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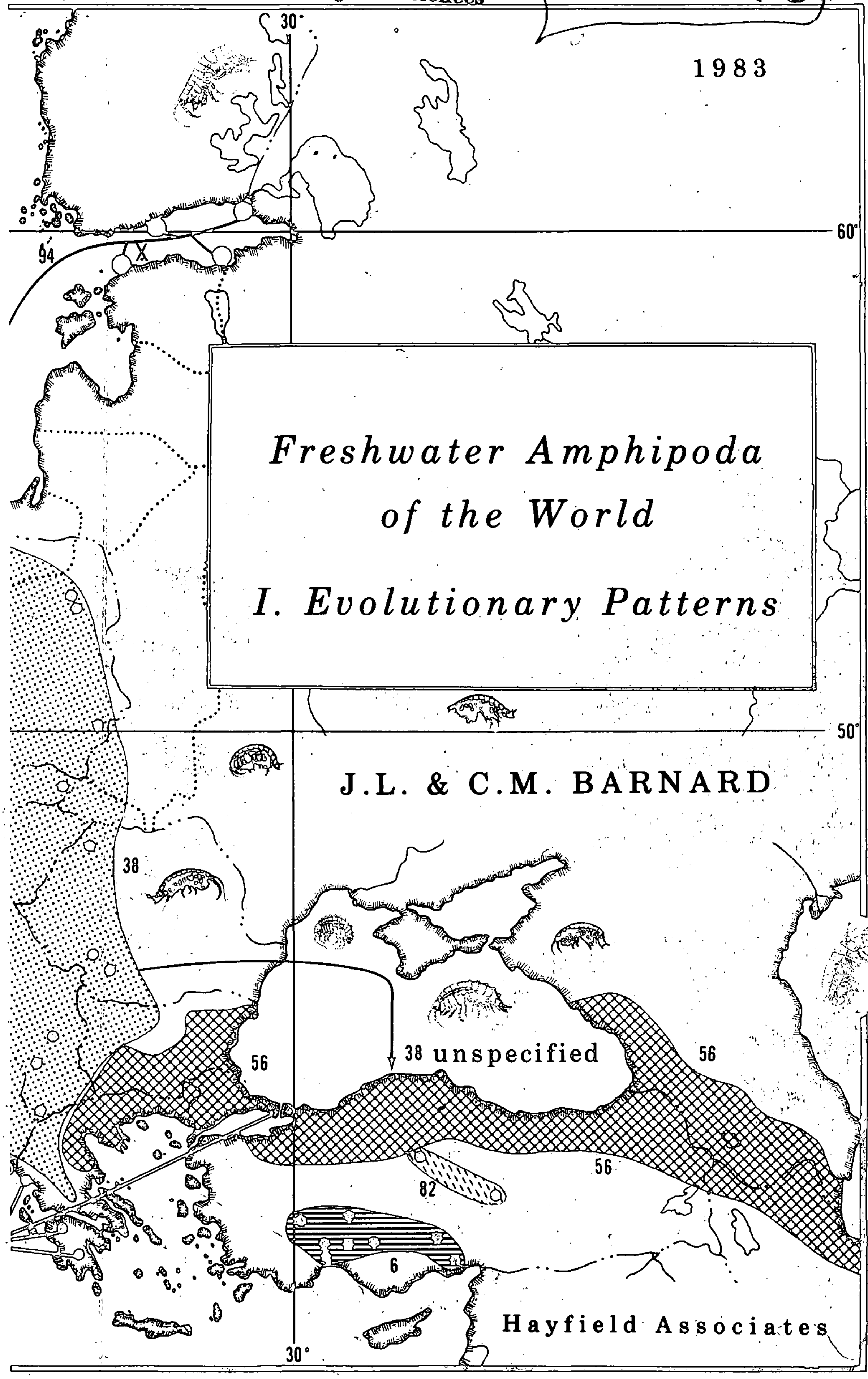
Maps, figures + discussions

104



1983

Freshwater Amphipoda of the World

I. Evolutionary Patterns

J.L. & C.M. BARNARD

Hayfield Associates

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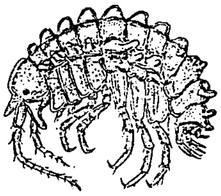

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1983 May 10 J L Barnard

ABSTRACT

Barnard, J. Laurens and Charline M. Barnard. Freshwater Amphipoda of the World: I, Evolutionary Patterns. II, Handbook and Bibliography. In 2 volumes. Hayfield Associates, xix + 830 pages, 50 figures, 7 graphs, 98 maps, 12 tables. 1983.--Amphipoda of the family formerly called Gammaridae (here called Section Gammarida) form the bulk of freshwater species throughout the world. They are highly diverse and dominant in Palearctica but decline progressively in Nearctica, Notogaea, Neotropica, Ethiopia and Paleotropica. The reasons for this pattern are proposed to be a result of vicarience and adaptation. Amphipoda are poorly adapted to the tropics, whether in freshwater or the seas. They are thus cold adapted. Through continental drift the freshwater species lost their habitat in Australia, probably in southern Africa and perhaps never gained it in South America. We propose that Amphipoda had attained their present morphological advancement by the late Paleozoic. The best explanation for their present distribution in freshwaters is found by pandemic dispersal during continental coalescence in the era of Pangaea. Corophiidans, not Gammaridans, are proposed to be the more primitive members of the order; but Gammaridans largely radiated in freshwater and have not been very successful in the oceans.

The massive amphipod fauna of Lake Baikal is believed to have originated mainly from ancestors derived from early Crangonyctoids and, though this derivation may have been associated remotely with brackish water in early tectonic gulfs, the major evolutionary deployment has been in freshwater from strictly freshwater ancestors. The derivative and widely common west Palearctic Gammarus scarcely differs from Baikalian genera and is believed to be an entirely freshwater product; its modern marine species are believed to be emigrating from freshwaters into the sea. In this same way the diverse PontoCaspian fauna had a freshwater ancestry and never adapted to the oceans sufficiently to populate the Mediterranean; the drying of that basin in the Pliocene affected only slightly some Niphargids and Sarothrogammarids that otherwise survived elsewhere. The main PontoCaspian amphipod fauna is believed therefore to be a relict of the sea.

