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Comparison of oostegite shapes in some gammaroidean species (Crustacea: Amphipoda)

D.H. Steele
Dept. of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1B 3X9

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Abstract

Within the superfamily Gammaroidea oostegites vary from broad (primitive) to narrow (advanced). Broad oostegites are found in members of the Acanthogammaridae, Macrohectopidae and a few of the Gammaridae. Most species of the family Gammaridae have broad anterior oostegites and narrow posterior ones. Marine *Gammarus* species and *Echinogammarus* show a narrowing trend in the anterior oostegites as well.

Résumé

Dans la superfamille Gammaroidea les oostégites varient depuis ceux élargis (aspect primitif) à ceux étroits (aspect évolué). Des oostégites larges sont présents chez des membres des familles Acanthogammaridae, Macrohectoptidae, et chez certains Gammaridae. La plupart des espèces de la famille Gammaridae ont des oostégites antérieurs larges et des oostégites postérieurs étroits. On observe chez les espèces marines de *Gammarus* et chez *Echinogammarus* une tendance au rétrécissement aussi pour les oostégites antérieurs.

Introduction

Prior to 1977, gammarid amphipods (family Gammaridae) made up the major portion of all described species and genera of amphipods. Bousfield (1977) revised this group and assigned the species to six superfamilies, each containing several families. Subsequently this revision was extended to all gammaridean amphipods (Bousfield, 1979; 1982; 1983).

While these revisions have found support, not all of the changes have been accepted (e.g. Barnard & Barnard, 1983; Barnard & Karaman, 1980; Lincoln, 1979; Ruffo, 1982; and Stock, 1980). As a result, amphipod taxonomy, especially as it relates to the family Gammaridae "is still in a state of flux" (Stock, 1980).

The purpose of the present study is not to resolve this controversy, since this is probably impossible given our present inadequate data base, but rather to illustrate how the structure of the brood pouch can provide data that will contribute to the resolution of the problem.

Oostegites have been recognized as morphological structures that should be more stable ("change resistant") than the traditional characters of the mouthparts, antennae, telson, etc. (Bousfield, 1977). However, I have concluded (Steele, in press) that the appearance of the major amphipod superfamilies has predated changes in the oostegites, since several of the superfamilies contain the full range of oostegite types. Thus the structure of the brood pouch should not be used to demonstrate relationships between major groups of gammaridean amphipods but may be used to follow trends within these groups. The present study consists of an analysis of the structure of the oostegites in some of the species in the superfamily Gammaroidea, which prior to 1977 were all placed in the family Gammaridae.

Methods

Previous characterizations of the oostegites for taxonomic purposes have been based on observations of one or two oostegites. However, this is inadequate as the oostegites on adjacent peraeopods can differ markedly. The oostegites attached to the second to fifth peraepods function as a unit to form the brood pouch and the structure of all of them must be considered. They are numbered here according to the peraeopod to which they are attached.

The illustrations have been adjusted such that oostegite three is of the same size on each figure. Only the basal setae on the anterior and posterior margins and the distal setae have been illustrated. In order not to prejudge the situation, the "gammarid" species have been referred to as *Gammarus*. A number of other species have been examined which are not illustrated here.

Results

For comparative purposes, the species have been grouped more or less as outlined by Bousfield (1977; 1982; 1983).

Gammaracanthus loricatus (Sabine, 1821) (Fig. 1A) is here considered to have the most primitive type of brood pouch (see discussion). The oostegites are all broad, with relatively short marginal setae that extend to the base of the oostegite. *Gammaracanthus* was placed in the family Acanthogammaridae by Bousfield (1977), but the bilobed structure of its gills indicates that its affinities probably lie elsewhere. In the family Acanthogammaridae the available specimen of *Garjajewia sarsi* Sowinsky, 1915 (Fig. 1B) lacked marginal setae, probably indicating ovarian diapause. The oostegites are similar in shape to those of *Gammaracanthus*, except that four and five are more elongated and five is also slightly narrowed. However, in *Spinacanthus parasiticus* (Dybowsky, 1874) (Fig. 1C) of the same family, the oostegites are similar to those of the freshwater *Gammarus* (Fig. 2).

