

Chromosome numbers of Fennoscandian glacial relict Crustacea

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Chromosome numbers and karyological characteristics were examined during spermatogenesis in *Saduria entomon* ($n=30$), *Mysis relicta* ($n=52$), *Pontoporeia femorata* ($n=14$) and *P. affinis* ($n=26$) from the northern Baltic Sea, and in *Mysis relicta* ($n=52$), *Pallasea* (*Pallasiola*) *quadrspinosa* ($n=26$) and *Gammaracanthus lacustris* ($n=19$) from Lake Pääjärvi, southern Finland. The chromosomes of the postglacial immigrants *Gammarus lacustris* and *G. pulex* were also recorded ($n=26$). These observations suggest karyological differentiation of the originally subarctic marine amphipods *Pontoporeia femorata* and *Gammaracanthus lacustris* from *Pontoporeia affinis*, *Pallasea quadrspinosa* and *Gammarus* spp. evolved in Palearctic freshwater bodies.

1. Introduction

The glacial relict macrocrustaceans are a phylogenetically heterogeneous group, belonging to the peracaridan orders Isopoda, Amphipoda and Mysidacea. Our knowledge of peracaridan karyology is scanty compared to that of the higher decapods with their exceptionally high and variable chromosome numbers ($n=42$ –188) (Niiyama 1959). The review by Hedgecock et al. (1982) gives the chromosome numbers of 33 species of Amphipoda and 44 species of Isopoda. Information on chromosome numbers in Mysidacea is based mostly on Holmquist's (1959, 1973, 1975) investigations.

In the present study the chromosomal relationships of glacial relict crustaceans inhabiting Fennoscandian lakes and the northern Baltic Sea are reviewed to elucidate the role of karyological techniques in crustacean phylogenetic research.

2. Material and methods

Crustaceans for the present investigations were collected before their breeding season in the autumn from the northern Baltic Sea in the Tvärminne archipelago and from the deep oligotrophic Lake Pääjärvi in southern Finland. In addition, freshwater *Gammarus* populations were studied

in smaller ponds at Oulanka and Kevo in northern Finland and eutrophic Lake Ormajärvi near the village of Lammi. Conventional dredging methods and vertical nets were used in sampling. The glacial relict populations investigated, together with their characteristic habitats, are indicated in Table 1.

Testicular tissues were dissected and washed in cold distilled water for hypotony and fixed in 1:3 acetoethanol. The gonads were then stained in propionic or acetic orcein for 1–3 h, squashed in 45% acetic acid under coverslips, and mounted in glycerin. In *Pontoporeia* the Giemsa stained air-drying technique (Salemaa 1979) was also applied.

The chromosome counts were carried out from the synchronously dividing cysts of spermatocytes. In addition to the first meiotic division, gonimiotosis and the second meiotic division were also investigated when available. Several metaphase plates were investigated in each species.

3. Results and discussion

The chromosomes of the north-European glacial relict crustaceans illustrate three main principles of peracaridan karyology:

1. *Mysis relicta* (Fig. 1I) with its high haploid number and small and compact bivalents has a karyotype resembling that of decapods. The same chromosome number ($n=52$) was found in both

the lake and the brackish water populations examined. Our observations also agree with Holmquist's (1959) findings of approximately 100 mitotic chromosomes in several *Mysis* populations.

Although chromosome numbers as low as $n=16$ in *Anchialina agilis* and $n=24$ – 34 in *Neomysis integer* have been reported, the larger species like *Mysis mixta*, *M. littoralis* and *Praunus* spp. closely resemble *M. relicta* in their chromosome size and number (Holmquist 1959, Salemaa 1986).

2. The chromosome numbers of *Saduria entomon* ($n=30$), *P. quadrispinosa* (Fig. 1C) and *Gammarus* spp. (Fig. 1G, H) ($n=26$) correspond to the modal numbers established earlier for Isopoda ($n=29$ in Idoteidae) and Amphipoda ($n=26$ in Gammaridae) (Hedgecock et al. 1982). Again, *Pallasea quadrispinosa*, which has endemic Baikalian progenitors in Siberia, has an identical chromosome number ($n=26$) to those of the European gammarids of freshwater origin examined.

