AUSTRALIAN MUSEUM MEMOIR 18

Papers from the Conference on the Biology and Evolution of Crustacea

HELD AT THE AUSTRALIAN MUSEUM
SYDNEY, 1980

Edited by

JAMES K. LOWRY

The Australian Museum, Sydney

Published by order of the
Trustees of the Australian Museum

Sydney, New South Wales, Australia
1983

Manuscripts accepted for publication 1 April, 1982

AUSTRALIA AS A MAJOR EVOLUTIONARY CENTRE FOR AMPHIPODA (CRUSTACEA)

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SUMMARY

The morphology of modern amphipods is used in place of a cogent fossil record to conclude that amphipods existed in the early Mesozoic during Pangaea. A freshwater group called crangonyctids was distributed at that time over most of the continental coagulum. Freshwater amphipods abhor tropical environments so that the modern dispersal of continents has resulted in widely dispersed relict fragments of crangonyctids. North America remains heavily populated with these animals whereas South Africa and Australia are now poorly endowed owing to climate. Eurasia is poorly endowed with crangonyctids because of the later evolution of more successful freshwater amphipods such as gammarids and niphargids, neither of which reached the southern hemisphere. South America lacks any of the mentioned groups, having a freshwater amphipod fauna of unique character except for bogidiellids shared with other world regions.

Marine amphipods also are cold-adapted. This characteristic in part provides a global ecological effect best represented in Australia and known as ends-of-the-earth phenomenon. The warm-temperate region of southern Australia therefore comprises a large isolated reservoir of amphipods dominated by groups poorly represented elsewhere. Parts of certain families have exploded evolutionarily in Australia. These include Phoxocephalidae, Dexaminidae and Urohaustoriidae. Australia is seen primarily as a huge environment capable of containing a diverse assemblage of these taxa and is not necessarily the place of origin for these and other taxa. However, Australia retains the most primitive living phoxocephalid (*Pontharpinia*).

A new classification of amphipods based on fleshy telson is promulgated and criticised. Two new families and two new genera are also created to fill obvious gaps in Australian taxonomy.

A prospectus treats new research needed, especially that which requires morphofunctional investigation.

Introduction

Evidence that Australia is a major evolutionary centre and refugium for both freshwater and marine Amphipoda (Crustacea) is presented in this paper. The evidence thrusts the presumed origins of the group back into the early Mesozoic during the time of Pangaea.

The evolutionary system, dispersal knowledge recently gained about Australian amphipods, and new ideas on classification are all interrelated. Two data bases, on freshwater and marine facts, will be presented here, then discussed and problems raised. The faunule in Australia is summarised and a prospectus treats the many investigations now required to clarify not only certain facts but the tentative conclusions drawn herein. Research to be done in the Australian region is of major importance.

A new subordinal classification of the order Amphipoda based on telson is presented in which the group is reduced to 3 suborders, Corophiidea, Gammaridea, and Hyperiidea, part of the old Gammaridea being removed to join Caprellidea to form the Corophiidea.

Objections to certain hypotheses and alternative explanations for several conditions are provided by the second author, Karaman, in Notes a, b, c, and d in Appendix 2.

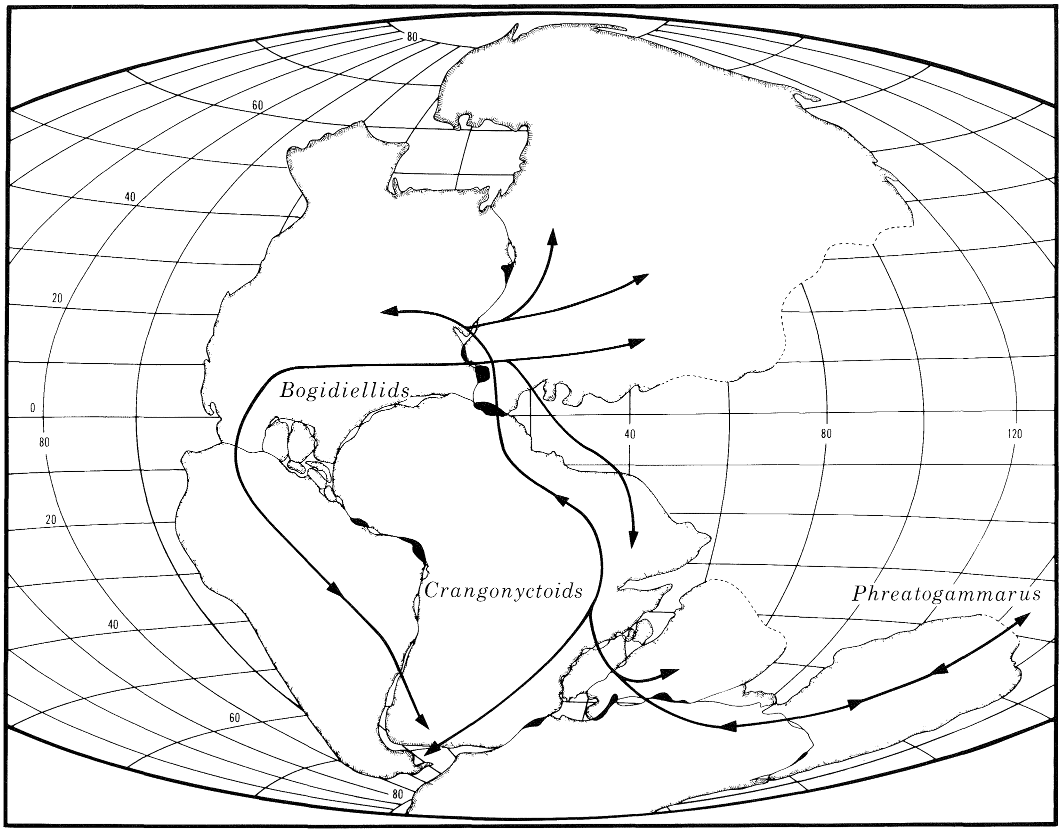

Fig. 1. Pangaea. Hypothetical pathways of amphipod groups based on modern distributional remnants.

Methods and procedures

The adjectival ending "id" refers to a group of amphipods conceivably at the level of family; "oid" refers to a group at the level of superfamily; "in" refers to a group at subfamily level.

The intent of this work is neither to create nor honour nor perhaps misuse many family and superfamily names published by others. Our concept of these categories is almost completely distinct from that of others and we often disagree between ourselves (see Appendix 2). We believe that a cluster to be honoured with a family name (*sensu lato*) should have a positive, describable and keyable distinction from other similar clusters and that all of the members of the cluster be so endowed. Clusters should be monophyletic.

This work borrows heavily from 2 unpublished books, "The Freshwater Amphipoda of the World" by J.L. Barnard and C.M. Barnard, in press, and "The Families and Genera of Gammaridean Amphipoda" by J.L. Barnard and G.S. Karaman, in preparation (since 1973, not yet completed).

Freshwater data base

1. Australia (= Notogaean), South Africa (= Ethiopian), Eurasia (= Palearctican) and North America (= Nearctican) have freshwater amphipods with many characters in common, including the presence of sternal gills. These amphipods are classified by Bousfield (1977) as Crangonyctidae. Several taxa of crangonyctids actually lack sternal gills but can be included in the group by internal goodness of fit through cladistic (descent and apomorphy) or phenetic (similarity) clustering. Actually they can be included by the simple phyletic process of finding their grossly closest morphological relatives which are themselves crangonyctids. Crangonyctids without sternal gills technically fall into the classic family Gammaridae which is restricted by Bousfield (1977) to a narrower content than in earlier times.

2. No modern marine pathways for crangonyctids are known to occur between Australia and South Africa, nor between Australia and Eurasia, nor between South Africa and North America, nor any mixture among these elements (J.L. Barnard, 1972b). In other words, there are no living marine relatives of crangonyctids in the seas around Australia or South Africa. In the context of marine groups identified through an extensive literature there appear to be no possible connections between freshwater crangonyctids of Holarctica and the southern hemisphere by oceanic connections in modern seas.