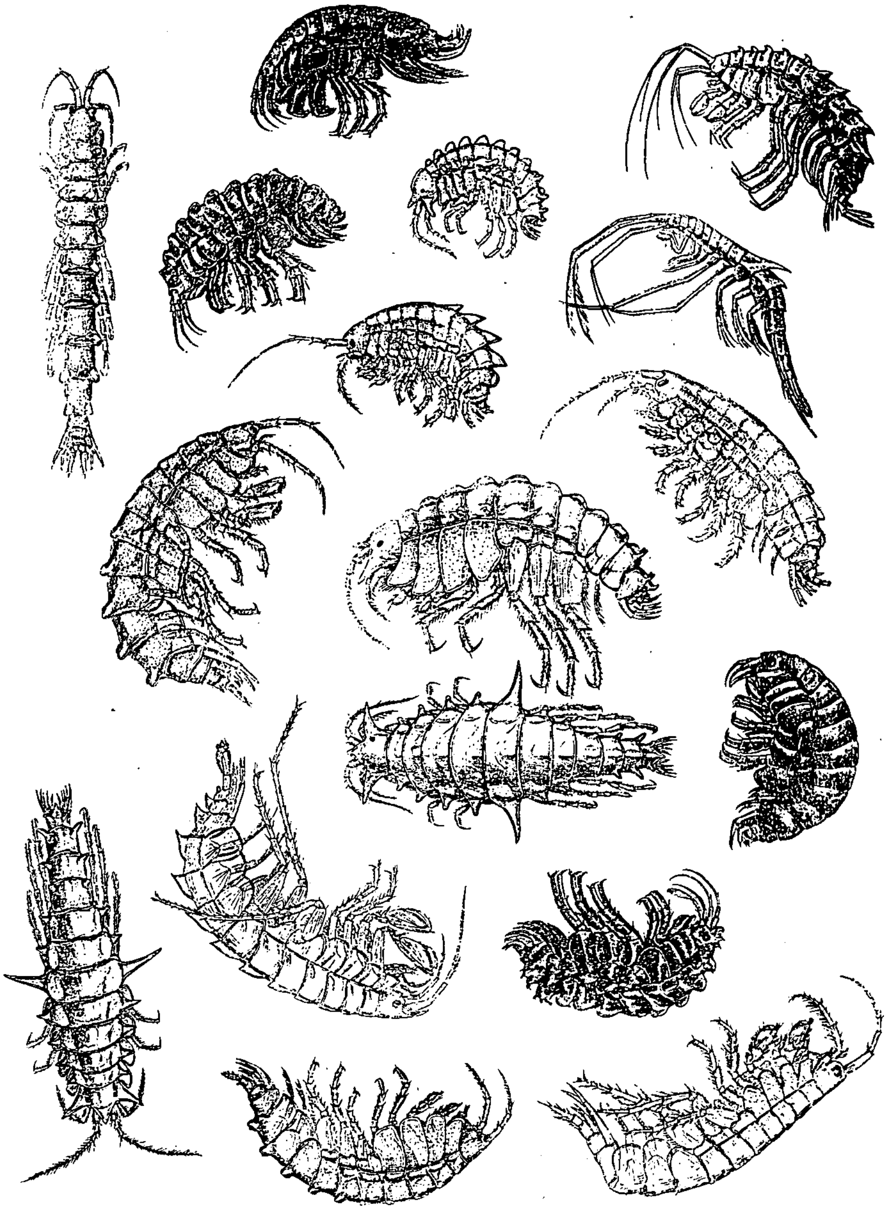
This treatise contains a fully developed generic Handbook to the world Gammarida with phyletic and geographic keys, nomenclature and diagnoses, and with all major characters and lines of diversity illustrated. Each genus has a full list of species, major references, and subspecies. A newly invented system of geographic reporting is given so as to describe the distribution of every species. Maps of most species distributions outside of Baikal and the PontoCaspian are presented. Appendices include lists of Baikalian and PontoCaspian taxa and nomenclatural indexes for Baikal. A bibliography of 1735 citations covers the taxonomy, systematics, biogeography and evolution of freshwater amphipods since 1758.

Dedicated to the pioneers, Benedict N. Dybowsky and Stanko Karaman

Table of Contents

Genera discussed in each section placed in brackets.

Figure 1 is on page 18
Other Figures, Graphs and Maps Fall at the End of Part I (this volume).
See Notes on Figures, Graphs and Maps at end of Table of Contents
LEGEND for Figures is on Graph 5, page 257



Freshwater Amphipoda of the World, Part I, Evolutionary Patterns

By J. Laurens Barnard* and Charline M. Barnard*

Introduction

Amphipoda of the family Gammaridae (sensu lato) contain some of the most primitive living members of the order. The group is very large (210+ genera and 1350+ species) and is mainly distributed in fresh waters of the world (Table 1). Only 50+ genera and 350+ species occur in the seas. More than half of the taxa (almost 110 genera and 900 species) occur in the freshwaters and inland seas of Palearctica and almost 30 percent of these species occur in Lake Baikal (45 genera and 262 species). The taxonomy of this group grows ever more complex as new taxa are discovered and older taxa are found to be described inadequately. The literature is scattered through hundreds of articles, many of which are difficult to obtain except by resident biologists in the country of origin. The most recent monograph of the group was written by Stebbing (1906) in his overview of all Gammaridea and is now severely out of date. The marine genera were treated by J.L. Barnard (1969c) in his overview of marine Gammaridea but this work is also out of date owing to the rapid increase of study in Amphipoda as a whole. An index to the taxa of the group (J. L. Barnard, 1958c) now needs hundreds of alterations and additions in nomenclature. A new index is in preparation by J.L. Barnard and C.M. Barnard and a new generic monograph by Barnard and Karaman but these efforts will not be ready until the mid 1980s. Bousfield (1977) presented a new and partly valuable classification of the group in outline form.

The diffusion of taxonomic knowledge in this group not only frustrates taxonomists but must prevent other biologists from studying many important topics about these animals and from using them as models and subjects in the study of ecological problems and especially as tools in impact surveys of environment. Amphipods are a very conspicuous and important part of many freshwater and marine ecosystems.

The purpose of this essay is to present some ideas about the overall evolutionary system in the group and to set this in a geographic framework. The old idea that freshwater Gammaroid amphipods are of direct marine origin is overturned in favor of the idea that the Crangonyctoid and Gammaroid groups, though remotely marine, descended from inherently freshwater Paleozoic ancestors. Their freshwater inhabitation and evolutionary character are very old, but their extreme thermophoby prevents their expansion out of Holarctica and cool Notogaea. The taxonomy of the group is reordered. In this process many problems requiring study are focused upon, to which taxonomists, and especially other biologists in ecology, functional morphology and physiology, should be alerted.

More specifically, the purposes of this paper are to describe the kinds of characters found in amphipods, to increase attention on what heretofore have been considered to be minor or obscure characteristics, and to outline the kinds of information needed by taxonomists to understand the functional morphology of various attributes, thereby increasing their

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analytical acumen as to the evolutionary flow of adaptations. An evolutionary pattern is propounded based on progress from complex to simple morphology or from least to most specialized (plesiomorphic to apomorphic, i.e., ancestral to derived) in as parsimonious a fashion as possible, by employing the thesis that once an attribute is lost or severely altered, it cannot be reinstated in precisely the original condition (irreversibility of evolution).

This work had its first stirrings as a summary for American biologists who generally have ignored this topic, one presumes largely because its major sources are in languages other than English.

We are aware that this work, finished in August, 1979, will be outdated by the time it is published. Nevertheless, we wanted to discuss the state of Gammaridan taxonomy at the point found herein, which we believe represents the post-Sarothrogammarid phase of Stock (1974c) and the pre-Sectional stage of the 1980s when the entire order will have a distinctive classificatory state characterized by division of Gammaridea into taxonomic "sections." We believe that the present stage has the highest evolutionary content because we preserve many of the groups such as Sarothrogammarids, Metohiids, Fluviogammarids, Pontogammarids, Dikerogammarids, Weckeliids, and more than a dozen of others, that will be submerged nomenclaturally in the future. We hope our presentation will then become the introductory work for students wanting to understand the transition between the taxonomy of Stebbing (1906) and that of the twenty-first century, and how, suddenly in the 1960's and 1970's, our knowledge of the group reached the critical mass necessary to see some of evolutionary deployment within major subdivisions.

A few papers beyond 1978 are included in the bibliography as works we had consulted in manuscript courtesy of their authors.

Owing to its large size this work has been divided into 2 principal parts which have been structured to stand alone as much as possible. This first part (Evolutionary Patterns, see Table of Contents) introduces the subject, describes the evolutionary pattern in the Gammaridans, provides alternatives between text and graphic models (Graphs 1-7), discusses the distribution of major genera in the geographic regions and then devotes most of the narrative text to an elaboration of the taxonomy, morphology, evoluton, and distribution of the taxa within their native regions; twelve tables and 3 boxes on major distributions and subjects are included. A brief statement of facts is presented below. A section on non-Gammaridan amphipods found in freshwater follows. Appendices I-II include lists of taxa in the PontoCaspian Basin (I) and Lake Baikal (II), followed by (III) the Geographic Reporting System for the distribution of species. The diversity of form in Gammaridan Amphipods is shown in 50 figures. About 90 maps display: (1) the distribution of major groups during continental drift, (2) the geographic zones of Appendix III, and (3) the modern distribution of species ouside of Lake Baikal and the PontoCaspian Seas; code numbers for distributions are found in species lists of Appendices VI and VII.

