This article was downloaded by: [2007 Seoul National University] On: 26 December 2007 Access Details: [subscription number 779965008] Publisher: Taylor & Francis Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Natural History Publication details, including instructions for authors and subscription information:

http://www.informaworld.com/smpp/title~content=t713192031

Phylogenetic relationships among gammaridean

families and amphipod suborders

C. B. Kim^a; W. Kim^a

^a Department of Molecular Biology, College of Natural Sciences, Seoul National University, Seoul, Korea

Online Publication Date: 01 August 1993 To cite this Article: Kim, C. B. and Kim, W. (1993) 'Phylogenetic relationships among gammaridean families and amphipod suborders', Journal of Natural History, 27:4, 933 - 946 To link to this article: DOI: 10.1080/00222939300770571

URL: http://dx.doi.org/10.1080/00222939300770571

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: http://www.informaworld.com/terms-and-conditions-of-access.pdf

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Phylogenetic relationships among gammaridean families and amphipod suborders

C. B. KIM and W. KIM

Department of Molecular Biology, College of Natural Sciences, Seoul National University, Seoul 151–742, Korea

(Accepted 3 March 1992)

The phylogenies of gammaridean families and amphipod suborders have been investigated by cladistic methods. Sixteen morphological characters were used in this analysis. Five independent lineages identified from this analysis were Gammaridae, Crangonyctidae, Pontogeneiidae, Synopiidae plus Stegocephalidae, and one comprising the other groups considered in this study. The Talitroidea, consisting of Hyalidae and Talitridae, was monophyletic. Three families (Podoceridae, Caprogammaridae and Caprellidae), which all have a reduced abdomen, proved to be monophyletic, and this result suggests that the combination of the Corophioidea with Caprellidea would be monophyletic. The Hyperiidea showed a close affinity with leucothoid members such as Amphilochidae and Stenothoidae. The present phylogenetic scheme is compared with previous hypothetical schemes.

KEYWORDS: Amphipoda, gammaridean families, cladistic analysis, phylogeny.

Introduction

Phylogenetic relationships among suborders or superfamilies within the Amphipoda have been a subject of disagreement between amphipologists. The Amphipoda has been subdivided into three or four suborders: Gammaridea, Hyperiidea and Caprellidea versus Gammaridea, Hyperiidea, Caprellidea and Ingolfiellidea (Bousfield, 1982a; Bowman and Abele, 1982). Some workers regarded the Caprellidea and Hyperiidea as superfamilies of the Gammaridea. In the Gammaridea, which has been considered to be the most primitive suborder, proposed classifications and phylogenetic relationships among subgroups have been highly controversial compared with the other two suborders showing natural groupings (Bowman and Gruner, 1973, for Hyperiidea; McCain, 1970 and Vassilenko, 1974 for Caprellidea).

The classical scheme of classification and phylogeny of the Gammaridea was established by Bate (1862), Sars (1895) and Stebbing (1888, 1906). In their systems, the Lysianassidae, Phoxocephalidae, other mysid-like groups and Talitridae were treated as the most primitive groups. Barnard (1969), and Barnard and Barnard (1983) proposed a hypothetical phylogenetic system in which gammaridean families (or family groups) and the other two suborders (hyperiids and caprellids) were considered to have radiated from the basic gammarideans, such as sections Gammarida and Corophiida. Bousfield (1978, 1983) presented another classification and hypothetical phylogenetic relationships of amphipod suborders and gammaridean superfamilies.

	Characters
	1111111
Taxa	1234567890123456
Hypanc	000000000000000000
Gammaridae	00000000000000000
Crangonyctidae	000000000000100
Lysianassidae	1111000000000000
Pontogeniidae	0000000000000000
Liljeborgiidae	1111100000000000
Synopiidae	0001010000000000
Stegocephalidae	0011010000000000
Pardaliscidae	111110000000000
Hyperiidea	111111000000010
Phoxocephalidae	111110010000000
Oedicerotidae	110000010000000
Dexaminidae	110000000000001
Ampeliscidae	100000000000001
Amphilochidae	111110000000010
Stenothoidae	1111100000001910
Hyalidae	110200000000100
Talitridae	1102010000101900
Podoceridae	110000000002912
Caprogammaridae	2100001011012992
Caprellidae	2100001011112992

Table 1. Character data matrix. State 9 indicates missing data. Hypanc=hypothetical ancestor.

In his system, 19 gammaridean superfamilies were proposed (Bousfield, 1983). Bousfield's phylogeny was based on the supposedly primitive morphological features of carapace-bearing Mysidacea, which represent the primitive conditions in the Peracarida. No-one has yet proposed the phylogenetic relationships and classification of amphipod subgroups using objective means such as cladistic methods.

The aims of the present paper are the re-examination of previous phylogenetic theories, and the presentation of phylogenetic relationships among gammaridean families and amphipod suborders by cladistic methods.

Materials and methods

The gammaridean, caprellidean and hyperiidean amphipods deposited in the Department of Molecular Biology, Seoul National University were examined and the 16 morphological characters were scored (see below, and Appendix 1). Representative species of families or suborders were examined, and the characters for unavailable species and some characters in rare taxa (e.g. Crangonyctidae) were taken from the literature. The illustrations of characters examined were provided in Kim (1991).