Macrohectopus branickii (Dybowsky, 1874) (Fig. 1D), the sole representative of the family

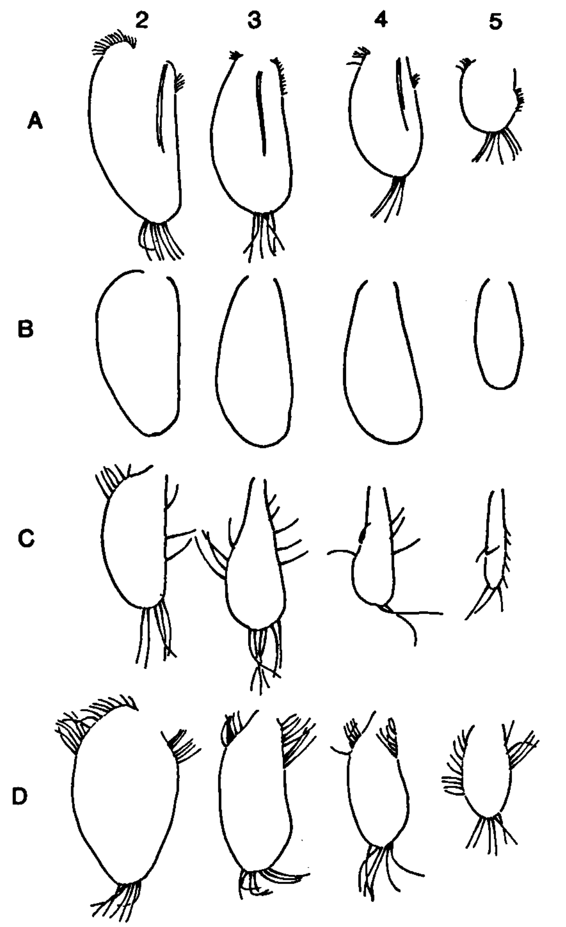

Fig. 1. Oostegites of Acanthogammaridae: A, *Gammaracanthus loricatus*; B, *Garjajewia sarsi*; C, *Spinacanthus parasiticus*; and Macrohectopidae: D, *Macrohectopus branickii*.

Macrohectopidae, has broad oostegites quite distinct from those in the Acanthogammaridae.

The brood pouch of the *Gammarus* species (Figs. 2, 3, 4) has a combination of broad and narrow oostegites. The anterior oostegites (two and often three) are broad, whereas four and especially five are narrow. The freshwater *G. fossarum* Koch, 1835, *G. minus* Say, 1818 and *G. roeseli* Gervais, 1835 have oostegites similar to those of *G. pulex* (Linnaeus, 1758) (Fig. 2A), whereas *G. lawrencianus* Bousfield, 1956, *G. fasciatus* Say, 1818, *G. locusta* (Linnaeus, 1758), *G. crinicornis* Stock, 1966, *G. duebeni* Liljeborg, 1852, *G. salinus* Spooner, 1947, *G. zaddachi* Sexton, 1912, *G. oceanicus* Segerstråle, 1947 and *G. wilkitzkii* Birula,