The second part, Handbook and Bibliography, is composed of appendices and contains: (IV) A Checklist of World Gammaridans; (V) Phyletic and Geographic Keys to the Genera of Gammaridan Amphipods; (VI) A Handbook with major references to genera, diagnoses, lists of species with their major citations and codes to cite the distribution for each species; and (VII) A

Handbook of Other Freshwater Amphipod Genera. A Bibliography of Freshwater Amphipoda represents our selection of crucial references to the taxonomy, morphology, evolution, and biogeography of the group but excludes such topics as ecology, physiology, and genetics.

Acknowledgments

A grant (1975 1978) from the Smithsonian Research Foundation (now defunct) provided the help of Carolyn L. Cox, the major illustrator of this work, with assistance from Debra Horner (11 of the base maps), and Marisa Costagliola Consini who executed the actual plotted charts on their bases and inked several of the plates). Later, a direct grant from the Congress of the United States of America permitted us to generate the manuscript from microcomputer diskettes and to have Irene F. Jewett and Deborah Feher ready the illustrations for press. Mr. Reggie Creighton of Smithsonian's Office of Computer Services designed our computer system and Elizabeth B. Harrison, Wendy K. Brown and Margaret B. Cairns operated the computer. At the Smithsonian Institution we had vital encouragement and help from the following persons: Dr. R.B. Manning, Janice Clark, Roland H. Brown, Dessie M. Best, Roscoe C. Johnson, and Dr. Fenner A. Chace, Jr.; Jack F. Marquardt, Chief of Accession Services of Smithsonian Library and his diligent staff, especially Mrs. Carolyn Sue Hahn, performed their usual miracles in helping us get obscure literature.

We benefitted from many consultations over many years with Dr. John R. Holsinger of Old Dominion University, Virginia, Dr. Gordan S. Karaman of the Freshwater Institute, Titograd (Lake Skadar), and from fruitful discussions over several years with Dr. Jan H. Stock and Dr. Sjouk Pinkster of the Institute of Taxonomic Research in Amsterdam. Also of great influence have been many years of association in the 1940s and 1950s with Dr. John S. Garth, Dr. John L. Mohr, and the late Dr. Olga Hartman of the University of Southern California. Other colleagues over the years have also been inspirational: Dr. W.J.M. Vader of the Tromso Museum, Norway Margaret M. Drummond and Dr. F.H. Drummond of Melbourne, Dr. D.J. Reish, California State College at Long Beach, Professor W. Stephenson of the University of Queensland, Professor W.D. Williams of the University of Adelaide (who also kindly received us earlier at Lake Windermere, and even earlier at Monash University, Melbourne). Dr. K. Jazdzewski of the University of Lodz very kindly loaned to us and later discussed with us important manuscripts before they were published; the staff of the library at the University of Amsterdam generously found many rare papers for us during our visit there in 1975; and we want to thank the following for their courtesies and help: Drs. M.P.D. Meijering and S. Husmann of the Max-Planck-Institut for Limnologie at Schlitz; Dr. A. Buikema of Virginia Polytechnic Institute at Blacksburg; Shirley M. Slack-Smith and Dr. Barry R. Wilson of Western Australian Museum (latter now at National Museum of Victoria); Dr. E.L. Bousfield of National Museum of Canada, Ottawa, who courteously gave us advance inspection of several of his manuscripts between 1973 and 1977; and John W. Chapman of California University at Santa Barbara for help with Corophium. We would like to recall and thank in print for the first time our early mentors of 30 to 35 years ago, the late Professor Dr. Max W. de Laubenfels, latterly of the University of

Facts and Conclusions about Amphipoda

(Date of analysis shown in parentheses)

1. Known species of Gammaridea (October 1978): 4786 (marine and freshwater).

2. Known genera of Gammaridea (1978): 763 (marine and freshwater).

3. Genera of freshwater Amphipods (1979): About 232 (Gammarida= 217, others= 15).

4. Species of freshwater Amphipods (1979): About 1088 (Gammarida= 982, others= 106).

5. More than 90 percent of freshwater Amphipods are in the Gammarida; the other 10 percent are in Talitroidea and minor groups.

6. Species of freshwater Amphipods by world region (1979): Palearctica, 764; Nearctica, 159; Neotropica, 60; Notogaea, 48; Ethiopian, 20; other, 37 (includes non-Gammaridans).

7. Species of world Gammaridans, including 358 marine species (1979): 1340.

8. Gammaridan species (1979): in Lake Baikal, 262; in PontoCaspian Basin, 83; in total Palearctica, 730; in Nearctica, 152.

9. Fossil Record; Several species of _Paleogammarus_ and _Gammarus_ in Baltic amber of Eocene, marvelously preserved, even with their parasites; but species of _Paleogammarus_ essentially identical to living species of _Crangonyx_; several organically imprinted species (in rocks of Sarmatian near Caspian Sea) of extinct genera _Andrussovia_ and _Praegmelina_ but very advanced semifossorial taxa with little phyletic information; finally there exist a few miscellaneous Cenozoic taxa of no gross evolutionary value.

10. Origins of Amphipoda: Undoubtedly group diverse and highly advanced at time of Pangaea in late Paleozoic. Modern distributional patterns resulting from dispersion of continents after era of Pangaea.

11. African rift lakes: No Amphipods yet known.

12. South American Amazonia Basin: Freshwater Amphipods few; epigean = several species of <u>Hyalella</u> (not Gammaridan); hypogean = several species of Bogidiellids (Gammaridan, possible descendents of Crangonyctoids).

13. Lake Titicaca: A swarm of <u>Hyalella</u> (not Gammaridan, of marine origin, very apomorphic).

14. Australia: Freshwater Amphipods mostly relicts of Pangaean Crangonyctids but a few marine crawlouts are present. Freshwater taxa lacking direct marine connection across wide modern seas to other continents.

15. <u>Gammarus</u>: A freshwater genus, with a few marine species emigrant from freshwater!

16. Nomenclature, new uses: Gammaridea, the major suborder of Amphipoda, name still used; Gammarida (217 genera), a section of the Gammaridea encompassing old concept of Gammaridae, now elevated; Gammaridae, now one family of Gammarida; Gammarids, a small group of genera related to <u>Gammarus</u>.

17. Most widely distributed freshwater species of Amphipods: <u>Gammarus lacustris</u>, Holarctic; <u>Gammarus pulex</u>, Palearctic; <u>Pallasiola quadrispinosa</u>, glacial lakes relict; <u>Crangonyx subterraneus</u>, Europe and southern England; <u>Stygobromus ambulans</u>, Eastern Europe and West Asia; <u>Gammarus roeselii</u>, France to Turkey; <u>Gammarus fasciatus</u>, Wisconsin to Quebec to North Carolina.

Oregon, the late Professor Tage Skogsberg of Stanford University, and Professor Dr. Irene S. McCulloch of the University of Southern California, without whom we would not have become zoologists; the late Dr. Waldo L. Schmitt of Smithsonian also gave us early encouragement (1948) and support in the 1960s; finally to Prof. J. Wyatt Durham of the University of California and the late Dr. E. Yale Dawson, latterly of the Smithsonian, both of whom sharpened our taxonomic teeth. The person who specifically drew us into the study of peracarids in the 1940s, Dr. Robert James Menzies, our peer, recently died, too prematurely to read our heartfelt thanks for years of support and generosity. This work is dedicated to four of our valued and fearless colleagues, Dr. Howard Winter, Dr. E. Yale Dawson, Dr Robert James Menzies and Dr. Rita Schaefer, who lost their lives prematurely to the cause of biology.