One or two representative monophyletic families were selected from each of Bousfield's superfamily because his gammaridean superfamilies (Bousfield, 1978, 1983) may be polyphyletic or paraphyletic groups. We excluded ill-defined groups (e.g. Hadziidae, Melitidae and Calliopiidae) and unresolved groups (which include Pontogammaridae, Typhlogammaridae, and Acanthogammaridae).

A data matrix was prepared, comprising 17 gammaridean families plus two caprellid families together with hyperiids, utilizing 16 morphological characters (Table 1). If multistates of a character were found in a group, the major state was selected as representative.

The data matrix was analysed using the PAUP (Phylogenetic Analysis Using Parsimony) Version 3.0k program (Swofford, 1990). The options employed were heuristic search, CLOSEST addition, TBR branch-swapping, and MINF optimization.

The nomenclature of Barnard (1969), Barnard and Barnard (1983), and Barnard and Karaman (1991) has been followed.

Characters and scoring

An attempt was made to list all morphological characters that previous authors had used in classification. Different types of oostegites (broad, sublinear, linear) are widely dispersed throughout groups without any obvious correlation with relationships deduced using other characters. The shape and sexual dimorphism of gnathopods give trouble in deciding their polarity. There are at least nine types in calceolus correlated with nine different family groups (Lincoln and Hurley, 1981). However, the majority of genera and species of each group have lost calceoli, and thus calceoli are of no value as phylogenetic characters. Analyses including these characters gave rise to parsimonious trees with very low consistency indices (CIs) (0.3-0.4) and high *f*-ratio. Trees having low CIs and high *f*-ratios contain many character reversals and convergences. Such characters were therefore excluded from the present analysis because too many reversals and convergences appearing in trees obstruct reasonable interpretation.

Characters were also excluded when the state of the character was the same for all taxa, i.e. giving it no value in the analysis. Thus 16 phylogenetically informative characters (see below) were used in this analysis.

Bousfield's phylogenetic scheme (1978) was based on the speculative primitive conditions of the Amphipoda, as evidenced in carapace-bearing Mysidacea and Cumacea. Watling (1981) pointed out two difficulties in assuming that cumaceans and mysids are representative of the plesiomorphic condition for amphipods, and rejected Bousfield's scheme. Watling proposed a syncarid-like ancestral eumalacostracan as the ancestor of amphipods (Watling, 1981, 1983). Recently, Schram (1986) reassociated Amphipoda and Isopoda as sister groups and juxtaposed an Amphipoda-Isopoda clade with the Mictacea. However, due to extreme specialization in many syncarid and mictacean appendages, it is difficult to use syncarid and mictaceans strictly as an outgroup to polarize the character states in the amphipods. Experiencing difficulties in the selection of an outgroup, we have selectively used characters of the 'Basic marine gammaridean' (Barnard and Karaman, 1991) and combined these characters with those of 'Primitive amphipod' (Barnard and Barnard, 1983). These combined features were regarded as characteristics of the hypothetical ancestor, and polarity of each character was selected by comparing the state of each character with that shown in this hypothetical ancestor (hypanc, see Table 1).

The characters were scored using a multistate system: viz. the ancestral state = 0, the derived state = 1, the further derived state = 2. A score of 9 = missing data, indicating that the appendage is absent in that group.

The characters were ordered except for the telson. The use of ordered, multistate characters implies a linear transformation series, so that the most derived state (2) evolved from the ancestral state (0) via the intermediate state (1).

1. *Maxilla 1, inner lobe*: (0) Large and densely setose marginally; (1) small and sparsely setose marginally; (2) absent. Bousfield (1978) also considered a well-developed inner lobe to be plesiomorphic. Gammaridae, Crangonyctoidae, Pontogeneiidae, Synopiidae and Stegocephalidae show the ancestral state. The other groups

show the derived state. The possession of a derived state maxilla 1 with reduced inner lobe is typical of Dexaminidae, Lysianassidae and Phoxocephalidae which contain basic members exhibiting the ancestral state. A further derived state is seen in Caprogammaridae and Caprellidae, both of which have no inner lobe.

2. *Maxilla 2, lobes*: (0) Broad, and densely setose marginally and facially; (1) narrow or small, and sparsely setose marginally and facially. Bousfield (1978) also regarded a well developed maxilla 2 as exemplifying the ancestral state. The ancestral state, with well developed lobes of maxilla 2, is found in Gammaridae, Crangonyctidae, Synopiidae, Stegocephalidae and Ampeliscidae. The derived state is found in the other groups. Typically in Dexaminidae, Lysianassidae, and Phoxocephalidae, the derived state is shown, although in basic members the ancestral state is exhibited.

3. *Mandible, molar*: (0) Strongly developed and triturative; (1) weakly developed and smooth or molar absent. A strongly developed and triturative (= grinding surface composed of ridges and teeth) molar is found in other peracarids which can (more or less) be regarded as an outgroup. Gammaridae, Crangonyctidae, Pontogeneiidae, Synopiidae, Oedicerotidae, Dexaminidae, Ampeliscidae, Hyalidae, Talitridae, Podoceridae, Caprogammaridae and Caprellidae all show the ancestral state. The derived state is found in the other groups.

