BIOCHEMICAL SYSTEMATIC RELATIONSHIPS AMONG THE FRESHWATER AMPHIPODS GAMMARUS VARSOVIENSIS, G. LACUSTRIS AND G. PULEX

BY

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ABSTRACT

The systematic position of the freshwater amphipod G. varsoviensis Jazdzewski from northern Poland and Germany, split off recently from G. lacustris Sars in the same area, was assessed by allozyme electrophoresis. A distant evolutionary relationship between the two species was indicated, similar to that between them and G. pulex (L.), and to those earlier recorded between marine and freshwater Gammarus spp. (genetic identities I = 0.1-0.2). The neutral terms currently used for subdivisions of the genus, such as the G. pulex group which includes the three species studied, refer to units too ancient to have retained traces of a common ancestry at the allozyme level; adoption of subdivisions based on phylogenetically closer, genetically identifiable relationships is suggested.

INTRODUCTION

The distribution of the freshwater amphipod Gammarus lacustris G. O. Sars, 1863, comprises much of the northern holarctic region and of central Asia (e.g., Schellenberg, 1937). Despite the unusually wide range and considerable morphological variability, the species is currently regarded as monotypic in Eurasia (Segerstråle, 1954; Pinkster, 1972; Jazdzewski, 1975; Karaman & Pinkster, 1977; Barnard & Barnard, 1983). Yet, while dismissing any former suggestions of taxonomic subdivision, Jazdzewski (1975) split off from G. lacustris a new species, G. varsoviensis, with a restricted distribution centered in Poland and largely overlapping that of G. lacustris in the area.
Karaman & Pinkster (1977) treat *G. lacustris* and *G. varsoviensis* as members of the *G. pulex* group, one of three morphologically delineated, conventional infrageneric divisions of freshwater *Gammarus* spp. Until the 1930s, *G. lacustris* was actually often confused with *G. pulex* (L., 1758), the other main freshwater *Gammarus* species indigenous in northern continental Europe. *G. pulex* itself has been subject to extensive taxonomic subdivision in western Europe (see Scheepmaker, 1990). The systematics of this group (excluding *G. lacustris*) even in this well-studied area, are far from clear, however. Crossbreeding experiments often give results inconsistent with morphological taxonomic criteria (e.g., Goedmakers, 1972; Pinkster, 1983; Scheepmaker, 1990). Moreover, allozyme studies have revealed strongly differentiated lineages, whose distributions may be related to zoogeographical history, but not always to the conventional species boundaries defined by morphology or interbreeding ability (Scheepmaker, 1990).

Comparable levels of genetic differentiation have recently been found within the Fennoscandian *Gammarus lacustris*, which suggests a complicated zoogeographical history and systematic substructuring also for this taxon (Vainio & Väinölä, in prep.). The relationship of *G. varsoviensis* to this new diversity is unclear. Thus, considering the new data on biochemical systematics of both *G. lacustris* and species closely allied with *G. pulex*, and the general criticisms on the value of morphological characters in gammarid taxonomy (Pinkster, 1983, 1988), we found it of interest to examine the status of *G. varsoviensis* by the allozyme method, through assessing its affinities with *G. lacustris* and *G. pulex* from the same area.

**MATERIAL AND METHODS**

**Species and samples**

The habitat of *Gammarus varsoviensis* in central and northern Poland involves both stagnant and running waters. A majority of the records are from the middle Vistula river system, linked to other localities through canals connecting neighbouring drainage basins (Notec in Poland, Neman and Pripet in Belarus, Spree and Elbe in Germany) (Jaźdżewski, 1975). An important role of the canal connections in the recent dispersal history of the species has been proposed (Jaźdżewski, 1980).

The main distribution of *G. lacustris* in Poland and Germany comprises the northern lakelands, but also extends to central eastern Poland (Jaźdżewski, 1975). The distributional pattern in Scandinavia suggests that the species can effectively spread with birds, and has therefore been able to colonize much of the once glaciated northern areas, from more than one center of dispersal in Europe (Segerstråle, 1954; Vainio & Väinölä, in prep.). By contrast, *G. pulex* is more dependent on direct water connections (Segerstråle, 1954); the post-glacial colonization was probably from the southwest. In Poland, the range of *G. pulex* overlaps with that of *G. lacustris* in the northwest, but the species is