We thank C.W. Hart, Jr., who raised money for our work in its early days and Dr. R.P. Higgins who introduced us to the computer as a research tool. We will forever remember the moral support of Dr. R.B. Manning during the five discouraging years during which we tried to get our work published in other media. To the dozens of people outside of Washington, D.C., including the dozens of graduate students, who liked our work, we

give special thanks for illumination during our darker days. That we ultimately decided to publish this work with our own resources came from assurances by Dr. Holsinger, Dr. Vader, Dr. Manning and Dr. Watling that we had something to offer. We apologize to our readers for the necessity to pay a token fee for our volumes and that its reproduction is marginal; but it is presented the way we wanted it.

From the day of our arrival at Smithsonian in 1964, Secy. S. Dillon Ripley has generously encouraged our research and monetarily supported our extensive field work throughout the world, giving us the opportunity to see and work in Australia, New Zealand, Hawaii, Malaysia, Indonesia, New Guinea, Micronesia, Polynesia, the Galapagos, Panama, Mexico, China, South America, Africa and Europe. His inspiration has been crucial to the completion of this work. Not endorsed by Smithsonian Inst.

Background

(Tables 1 and 2 and "Facts and Conclusions" Above)

Amphipoda are unusual animals and unusual crustaceans. They are unusual animals because they have a preponderant affinity for cold waters, whether marine or freshwater; and they are unusual crustaceans because they, like the few other groups of Peracarida, brood their offspring.

The character of the marine fauna of Amphipoda, especially Gammaridea, has been treated by J.L. Barnard (1962b, deep sea; 1965, tropics; 1969c, world; 1970, Central Pacific; 1972a, Australia; 1972b, New Zealand; 1977, tropics again) but these "obscure" papers have largely been overlooked by the general biological community. The unusual character of Amphipoda goes largely unheralded in textbooks on morphology, ecology and biogeography; for example, several conclusions about freshwater amphipods in Hutchinson (1967) are erroneous. It is time for generalists to read some amphipod papers!

In the oceans, Gammaridea are cool adapted; in other words, their generic diversity is greatest in boreal waters, whereas the tropics have relatively few genera with large numbers of species and most of the small genera are inquilinous; the large tropical genera are nestling, fossorial and inquilinous and exhibit the common biological distribution pattern of tropical dominance with polewards diminution. But the boreal zones themselves contain many endemic genera with great species diversity. Close to half of the familial plesiomorphs live today in cool waters; are these relicts or, more plausibly, are they survivors of their original thermal preference? In precisely homologous fashion, the pelagic waters resemble the benthic waters, with the greater diversity of nektonic amphipods occurring in bathypelagic and not epipelagic waters. In his several works cited above, J.L. Barnard supports the ideas of Bruun (1957:667), Menzies and Imbrie (1958:208), and Menzies, Imbrie and Heezen (1961:79) that the oldest members of the fauna today live in bathyal waters which are the relict of pre-Oligocene abyssal seas. Water in abyssal depths colder than 4* C is a young world phenomenon. Amphipods are so poorly adapted to warm waters that they stagnate there evolutionarily. Hence, important evolutionary events of Amphipoda remain centered in cool waters 4-12* C in bathyal depths.

The coolwater orientation of amphipods is also found in freshwaters. Tropical and warm-temperate freshwaters have few amphipods whereas Holarctic waters have hundreds of species; similar cold environments in the southern hemisphere are confined to the narrow part of South America where almost no Gammarideans have been found; southern Africa and Australia have a few species of Crangonyctoids surviving the misfortune of continental drift into warm climes.

The following coincidences occur in Gammaridean Amphipoda: (1) The close similarity between North American and Southern Australian freshwater Amphipoda; (2) the absence of marine remnants linking freshwater faunas across wide ocean basins; (3) the extremely similar morphology of several generic groups between Lake Baikal and the Caspian Sea; (4) the parallelism of congeners in freshwater Australia and South Africa; and (5) the convergence of PontoCaspian Gammaroids and the widely spread but mostly antiboreal Phoxocephalids.

The great freshwater clusters of amphipods are centered in Palearctica and Nearctica, especially in Lake Baikal, the PontoCaspian Basin, the running waters of Europe and America and subterranean systems in general. The rainforest tropics of Africa seem almost to be devoid of amphipods. The great rift lakes in the savannahs also seem to lack amphipods; oriental rainforests appear almost to be devoid of amphipods and the few taxa recovered in India, Bengal, Southeast Asia and Indonesia are almost all of subterranean character. Most of the amphipods of Australia are found in the cool south, none so far having been found in the torrid north, and most of the southern members come from the highest altitudes or from subterranean sources. In the American tropics the only freshwater amphipods of the Gammaridan section of Gammaridea (which has most of the freshwater amphipods of Holarctica) are of subterranean character and the only epigean species belong to an American endemic genus, Hyalella, supposed to have emerged from the sea long after the breakup of Pangaea. Hyalella is the first successful tropical epigean genus and is confined to America. Though a few species occur in lowlands of North America and the Amazonian Basin, most of the species occur in the alpine Lake Titicaca.

Brooding of offspring hypothetically should lead to relatively low dispersal rates and high degrees of endemism and speciation (given many other coincidences). This seems to be supported by the large species flocks of amphipods in Lakes Baikal and Titicaca, in the running freshwaters of Europe, especially France and Spain, in the underground systems of Europe, centered in Yugoslavia, and in the marine swarms found in the Okhotsk Sea, southern Australia and other places. Yet, the distribution of marine amphipods is very peculiar. Certain deep sea species thought to be demersal are cosmopolitan, so that the brooding of young and absence of larvae have not restricted dispersal. Certain deep-sea species tied to the benthos show wide speciation or considerable evolutionary chatter or morphism (Dunbar, 1972). Finally, despite the assumed great age of Amphipoda proposed herein, the entire Amphipodan fauna of the North Atlantic Ocean appears to be strongly apomorphic, except possibly for a few species in cosmopolitan genera.

Our capsule version of amphipods, based on works cited above and on the new conclusions documented in the present work, is as follows: Amphipoda existed in the Paleozoic in fully modern morphology. Their origins are unknown but their line of descent proceeds through the Corophiida, a large marine section living today, characterized by fleshy telson. The section Gammarida, descendent from Corophiida, already existed in the era of Pangaea, inhabited freshwater as sternobranchiate Crangonyctoids, evolved rapidly during the early continental drifting as a result of invading the brackish gulf waters and, emerged as the modern Gammaroids, lacking sternal gills. We conclude that the parallelism between Holarctic (Laurasian) and Gondwana freshwater taxa descends from the era of Pangaea when the continents were coalesced and free exchange could take place by freshwater pathways. There remains no evidence within modern shallow seas in the southern hemisphere of any pandemic marine dispersal of ancestral taxa that could account for the freshwater parallels (J.L. Barnard, 1972a:5,1972b:20). There are however, a few marine taxa, the Cheirocratids, that point to a common marine pathway dating from Pangaea; this suggests that Cheirocratids occurred in marine waters at the same time as pangaenic freshwater Crangonyctoids. Cheirocratids are, however, apomorphic and cannot be placed on the ancestral side of Crangonyctoids (see "Box, The *Cheirocratus* Case" in the Table of Contents). Crangonyctoids today survive as very attenuate freshwater relicts in southern Africa, southern Australia and burgeoning postglacial radiates in Nearctica, mainly surviving underground.