4. *Mandible, palp*: (0) Strongly developed and 3-articulate; (1) weakly developed or article 3 absent; (2) absent. A strongly developed, 3-articulated palp is shown in other peracarids, especially mysidaceans. The ancestral state is found in Gammaridae, Crangonyctidae, Pontogeneiidae, Oedicerotidae, Dexaminidae, Ampeliscidae, Podoceridae, Caprogammaridae and Caprellidae. The derived state is found in the other groups. In Hyalidae and Talitridae the palp is absent (further derived state).

5. *Maxilliped, inner plate*: (0) Well developed; (1) reduced or fused. In most amphipod groups the ancestral state is exhibited. A derived state, with reduced inner plate, is shown in Phoxocephalidae, Liljeborgiidae, Hyperiidea, Pardaliscidae, Amphilochidae and Stenothoidae. Hyperiidea also show inner plates which are fused into a single plate.

6. *Maxilliped*, *palp*: (0) 4-Articulate and unguiform; (1) article 4 of palp reduced or palp absent. In most amphipod groups the ancestral state is found, Synopiidae, Stegocephalidae and Talitridae have a palp with article 4 reduced. In Hyperiidea the palp is absent.

7. Coxae 1-4: (0) Present, deep and large or small and shallow; (1) vestigial or absent. In gammaridean families and Hyperiidea the ancestral state is shown. The derived state is found in Caprogammaridae and Caprellidae which either have coxae 1-4 vestigial or lacking.

8. *Pereopods* 5-7: (0) Rather subequal in size and form; (1) unequal in size and form, and articles broadly expanded and strongly spinose and/or setose (= fossorial). Bousfield (1978, 1983) considered fossorial pereopods 5-7 to be apomorphic. In most groups the ancestral state is shown, while in fossorial groups such as Oedicerotidae and Phoxocephalidae the derived state is found.

9. Number of gills: (0) Occur on coxae 2–7 (or 6); (1) occur on coxae 2–4. The ancestral state is shared by gammaridean families and Hyperiidea. Caprogammaridae and Caprellidae display the derived state.

10. *Number of oostegites*: (0) Occur on coxae 2–5; (1) occur on coxae 3–4. The ancestral state is found in the gammaridean families and Hyperiidea. The derived state is retained only in the Caprogammaridae and Caprellidae.

11. *Pleopods*: (0) Well developed; (1) reduced or absent. In most groups the ancestral state is shown. The Talitridae and Caprellidae have pleopods reduced or lacking. The loss of pleopods is the mark of a sedentary life of Caprellidae and of terrestrial habits in Talitridae.

12. Uropods 1 and 2: (0) Biramous; (1) uniramous or vestigial. The ancestral state appears in gammaridean families and Hyperiidea. The derived state is shown in Caprogammaridae and Caprellidae which have uniramous and vestigial uropods 1 and 2, respectively.

13. *Rami of uropod 3*: (0) Biramous; (1) uniramous; (2) absent. The ancestral state is exhibited by most groups, while Stenothoidae and Talitridae have a uniramous uropod 3 (= derived state). A further derived state is shown in Podoceridae, Caprogammaridae, and Caprellidae, all of which lack uropod 3 rami.

14. *Size of rami if biramous*: (0) Equal or subequal; (1) unequal. Most amphipod groups show the ancestral state, except Crangonyctidae and Hyalidae which bear unequal rami. Scores of 9 were attributed to the Stenothoidae, Talitridae, Podoceridae, Caprogammaridae and Caprellidae, all of which have uropod 3 uniramous or lacking.

15. Shape of telson: (0) Lobes separated, deeply or narrowly; (1) lobes fused entirely. The entire telson frequently appears in most other peracarids and so Barnard and Barnard (1983) regarded the non-laminar, entire telson of domicolous amphipods such as Corophioidea to be primitive. Bousfield (1978, 1983) and Barnard and Karaman (1991), however, considered the bilobed and laminar telson of non-domicolous amphipods (e.g. Gammaridae) as the ancestral state. Moreover, the function of the telson in amphipods is not fully understood. Outgroup comparison is uninformative in this case. Therefore, this transformation must be treated as unordered.

16. *Urosome*: (0) Free; (1) at least 2 urosomites fused; (2) urosomite 1 distinctly elongate or urosomites absent. In most amphipod groups the ancestral state is shown. The derived state is exhibited by the inquilinous Dexaminidae and the tube-dwelling Ampeliscidae. A further derived state is found in the sedentary groups (Podoceridae, Capregammaridae and Caprellidae) which have urosomite 1 distinctly elongated or lack urosomites.