3. Freshwater amphipods of the gammarid-crangonyctid family group abhor the tropics. They apparently are adapted to cold waters and cold climates. However, a closely descendent group, the bogidiellids, has invaded subterranean habitats in tropical South America. Tropical epigean amphipods are absent in Asia, Africa and Australia at least in rainforest regimes or in the wettest northern parts of Australia. In the South American tropics the family Hyalellidae, with sternal gills independently evolved, has invaded certain epigean habitats. A modern tropical freshwater pathway for gammarids and crangonyctids does not exist because these taxa cannot cross the "Sonoran" deserts nor the equatorial rainforests nor tropical seas. In a few places some marine taxa have emerged into freshwater habitats and have converged towards the gammarid morphology but these apparently can be sorted away from the truly crangonyctid groups.

4. The crangonyctids can be considered to be plesiomorphic to gammarids in light of the general structure of amphipods which seems to have an evolutionary deployment proceeding from morphologically complicated to morphologically simplified (Barnard, 1969). Most of the characters for which one can construct plesiomorphic-apomorphic sequencing proceed from complex to simple and this dominantly fits a parsimonious and logical biogeographic picture. For example, the basic crustacean biramous antennal condition is progressively reduced to uniramous; the basic body segmentation is reduced; the fleshy uncleft telson is progressively laminated and cleft; the mouthparts are progressively degenerated; etc. One must note that amphipods generally are poor material for cladogenesis because of this negative progression (noting Ashlock, 1974).

5. Freshwater amphipods of a group known as austroniphargids occur in Madagascar. They bear coalesced urosomites and supposedly lack sternal gills. They could either be marine crawlouts or more parsimoniously they could be considered descendents of African crangonyctoids. No absurdities in phenetics, cladistics or evolutionary methods are known to prevent this assumption.

6. Freshwater amphipods of India and at least one genus of Australian freshwater amphipods (*Giniphargus*) are likewise assumed to be marine crawlouts because their closest ancestors morphologically and geographically live in the sea. There are very few and poorly studied taxa yet known in this category so that much more information needs to be gathered in this regard.

7. All insular freshwater amphipods from places such as Reunion, Andaman, Java, Bismarck, Hawaii, and Galapagos, can be parsimoniously best related to adjacent marine taxa. These are genera such as *Paraniphargus, Psammoniphargus, Galapsiellus, Anchialella, Rotomelita.*

8. The hadziids, which occur predominantly in limestone aquifers of central America, Caribbean Sea islands (Stock, 1977), margins of Mediterranean Sea and some Pacific coral atolls, have several blind marine species also. This distribution is predominantly Tethyan. A tightly parallel group with parsimonious ancestry in the marine ceradocids (*Ceradocus*) is the weckeliids, which occur only in the Caribbean part of the Tethyan sphere. Their ecology is similar to hadziids.

9. The Pontocaspian basin, today composed of remnants such as the Caspian, Black and Aral Seas has a diverse amphipod fauna. Part of the fauna is clearly of marine origin, genera such as *Corophium* and *Pseudalibrotus* being invaders either directly from the sea or from glacial sluicing which brought them from the shallow arctic sea into the drainage pattern of the Pontocaspian basin (Segerstrale, 1962). *Corophium* may be a holdover from Tethyan eras but if a Tethyan connection was supreme at one time the evidence is now poor. Many other possible marine and brackish Gondoasiatic genera simply left no impact on this basin (for example *Grandidierella* is not represented). The marine influence to us therefore appears to be entirely post-Tethyan, or at least the survivors have that character. The great majority of the fauna is of gammarid morphology, being composed of apomorphic genera from ancestors like *Gammarus* and *Echinogammarus.* But one group, which we call gmelinids, has a fossil ancestry in Miocene imprints (*Andrussovia, Praegmelina*). If these fossils clearly have aequiramous uropod 3 then their gmelinid descendents do not pass through *Echinogammarus* and therefore they form a subsidiary group. They may be an earlier holdover and be in the process of extirpation by the echinogammarids such as *Dikerogammarus* and *Niphargoides.* The sequencing descent is very good in these organisms, so close at times that Karaman and Barnard (1979) implied a large share of the species could be included within a few supergenera, themselves blending together.

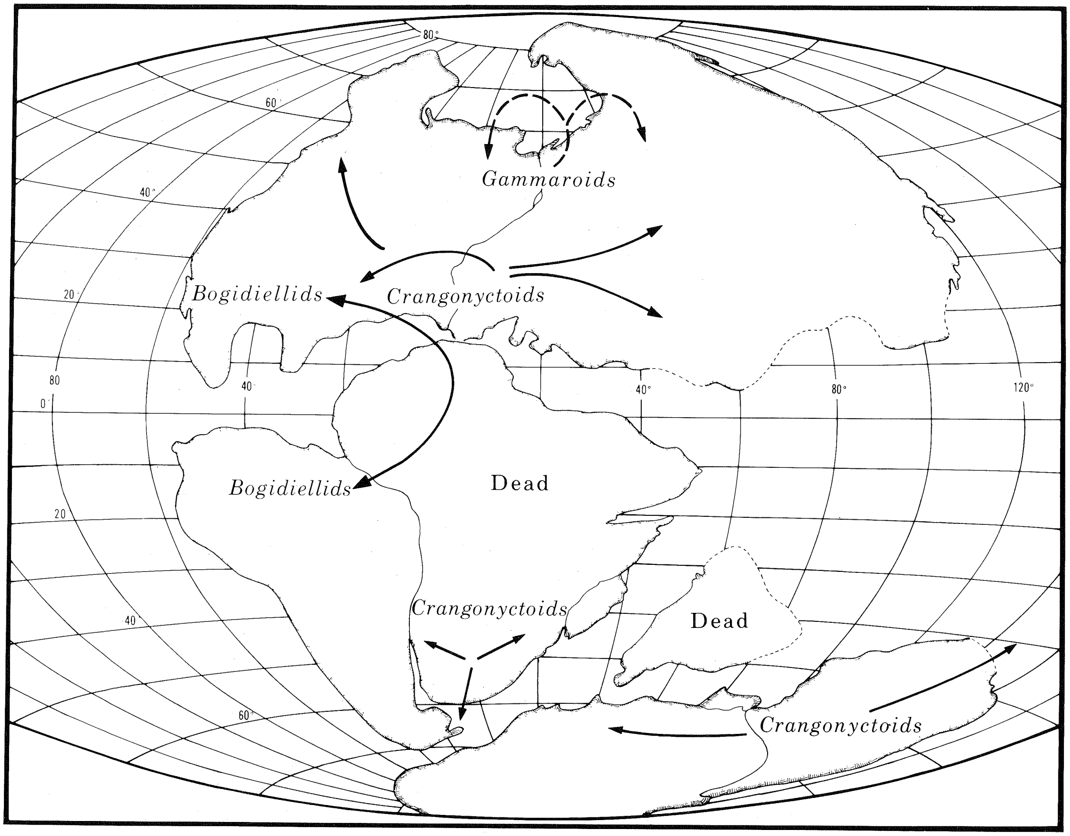

Fig. 2. Later Tethyan era. Crangonyctids now disjuncted. Gammaroid group (or *Gammarellus*) possibly developing now in northern sinuses.

The Pontocaspian amphipods are dominated by fossorial (burrowing) kinds owing to the great shallowness of the system and the high proportion of benthos to water volume. There are many congruencies in morphology between pontogammarids and Phoxocephalidae (Barnard and Drummond, 1978) but the ecological and biogeographic facts are all wrong at present to justify this relationship. Most taxonomists, including Karaman, believe that the congruencies between phoxocephalids and pontogammarids are entirely due to their similar ecological requirements and their remarkable similarities are a result of convergence. Once again, an amazing parallelism has arisen in Amphipoda, similar to that between the west Palearctic gammarids and the Baikalian microcosm.