In freshwater, Gammaroids succeeded Crangonyctoids, but long after Pangaea had dispersed, Gammaroids, if they occurred elsewhere, became extinct everywhere except in Holarctica. A few Crangonyctoids apparently survive as a descendent group, known as Bogidiellids, which inhabits subterranean Neotropica and Palearctica. Otherwise, Neotropica has been invaded by a strongly apomorphic group, the Hyalellids. The few Crangonyctoids of Palearctica, mostly hypogean, apparently are being extinguished or constrained by the later marine incursors, the Niphargids.

There are many parallels between Baikalian and Caspian taxa that can be explained by convergence in evolution controlled by similarities in ancestral forms and similarities in environment but some of the coincidences in ornamentation are so spectacular as to suggest direct interchange of certain taxa. However, the characters dealt with in analyzing Gammaridean evolutionary deployment are so subtle that only a cursory overview of the true interrelationships can be made in this decade. A great deal of functional morphology must be undertaken before conclusions can be drawn as to the exchange of Baikalian and Caspian taxa.

An analogous case that is apparently convergence involves the amazing morphological parallels between PontoCaspian Gammaroids and Australasian Phoxocephalids. The fossorial characters we might have thought to be subtle in the 1970's may be found in the 1980's to be replicated several times in Gammaridea as a result of natural selection on remote genosomes (genotypes) rather than as markers of genetic similarities. Barnard and Drummond (1978:36) called attention to these convergences but pointed out the absurd geographic and thermal framework involved between the PontoCaspian environment of the Cenozoic and that of modern Australasia.

The critical questions to be asked are as follows: (1) If amphipods are cryothermic how did they pass through equatorial zones of Pangaea in their migration from one cool zone to another in freshwaters?; (2) Can no possibility of connection between PontoCaspian Gammaroids and Australasian

Table 1A - World Distribution of Gammaridans (June 1979)

Region	Genera	Species	Additional Subspecies (Endemic)
Baikal	45	262	77
PontoCaspian	30	76	2
Marine	53	358	-
Palearctic	37	217	175
Holarctic*	6	344	-
Nearctic	11	16	5
Neotropic	6	15	-
Ethiopian	4	18	-
Notogaean	7	24	-
New Zealand	3	8	-
Paleotropics	1	1	-
IndoPacific Freshwater	10	13	-
Antiboreal Island Freshwater	2	3	-
Other Anchialine	2	5	-
TOTAL	217	1360	259

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*Note: The table is constructed so that polypatric genera, such as *Gammarus*, are placed only once, in this case classified as Holarctic, along with *Crangonyx*, *Echinogammarus* and others. In Table 1B, however, the species of these polypatric genera are divided into their specific regimes, so that the genus *Gammarus*, for example, is divided into its marine, Palearctic and Nearctic components and the species thereby allotted precisely.

TABLE 1B.--By dividing Holarctic genera and species into regimes following corrections are made.

Region	Genera	Species	
Baikal	46	262	(and 1 non-endemic species)
Caspian	32	83	(and 2 non-endemic species)
Palearctic	42	385	
Nearctic	16	152	
Neotropic	7	28	(all Bogidiellas put here)
Marine	55	378	(added *Gammarus*, *Echinogammarus*)
Other non-Gammaridans	21	97	

TABLE 2.--Freshwater Gammaridae of the world, classified into major habitat-regions, listing genera and numbers of species; brackets enclose genera with exotic distributions. Maps showing distribution are also listed.

Region	Species	Map Number
East Palearctic Hypogean		
Eoniphargus	1	22
Procrangonyx	1	22
Pseudocrangonyx	9	22
Anisogammarids	3	50-52
Mostly western and middle Palearctic epigean		
Gammarus (plus 14 marine)	102	23-37
Echinogammarus (plus 7 marine)	37	39-44, 47a,b
Crangonyx	4	11-13,46
Tadzhikistania	2	24
Lusigammarus	2	44, 45
Fontogammarus	2	45
Comatogammarus	1	46
Pectenogammarus	1	45
Bathyonyx	1	--
Mostly western Palearctic hypogean		
Niphargus	133	59-64
[Stygobromus]	16	13-17,46
[Bogidiella]	14	18-21
Salentinella	11	57
Sarothrogammarus	5	46
Hadzia	3	55
Metacrangonyx	3	58
Neogammarus	3	45
Rhipidogammarus	3	38, 45
Anopogammarus	2	45
Niphargellus	2	65
Tadzocrangonyx	2	24
Metahadzia	4	55
Issykogammarus	1	19
Afridiella	1	19, 54
Longigammarus	1	45

Ilvanella	1	45
Metohia	1	45
Accubogammarus	1	45
Zenkevitchia	1	45
Typhlogammarus	1	45
Pygocrangonyx	1	58
Microniphargus	1	65
Parasalentinella	1	65
Psammogammarus	3	55
Pseudoniphargus	1	58
Pontoniphargus	1	65
Haploginglymus	1	59,no.20
Carinurella	1	65
Niphargopsis	2	65
Glacial Relicts		
Gammaracanthus	1	49
[Pallasiola]	1	38
[Pontoporeia]	1	--
PontoCaspian		
Stenogammarus	7	--
Dikerogammarus	7	38,47c
Obesogammarus	6	48a
Pontogammarus	6	47d
[Echinogammarus]	5	--
Yogmelina	5	--
Amathillina	5	48c
Niphargogammarus	4	--
Akerogammarus	3	--
Euxinia	3	--
Niphargoides	3	--
Paraniphargoides	3	--
Gmelina	2	--
Gmelinopsis	2	--
Turcogammarus	2	38
Cardiophilus	2	--
Sowinskya	1	--
Derzhavinella	1	--
[Gammaracanthus]	1	--
Kuzmelina	1	--
Axelboeckia	1	--
Jugogammarus	1	38
Shablogammarus	1	38
Cephalogammarus	1	--
Lanceogammarus	1	--

Baku	1	--
Iphigenella	1	--
Pandorites	1	--
Behningiella	1	--
Zernovia	1	--
Uroniphargoides	1	--
Compactogammarus	1	--
[Pontoporeia]	1	--
[Gammarellus]	1	--
Baikal		
Micruropus	34	--
Eurybiogammarus	25	--
Poekilogammarus	18	--
Hyalellopsis	16	--
Pallasea	14	--
Acanthogammarus	13	--
Philolimnogammarus	12	--
Eulimnogammarus	10	--
Corophiomorphus	10	--
Carinurus	6	--
Spinacanthus	5	--
Macropereiopus	5	--
Crypturopus	5	--
Fluviogammarus	4	--
Carinogammarus	4	--
Pseudomicruropus	4	--
Parapallasea	3	--
Abyssogammarus	3	--
Ceratogammarus	3	--
Odontogammarus	3	--
Plesiogammarus	3	--
Garjajewia	3	--
Boeckaxelia	3	--
Coniurus	3	--
Ommatogammarus	3	--
Echiuropus	3	--
Homocerisca	3	--
Pachyschesis	3	--
Heterogammarus	2	--
Metapallasea	1	--
Paragarjajewia	1	--
Lobogammarus	1	--
Hakonboeckia	1	--
Polyacanthisca	1	--
Eucarinogammarus	1	--

