GENETIC RELATIONSHIPS AMONG NORTH-WESTERN EUROPEAN GAMMARIDAE (AMPHIPODA)

BY

ARNFINN SKADSHEIM
Øye Havbruk A/S, P.O. Box 66, N. 4484 Øyestranda, Norway

and

HANS REDLEF SIEGISMUND
Zoological Institute, University of Munich, Seidstrasse 25, D-8 Munich 2, Federal Republic of Germany

INTRODUCTION

Historically the classification of species in the family Gammaridae sensu Lincoln (1979), whose terminology we have chosen to follow in this paper, has been subjected to many changes. Around 1850 several species were described in the genus Gammarus Fabricius, 1775 (see for example Rathke, 1843; Lilljeborg, 1852, 1855; Sars, 1863) but later, especially in the beginning of the 20th century, most of the descriptions were rejected and/or returned to the three classical species Gammarus pulex (L., 1758), Chaetogammarus marinus (Leach, 1815) and Gammarus locusta (L., 1758). At that time Sexton (1912) initiated rearing and crossing experiments of several Gammarus forms. Her description of Gammarus zaddachi in 1912 was, however, first accepted in the next phase around 1930 to 1950 when most of the present marine and brackish water species were described. Stock (1967) settled the marine species picture in north-western Europe to the present state when he separated the G. locusta-complex into seven species. The controversy about the higher classification in Gammaridae is reflected in Bousfield (1977, 1979a, 1981, 1983) and Karaman & Barnard (1979); Barnard & Karaman (1980); Barnard & Barnard (1983). As appears from this sample of papers, possibly convergent evolution of morphological characters renders classification above the species level very difficult. Lincoln (1979) partly followed Bousfield (1977) and recognized four genera: Gammarus, Chaetogammarus Martynov, 1925, Eulimnogammarus Bazikalova, 1945 and Pectenogammarus Reid, 1940.

The occurrence of species groups in well defined habitats or geographical regions has been used for placing these groups in their own genus. Karaman (1931), for example, introduced Rivulogammarus to separate freshwater and marine species, but Stock (1969a) showed that Rivulogammarus must be rejected.
as a generic name according to the rules of the International Code of Zoological Nomenclature. Comprehensive reviews of the systematics of freshwater *Gammarus* are presented by Karaman & Pinkster (1977a, b); Barnard & Barnard (1983). Sket (1971) proposed *Lagunogammarus* as a new genus covering the species *G. zaddachi*, *Gammarus salinus* Spooner, 1947 and *Gammarus oceanicus* Segerstråle, 1947 that occur under estuarine conditions plus the arctic species *Gammarus wilkitzkii* Birula, 1897 and *Gammarus setosus* Dementieva, 1931, and this genus is now accepted by Bousfield (1979b). Members of *Eulimnogammarus* were believed to occur only in Lake Baikal and in the Arctic region, until Stock (1969) placed a new species from the inland waters of Spain and two additional species in this genus. Pinkster & Stock (1970) and Pinkster (1973) placed additional European species in *Eulimnogammarus*. Pinkster disregarded a possible immigration to Europe from Lake Baikal and suggested that the genus must have been in both areas since the Miocene.

An important morphological trait that has been used for the separation of species into genera is the form of uropod 3. Schellenberg (1937) suggested *Marinogammarus* as a subgenus for species with a reduced inner ramus of uropod 3. Sexton & Spooner (1940) raised *Marinogammarus* to generic rank. Stock (1968), however, pointed out that *Marinogammarus* was a junior synonym of *Chaetogammarus*. Many Gammaridae from Eurasia are characterized by a reduced inner ramus in uropod 3, in combination with simple gills and no projection of the basis of pereopod 7 (Stock, 1971). Stock recognized three major groups based on these traits: the *Sarothrogammarus*-group, the *Echinogammarus*-Chaetogammarus-group and the *Eulimnogammarus*-group, Karaman (1975) synonymized *Chaetogammarus* and *Pectenogammarus* with *Echinogammarus* and in (Karaman, 1977) he also questioned the separation of *Sarothrogammarus* from *Echinogammarus*. Barnard & Karaman (1980) relied only on uropod 3 as a distinguishing character, and regarded even the *Gammarus-Echinogammarus* grouping as a temporary classification, but Bousfield (1983) pointed to the high degree of intermediate characters that describe the whole superfamily Gammaroidea, and he regarded the characterization of Barnard & Karaman (1980) as unrealistically rigid.

Few fossils are available to support the morphological principles for phylogenetic classification (Hessler, 1969), and the oldest *Gammarus*-like fossil has been dated back only to Upper Eocene (Just, 1974). Bousfield (1979b) suggested that the whole superfamily Gammaroidea could have diversified during the last 50 million years, and in Bousfield (1983) he indicated that Amphipoda may be older than expressed earlier. Barnard & Barnard (1983) propose an origin even before the breakup of Pangea.

Holmes (1975) used numerical taxonomic techniques to compare morphological measurements of thirteen *Gammarus* and *Marinogammarus* species. His analysis mainly confirmed the differences between the two genera. Another taxonomic approach was that of Orian & Callan (1957) who studied