10. Lake Baikal in Siberia, just north of Mongolia, contains more than 40 genera and about 300 species of gammarids. One of these, *Macrohectopus,* is so bizarre that it may have a distinctive origin but all others can be envisioned as having one ancestor. Again, most taxonomists believe this genus is autochthonous. The Baikalian faunule has diverged into pelagic, nestling, fossorial, and inquilinous kinds of taxa, with pelagic and nestling kinds dominant because of the high proportion of water to benthos in this deep lake (containing 20 per cent of the world's fresh water). The fossorial kinds are so close morphologically to Pontocaspian fossorial types that if they are polyphyletic and simply convergent then little damage would be done internally to the gammarid classificatory system. On the other hand, Bazikalova (1945), Koshov (1963), and others have proposed 4–6 ancestral kinds to the Baikalian amphipod fauna with biogeographic pathways from Pontocaspian and glacial lakes through Siberian ice lakes. Neither alternative, the mono- or the polyphyletic view, is empirically supported at present and these may be only tempests in a teacup.

The immense diversification seen in west Palearctic gammarids out of *Gammarus* and *Echinogammarus* and the fossil *Andrussovia* and *Praegmelina* through various sarothrogammarids, and dikerogammarids, into gmelinids, pontogammarids, and compactogammarids is so overwhelming that to have this repeated in the Baikalian microcosm with results selected by the environment is not difficult to accept.

Marine data base

1. The data bases for Gammaridea presented by Barnard (1962, 1965, 1969, 1976) remain mostly true, having been diversified and strengthened through subsequent description of numerous new taxa in a field (amphipodan systematics) that has exploded in the past decade. This data base shows that at generic level Gammaridea are more poorly developed in the tropics than one might expect (but notice the positive statement of item 2 below and that the taxa of the deepest seas are more apomorphic than those of the upper deep sea just below the continental shelf). In other words, the Bruun (1957) idea of ancient deep-sea taxa being displaced upward by cooling of the deep seas has not yet been disputed, at least in Gammaridea. One major modification now must be added; herein we realign the Amphipoda to make Corophioidea the most plesiomorphic of groups and this adds a strong tropical aspect to normalise the plesiomorphic content of the tropical fauna as in other groups. Taxa orbiting about the old Gammaridae (*sensu lato*) are still considered to be the most plesiomorphic of the Gammaridea but not of the Amphipoda as a whole (but see Note b, Appendix 2).

2. About 68 marine families of amphipods (barring hyperiidean kinds) occur today (J.L. Barnard, 1969, 1977, Bousfield, 1979) (see Appendix 1, taxa marked with *). About 35 of these are believed to be tropically plesiomorphic, whereas most of the remainder have their most primitive members in cold waters (J.L. Barnard, 1976) (Appendix 1, herein, cold taxa marked with †). About one third of the 33 coldwater taxa occur mainly in the deep sea or in cold pelagic waters. The 21 families of hyperiids listed in Bowman and Grüner (1973) could be added to this total. There is also strong coldwater representation in 7 of the 35 tropically plesiomorphic families mentioned above. Therefore Amphipoda are strongly developed in cold waters.

3. In Australia there is strong centrifugal character to 12 of the 68 families, here listed in order from strongest to weakest in focus: Dexaminidae, Phoxocephalidae, Urohaustoriidae, Zobrachoidae, Paracalliopiidae, Exoedicerotidae, Ochlesidae, Phliantidae, certain parts of Podoceridae and Stenothoidae (especially the thaumatelsonins), very weakly Platyischnopidae and Colomastigidae.

Australia is a centre or subsidiary centre for these families because of occurrence of plesiomorphs and/or great diversity of familial components or because of the occurrence of deployment sequences (Fig. 4 shows some of the strongest examples of these taxa). The "ends-of-the-earth" phenomena in marine amphipods discussed by Barnard (1972a, 1972b, 1974, 1976) prevail.

4. Other areas of the world do not have such a broad and sharp focus on families, the following notable exceptions being: Bateidae—Central America; Haustoriidae—New England (North America); Pontoporelidae—North Atlantic; Mesogammaridae, Gammaroporeidae, Anisogammaridae, Dogielinotidae and Najnidae—North Pacific; Hadziidae—Tethyan; Ceinidae—New Zealand; Plioplateidae, Temnophliidae, Kuriidae—South Africa (or Africa). Some of these are also shown on Fig. 4. Urohaustoriidae and Zobrachoidae are new families in press by Barnard and Drummond.

5. The fossil record for amphipods (Hurley, 1973) is confined to (1) Baltic ambers of Eocene age in which are well preserved such taxa as *Paleogammarus balticus* Lucks, a species so close superficially to modern crangonyctids that no justification for the genus can be made apart from great age; and (2) imprints in Miocene Sarmatian sediments near the Caspian Sea, contain taxa completely united to the special elements now living in the modern Pontocaspian basin. No fossils with plesiomorphic content are known. The occurrence of sternal gills on the Eocene amber fossils has not been demonstrated.

6. One genus of corophiidean amphipod, *Paracorophium,* is found in Australia, New Zealand and South America. This genus is largely limited to freshwater and is an exceptional genus in this superfamily, which is composed largely of marine taxa. One assumes the distribution of *Paracorophium* to be a result of continental drift.

Discussion

If the information presented in the data bases above is true the only pathway for crangonyctids between Holarctica and Notogea would have occurred in the Paleozoic or early Mesozoic when continental coalescence occurred at a time often denoted as Pangaean (including Laurasian). At that time the Indian subcontinent was near South Africa, Antarctica and Australia (Fig. 1); South America was pressed near Africa; and Eurasia and America were contiguous. A continuous pathway would have been provided for freshwater animals to disperse elsewhere.

The modern distribution of freshwater amphipods suggests that crangonyctids were widespread in Pangaea, never reached or died out from South America but bloomed in North America (Figs. 2, 3). Owing to severe ecological changes they exist only as remnants in Australia and South Africa. Owing to the evolution of competitive gammarids and niphargids which took hold primarily in Palearctica, crangonyctids have almost reached extinction there (but see Note c, Appendix 2). Only a few species survive in west Palearctica, whereas the east margin of Palearctica retains some highly derived, mostly subterranean crangonyctids such as *Pseudocrangonyx* and *Protocrangonyx.*

Problems: Today freshwater gammarid-crangonyctid amphipods abhor the tropics. One must therefore presume a cool-water pathway between Holarctica and Notogaea existed earlier. Today gammarid-crangonyctid amphipods live in South America only as descendent hypogean bogidiellids; and in India and middle Africa they are extinct. Either the amphipods or Pangaean environmental conditions were different then from what they are today. Just because marine crangonyctids do not exist today we cannot assume they did not exist during Pangaea. Thus, Australian and Nearctic freshwater crangonyctids could be relicts of pandemic marine forms now extinct. This is supported by the lack of primary freshwater fish interchange north to south in the fossil record (Darlington, 1957). The absence of crangonyctids in South America matches the situation in spiders noted by Besch (1969), who thought that South Africa pulled away early. But too many diverse and conflicting distribution patterns that could have been affected by continental drift exist in animal and plant groups so that virtually any desirable solution can be extracted from general biotic data (Keast, Erk and Glass, 1972).

The gammarids and their immediate descendents probably had a Laurasian origin. None has ever been found south of the Sahara or "Sonoran" deserts. A few of them retain or acquired a salt tolerance so that a few species of *Gammarus* and *Echinogammarus* have been able to penetrate into the very shallow seas and their margins in Holarctica. One suspects a case could be made for descent of gammarids from crangonyctids through loss of sternal gills, thereby improving physiological adaptations to osmotic problems such that a few could invade the sea. This may all have occurred during the breakup of Laurasia when so many rift lakes became brackish. Gammarids exploded in southwest Palearctica and escaped to, but poorly bloomed in, Nearctica where crangonyctids have been able to hold on and diversify. In west Palearctica, gammarids (*Gammarus, Echinogammarus*) spun off numerous genera into marginal ecoisolates such as estuaries, pebble-beach aquifers, and the great Pontocaspian basin where dozens of genera were spawned. The salt tolerance again is apparent but we believe that the amphipod fauna of Pontocaspia, apart from the obvious marine imports such as *Corophium,* is strictly of freshwater origin, from gammarids working outward towards salty waters. This is entirely opposite to all other opinions heretofore offered. We think this argument is strengthened by the inability of any gammarids to escape by sea routes outside Holarctica and for any but the most plesiomorphic (*Echinogammarus*) to escape out of the Pontocaspian Basin into the Mediterranean Sea.