Results and discussion

Four shortest trees (39 steps) were obtained, with a consistency index of 0.641. All four trees were fully resolved, with an *f*-ratio of either 0.0816 (Fig. 1) or 0.0738

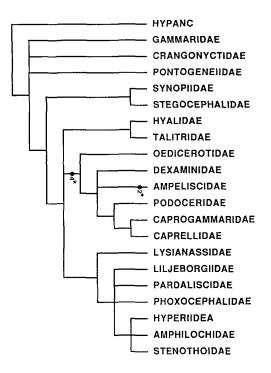


FIG. 1. Cladogram for amphipod subgroups (*f*-ratio of 0.0816). HYPANC = hypothetical ancestor. Numbers refer to characters listed in text. * Character reversal.

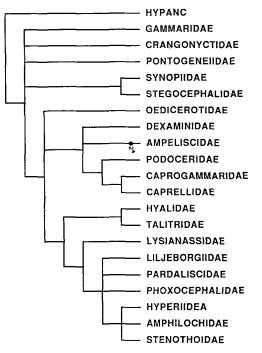


FIG. 2. Cladogram for amphipod subgroups (f-ratio of 0.0738). HYPANC = hypothetical ancestor. Numbers refer to characters listed in text. * Character reversal.

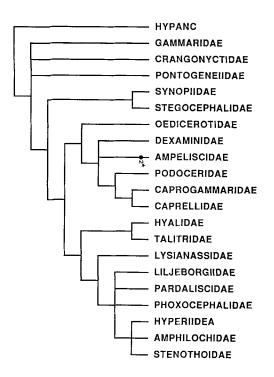


FIG. 3. Cladogram for amphipod subgroups (*f*-ratio of 0.0738). HYPANC = hypothetical ancestor. Numbers refer to characters listed in text. * Character reversal.

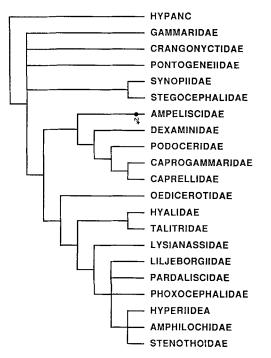


FIG. 4. Cladogram for amphipod subgroups (*f*-ratio of 0.0738). HYPANC = hypothetical ancestor. Numbers refer to characters listed in text. * Character reversal.

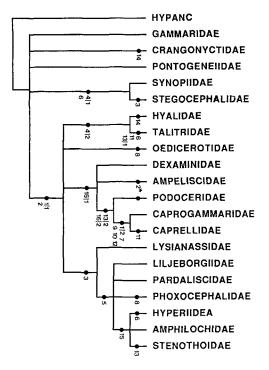


FIG. 5. The phylogenetic relationships of amphipod subgroups. A strict consensus tree. HYPANC = hypothetical ancestor. Numbers refer to characters listed in text. * Character reversal.

(Figs 2-4). The Oedicerotidae, Dexaminidae, Ampeliscidae, Podoceridae, Caprogammaridae and Caprellidae, as shown in Fig. 1, are monophyletic, sharing an apomorphy of redeveloping mandibular palp (character 4). A presumed function of the mandibular palp is the cleaning of the anterior cephalic space between the antennae. Amphipods without a palp often have a few antennal setae projecting into that space to trap particles. Moreover, amphipods have been observed cleaning that space with gnathopod 1 (Barnard and Karaman, 1991). If the phylogenetic hypothesis represented in Fig. 1 is selected, we would have to accept a non-economic notion that the mandibular palp redeveloped in this group. However, such incomprehensibility is not found in Figs 2–4. In these three trees character 2 (inner lobe of maxilla 2) is reversed on the ampeliscid clade. Ampeliscids are infaunal deposit and filter feeders. According to their habits they may need elaborate setae on maxilla 2 inner lobe which filters particles of different sizes (Croker, 1967). Their reacquisition of a well-developed maxilla 2 may be understandable in this respect. Trees depicted in Figs 2-4 are different from each other in the positions of the Synopiidae-Stegocephalidae and oedicerotid clades. Since three trees have no character reversals, except for character 2, and bear the same f-ratio (0.0738), we cannot conclude which is the best hypothesis. We have selected the strict consensus tree (Fig. 5) as the preferred phylogenetic hypothesis.

Five lineages diverge from the hypothetical ancestor. Gammaridae and Pontogeiidae retain all ancestral states of each character and they are presumed to have evolved early, as suggested by previous researchers (see Bousfield, 1978; Barnard and Karaman, 1991). Crangonyctidae contains about 125 species in six genera, all of which are limited to freshwaters and subterranean systems in the northern hemisphere (Bousfield, 1982a). They are considered to be a very ancient continental freshwater group and were most probably derived from potogeneioidean-like marine stock (Bousfield, 1978). The crangonyctid clade is characterized by the presence of unequal rami on uropod 3 (character 14). The Synopiidae, in spite of its proposed close relationship with Paradaliscidae (Bousfield, 1978), has proved to be the sister group of Stegocephalidae in this analysis. They share with their common ancestor the lack of a mandibular palp (character 4) and a reduced maxillipedal palp (character 6). The stegocephalid clade is identified by having a reduced mandibular molar (character 3).

