60% of the body length. The specimen was sent to the present author, who determined it as f. *brevicornis* on account of the shortness of the antennae as compared with *filicornis*.[1]

The disclosure of the aberrant male from Great Bear Lake prompted re-examination of Henson's male from L. Cayuga. This specimen is still available in the collections of the present author and there is a mount of the second pair of antennae, pereiopod pair 7 and uropod pair 3. Close examination of this material has revealed the following facts: the peduncle of the second pair of antennae represents the same intermediate stage as f. *intermedia* (Fig. 14); as in this form the flagella comprise only a few long segments (6); pereiopod pair 7 is of the adult type, the number of peglets being comparatively low (13) as in the form *intermedia;* the depression of the first urosome segment is intermediate and the third pair of uropods are of the adult type.

In view of these similarities between f. *intermedia* from Great Bear Lake and Henson's male from Cayuga, I regard the latter as belonging to f. *intermedia*.

Discussion

In my paper of 1937 attention was drawn to the fact that in the Eurasian *Pontoporeia affinis* no examples of the tendency towards neoteny observed in North American populations was known. This difference also holds good today and is even more accentuated by the disclosure of a new neotenic male form the latter area, in addition to f. *brevicornis*.

It is of interest that signs of inhibition of normal development have also been observed in other crustaceans belonging to the group of glacial relicts. An example is the amphipod *Gammaracanthus relictus* (today regarded as a species of its own, cf. LOMAKINA 1952), a relict of European lakes. In this relict, the third epimeral plates are more or less square in

[1] Some points in HENSON's article of 1954 call for comment. When he (p. 579) says that »In a revision of the genus [*Pontoporeia*] (SEGERSTRÅLE 1937) it was pointed out that *filicornis* was identical to the penultimate stage of the normal male of *P. affinis*» it ought to have been stressed that the *filicornis* mentioned in this connection was that meant by ADAMSTONE (= *brevicornis*) and not SMITH's *filicornis*.

shape and thus resemble the not fullgrown stage of the ancestral form, *G. loricatus*, which lives in the Arctic Sea: in the fully developed *loricatus* the postero-ventral angle of the plates concerned is acutely produced (EKMAN 1919, LOMAKINA 1952). A further example is provided by the relict amphipod *Pallasea quadrispinosa*, a freshwater species, apparently derived from the closely related *P. kessleri* of the Baikal region in eastern Siberia (SEGERSTRÅLE 1957). A large, lake-like spring in southern Finland has proved to harbour a populations of *P. quadrispinosa* which exhibits marked morphological reduction, the dorsal spines of the two abdominal segments, characteristic of the full-grown stage, being stunted or missing (SEGERSTRÅLE 1958).

As was earlier mentioned, in several lakes the male forms *filicornis* and *brevicornis* of *P. affinis* are found living side by side. The presence of f. *intermedia* in L. Cayuga shows that all three male forms known today may even occur in the same lake. As regards the prehistory of *brevicornis*, a form whose range has proved to comprise a wide area in North America, some comments may be made. Two alternatives are to be reckoned with: (1) either this male form has developed independently in each of the lakes inhabited, or (2) it has spread from a common centre. In view of the marked morphological uniformity of the form concerned over its whole range and the special conditions for dispersal prevailing during the melting phases of the last glaciation, the latter alternative seems more likely. If one considers the extension of the ice-dammed (proglacial) lakes which existed successively in North America during that time (cf. FLINT 1957, p. 345), as well as topographical facts, one is led to the conclusion that the *brevicornis* male form may have evolved in the region of L. Superior, including L. Nipigon, from which centre it was then able to spread over the Great Lakes region, and even to L. Cayuga (cf. GREEN 1965, p. 7: »Evidence indicates that Cayuga has existed as a separate lake three times and was the last of the Finger Lakes to be connected to the large proglacial lake when the ice retreated»).

The morphological variability of the North American *P. affinis* disclosed so far refers to the strongly modified adult male. As far as the female is concerned, no differentiation is known. In view of the fact that the mature female exhibits practicaly no modification, except the appearance of the brood-plates, splitting into different forms is hardly to be expected. Restriction of morphological divergences to the male only is not a unique phenomenon. An example is provided by the isopod *Jaera albifrons* (*J. marina*). As is well known, this crustacean comprises a group of subspecies or species which are recognizable in the males only, on the basis of the secondary sexual characteristics (see, for instance, NAYLOR et al. 1961, NAYLOR and HAAHTELA 1966).

Acknowledgements. The author wishes to express his thanks to the following North American colleagues, who put at his disposal the new material of *Pontoporeia affinis* on which the present paper is based: Drs. W. P. ALLEY and D. C. CHANDLER, Great Lakes Research Division, University of Michigan, Ann Arbor; Dr. E. L. BOUSFIELD, National Museum of Natural History, Ottawa; Dr. TH. E. BOWMAN, Division of Marine Invertebrates, Smithsonian Institution, Washington, D.C.; Prof. R. O. BRINKHURST, Department of Zoology, University of Toronto; Dr. R. H. GREEN, Department of Zoology, University of Manitoba, Winnipeg; Dr. J. HILTUNEN, Bureau of Commercial Fisheries, Ann Arbor, Michigan; Dr. L. JOHNSON, (by the time of sending material working at) Arctic Biological Station, Fisheries Research Board of Canada, Montreal; Dr. G. R. MARZOLF, Department of Zoology, Kansas State University. Mrs. JEAN MARGARET PERTTUNEN, B. Sc. Hons., has checked the English text, for which also sincere thanks are expressed.

The present work was supported by a grant awarded by Helsinki University.

References

ADAMSTONE, F. B. 1928: Relict amphipods of the genus *Pontoporeia*. *Trans. Amer. Microsc. Soc.* 47, 366–368.