3. Earlier reports on the chromosomes of Amphipoda emphasize the low rate of karyological differentiation of these crustaceans (e.g. Orian and Callan 1957, Salemaa 1984a). However, recent observations of exceptional chromosome numbers in the species *Pontoporeia femorata* (Fig. 1A, B) ($n=14$), *Gammaracanthus lacustris* ($n=19$) (Fig. 1D–F) and in the endemic *Gammarus* species inhabiting the ancient Macedonian lake Ohrid (Salemaa 1984b, 1985, 1986), suggest

Table 1. Haploid chromosome numbers (n) of the species of glacial relict Crustacea. Sampling sites and characteristic habitats.

Species	Sampling site and habitat	n
Mysidacea		
<i>Mysis relicta</i> Lovén	Tvärminne and Pääjärvi, pelagial	52
Isopoda		
<i>Saduria entomon</i> L.	Tvärminne, soft mud bottom	30
Amphipoda		
<i>Gammaracanthus lacustris</i> G. O. Sars	Pääjärvi, profundal	19
<i>Gammarus lacustris</i> G. O. Sars	Oulanka and Kevo, ponds	26
<i>Gammarus pulex</i> (L.)	Ormajärvi, littoral vegetation	26
<i>Pallasea (Pallasiola) quadrispinosa</i> G. O. Sars	Pääjärvi, profundal	26
<i>Pontoporeia affinis</i> Lindström	Tvärminne, soft mud bottom	26
<i>Pontoporeia femorata</i> Kroyer	Tvärminne, soft mud bottom	14