The group containing the other families is recognized for bearing maxilla 1 with reduced inner lobe (character 1) and maxilla 2 with reduced lobes (character 2). The oedicerotid clade is characterized by the presence of unequal and fossorial percopods 5-7 (character 8). The talitroid group, containing Hyalidae and Talitridae, is monophyletic, supported by the absence of mandibular palp (character 4.2). The group comprising Dexaminidae, Ampeliscidae, Podoceridae, Caprogammaridae and Caprellidae is distinguished by the presence of fused urosomites (character 16.1). A group comprising Podoceridae, Caprogammaridae and Caprellidae seems to have been descended from a common ancester which had lost the rami of uropod 3 (character 13.2) and had urosomite 1 elongate or urosomites lacking (character 16.2). Barnard (1973a) suggested re-evaluation of the Caprellidea as a gammaridean superfamily based on the morphological link (based on development of abdomen) between Podoceridae and Caprellidea seen in the Caprogammaridae. Barnard and Karaman (1983), and Barnard and Barnard (1983) proposed three amphipod suborders, Gammaridea, Hyperiidea and Corophildea, and separated the Caprogammaridae from the Caprellidea, placing it within the superfamily Corophioidea in Corophiidea. It is commonly accepted that the Caprellidea were derived from a podocerid-like ancester (McCain, 1970; Laubitz, 1977, 1979; Bousfield, 1978). This indicates paraphyly of Corophioidea, and monophyly of Corophioidea plus Caprellidea. The present result suggests the monophyly of the group embracing Podoceridae, which represented the Corophioidea, Caprogammaridae and Caprellidae. Thus, the combination of the Corophioidea with the Caprellidea would be a monophyletic grouping, and the Corophioidea without the Caprellidea is paraphyletic. The present analysis also supports the interpretation of the Caprellidea as a superfamily of the suborder Corophiidea, but does not support the placement of the Caprogammaridae in the Corophioidea. However, data on more families of Corophioidea need to be analysed to clarify the classification of Corophioidea and Caprellidea.

The group containing Lysianassidae, Liljeborgiidae, Pardaliscidae, Phoxocephalidae, Hyperiidea, Amphilochidae and Stenothoidae is recognized, as all bear a reduced mandibular molar (character 3). Liljeborgiidae, Pardaliscidae, Phoxocephalidae, Hyperiidea, Amphilochidae and Stenothoidae are descendants of an ancestor with maxilliped inner plate reduced (character 5). In spite of its suggested close affinity with Paradaliscidae (Bousfield, 1978), Hyperiidea show a close relationship with Amphilochidae and Stenothoidae. They are distinguished by the possession of an entire telson (character 15). No resolution among these three families was obtained. The hyperiid clade is characterized by the absence of a maxillipedal palp (character 5). Prior to the present scheme, two intuitive schemes of amphipod phylogeny were proposed without using cladistic methods. The present scheme supports 'hypothetical phylogenetic relationship of amphipod suborders and gammaridean superfamilies' proposed by Bousfield (1978, fig. 6) vis-a-vis the relationships of Dexaminidae, Ampeliscidae, Podoceridae, Caprogammaridae and Caprellidae. But Bousfield's scheme differs considerably from the present one in the relative affinities among the other groups. His scheme was founded primarily on the basis of the characters of the pelagic terminal male and the calceolus. These two characters are not congruent with the relationships deduced using other characters, and the information on these character states is not available for many groups.

The 'evolutionary pattern of suborders in Amphipoda' proposed by Barnard and Barnard (1983, graph 1) is very different from the present scheme. It was based solely on the telson form. According to that scheme, four major lineages diverged from the Corophiidea, regarded as the hypothetical ancestral group. One lineage consisted of Gammarida and Talitrida, the second of Caprellida alone; the third embraced the Caprogammaridae, and the fourth comprised the Hyperiidea. As pointed out by Barnard and Karaman (1991), our understanding of the significance of the telson as an evolutionary marker will not be clarified until a clear understanding of its function emerges. Therefore Barnard and Barnard's scheme must be reserved for future evaluation.

Conclusions

The present phylogenetic scheme is not necessarily to be seen as a replacement for previous schemes: it is, however, an attempt to generate testable hypotheses. Information on the shape and attachment point of gills would usefully supplement the present scheme.

Analysis of precopulatory mating behaviour and sexual dimorphism of appendages, especially gnathopods, can produce valuable information for reconstructing amphipod phylogeny. Conlan (1991) summarized precopulatory mating behaviour (mate guarding by carrying; mate guarding by attending; non-mate guarding) as a character useful for the recognition of amphipod superfamilies or suborders, and hypothesized that mate guarding had arisen more than once from non-mate guarding ancestors. However, due to the poverty of information on precopulatory mating behaviour for many amphipod taxa and its diversity at the family level, this character was unusable in the present study. Molecular studies, such as those of Kim and Abele (1990), and Spears *et al.* (1992) on decapod crustaceans, will provide another independent tool for testing various phylogenetic and classificatory schemes within the Amphipoda.

Acknowledgements

We wish to thank the late Dr J. Laurens Barnard for his encouragement and kind help in the collection of valuable literature. Dr L. Watling, Professor P. G. Moore, Dr S. Y. Moon, Dr M. K. Shin, and two anonymous reviewers contributed valuable comments that improved the manuscript. This work was partially supported by the Basic Science Research Institute programme, Ministry of Education, 1989–1992, ED 89-43.