Gammarids cannot even compete with their close vicariants, the Anisogammaridae, in the Pacific Ocean. And the anisogammarids have not escaped the North Pacific shallows.

Problems: If Corophioidea (see following chapter) are to be accepted as a good plesiomorphic marine group representing to some extent the best ancestral content of the order Amphipoda, then the direction from corophiideans to gammarideans is well expressed in the *Gammarellus* group where the telson is uncleft but no longer fleshy. *Gammarellus* could, at the very least, form a model for this evolutionary stage. It retains an accessory flagellum and can thus form a mode ancestral to both crangonyctids and gammarids and the various calliopiid-eusirid taxa (the latter mostly marine and showing loss of accessory flagellum but frequent retention of uncleft telson). *Gammarellus* survives today in the icy brackish shallows of the Arctic Ocean and coasts of Mediterranean Sea and Black Sea also. This jogs one's intuitive idea that crangonyctids had a Gondwanan origin from a *Gammarellus-Gammaropsis*-like ancestor, whereas gammarids (*Gammarus*) were spun off evolutionarily from crangonyctids during a brackish cycle through some tectonic rift or sinus borealis. Sites of origin and flow of distribution are therefore contentious at the moment.

Sternal gills are another problem. They occur in various crangonyctids but are lost in highly apomorphic members in both Australia and west America. They also occur in the remote hyalellids of South America and in a few other taxa such as *Sternomoera* (a pontogeneiid) of subterranean Japan and brackish *Pontoporeia* of the North Atlantic Ocean. One may construct an immense tree (not a true cladogram) to get from crangonyctids to hyalellids while retaining sternal gills, but it is preposterous and nonparsimonious. A much simpler system can be envisioned to get from crangonyctids to *Sternomoera* and *Pontoporeia* (indeed we herein remove the pontoporeiids from separate superfamilial status to low position near the gammarids). One must nevertheless conclude that sternal gills have arisen more than

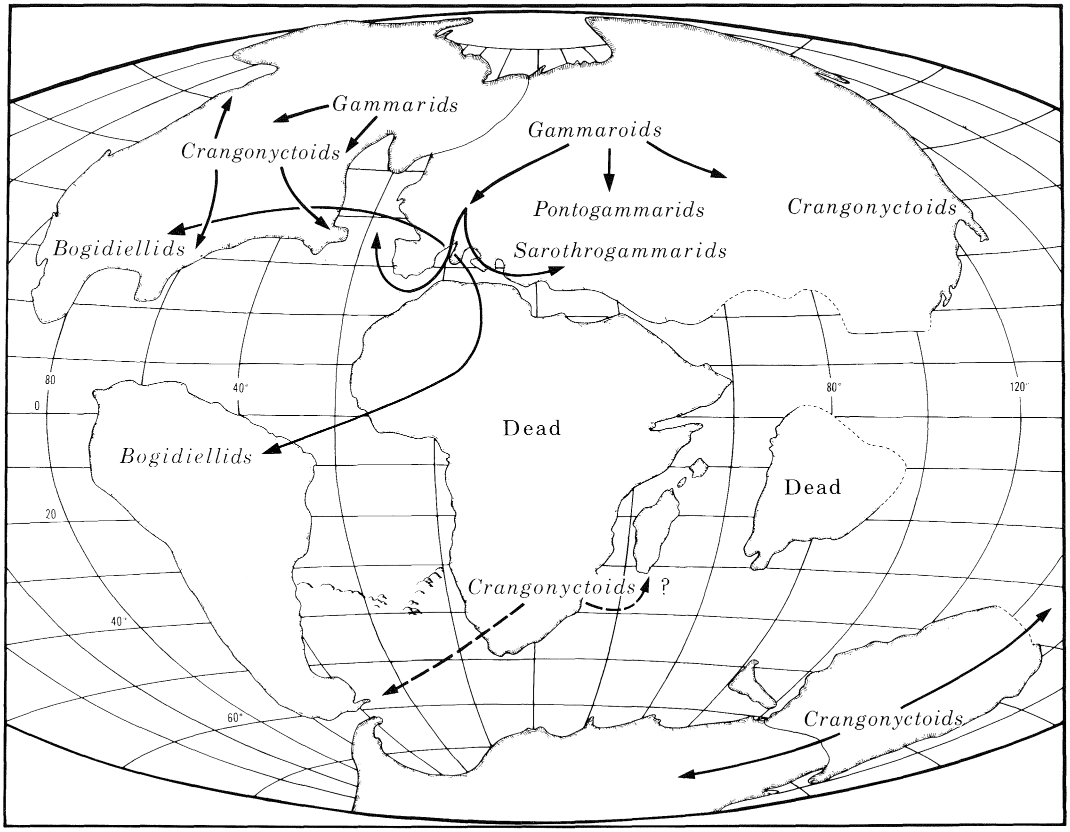

Fig. 3. Crangonyctids close to being split into 4 modern disjunctions (Nearctica, Palearctica, Ethiopian = South Africa, and Notogaean, with outposts in Falklands and Madagascar). Gammaroids will be split later by Nearctic part remaining poorly developed. Bogidiellids probably is a diversely polyphyletic group but one genus, *Bogidiella,* has definite intercontinental distribution as shown.

once in amphipods. Therefore, one must ask if sternal gills did not arise separately in Laurasia and Gondwanaland to produce parallel apomorphs (but see Note c, Appendix 2). We have no answer.

Classification and phylogeny

An evolutionary pattern in gammaridean Amphipoda was produced by Barnard (1969) and then updated by Barnard (1974). A revised classification and phylogeny of Amphipoda were produced by Bousfield (1978). Barnard's evolutionary tree was based on the plesiomorphy of accessory flagellum, 'basic' mouthparts, large coxae and dominance of gnathopod 2 in males, and worked outward towards specialisations such as pygidisation (modification of pleon by losses and fusions) and losses of structures such as in mouthparts and accessory flagellum.

Bousfield's tree and classification are based on the morphology of the reproductive male in which 4 kinds are recognised.

Both schemes recognise what has long been known, that there are corophioid (podocerid) amphipods which are clearly the ancestors of Caprellidae (Note a, Appendix 2), and that there is a greater Talitroidea group, and the following smaller groups conform: oedicerotids, stegocephalids, bogidiellids, and lysianassoids, ampeliscids, etc. Otherwise there is little but occasional similarity in certain juxtapositions. Barnard's scheme is mainly classificatory (rigid definitions) but has the advantage that all members in a group bear the class characters, whereas Bousfield's scheme is mainly evolutionary (indefinable clusters) and has the disadvantage that most of the individuals in a species lack the group characters

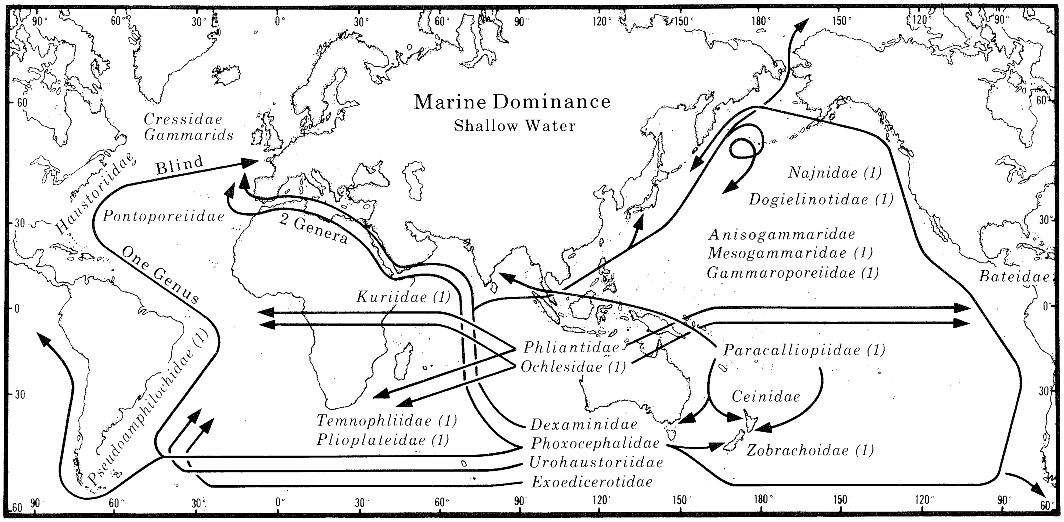

Fig. 4. Marine dominance by families in Australia. All but one North Pacific family are monotypic. Arrows show apomorphic shoots outward from Australia. Most other marine families have much wider distributions than those shown.