Table 2

Cheirogammarus	1	--
Brandtia	1	--
Dorogammarus	1	--
Gmelinoides	1	48b
Baikalogammarus	1	--
Gammarosphaera	1	--
Macrohectopus	1	--
Nearctic epigean		
[Gammarus] [and 3 marine]	10	23-37
[Echinogammarus] [and 3 marine]	0	39-44,47a,b
Crangonyx	21	11-13,46
Anisogammarids	3	50-52
Nearctic hypogean		
Stygobromus	96	13-17,46
Bactrurus	3	12
Allocrangonyx	2	12
Mayaweckelia	2	56
Mexiweckelia	2	56
Artesia	1	56
Parabogidiella	1	56
Paramexiweckelia	1	56
Texiweckelia	1	56
Allotexiweckelia	1	56
Holsingeria	1	56
Texiweckeliopsis	1	56
Neotropics hypogean		
Metaniphargus	8	56
Bogidiella	8	18-21
Saliweckelia	2	56
Spelaeogammarus	1	18
Paraweckelia	1	56
Alloweckelia	1	56
Weckelia	1	56
Pseudingolfiella	1	18
Galapsiellus	1	53
Anchialella	1	53
Neotropics epigean		
Falklandella (really Ethiopian import by tectonics)	2	18

Table 2

Ethiopian (plus South Africa)		
Paramelita	12	9-10
Sternophysinx	3	18
Austroniphargus	2	54
Bollegidia	1	18-19,54
Sandro	1	54
[Melita]	1	54
Notogaean		
Neoniphargus	10	6-8
Austrogammarus	6	6-7
Uroctena	3	7
Perthia	2	7
Hurleya	1	7
Protocrangonyx	1	7
Giniphargus	1	8
Pseudomoera	2	8
New Zealand		
Phreatogammarus	3	7
Paraleptamphopus	2	6-7
Paracrangonyx	1	8
Kerguelen		
Kergueleniola	1	54
[Pseudingolfiella]	1	18, 54
Paleotropical		
[Psammogammarus]	1	53, 54
Paraniphargus	2	54
Indoniphargus	1	54
Psammoniphargus	1	54
Nainaloa	1	53
Tegano	1	53
Rotomelita	3	53
North Pacific Marine Ingressors		
Jesogammarus	1	50-52
Ramellogammarus	4	50-52
Annanogammarus	1	50-52
Eogammarus	2	50-52

Phoxocephalids be accepted because the warm tropical barrier would prevent transmigration; (3) Given a late Paleozoic origin how can so many distributional anomalies remain in such an old but otherwise very abundant and successful group (Amphipoda), if not then controlled by this difficulty of adaptation to tropical environments of all kinds? The open niches must therefore be so vast that whole categories of morphofunction that might be filled by amphipods are vacuous in certain biogeographic regions. (4) Are amphipods only now exploding (speciating and rapidly radiating) because the cold polar and deep-sea environments attended by cool-temperate environments have opened up in the later Cenozoic? (5) Are tropical amphipods such generalists that they are driving other genera polewards? Or, is some other group affecting Amphipoda?

In the oceans the abhorrence of warmth has driven amphipods towards two antitropical bands in cool waters. The tropics retain a few highly speciated cosmopolitan genera, a few smaller mostly inquilinous endemic genera and remnants of a few coolwater genera passing back and forth from boreal to antiboreal. The following of cool isotherms across the tropics apparently hinders dispersal because descent into dark waters is often evolutionarily fatal. Large anomalies occur as a result of this antitropical adaptation; for example, the marvelously fossorial family Phoxocephalidae is largely contained in antiboreal waters and has barely begun its escape and radiation into boreal waters. On the other hand some of the niche functions of the fossorial Phoxocephalids are still held, and perhaps may be in the process of being expanded, by the modern Oedicerotids (the primitive Oedicerotids remain largely in the southern hemisphere). In the southern hemisphere the long persistence of Phoxocephalids apparently has resulted in their invasion of inquilinous niches whereas their inquilinous place in the cold north is apparently held by Pleustids.

This turnabout of view on the history of freshwater amphipods should have consequence on modern ecological research. For example, our version of this history means that marine members of Gammarus and Echinogammarus are apomorphic and moving into the sea, not that they are plesiomorphic and invading freshwaters from the sea. This may well put quite a new slant on the burgeoning science of freshwater ecology where it concerns certain amphipods.

Classification

The classic Gammaridae have been divided into superfamilies and families by Bousfield (1977). This division has merit in reducing the unwieldiness of a diverse group and setting the background for more intensive focusing on interrelationships of the various subgroups. It goes counter to the general trend in biological taxonomy to amalgamate the higher taxa into fewer but larger groups with emphasis on subfamilies and supergenera but this is of little concern to carcinologists who historically have split their groups into finer and finer clusters at high levels. To some extent this is justified by the Hennigian principle of antiquity because most Crustaceans appear to be extremely old. Though many of them, such as amphipods, appear on the surface to be morphologically homogeneous, they nevertheless are distinguishable as clusters at fine levels of observation.

Since 1906, Gammaridean taxonomy has been based on the system proposed by Stebbing, the Gammaridea forming one of four (fourth added since 1906) suborders. The Gammaridea were divided into 42 families. Since that time up to 1976 a net seven families have been added but mainly have been fitted into the Stebbingian system. To make the Stebbingian system work, many adjustments were made by J.L. Barnard (1964,1969) primarily through synonymy of clearly and broadly intergradational groups. For example, the Eusiridae, Calliopiidae and Pontogeneiidae were amalgamated so as to maintain a workable systematic system within the overall framework of limited familial groups proposed by Stebbing. This was criticized by Bousfield (1973, 1977) and was rejoined by Barnard and Karaman (1975) who pointed out the need to maintain stability in any system of classification without mixing two kinds of systems, lumped and fragmented.

Reorganization of the Gammaridea commenced with Bulycheva (1957a) who created the superfamily Talitroidea for three families. Because the remaining Gammaridea were left unordered at superfamily level this immediately created a classificatory system in theory operating at two levels. Nevertheless, this was easily handled because of the general morphological remoteness of the group. Creation of the Talitroidea simply provided an umbrella for the 3 families. Later, J. L. Barnard (1972a) realigned the Talitroidea by minor fragmentation and addition of old families such as Phliantidae and creation of new ones, such as Ceinidae. The Corophioidea, an old superfamily from last century, was re-elevated by J.L. Barnard (1973) to contain several of the domicolous families and J.L. Barnard (1969c, 1974) published a pattern of evolutionary flow showing the nuclei of other superfamilies. Many of these superfamilies are now being ordered by various taxonomists.

For a few years various new taxa proposed by these students must remain out of balance with each other in the hierarchy until the new system of superfamilies and sections throughout the suborder can be completed. At that time, then, the Amphipoda will be organized in the same way as other Crustacean orders, such as the Decapoda.

The extraction of many new superfamilies by Bousfield (1977) out of the old Gammaridae is, one hopes, the apogee of splitting in this group and the penultimate step to the final ordering of the Gammaridea as a whole. There is little doubt that a superfamily Gammaroidea exists as a foil for Corophioidea and Talitroidea and there will come some future justification for use of higher categories such as section (for example, Gammarida). Unfortunately, as will become evident to the reader of this essay, the formalization of the familial and superfamilial nomenclature by Bousfield is not yet a workable proposition because many of the clusters are, for the most part, not taxonomically discrete. The problem is more than just a minor exception here and there. Such taxal groups as Anisogammaridae are perfectly discrete because their species universally share accessory coxal gills not found in any other Gammaridans, but most of the other clusters are broadly connected to each other by long series of intergrading genera. For example, Karaman and Barnard (1979) have shown the untenability of the superfamily Bogidielloidea, which actually contains a wide array of transitional morphs between Crangonyctoids and the ultimate interstitial genus Pseudingolfiella. If these integrading genera could be arranged along simple radii, then one could define arbitrary points of no return in morphological condition and thereby define superfamilies. But, without a significant fossil record and the unlikelihood that any will ever be discovered, and the present incapability of detecting any inherent taxal memory of such history, the species have to be arranged on a scrambled network of converging and diverging lines. The complexity of the tangles prevents nomenclatural divisions of a certitude so easily constructed by Bousfield.