References

- BARNARD, J. L., 1960, New bathyal and sublittoral ampeliscid amphipods from California with an illustrated key to Ampelisca, Pacific Naturalist, 1, 1–36.
- BARNARD, J. L., 1962, Benthic marine Amphipoda of southern California: Families Tironidae to Gammaridae, *Pacific Naturalist*, **3**, 73–115.
- BARNARD, J. L., 1966a, Submarine canyons of southern California. Part V, systematics: Amphipoda, Allan Hancock Pacific Expeditions, 27, 1-166.
- BARNARD, J. L., 1966b, Benthic Amphipoda of Monterey Bay, California, Proceedings of the United States National Museum, 119, 1-41.
- BARNARD, J. L., 1969, The families and genera of marine gammaridean Amphipoda, Bulletin of the United States National Museum, 271, 1–535.
- BARNARD, J. L., 1970a, Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands, Smithsonian Contributions to Zoology, 34, 1–286.
- BARNARD, J. L., 1970b, The identity of *Dexamonica* and *Prinassus* with a revision of Dexaminidae (Amphipoda), *Crustaceana*, **19**, 161–180.
- BARNARD, J. L., 1972a, The marine fauna of New Zealand: algae-living littoral Gammaridea (Crustacea, Amphipoda), *Memoir of the New Zealand Oceanographic Institute*, **62**, 1–216.
- BARNARD, J. L., 1972b, A review of the family Synopiidae (= Tironidae), mainly distributed in the deep sea (Crustacea: Amphipoda), Smithsonian Contributions to Zoology, 124, 1–94.
- BARNARD, J. L., 1973a, Revision of Corophildae and related families (Amphipoda), Smithsonian Contributions to Zoology, 151, 1–27.
- BARNARD, J. L., 1973b, Deep-sea Amphipoda of the genus Lepechinella (Crustacea), Smithsonian Contributions to Zoology, 133, 1–31.
- BARNARD, J. L., and BARNARD, C. M., 1983, Freshwater Amphipoda of the world, I: Evolutionary patterns and II: Handbook and Bibliography (Mt Vernon, VA: Hayfield Associates), 830 pp.
- BARNARD, J. L. and DRUMMOND, M. M., 1978, Gammaridean Amphipoda of Australia. Part III. The Phoxocephalidae, *Smithsonian Contributions to Zoology*, **245**, 1–551.
- BARNARD, J. L. and KARAMAN, G. S., 1983, Australia as a major evolutionary centre for Amphipoda (Crustacea), *Memoirs of the Australian Museum*, **18**, 45–61.
- BARNARD, J. L. and KARAMAN, G. S., 1991, The families and genera of marine gammaridean Amphipoda (except marine gammaroids), Parts 1 and 2, *Records of the Australian Museum Supplement*, 13, 1–866.
- BATE, C. S., 1862, Catalogue of the Specimens of Amphipodous Crustacea in the Collection of the British Museum (London: British Museum (Natural History)), 399 pp.
- BELLAN-SANTINI, D., 1972, Invertébrés marine des XIIème et XVème Expeditions Antarctiques Françaises en Terre Adélie 10. Amphipodes Gammariens, *Tethys*, **4** (Suppl.), 157–238.
- BOUSFIELD, E. L., 1973, Shallow-water gammaridean Amphipoda of New England (Ithaca and London: Cornell University Press), 312 pp.
- BOUSFIELD, E. L., 1978, A revised classification and phylogeny of amphipod crustaceans, *Transactions of the Royal Society of Canada*, **4**, 343–390.
- BOUSFIELD, E. L., 1982a, Amphipoda, in S. P. Parker (ed.), Synopsis and Classification of Living Organisms (New York: McGraw-Hill), pp. 241–285.
- BOUSFIELD, E. L., 1982b, The amphipod superfamily Talitroidea in the northeastern Pacific region. I. Family Talitridae: systematics and distributional ecology, *Publications in Bio*logical Oceanography of the National Museum of Natural Sciences, Canada, 11, 1-73.
- BOUSFIELD, E. L., 1983, Updated phyletic classification and palaeohistory of the Amphipoda, in F. S. Schram (ed.), *Crustacean Phylogeny*, Vol. 1 of *Crustacean Issues*, F. S. Schram (ed.) (Rotterdam: A. A. Balkema), pp. 257–277.
- BOWMAN, T. E., 1973, Pelagic amphipods of the genus *Hyperia* and closely related genera (Hyperiidea: Hyperiidae), *Smithsonian Contributions to Zoology*, **136**, 1–76.
- BOWMAN, T. E. and ABELE, L. G., 1982, Classification of the recent Crustacea, in L. G. Abele (ed.), Systematics, the Fossil Record and Biogeography, Vol. 1 of The Biology of Crustacea, D. E. Bliss (ed.) (New York: Academic), pp. 1–27.
- BOWMAN, T. E. and GRUNER, H. E., 1973, The families and genera of Hyperiidea, *Smithsonian* Contributions to Zoology, **146**, 1-64.