(since only terminal males of a few plesiomorphic species in each group have the class characters; other specimens have to be identified by approximations).

Barnard now proposes another scheme which reconstructs the Amphipoda at suborder level but which downgrades the significance of Bousfield's superfamilies and maintains some of the web-like structure of the earlier Barnard schemes.

This proposal recognises the plesiomorphy of the solid fleshy telson in Corophioidea and Caprellidea and joins them together into a suborder Corophiidea (but see Karaman's Note b, Appendix 2). This removes the Corophioidea and the Caprogammaridae from the suborder Gammaridea and leaves it to hold other amphipods. The suborder Hyperiidea is maintained as an assemblage which early lost the palp of the maxilliped and the suborder Ingolfiellidea is placed under Gammaridea as nothing more than a bogidiellin with altered operation of dactyls on gnathopods (but see Note e, Appendix 2).

The order Amphipoda is therefore reduced to 3 suborders on fleshiness (Corophioidea, Hyperiidea) and lamination (Gammaridea) of telson. Forms with fleshy telson are considered plesiomorphic because the laminar telson is considered to be a specialisation abnormal to basic crustaceans. Though not Hennigian, Barnard believes this to be a very workable classification because more than 95 per cent of all amphipod specimens can be classified instantly into suborders.

The classification is presented in Appendix 1 and Fig. 5. It places the suborder Corophiidea first (upper left) as most plesiomorphic, showing that these amphipods represent only a small part of the total order and are divisible into only 2 superfamilies, the Corophioidea and the Caprelloidea, neither of which is worth much because the two groups grade into each other so broadly through the Podoceridae, Caprogammaridae and Caprellidae (with 4 other residual families not mentioned).

The Corophiidae was divided into additional families by Bousfield (1973) and although Bousfield's method has great interest and possible merit we have not reanalysed this situation.

The suborder Gammaridea continues to have the Gammaridae or similar taxa at its base, for example, those taxa that resemble primitive corophioids (such as *Gammaropsis*) except in telson. In other words, gnathopod 2 is fully developed and strongly prehensile (Barnard, 1969) but the telson is laminar, not fleshy.

At the base of the Gammaridae are placed the crangonyctids which contain relict sternobranchiate genera now confined to freshwaters of southern Australia, southern Africa, sketchily in Palearctica and in a blooming condition in Nearctica. Their descendents, various subterranean bogidiellins, occur prominently in the west Tethyan region but especially in South America where orthodox crangonyctids have disappeared. The dispersal of crangonyctids had to occur when all the continents were coalesced as they have no connection whatsoever with marine amphipods. Neither the crangonyctids nor the

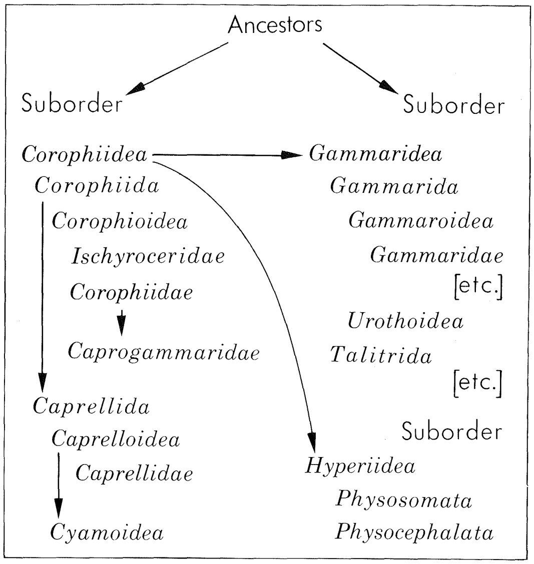

Fig. 5. Higher groups of order Amphipoda.

bogidiellids can be recognised nominally as families because neither of them has technical definitiveness. They simply represent large diffuse clusters of genera which can be interrelated by use of phyletics, phenetics or cladistics when seeking nearest relatives but a crangonyctids without sternal gills or one without notched spines on the palms of the gnathopods is not definitively distinct from gammarids.

New groups of crangonyctids are proposed to clean up the evolutionary classification and to show the phyletic order Barnard conceives. But none of these is a very good group beyond cluster level although one can clearly invoke such 'all or none' characters as bifidation of coxal gill 2 in *Allocrangonyx* to raise it so as to typify family level or the fusion of urosomites to validate Austroniphargidae. Barnard and Karaman (1974) warned against premature formalisation of names but this has not been taken seriously by anybody. We are now beginning to be burdened by many superfluous and even foolish names as high as at superfamily level (for example Niphargoidea, a cluster not worth recognition at more than supergeneric level).

The old Gammaridae, *sensu lato,* of Stebbing's (1906) concept was narrowed stringently by Bousfield (1973, 1978) but in reality about all that has happened is that it has been upgraded to a superfamily (or it could be elevated to a section* "Gammarida" if one could define it in some way). It remains as indefinable as it ever was, regardless of categorical level. Our concept of the contents and their phyletic order is presented in Appendix 1 in very skeletal form, taken from the Barnards' (in press) forthcoming book "The Freshwater Amphipoda of the World". As in almost all other Gammaridea at any level, there is very little complete discontiguity between or among groups. Gaps between clusters are not absolute, only pinched places between clumps. For example, we follow the convention of European specialists that strongly honours the parviramous uropod 3 of *Echinogammarus* as a strong distinction from *Gammarus,* but only with tongue in cheek, because so many bridges occur across this boundary (for example, *Gammarus roeseli* to *Echinogammarus annandalei*).

The old Gammaridae contained some clusters or cluster fragments that can be removed, such as Anisogammaridae, about the only group that can be rigidly defined (with accessory coxal gills), or the Macrohectopinae (based on the mysidiform Baikalian genus *Macrohectopus,* raised to family level by Sowinsky, 1915, honoured by Bousfield, 1978, but here removed to the vicinity of weyprechtiins in the Melphidippidae). Here, Bousfield must be looking at reproductive males while we are looking at gnathopods and telson.

Proceeding past the Melphidippidae, a rather strong cluster, one finds the Hadziidae, a weak cluster with little to recommend it except some ecological facts. Bousfield recognises it as a family in Melitoidea, a superfamily which we here reduce to family or lower level and equate with and then rename as hadziids (which has priority). We can't define this melitid-hadziid group in more than negative terms; the

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*The term "section" is a taxonomic category between suborder and superfamily.

component taxa are largely in the ocean or in Tethyan nearshore limestones and lack coxal gill 7, lack sternal gills, lack calceoli, and lack notched spines on gnathopods (or do they?). Without any positive features they are simply a residue of indefinable things. Some of these leftovers are worse (more degenerate) than others and therefore can be clustered: for example, the *Metacrangonyx* group lacking inner ramus on uropod 3.