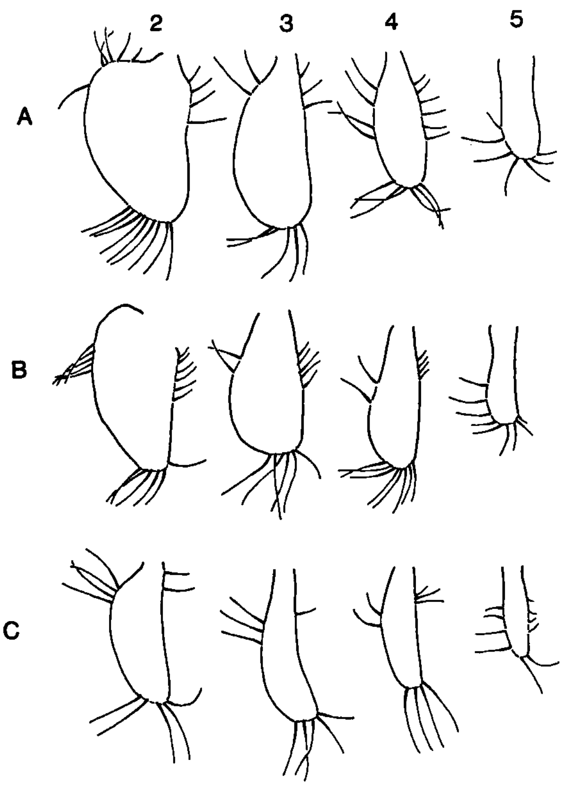

Fig. 2. Oostegites of freshwater Gammaridae with subequal rami on uropod 3: A, *Gammarus pulex*; B, *Gammarus pseudolimnaeus*; C, *Gammarus pseudosyriacus* Karaman & Pinkster, 1977.

1897 have oostegites similar to the marine species illustrated in Fig. 3. The species with markedly unequal rami on uropod 3 (*Echinogammarus* grouped in Fig. 4) tend to have narrower oostegites than those with subequal rami. However, *Echinogammarus stoerensis* (Reid, 1938) (Fig. 5C) has quite different oostegites. In this species, oostegites two, three, and four are expanded, and only oostegite five is narrow. *Eogammarus oclairi* Bousfield, 1979 (family Anisogammaridae) (Fig. 3D) has oostegites that are indistinguishable from those of *Gammarus*.

In many species of *Gammarus*, oostegite two and to a lesser extent oostegite three are curved and have a concave posterior margin (Figs. 2, 3, 4). In others such as *G. pulex* and *G. pseudolimnaeus* Bousfield, 1958 (Figs. 2A, B) these oostegites have a straight posterior margin similar to that found in *Gammaracanthus* (Fig. 1A) or *Crangonyx* (Fig. 5A).

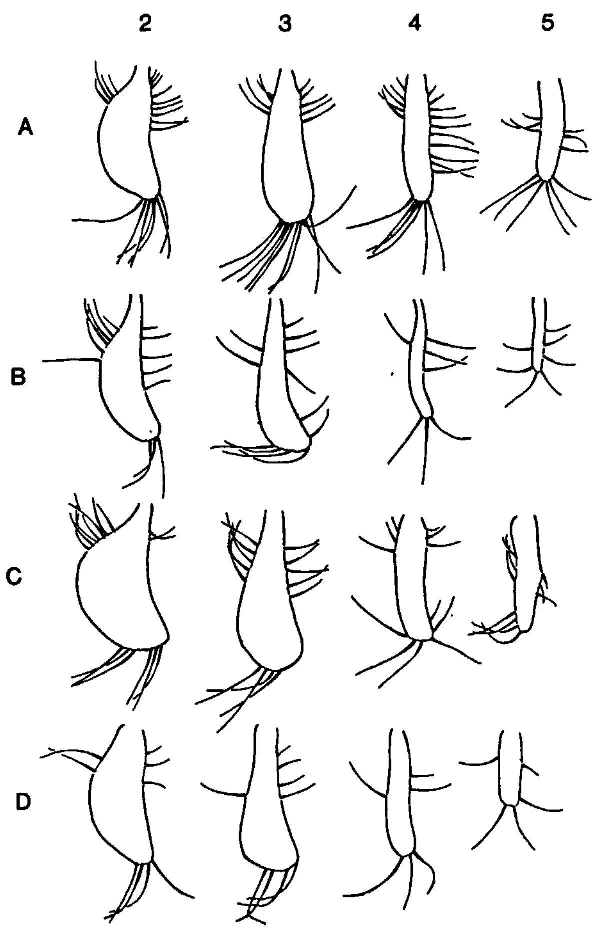

Fig. 3. Oostegites of marine Gammaridae with subequal rami on uropod 3 and Anisogammaridae: A *Gammarus setosus* Dementieva, 1931; B, *Gammarus mucronatus* Say, 1818; C, *Gammarus tigrinus* Sexton, 1939; D, *Eogammarus oclairi*.