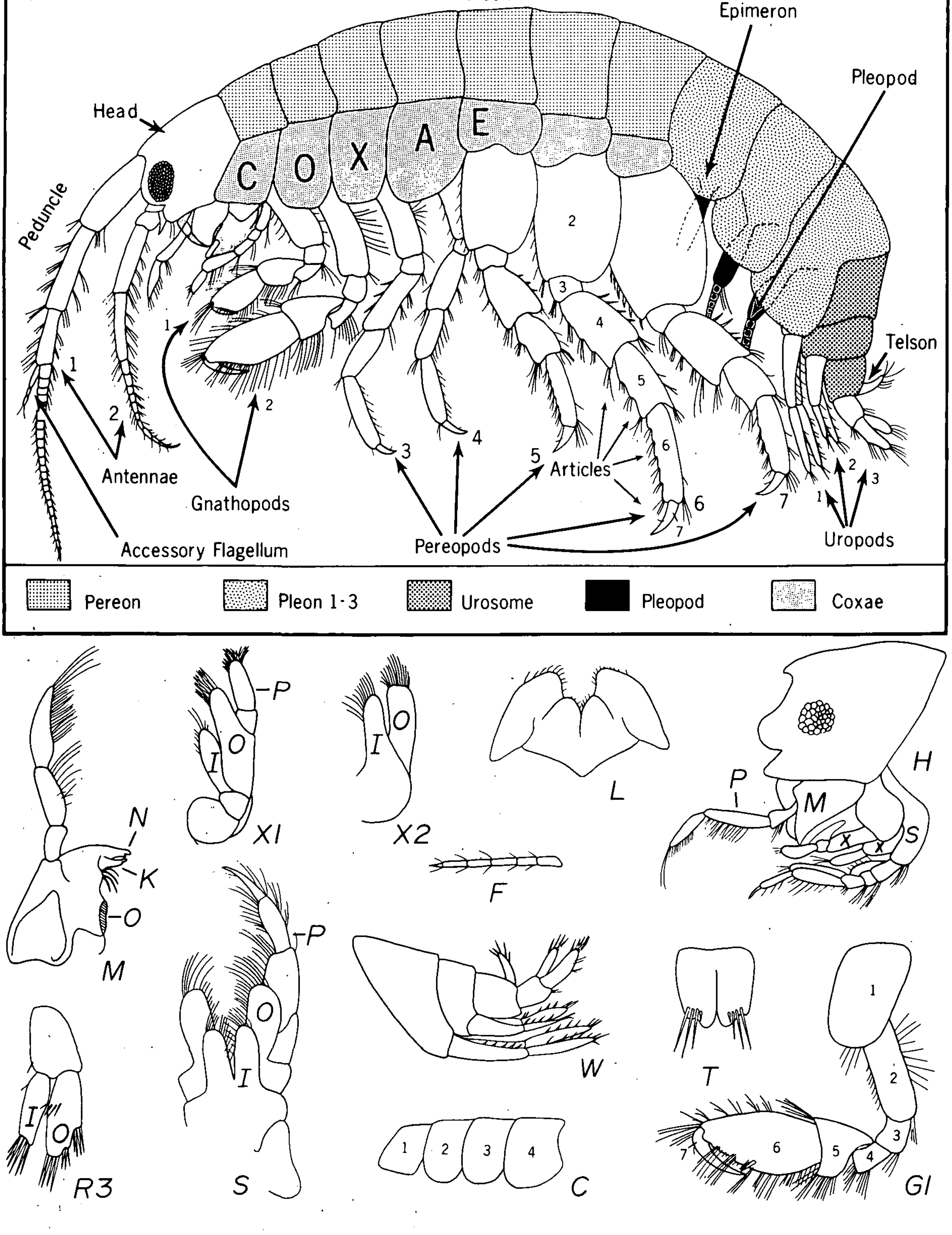
Taxonomy (or simple classification) does not reflect the evolutionary deployment in the group to an extent adequate to make neat familial and superfamilial clusters. One cannot write a simple key to the families proposed by Bousfield (1978) without engaging numerous exceptions that would prevent proper generic placement of many species not by morphology alone. When the time comes that species are identified at molecular levels or by microgeographic means, then one might be able to define some of the proposed families adequately.

Although a degree of cluster recognition should be accepted, it should be reserved for evolutionary papers (Barnard and Karaman, 1975) and not made into formal Linnaean nomenclature until discontiguities can be demonstrated.

The forward leap from the 19th century Stebbingian system to a supersplit manifold or multilevel system employing all available nomenclatural categories is simply too great a jump too swiftly. Not enough preparation has been made. The amount of dialectics about these proposals has been minimal, involving a few students such as Chevreux, Schellenberg, Ruffo, the Karamans, Stock, Holsinger, Sket and a few others. The number of papers has been few. The number of family trees actually proposed and widely discussed has been few; in fact one of the few actually depicted was by A. Mateus (1974a). Even Bousfield has written very little background on his suddenly proposed system. Virtually no one except Barnard and Karaman (1975) has challenged any presentation nor warned of pitfalls nor has pointed out gross inaccuracies and absurdities.

The problem is that Amphipods are not only richly furnished with characters but also have radiated into many avenues while often retaining plesiomorphic characters. Many of the advancements involve loss of structure rather than gain of new attributes. Several groups such as Lysianassoidea and Corophioidea (perhaps the most plesiomorphic) have, by chance, been isolated morphologically from the others by adequate extinction of intermediate taxa but groups such as the Gammaroidea (better Gammarida for this purpose) have lost almost no links between clusters. The clusters have too much interfingering to justify their nomenclatural recognition. We already deal routinely with 250+ characters and, lately, descriptions are appearing that consider 500+ characters, so that there is no dearth of analysis. Some of the clusters are clearly polyphyletic. These are gradational, to wit, they are composed of taxa with common characters arrived at by convergence of two distinct ancestral lines. Many other taxa might be called "universal matchers," those which have a mix of characters allowing one to hypothesize several points of classification. For example, one might consider the Brazilian troglobite, Spelaeogammarus, as (1) a Crangonyctid without sternal gills; (2) a prototype of the Bogidiellids with plesiomorphic coxae; or (3) a freshwater immigrant from the sea, with so-called Hadzioid (or Melitoid) ancestry. A system that cannot handle Spelaeogammarus and dozens like it is not a good Linnean taxonomic system, though such a system has value to an evolutionist.

Figure 1


Pereon
Epimeron
Pleopod
Head
Peduncle
COXAE
Telson
1
2
Antennae
Gnathopods
Accessory Flagellum
3
4
5
6
7
Articles
Pereopods
1
2
3
Uropods
Pereon
Pleon 1-3
Urosome
Pleopod
Coxae
N
K
O
M
P
O
I
X1
I
O
X2
L
F
P
M
H
S
X
X
P
O
I
S
W
T
I
O
R3
1
2
3
4
C
1
2
3
4
5
6
7
G1

There is not going to be much early agreement among the dozens of working taxonomists in amphipods as to the limits of the umbrellar group, Gammarida, into which the various superfamilies of Bousfield must go. There are many so-called Eusirids, Calliopiids, Pontogeneiids and other taxa with immediate roots in Gammaridans. Therefore, even the limits of the old Gammaridae may never be agreed to.

For these reasons we abandon here the use of formal Linnean names for superfamilies and families within the old Gammaridae though we often use these in the informal evolutionary sense; and we redefine and recompose many of those groups as seen in Appendix IV.