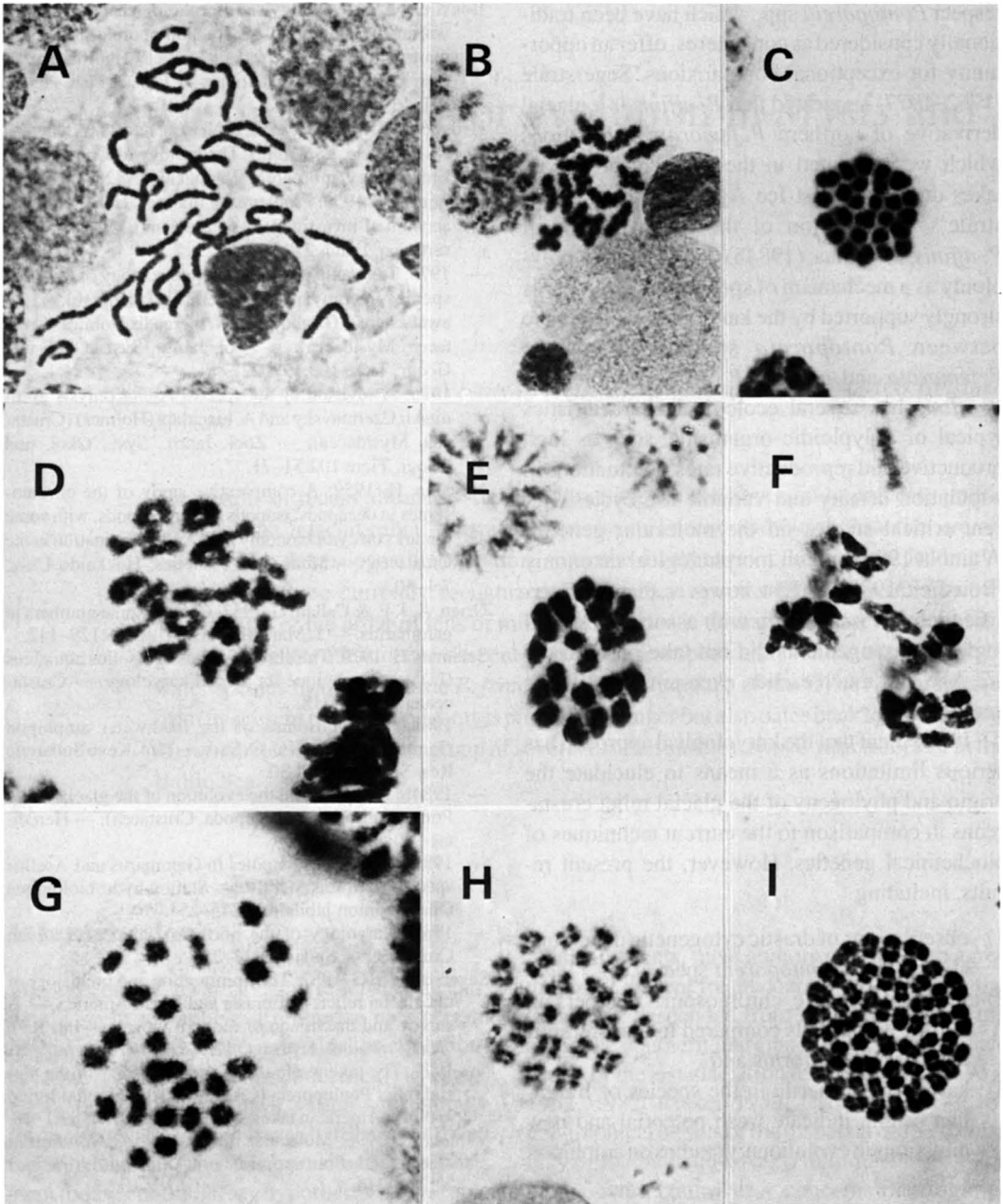


Fig. 1. Chromosomes of the glacial relict Crustacea. *Pontoporeia femorata*: late goniomitotic prophase, $2n=28$ (A), diakinesis, $n=14$ (B). *Pallasea (Pallasiola) quadrispinosa*: I meiotic metaphase, $n=26$ (C). *Gammaracanthus lacustris*: diakinesis, $n=19$ (D), I meiotic metaphase, $n=19$ (E), I meiotic anaphase with heterokinetic pair of chromosomes (F). *Gammarus pulex*: I meiotic metaphase, $n=26$ (G), II meiotic metaphase, $n=26$ (H). *Mysis relicta*: I meiotic metaphase, $n=52$ (I).

that substantial chromosomal rearrangements occasionally take place in Amphipoda too. In this respect *Pontoporeia* spp., which have been traditionally considered as congeners, offer an opportunity for exceptional comparisons. Segerstråle (1962, 1977) suggested that *P. affinis* is a glacial derivative of northern *P. femorata* populations which were isolated in the Siberian proglacial lakes during the last Ice Age. Adopting Segerstråle's presumption of the recent origin of *P. affinis*, Salemaa (1984b) hypothesized polyploidy as a mechanism of speciation. This view is strongly supported by the karyological difference between *Pontoporeia* species ($2n=28$ in *P. femorata* and $n=52$ in *P. affinis*). Moreover, *P. affinis* has several ecological characteristics typical of polyploidic organisms, such as high productive and reproductive rates, fluctuations in population density and variable life cycles. Recent critical studies on the molecular genetics (Väinölä 1990) and on morphological taxonomy (Bousfield 1989) suggest, however, that the diversification in *Pontoporeia* with associated karyological rearrangements did not take place in the Ice Age, but much earlier, even tens of millions years ago.

It is evident that the karyological approach has serious limitations as a means to elucidate the origin and phylogeny of the glacial relict crustaceans in comparison to the current techniques of biochemical genetics. However, the present results, including

- 1) observations of drastic cytogenetic differentiation among *Pontoporeia* species,
- 2) low and variable chromosome numbers in marine amphipods compared to undifferentiated freshwater forms and
- 3) karyological inertia in the species of Baikalian origin, indicate fresh potential and new directions in evolutionary studies on amphipod Crustacea.

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