The "*Gammarus*" species of Tasmania were assigned to the Crangonyctoidea by Bousfield (1977) and assigned to the genera *Austrogammarus* and *Antipodeus* by Williams & Barnard (1988). However, observations of live specimens of *Antipodeus* showed they behaved much like northern hemisphere *Gammarus* rather than *Crangonyx*. In particular, they walk on their sides (rather than upright) using peraeopods five, six and seven reflexed over their dorsal surface. This is a specialized form of locomotion typical of *Gammarus* and not yet observed in the other amphipod groups, including the crangonyctoids. The oostegites of *Antipodeus niger* Williams & Barnard, 1988 conform to the *Gammarus* type (Fig. 5B) rather than to *Crangonyx* (Fig.

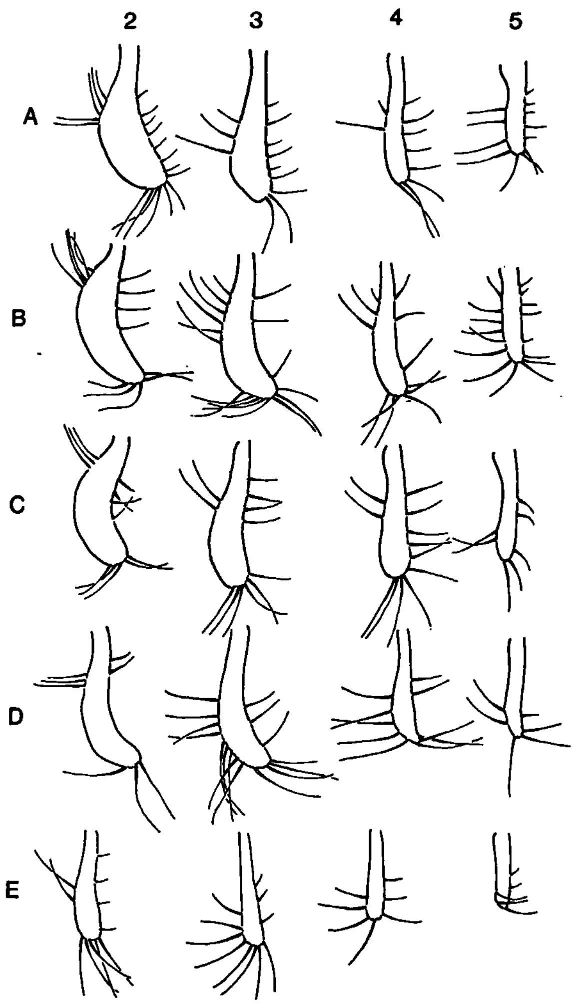

Fig. 4. Oostegites of Gammaridae with markedly unequal rami on uropod 3: A, *Echinogammarus marinus* (Leach, 1815); B, *Echinogammarus finmarchicus* (Dahl, 1938); C, *Echinogammarus obtusatus* (Dahl, 1938); D, *Echinogammarus planicrurus* (Reid, 1940); E, *Echinogammarus foxi* (Schellenberg, 1928).