There are scarcely any but ecological reasons to recognise hadziids, weckeliids and melitids and out of all of this, the completely negative niphargids, which are only barely definable from eriopisellids, are here reduced from superfamily level to supergeneric level.

Having lost almost everything, coxal gill 7, sternal gills, differentiated gnathopods, notched gnathopodal spines, thick bodies, deep coxae and long inner ramus of uropod 3, and having developed only in a majority of taxa a long article 2 on the outer ramus of uropod 3, a character replicated in eriopisellids and certain crangonyctids, niphargids are the ultimate evolute in the gammaroids, *sensu lato*. Apart from ingolfiellids and crangonyctids (and bogidiellids) they also have the strangest ecology (stygobionts) and perhaps strangest behaviour (errant) of any gammaroids. But they are not a good, definable cluster and there is no evidence they are not simply one more variation on a theme, similar to eriopisas and eriopisellins.

All of the other families listed in sequence in Appendix 1 starting with Eusiridae also form an outline of taxa listed for the purpose of item 2 of Marine Data Base showing total marine families. The Gammaroidea contain a wide assortment of families besides the classical Gammaridae. The Talitroidea contain several families already consolidated earlier in the literature. The remaining families must remain unordered until they are better understood.

The Australian faunule

The freshwater Amphipoda of Australia today are strongly constrained descendents of a fauna common to much of Pangaea of pre-Jurassic times (Figs 1-3). These crangonyctids today bloom in North America, are holding on in east Palearctica but are almost or fully extinct elsewhere, except for the remarkable and primitive New Zealand *Phreatogammarus*. Crangonyctids are antitropical and one would expect their environment to disappear if Australia pushes northward completely into the tropics. In Australia crangonyctids can be described as relicts because one assumes they were much more diverse when the Australian climate was wetter and colder. In Europe they have been largely extirpated by gammarids and niphargids (but see Karaman's Note c, Appendix 2). Australian and South African crangonyctids are very closely connected. As far as is known, crangonyctids never reached South America or went extinct, but may be represented by the apomorphic *Spelaeogammarus* and various bogidiellins which one presumes were also in existence and distributed among the continental fragments during Pangaea. The austroniphargids of Madagascar have the appearance of apomorphic crangonyctids.

Approximately 12 of the 68 major family groups of so-called gammaridean amphipods in the sea have a strong focus on Australian shores, especially in the warm-temperate outpost of the southern half (Fig. 4). This may both be a place of action and a refugium for the remnants of evolutionary deployment in all of certain families and subdivisions of other families. No other marine place on earth holds even half as many such family centres; of course, a significant share of the marine families is either subcosmopolitan or confined to cold waters. This makes the Australian dominance more superior.

We have reconstructed the order Amphipoda on the basis of telsonic apomorphy to proceed from a primitive suborder Corophiidea, containing former gammarideans with fleshy telson and including the Caprellidea, outward to the newly restricted Gammaridea, from which the corophioids have been removed (Fig. 5). The Ingolfiellidea are sunk into the Gammaridea and the Hyperiidea are retained as an early branch from Corophiidea in which the telson retains more of its plesiomorphy than does the average gammaridean telson and in which the maxillipedal palp is lost. New taxa described are Paracalliopiidae, Exoedicerotidae, and *Austrocrangonyx* (Appendix 3). We have also proposed a system of evolutionary deployment within the section Gammarida, distinct from the Bousfieldian system (Appendix 2 and Fig. 6). Much of this is based on knowledge of Australian taxa.

Prospectus

1. Continue study of morphology, function and ecology of crangonyctoids to find proof whether or not Nearctic and Notogaean taxa are homologous or monophyletic or at least sister groups with a common ancestor.

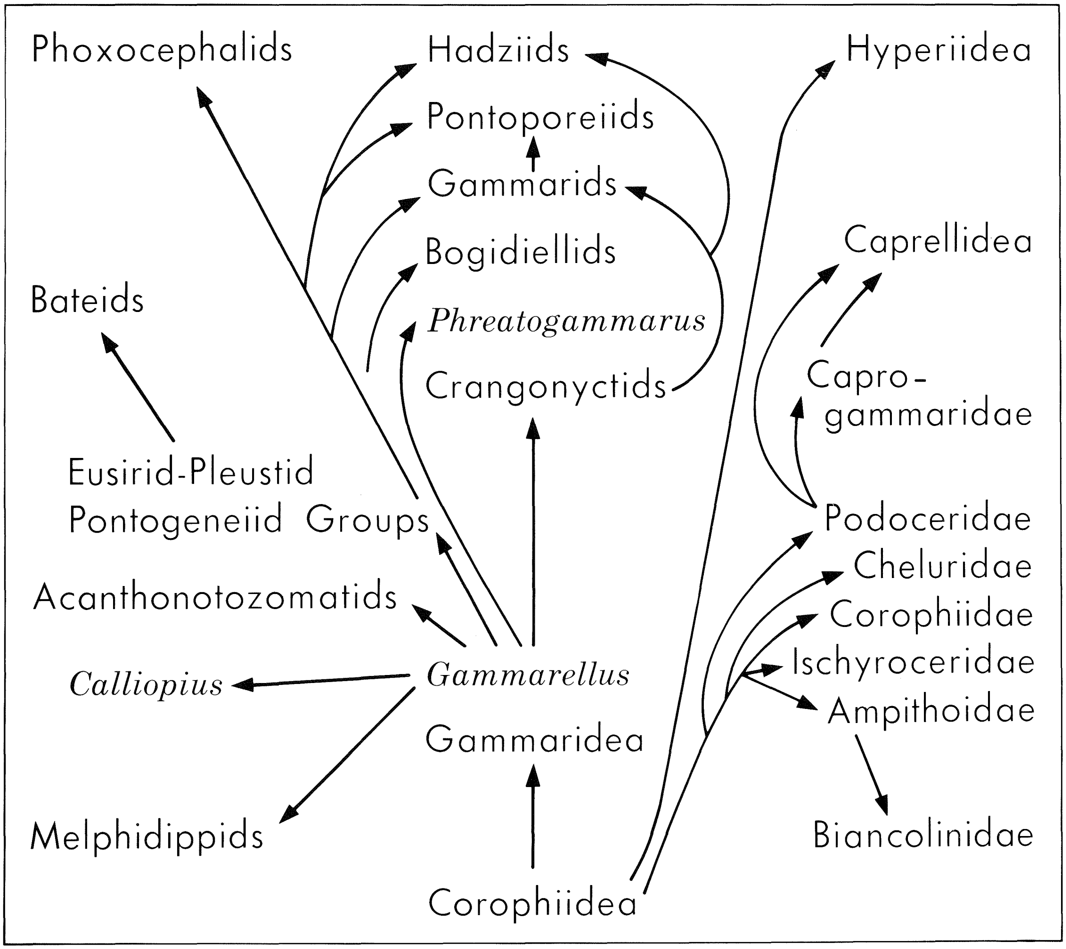

Fig. 6. Tree of relationships showing mostly primitive amphipod groups. Many apomorphs such as *Talitroidea* are omitted. Made to show total contrast with tree of Bousfield (1978).

2. Work out a theory of the development of sternal gills in amphipods. Are sternal gills of crangonyctoids and hyalellids and other amphipods homologous or are they structurally distinct and of differing origins? How can apomorphic species of *Stygobromus* survive without sternal gills? Drummond (*in litt.*) has suggested to us they may be mainly osmotic rather than respiratory as in certain insects. How useful are they to the species known to have them? Can they be removed and not affect survival?

3. Develop ecological theory on sequential relationships between crangonyctids and gammarids. Is one or the other plesiomorphic or are they sister groups with a common ancestor? Develop a model of an ancestor and its ecology, especially its osmotic problems and potential.

4. How are gammarids better adapted than crangonyctids in west Palearctica and why are gammarids so much less well adapted than crangonyctids in Nearctica? Is this entirely the late arrival of gammarids?