BOUSFIELD, E. L. 1958: Fresh-water amphipod crustaceans of glaciated North America. *Canad. Field-Nat.* 72, No. 2, 55–113.

EKMAN, S. 1913: Zwei neue europäische Arten der Amphipodengattung *Pontoporeia* Kröyer. *Ark. Zool.* 8 (8), 12 pp.

—»— 1919: Studien über die marinen Relikte der nordeuropäischen Binnengewässer. VI. Die morphologischen Folgen des Reliktwerdens. *Intern. Rev. Hydrobiol. Hydrogr.* 8, 477–528.

FLINT, R. F. 1957: Glacial and Pleistocene geology. New York.

GREEN, R. H. 1965: The population ecology of the glacial relict amphipod *Pontoporeia affinis* Lindstrom in Cayuga Lake, New York. Doctoral thesis (Cornell University), 116 pp.

—»— 1968: A summer-breeding population of the relict amphipod *Pontoporeia affinis* Lindström. *Oikos* 19, 191–197.

HENSON, E. B. 1954: *Pontoporeia affinis* var. *brevicornis* in Cayuga Lake, N.Y. *Ecol.* 35, 579.

JUDAY, CH. & E. A. BIRGE 1927: *Pontoporeia* and *Mysis* in Wisconsin lakes. *Ecol.* 8, 445–452.

LINDSTRÖM, G. 1855: Bidrag till kännedomen om Östersjöns invertebrat-fauna. *Öfv. Kgl. Vet. Ak. Förh.*, årg. 12, 49–73.

LOMAKINA, N. B. 1952: Proizhozhdenie lednikovyh reliktovyh amfipod v svjazi s voprosom o pozdneledni kovom belomorsko-baltiiskom soedinenii. *Uchenye Zapiski Karelo-Finskovo Universiteta, Biologicheskie Nauki* 4, 110–127. (Translation by W. E. Ricker: The origin of glacial relict amphipods in relation to the question of the post-glacial connection between the White Sea and the Baltic; distributed by The Fish. Res. Bd. of Canada, Arctic Unit, Montreal, Translation Ser. No. 390.)

MARZOLF, G. R. 1965: Vertical migration of *Pontoporeia affinis* (Amphipoda) in Lake Michigan. *Univers. Mich., Great Lakes Res. Div.*, Publ. No. 13, 133–140.

MCNAUGHT, D. C. & A. D. HASLER 1966: Photoenvironments of planktonic Crustacea in Lake Michigan. *Verh. Internat. Verein. Limnol.* 16, 194–203.

MUNDIE, J. H. 1959: The diurnal activity of the larger invertebrates at the surface of Lac La Ronge, Saskatchewan. *Can. J. Zool.* 37, 945–956.

NAYLOR, E. & I. HAAHTELA 1966: Habitat preferences and interspersion of species within the superspecies *Jaera albifrons* Leach (Crustacea:Isopoda). *J. Anim. Ecol.* 35, 209–216.

NAYLOR, E., D. J. SLINN & G. M. SPOONER 1961: Observations on the British species of *Jaera* (Isopoda: Asellota). *J. mar. biol. Ass. U. K.* 41, 817–828.

NORTON, A. H. 1909: Some aquatic and terrestrial crustaceans of the state of Maine. *Proc. Portland Soc. Nat. Hist.* 2, 245–255.

SEGERSTRÅLE, S. G. 1937: Studien über die Bodentierwelt in südfinnländischen Küstengewässern. III. Zur Morphologie und Biologie des Amphipoden *Pontoporeia affinis*, nebst einer Revision der *Pontoporeia*-Systematik. *Commentat. Biol.* (Soc. Sci. Fenn.) 7 (1), 183 pp.

—»— 1957: On the immigration of the glacial relicts of Northern Europe, with remarks on their prehistory. *Ibid.* 16 (16), 117 pp.

—»— 1958: On an isolated Finnish population of the relict amphipod *Pallasea quadrispinosa* G. O. Sars, exhibiting striking morphological reduction, with remarks on other cases of morphological reduction in the the species. *Ibid.* 17 (5), 33 pp.

—»— 1967: Observations of summer-breeding in populations of the glacial relict *Pontoporeia affinis* Lindström (Crustacea Amphipoda), living at greater depths in the Baltic Sea, with notes on the reproduction of *P. femorata* Kröyer. *J. exp. mar. Biol. Ecol.* 1, 55–64.

SMITH, S. I. 1874: Crustacea of the fresh waters of the United States. *Rep. U. S. Commissioner Fish and Fisheries*, Part 2 for 1872–73, 637–665.

STEBBING, T. R. R. 1906: Amphipoda. I. Gammaridea. *Das Tierreich* 21.

WALDRON, K. D. 1953: A new subspecies of *Pontoporeia affinis* in Lake Washington, with a discussion of its morphology and life cycle. (Mimeo., University of Washington), 78 pp.

WELLS, L. 1960: Seasonal abundance and vertical movements of planktonic Crustacea in Lake Michigan. *U. S. Dept. Int., Fish Wildlife Serv., Bureau of Commerc. Fish., Fish. Bull.* 172, from *Fish. Bull. Fish Wildlife Serv.* 60, 342–369.

—»— 1969: Daytime distribution of *Pontoporeia affinis* off bottom in Lake Michigan. *Limn. Oceanogr.* 13, 703–705.

Address of the author:
Institute of Marine Research,
Biological Division,
Bulevarden 9 A,
Helsinki/Helsingfors, Finland

Communicated November 16, 1970
Printed February 1971

Keskuskirjapaino—Centraltryckeriet
Helsinki—Helsingfors