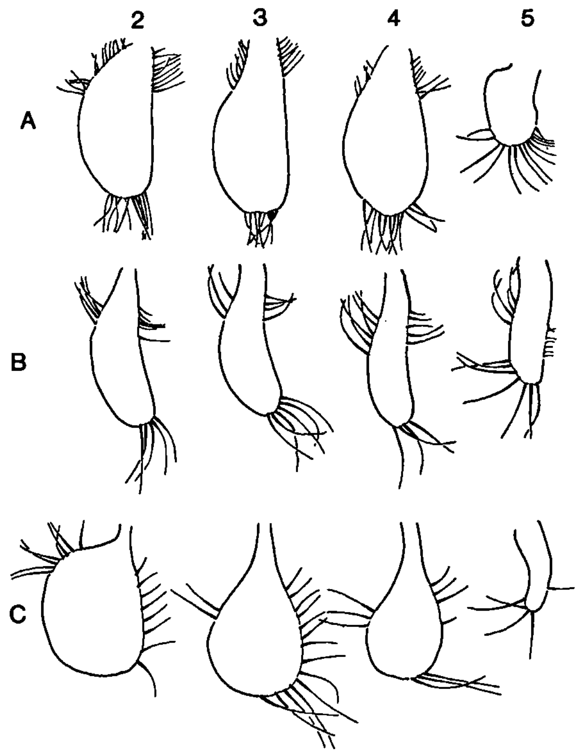

Fig. 5. Oostegites of Gammaroidea: A, *Crangonyx richmondensis* Ellis, 1940; B, *Antipodeus niger*; C, *Echinogammarus stoerensis*.

5A). It might be noted that crangonyctoids do occur in Tasmania, but none with developed oostegites were available for study.

Discussion

Although the oostegites of only a small fraction of the described gammaroidean species have been investigated, it is possible to make some tentative generalizations. Within the superfamily Gammaroidea the oostegites vary from broad to narrow, in a pattern parallel to that described for the Haustorioidea (Steele, in press). This observation supports the conclusion that the oostegites have evolved independently in the major amphipod groups.

A broad oostegite with short setae which is found in mysids, isopods and amphipods is the most primitive type, whereas a narrow oostegite with long setae known only in amphipods is the advanced type.

Within the Gammaroidea, the Acanthogammaridae (*Gammaracanthus*, *Garjajewia*) have the most primitive type of brood pouch. However, the structure of the brood pouch on *Spinacanthus* indicates that either it has evolved towards the gammarid type (see below) or, as seems more likely, the species has been misclassified.

The Macrohectopidae (*Macrohectopus*) and Crangonyctidae (superfamily Crangonyctoidea) have broad oostegites but of somewhat different shape (especially oostegite two) from the Acanthogammaridae.

There is an overall similarity in the brood pouch structure of members of the Gammaridae. The brood pouch is composed of a mixture of narrow (posterior) and broad (anterior) oostegites. The similar brood pouch of the Anisogammaridae (*Eogammarus oclairi*) indicates that the two families are closely allied. It should be noted, however, that *Priscillina* (Haustorioidea) also has a combination of broad and narrow oostegites (Steele, in press).

Within the Gammaridae there is continual variation in the oostegites, particularly in the narrowing of the anterior ones, so that in some species all the oostegites are narrowed. It is difficult therefore to accept as valid the genus *Lagunogammarus* established by Sket (1971) on the basis of the shape of its oostegites and of all the other genera and subgenera based on other characters that were summarized by Bousfield (1977). The synonymy summarized by Karaman (1982) in which *Rivulogammarus*, *Carinogammarus*, and *Lagunogammarus* are synonymized with *Gammarus*, and *Pectenogammarus*, *Eulimnogammarus* (European records), *Chaetogammarus*, *Marinogammarus*, *Homoeogammarus*, *Ostiogammarus*, and *Parhomoeogammarus* are synonymized with *Echinogammarus* seems most satisfactory at the present time.

All *Echinogammarus* (markedly unequal rami on uropod three) tend to have narrowed and curved anterior oostegites. *Echinogammarus stoerensis* has the only atypical brood pouch. This, plus its other known differences from typical gammarids, suggests that it should be reexamined critically to reassess its generic position.