5. Reconstruct all osmotic sequencing and other data to test the hypothesis that marine species of *Gammarus* have ultimate freshwater ancestry. Ditto for various Pontocaspian taxa.

6. Study the functional reasons for tropical antipathy in freshwater gammarids. Make ecological comparison between general gammaroid facies and talitroid facies (the freshwater hyalellids of Neotropica).

7. Intensify study of the rare tropical freshwater gammarids such as *Indoniphargus* and

Paraniphargus and in the former make ecofunctional and morphologic analyses seeking links to crangonyctoids. The purpose is to determine if *Indoniphargus* is a relict of Gondwanan crangonyctoids. How do marine taxa such as *Paraniphargus* and *Rotomelita* so easily invade freshwater? *Paracalliope,* a non-gammarid but potentially remote descendent of crangonyctoids, needs strong focus. That genus may also be interpreted as a freshwater relict of the basal stock near marine Oedicerotidae.

8. Focus on *Phreatogammarus,* the New Zealand endemic with 3 species. Do the many generalised plesiomorphic characters imply a transitional mode between marine and freshwater crangonyctoids, or is *Phreatogammarus* simply a relict now moving outwards to the sea on an impoverished archipelago?

9. Is the generally low generic diversity (and relatively low morphologic diversity) of Notogaean-New Zealand-South African-Falklandian crangonyctoids evidence of eternal Gondwanan stagnation of environment? Balance this diversity against the similar low Nearctic diversity and then compare to the Baikalian explosion in gammarids. West Palearctic gammarid diversity, though reduced recently by us through synonymies, is also very striking. Are these diversities simply the result of Hennigian commonness or (more probably) certain favourable ecological circumstances?

10. Balance the roots of stenothermy and competition in assessing the reasons for tropical abhorrence in amphipods. This abhorrence in epigean forms is close to 100 per cent (except hyalellids, one tropical genus so far) but at generic level it is also rather high in marine shallows. Is there such a thing as stenothermy—a genetically controlled intolerance of tropical waters for thermal reasons—or is there a stenocompetitive factor also involved? To what extent do these factors explain the absence of amphipods in African rift lakes? One must note generally that amphipods are of low diversity in freshwater lakes other than Baikal, Titicaca, Ohrid and Pontocaspia.

11. Determine the lowest thermal limits of a cold era fossil pathway between Laurasia and Gondwana during which time freshwater amphipods could migrate between Nearctica and Notogaea.

ACKNOWLEDGEMENTS

We thank the following assistants and illustrators for their help over several years: Carolyn L. Cox, Marisa C. Consoli, Irene F. Jewett, Elizabeth B. Harrison and Janice Clark. Dr S. Dillon Ripley, Secretary of the Smithsonian Institution, gave us several valuable ideas.

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APPENDIX 1, GROUPS OF AMPHIPODS

Nomenclature often restricted to "in", "id" and "oid" endings so as not to create or submerge taxa; comments in parentheses show subordination of groups considered by Bousfield (1978) to be situated at higher level. * = Marine Family Group; † = Cold Centre.

- Suborder Corophiidea
  - Superfamily Corophioidea (at best gradational)
    - *Corophiidae (Aorids, Photids, Isaeids)
    - *Ischyroceridae
    - *Ampithoidae
    - *Biancolinidae
    - *Cheluridae
    - *Podoceridae
    - *Caprogammaridae
  - Superfamily Caprelloidea (at best gradational)
    - *Caprellidae (and 4 residual families)
    - *Cyamidae
- Suborder Gammariidea
  - Superfamily Gammaroidea
    - Crangonyctids (reduced from superfamily level)
      - Phreatogammarins (new) (Phreatogammarus group of Bousfield)
      - Paramelitins
      - Neoniphargins (reduced)
      - Sternophysingins (new)
      - Crangoncytins (reduced)
      - Pseudocrangonyctins (new)
      - Allocrangonyctins (new)
      - Austroniphargins (new)
      - Spelaeogammarins (new)
      - Bogidiellins (reduced from superfamily level)
    - Gammaridae
      - Gammarins (Gammarus group)

  - Brandtia group
  - Echinogammarus group
  - Metohia group (vaguely Typhlogammaridae of Bousfield)
  - Fluviogammarus group (artificial)
  - Acanthogammarus group (Acanthogammaridae of Bousfield)
  - Dikerogammarus group
    - Gmelina subgroup
    - Dikerogammarus subgroup
  - Pontogammarus group (Pontogammaridae of Bousfield 1978)
    - Pontogammarus subgroup
    - Compactogammarus subgroup
  - Cardiophilus group (gradational) (Behningiella-Zernovia group of Bousfield)
  - †*Pontoporeia group (reduced from superfamily level)
  - Macropereiopus group
  - Micruropus group
  - Hyalellopsis group
- †*Mesogammaridae
- †*Gammaroporeiidae
- †*Eoniphargids (new)
- †*Anisogammaridae
- †*Melphidippidae
  - Weyprechtiins (new)
  - Cheirocratins (new)
  - Hornelliins (new)
  - Megaluropins (new)
  - Argissins
  - Melphidippins
  - Macrohectopins
- *Hadziids
  - Ceradocins (new)
    - Ceradocus group (or to include Paraweckelia subgroup)
    - Paraceradocus group
    - Maera group
      - Maera subgroup
      - Elasmopus subgroup
      - Beaudettia subgroup
    - Parapherusa group
  - Ceradocopsins (new)
  - Gammarellins (new)
  - Weckeliins (new) (founder is Paraweckelia subgroup above)
      - Paraweckelia subgroup
      - Weckelia group
  - *Hadziins
  - Metacrangonyctins
  - *Melitins
    - Melita group
    - Eriopisella group
    - Salentinella group
    - Pseudoniphargus group
    - Niphargus group (Niphargoidea and Niphargidae of Bousfield)
- †*Eusiridae (= Calliopiidae, Pontogeneiidae)
- †*Bateidae
- †*Pleustidae
- †*Carangoliopsidae
- †*Laphystiopsidae
- †*Acanthonotozomatidae (= Paramphithoidae) (= Amathillopsidae)
- *Urothoidae
- †*Phoxocephalidae
- *Platyischnopidae
- *Urohaustoriidae (new)
- †*Haustoriidae
- †*Zobrachoidae (new)

Superfamily Talitroidea

*Hyalidae
*Hyalellidae (also has freshwater taxa)
Talitridae
†*Dogielinotidae
†*Najnidae
†*Ceinidae
Chiltoniinae
*Plioplateidae
*Phliantidae
*Kuriidae
†*Temnophliidae
Unordered families
*Liljeborgiidae
*Sebidae
†*Lysianassidae
†*Synopiidae
†*Pardaliscidae
†*Stilipedidae
†*Hyperiopsidae
†*Astryridae
†*Maxillipiidae
†*Vitjazianidae
†*Dexaminidae (submerging all other dexaminoids)
*Colomastigidae
*Ampeliscidae
†*Exoedicerotidae (new)
†*Oedicerotidae
†*Paracalliopiidae (new)
†*Stegocephalidae
†*Ochlesidae
†*Lafystiidae
†*Pseudamphilochidae
*Amphilochidae
†*Pagetinidae
*Nihotungidae
*Leucothoidae
*Anamixidae
*Stenothoidae (= Thaumatelsonidae)
†*Cressidae

APPENDIX 2, KARAMAN'S ANTITHESIS

Note a: Karaman believes that Caprogammaridae do not support the opinion that Corophioidea are ancestral to Caprellidea; he remarks they are close to Podoceridae but Barnard puts Podoceridae in the Corophioidea despite certain problems such as absence of tube-forming glands in various taxa. Barnard remarks that we may simply be failing to communicate to each other that Podoceridae are corophioideans.