- CONLAN, K. E., 1991, Precopulatory mating behavior and sexual dimorphism in the amphipod Crustacea, *Hydrobiologia*, **223**, 255–282.
- CROKER, R. A., 1967, Niche diversity in five sympatric species of intertidal amphipods (Crustacea: Haustoriidae), *Ecological Monographs*, **37**, 173–200.
- DICKINSON, J. J., 1983, The systematics and distributional ecology of the superfamily Ampeliscoidea (Amphipoda: Gammaridea) in the northeastern Pacific region. II. The genera Byblis and Haploops, Publications in Natural Sciences, National Museum of Natural Sciences, 1, 1–38.
- GURJANOVA, E., 1951, Bokoplavy morej SSSR i sopredel'nykh vod (Amphipoda, Gammaridea), Akademiia Nauk SSSR, Opredeliteli po Faune SSSR, **41**, 1–1029.
- GURJANOVA, E., 1962, Bokoplavy severnoi chasti Tixogo Okeana (Amphipoda, Gammaridea) chast' 1, Opred. po Faune SSSR, Akademiia Nauk SSSR, Opredeliteli po Faune, SSSR, 74, 1-440.
- HOLSINGER, J. R., 1977, A review of the systematics of the Holarctic amphipod family Crangonyctidae, *Crustaceana*, 4 (Suppl.), 244–281.
- HOLSINGER, J. R., 1978, Systematics of the subterranean amphipod genus *Stygobromus* (Crangonyctidae). Part II: species of the eastern United States, *Smithsonian Contributions* to Zoology, **266**, 1–144.
- KARAMAN, G. S., 1974, Revision of the family Pardaliscidae with diagnosis of genera, distribution of species and bibliography, Acta Adriatica, Institut za Oceanografiju i Ribarstvo, 15, 3–46.
- KARAMAN, G. S., 1980a, Revision of the genus Gitanopsis Sars 1895 with description of a new genera [sic] Afrogitanopsis and Rostrogitanopsis n. gen. (fam. Amphilochidae), Poljoprivreda i Sumarstvo, Titograd, 26, 43–69.
- KARAMAN, G. S., 1980b, Revision of genus *Idunella* Sars with description of new species, *I. sketi*, n. sp. (fam. Liljeborgiidae), *Acta Adriatica*, **21**, 409–435.
- KARAMAN, G. S. and PINKSTER, S., 1977a, Freshwater Gammarus species from Europe, North Africa and adjacent regions of Asia (Crustacea, Amphipoda) Part I. Gammarus pulexgroup and related species, Bijdragen Tot de Dierkunde, 47, 1–97.
- KARAMAN, G. S. and PINKSTER, S., 1977b, Freshwater Gammarus species from Europe, North Africa and adjacent regions of Asia (Crustacea, Amphipoda) Part II. Gammarus roeseligroup and related species, Bijdragen Tot de Dierkunde, 47, 165–196.
- KIM, C. B., 1991, A systematic study of marine gammaridean Amphipoda from Korea, unpublished PhD thesis, Seoul National University, Korea, 442 pp.
- KIM, W. and ABELE, L. G., 1990, Molecular phylogeny of selected decapod crustaceans based on 18S rRNA nucleotide sequences, *Journal of Crustacean Biology*, **10**, 1–13.
- KUDRJASCHOV, V. A. and VASSILENKO, S. V., 1966, A new family Caprogammaridae (Amphipoda, Gammaridea) found in the north-west Pacific, *Crustaceana*, **10**, 192–198.
- LAUBITZ, D. R., 1977, A revision of the genus Dulichia Krøyer and Paradulichia Boeck (Amphipoda, Podoceridae), Canadian Journal of Zoology, **55**, 942–982.
- LAUBITZ, D. R., 1979, Phylogenetic relationships of the Podoceridae (Amphipoda, Gammaridea), Bulletin of the Biological Society of Washington, **3**, 144–152.
- LINCOLN, R. J. and HURLEY, M. H., 1981, The calceolus, a sensory structure of gammaridean amphipods (Amphipoda: Gammaridea), Bulletin of the British Museum of Natural History (Zoology), 40, 103-116.
- Lowry, J. K., 1984, Systematics of the pachynid group of lysianassoid Amphipoda (Crustacea), Records of the Australian Museum, **36**, 51–105.
- LOWRY, J. K. and STODDART, H. E., 1983, The shallow-water gammaridean Amphipoda of the subantarctic islands of New Zealand and Australia: Lysianassoidea, *Journal of the Royal Society of New Zealand*, **13**, 279–394.
- MCCAIN, I., 1970, Familial taxa within the Caprellidea (Crustacea, Amphipoda), *Proceedings* of the Biological Society of Washington, **82**, 837–842.
- NICHOLLS, G. E., 1939, The Prophliantidae: a proposed new family of Amphipoda, with description of a new genus and four new species, *Records of the Southern Australian Museum*, 6, 309–334.
- SARS, G. O., 1895, An Account of the Crustacea of Norway with Short Descriptions and Figures of all the Species, Vol. 1, Amphipoda (Christiania: Cammermeyer), pp. 1–711.
- SCHRAM, F. G., 1986, Crustacea (New York: Oxford University Press), 606 pp.