The anterior oostegites of *Gammarus* vary from broad to narrow, but without a correlation with the groupings of Bousfield (1977). Sket (1971) distinguished freshwater from marine species of *Gammarus* by the shape of the second oostegite. Marine species have a gradually widening oostegite whereas freshwater species have a shoulder near the base. However, the distinction is better characterized by the straight posterior margin found in the freshwater species both in North America and Eurasia and the curved margin of marine and estuarine forms (Figs. 2 & 3). Even a freshwater species such as *Gammarus fasciatus*, which is closely related to the marine *G. tigrinus* Sexton, 1939 and *G. lawrencianus* and thus probably of marine origin, has curved anterior oostegites. Cole (1985) showed *G. fasciatus* as having a straight posterior margin, but it is distinctly curved in all the specimens I have examined from southern Canada. The *Gammarus pecos* complex of species found in the sulfatochloride springs of Texas and New Mexico also have a curved margin and most probably a marine origin.

The structure of the brood pouch of the Tasmanian *Antipodeus*, together with its specialized manner of walking, indicates that it belongs in the Gammaridae rather than in the Crangonyctoidea. It seems more closely allied to *Echinogammarus* (Gammaridae) than to *Eogammarus* (Anisogammaridae).

From this analysis of oostegite structures it can be speculated that the gammaroid amphipods originated in the fresh waters of Eurasia where the primitive Acanthogammaridae are now most abundant. *Gammaracanthus* has spread into the dilute surface waters of the Arctic Ocean, but has readily reinvaded fresh water in Canada and Europe. The broad oostegites of freshwater species indicates that the Gammaridae also developed in fresh water. They have subsequently moved into estuaries and to the margins of the oceans. In these marine habitats the oostegites are narrower. Reinvasions of fresh water have then taken place by species such as *Gammarus fasciatus* and the *Gammarus pecos* complex. As a result of this complex history, the gammaroid fauna at any location is likely to comprise species of several different backgrounds.

References

Barnard, J.L. & C.M. Barnard, 1983. Freshwater Amphipoda of the world, 1: 1–358; 2: 359–830 (Hayfield Associates, Mt. Vernon, Virginia).

Barnard, J.L. & G.S. Karaman, 1980. Classification of gammarid Amphipoda. Crustaceana, Suppl. 6: 5–16.

Bousfield, E.L., 1977. A new look at the systematics of gammaroidean amphipods of the world. Crustaceana, Suppl. 4: 282–316.

Bousfield, E.L., 1979. A revised classification and phylogeny of amphipod crustaceans. Trans. roy. Soc. Can., (4) 16: ("1978"): 343–390.

Bousfield, E.L., 1982. Amphipoda. Gammaridea. In: S.P. Parker (ed.), Synopsis and classification of living organisms: 255–285 (McGraw-Hill Book Co., New York).

Bousfield, E.L., 1983. An updated classification and palaeohistory of the Amphipoda. In: F.R. Schram (ed.), Crustacean phylogeny. Crustacean Issues, 1: 257–277 (Balkema, Rotterdam).

Cole, G.A., 1985. An analysis of the Gammarus-pecos complex (Crustacea, Amphipoda) in Texas and New Mexico, U.S.A. J. Ariz.-Nev. Acad. Sci.,. 20: 93–103.

Karaman, G.S., 1982. Family Gammaridae (sensu lato). In: S. Ruffo (ed.), The Amphipoda of the Mediterranean. Mém. Inst. océanogr., 13 (1): 245–360.

Lincoln, R.J., 1979. British marine Amphipoda: Gammaridea: 1–658 (British Museum (Natural History), London).

Ruffo, E. (ed.), 1982. The Amphipoda of the Mediterranean. Mém. Inst. Océanogr., 13 (1): 1–364.

Sket, B., 1971. Zur Systematik und Phylogenie der Gammarini (Amphipoda). Bulletin Scientifique (Yougoslavie), (A) 16: 6.

Steele, D.H., in press. Is oostegite structure related to ecology or phylogeny? Hydrobiologia.

Stock, J.H., 1980. Regression model evolution as exemplified by the genus Pseudoniphargus (Amphipoda). Bijdr. Dierk., 50 (1): 105–144.

Williams, W.D. & J.L. Barnard, 1988. The taxonomy of crangonyctoid Amphipoda (Crustacea) from Australian fresh waters: Foundation studies. Rec. Austr. Mus., Suppl. 10: 1–180.

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