Note b: Karaman does not accept the theory of telsonic fleshiness having any high taxonomic validity. The telson is so variable even within one genus that its value is questioned. For example, *Niphargus duplus* has a fleshy telson in a genus otherwise defined as having a laminar telson; in *Bogidiella* the telson has progressed and regressed from fleshy to laminar; certain talitroids have a fleshy telson. Karaman continues to accept the standard classification within amphipods, 4 suborders of equivalent status, Hyperiidea, Gammaridea, Ingolfiellidea and Caprellidea. Caprogammaridae form the link between Gammaridea and Caprellidea. Corophioidea must be retained in Gammaridea. They are not the oldest of living amphipods and are only one additional adaptation of primary gammaridean amphipods with highly specialised characters. There are no fossil records to substantiate any theories of evolution within amphipods.

Note c: Karaman believes the opposite; crangonyctids have arrived in Europe much later than gammarids. Most crangonyctids, especially *Synurella,* are now expanding because of their high vitality and resistance to variables in oxygen tension and temperature and other exigencies of subterranean life.

For example, certain crangonyctids have recently been imported by humans from America to England and Holland and are expanding. Probably crangonyctids arrived in America first but gammarids arrived in Europe first. This explains the differing dominances of the groups.

Note d: Variability within amphipod genera is high; for example, coxal gill 7 is present or absent within the basic European genus *Echinogammarus* and this is just one of the many anomalies within amphipods that prevent any clear classification in higher categories.

Note e: Karaman states that Ingolfiellidea are not as close to Gammaridea as they seem to be at first glance. Ingolfiellidea are well-defined in the special shape of gnathopods 1-2, having coalesced with the head the first and sometimes the second thoracic segments and often having articulate ocular lobes in marine species. In contrast there are so many other ill-defined amphipod groups that it is inappropriate now to deal with ingolfiellids in this way.

APPENDIX 3, NEW TAXA

Exoedicerotidae, new family

Type genus: *Exoediceros* Stebbing, 1899.

Composition: *Exoediceropsis* Schellenberg, 1931; *Bathyporeiapus* Schellenberg, 1931.

Diagnosis. Gammaridean Amphipoda with urosomites 1-3 separate, pereopod 7 elongate as in Oedicerotidae, dactyl elongate and setose; head ordinary (not galeate); eyes 2 and fully lateral. Accessory flagellum vestigial or absent, antennae of general gammaroid form, often with calceoli on flagella in one or both sexes. Mouthparts of primitve form, thus with all palps present and fully articulate or divided, all medial setae present; inner lobes of lower lip present. Gnathopods sexually diverse, wrists lobate or not, mittenform or not, palms obsolescent or poorly defined. Coxae overlapping, medium to elongate, sometimes variable between the sexes. Pereopods 3-4 with vestigial dactyls; except for pereopod 7 no pereopods with fossorial mechanisms. Pleopods and peimera ordinary. Outer rami of uropods 1-2 not shortened, rami well spinose. Uropod 3 magniramous, aequiramous, peduncle elongate, rami slender, lanceolate. Telson laminar, leaf-like, entire. Coxal gills sac-like, subovate, oostegites narrow, setose.

Relationships. Like Paracalliopiidae but dactyls of pereopods 3-4 vestigal, outer rami of uropods 1-2 not shortened, urosomites all free. Like Oedicerotidae but eyes paired and lateral. *Metoediceros* Schellenberg (1931) is like this taxal group but uropod 3 is severely reduced.

Paracalliopiidae, new family

Type genus: *Paracalliope* Stebbing, 1899. Unique.

Diagnosis. Gammaridean Amphipoda with urosomites 2-3 fused together, pereopod 7 elongate as in Oedicerotidae, dactyl elongate and setose; head ordinary (not galeate); eyes 2 and fully lateral. Accessory flagellum vestigial or absent, antennae of general gammaroid form, with calceoli on both flagella in one or both sexes. Mouthparts of primitve form, thus with all palps present and fully articulate or divided, all medial setae present; inner lobes of lower lip present. Gnathopods sexually diverse, wrists lobate, in female very small, mittenform, in male of enlarged mittenform kind, hands thus softly ovate, palms poorly defined except by unarmed corners. Coxae overlapping, medium to elongate, variable between the sexes (coxae 2-4 elongate in female). Pereopods 3-4 with normal dactyls; except for pereopod 7 no pereopods with fossorial mechanisms. Pleopods and epimera ordinary. Outer rami of uropods 1-2 slightly shortened, otherwise well spinose; uropod 3 magniramous, aequiramous, peduncle elongate, rami slender, lanceolate. Telson laminar, leaf-like, entire. Coxal gills sac-like, subovate, oostegites expanded, setose.

Relationships. Like Exoedicerotidae but dactyls of pereopods 3-4 well developed, urosomites 2-3 fused.

Austrogammarus Barnard and Karaman, new genus

Type species: *Gammarus australis* Sayce, 1901.

Diagnosis: Urosomites occasionally with transverse posterodorsal setation. Rostrum weak to obsolescent, lateral cephalic lobes weakly projecting, subrounded. Eyes potentially present or absent.

Antennae 1-2 elongate, antenna 1 longer than 2, ratio of peduncular articles generally = 22:15:7, accessory flagellum 3-6 articulate. Antenna 2 usually bearing paddle-shaped calceoli (at least in male).

Ratio of mandibular palp articles generally = 7:20:17, article 3 weakly falcate, setae = BDE. Labium lacking inner lobes. Maxillae medially setose, inner plate of maxilla 1 triangular, fully setose medially, outer plate with ?7 spines, palps ?symmetric. Inner plate of maxilla 2 with oblique facial row of setae. Maxillipedal palp articles 2-3 densely setose laterally or ventrally.

Coxae 1-4 elongate, strongly setose, coxa 1 not expanded below, not prominent, coxa 4 lobate, coxa 5 much shorter than 4. Gnathopods 1-2 of medium size, alike but male gnathopod 2 slightly enlarged and with shortened wrist, article 5 of gnathopod 1 and female gnathopod 2 as long as article 6, poorly lobed, article 6 alike in both pairs, palms weakly oblique, lacking bifid spines.

Pereopods 5-7 not elongate, article 2 weakly expanded, ovate to pyriform, lobed or unlobed, dactyls not spinose.

Epimera lacking vertical rows of setae on lateral faces. Rami of uropods 1-2 extending subequally, margins spinose, uropod 2 ?with basofacial armaments. Uropod 3 weakly extended, variramous, peduncle short, outer ramus 2-articulate, article 2 short, inner ramus generally reaching to M. 67 on article 1 of outer ramus in male but only to M. 50 in female. Telson short, cleft to base, lobes tumid, with dorsal and apical spination.

Variants. Anterior coxae often with posteroventral spines; peduncle of uropod 2 often setose.

Relationships. Differing from *Phreatogammarus* in the diverse rami of uropod 3 (they are unequal in size and armaments), short article 1 of mandibular palp and poorly spinose palms of the gnathopods; from *Paramelita* in the diversity of male and female gnathopods; longer inner ramus of uropod 3, more strongly setose maxillae and lack of vertical facial rows of epimeral setae. Differing from *Crangonyx* in the elongate inner ramus of uropod 3, fully cleft telson and absence of bifid spines on the gnathopodal palms.

Species: *australis* (Sayce, 1901); *haasei* (Sayce, 1902); Australia, Victoria, epigean, 2.

Austrocrangonyx Barnard and Karaman, **new genus.**

Type species: *Gammarus barringtonensis* Chilton, 1916.

Diagnosis: Like *Austrogammarus* but uropod 3 fully parviramous; maxillae poorly setose medially.

Variants. Accessory flagellum only 3-4-articulate; inner plate of maxilla 1 with only 3-7 setae; article 2 on outer ramus of uropod 3 present or absent; eyes occasionally absent.

Relationships. Differing from *Paramelita* in the similarity of male and female gnathopods and absence of facial epimeral setae.

Species: *antipodeus* (G.W. Smith, 1909): *barringtonensis* (Chilton, 1916); *mortoni* (Thomson, 1893); *?niger* (G.W. Smith, 1909); *ripensis* (G.W. Smith, 1909); Southeastern Australia and Tasmania, epigean to hypogean, 4 species and one probable species.