- SPEARS, T., ABELE, L. G. and KIM, W., 1992, The monophyly of brachyuran crabs: a phylogenetic study based on 18S rRNA, *Systematic Zoology*, **41**, 446–461.
- STEBBING, T. R. R., 1888, Report on the Amphipoda collected by H.M.S. Challenger during the years 1873–76, Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76, Zoology, 29, 1–1737.

STEBBING, T. R. R., 1906, Amphipoda I: Gammaridae, Das Tierreich, 21, 1-806.

- SWOFFORD, D. L., 1990, PAUP, Phylogenetic Analysis Using Parsimony, user's manual version 3 (Champaign, IL: Illinois Natural History Survey), 91 pp.
- VASSILENKO, S. V., 1974, Kaprellidy (morskie, Koizochke) morei SSSR i sopredel'nykh vod, Zoologicheskogo Instituta, Akademiia Nauk SSSR, Opredeliteli po Faune SSSR, 107, 1–288.
- WATLING, L., 1981, An alternative phylogeny of peracarid crustaceans, *Journal of Crustacean Biology*, **1**, 201–210.
- WATLING, L., 1983, Peracaridan disunity and its bearing on eumalacostracan phylogeny with a redefinition of eumalacostracan superorders, in F. S. Schram (ed.), Crustacean Phylogeny, Vol. 1 of Crustacean Issues, F. S. Schram (ed.) (Rotterdam: A. A. Balkema), pp. 213-228.

Appendix 1. Materials and references consulted for scoring characters.

Order Amphipoda Latreille, 1816

Suborder Gammaridea Latreille, 1803

- 1. Family Gammaridae Leach, 1814 Gammarus sobaegensis; Karaman and Pinkster (1977a, b) (Gammarus)
- Family Crangonyctidae Bousfield, 1973 Barnard and Barnard (1983); Holsinger (1977); Holsinger (1978) (Stygobromus)
- 3. Family Lysianassidae Dana, 1849 Orchomene obtusa; Lowry (1984); Lowry and Stoddart (1983); Gurjanova (1962)
- 4. Family Pontogeneiidae Stebbing, 1906 Paramoera koreana; Pontogeneia rostrata
- Family Liljeborgiidae Stebbing, 1899 Liljeborgia hwanghaensis; Barnard (1962) (Liljeborgia); Karaman (1980b) (Idunella)
- 6. Family Synopiidae Dana, 1855 Barnard (1972b)
- 7. Family Stegocephalidae Dana, 1855 Stegocephaloides sp.; Gurjanova (1951) (Andaniexis, Stegocephaloides, Stegocephalopsis, Stegocephalus)
- 8. Family Pardaliscidae Boeck, 1871 Karaman (1974)
- 9. Family Phoxocephalidae Sars, 1891 Grandifoxus bangpoensis; Mandibulophoxus mai; Barnard and Drumond (1978) (several species)
- 10. Family Oedicerotidae Liljeborg, 1865
 Monoculodes koreanus; Bousfield (1973) (Synchelidium americanum); Gurjanova (1951) (Westwoodilla sp.); Sars (1895) (several species); Gurjanova (1951) (several species)
- Family Dexaminidae Leach, 1814 Atylus collingi; Gurjanova (1951) (Dexamine); Barnard (1973b) (Lepechinella); Barnard (1972a) (Paradexamine); Barnard (1966a, b, 1970b) (Guernea); Nicholls (1939) (Prophlias anomalus)

946 Phylogenetic relationships among amphipod subgroups

- Family Ampeliscidae Costa, 1857 Ampelisca brevicornis; Ampelisca misakiensis; Barnard (1960) (Ampelisca); Dickinson (1983) (several species of Byblis and Haploops)
- 13. Family Amphilochidae Boeck, 1872 Gitanopsis koreana; Sars (1895) (Amphilochoides boecki); Barnard (1970a) (several species of Amphilocus; Gitana liliuokalaniae); Karaman (1980a) (Gitanopsis)
- 14. Family Stenothoidae Boeck, 1871
 Stenothoe valida; Gurjanova (1951) (several species); Bellan-Santini (1972) (Thaumatelson herdmani)
- 15. Family Hyalidae Bulycheva, 1957 Allorchestes angusta; Hyale rubra
- Family Talitridae Costa, 1857 *Platorchestia crassicornis*; *Trinorchestia longiramus*; Bousfield (1982b) (several species)
- Family Podoceridae Leach, 1814
 Podocerus hoonsooi; Gurjanova (1951) (Dulichia, Dyopedos, Xenodice frauenfeldti); Laubitz (1977) (Dulichia, Dyopedos)

Suborder Caprellidea H. Milne Edwards, 1830

- Family Caprogammaridae Kudrjaschov and Vassilenko, 1966 Kudrjaschov and Vassilenko (1966)
- 19. Family Caprellidae White, 1847 Caprella penantis; Vassilenko (1974)
- 20. Suborder Hyperiidea H. Milne Edwards, 1830 Bowman and Gruner (1973); Bowman (1973) (Hyperia)