Geographic Presentation

The Gammaridans discussed in this study occur primarily in five great environmental zones on earth: Baikalian, Caspian, extra-Holarctic (excluding Baikal-Caspian), Notogean, and marine. The first four are primarily freshwater microcosms, with evolutionary outflow into adjacent seas from the first three zones. In the almost uninhabited (for Gammaridans) Paleotropical and Neotropical zones and the weakly inhabited Ethiopian zone no outflow to the marine world has been perceived. In this group of primitive Gammarideans the marine world is so homogeneous for its morphological content that it does not require subdivisions. Its evolutionary content matches that of the freshwater microcosms.

The five major microcosms are imperfect because they have never been totally isolated from each other. Species have passed to and fro in moderate to very limited extent. The strongest interchange has occurred between Holarctica and Baikal, Holarctica and Caspian, Palearctica and Nearctica, whereas the weakest interchange has occurred from any zone to the Notogean in recent epochs. The main interchange in the latter region is presumed to have occurred in the age of Pangaea and has been severed ever since. Several interchanges have occurred from Holarctica to marine and back again, more weakly so in the Caspian and very weakly so in Baikal. Nevertheless, most of the living species in the five zones have evolved in situ. For this reason this report is arranged in a progression from primitive to derived. Where possible the main emphasis within the phyletic sections emphasizes the geographic position of the taxa. The general order commences with Notogean Crangonyctoids, their satellites, especially of Nearctica, then proceeds to the extra-Holarctic Gammaroids, and their marine offshoots, then proceeds outward to the Caspian and Baikalian groups, and finally terminates with the marine groups, and their repenetration into freshwater (Niphargids). In the microcosmic sections each genus is fitted into its group, the number of its known species enclosed in parentheses and a summary of its distribution often stated.

Figure 1. Upper, Plan of Amphipod. Lower, Dissected Parts, items labeled as follows: C, coxae; F, accessory flagellum; G, gnathopod; H, head; I, inner plate; K, lacinia mobilis; L, lower lip; M, mandible; N, incisor; O, outer plate; P, palp; Q, molar; R, uropod; S, maxilliped; T, telson; W, urosome; X, maxilla.

Genera are then distinguished in as brief and unitary form as possible. Where the groups are tightly knit these differences are sparsely stated, but where problem genera are inserted into the sequence, a more elaborate discussion of their interrelationships is required. Many genera are discussed in more than one place because they have a strong informational content on evolutionary problems. All cross comparisons can be found in the index. Evolutionary flow charts are provided for a few of the groups (Graphs 1-7) but all genera are not necessarily included in any group. The genera are listed in a loose phyletic order in Appendix IV (Checklist of Gammaridan Genera) because of the necessity to list genera in sequential groups rather than in webs; but much of this problem is handled in the evolutionary flow charts.

Phyletic and geographic keys to the genera (Appendix V) are provided to assist in understanding the position of, or distinctions among, various genera and groups. The keys are arranged alphabetically so that groups of genera can be segregated rather than being submerged in an intolerably long key. The subsidiary keys are not for identifying genera but for demonstrating that the genera are minimally distinct and organizable into loose groups. A key may actually contain taxa of several remote groups to show significant differences between groups, and one genus may appear in several keys to demonstrate its interrelationships or its "universality."

A Handbook to the Gammaridan Genera is presented in Appendix VI along with additional keys. Because Gammaridan groups are not fully discrete as shown in the keys of Appendix V, the evolutionary groups of the checklist (Appendix IV) are described genus by genus and more strongly diagnostic keys are presented for discrimination of the taxa in these groups. The members of the group are fitted together according to the precepts of the narrative text of this treatise. As many as possible are natural groups, though several, such as the <u>Cardiophilus</u> group, are clearly polyphyletic.

Methods and Textual Presentation

Owing to the many years over which this study was undertaken (1973-1979) and the long delay anticipated in press, some of the facts are out of date but our intention is to cover only the years up to 1978. Recounts of species numbers or additions to charts and graphs were not made consistently in line with new data received after January 1979. Certain data were frozen at that time though, where possible, taxonomic revisions have been added to the manuscript up to the time of submittal for publication if they do not disturb the concepts up through 1978. Distribution charts generally were frozen about March 1979 owing to the impossible expense of redraughting necessitated by any major revisions. Other data often were updated heavily in August, 1979, and rarely thereafter.

We devised a geographic system of data reporting which is explained in Appendix III. The numbers in brackets reported after each species in the taxal lists of Appendix VI are code numbers referring to world segments.

To avoid creating any formal names at levels between suborder and subfamily, all names of potential taxal groups are provided with "id" or "a" or "in" endings and the first letter capitalized. This calls attention to names that if cited in lower case might be considered to be formally recognized.

The broadly spectral and interwebbed evolutionary deployment in the Gammarida has caused us to set in apposition several points in the scheme by listing a genus in one group in the narrative text and in another group in the Handbook of Gammaridans (Appendix VI) or in the Checklist (Appendix IV) or in the evolutionary charts (Graphs 1-7). For example, Turcogammarus is placed in the Dikerogammarids in the text and in the Pontogammarids in the Generic Handbook. These counterproposals are not contradictory, rather they clearly demonstrate the strong linkages among groups and the flexible boundaries of the groups.

Arrows in the evolutionary charts (Graphs 1-7) indicate general evolutionary advancement and are not conclusive statements of direct descent. The evolutionary charts show the same bent for diversity we display in other places; they do not necessarily fit the schemes of the text precisely; rather they occasionally, diverge slightly so as to leave the impression that there is more than one way to interpret interrelationships among many Gammarideans. If, after scores of millions of manhours consumed by avian specialists, there can still remain differences of opinion about classification and descent of birds, then the few tens of thousands of hours spent by carcinologists have scarcely opened the prologue to the story on amphipods.

The morphological plates (Figures 1-50) are keyed to Appendix VI (The Handbook) and show the diversity of body form and appendages in Gammaridans.

To avoid countless cross comparisons and reduce the text to manageable proportions in the narrative description of relationships among the taxa in the groups commencing with the chapter "Freshwater Gammaridans" (see Table of Contents), the taxa are arranged in progressive orders of comparison. A model or basic genus is selected for each group and any genera subsequently discussed are compared either to the model or to the antecedent genera.

We suggest the reader, while perusing the narrative text, open the second volume of this work to Appendix IV (Checklist of World Gammaridans). This will assist the reader in keeping track of antecedent groups and genera already discussed. While the reader consults the Keys (Appendix V) or the Handbook of Gammaridans (Appendix VI) in the second volume, the illustrations and maps in the first volume may be viewed simultaneously.

Terms

A significant evolutionary trend in many lines of amphipods is one most familiarly described by such terms as neoteny, pedogenesis, foetilization or heterochrony. Only the last two terms are strictly applicable to amphipods because they lack larval stages; we do not hold that larval stages occur inside the egg before hatching. The preferable term "heterochrony" is used herein to denote the evolutionary progress from ancestors with fully developed characters typical of adults to descendents lacking those adult characteristics but retaining into adulthold the characters of the embryonic or juvenile stages seen in the ancestors. Neoteny is often defined as retention of larval characters in adult stages. By some definitions (Pennak, 1964), the term "neoteny" has been extended to include the situation seen in non-larvaceous amphipods and that term will also be employed. In most cases this term is applicable to gnathopods because these are the only appendages of amphipods on which any study has been made about transformation to adulthood from the juvenile condition. In many cases the neotenic situation to be described also fits the term "gynomorphic," where adult male gnathopods retain the form of adult females. Because juveniles and adult females have similar gnathopods, male gnathopod 2 is often the only appendage to transform in adulthood. In the following categories of terms phyletic order is favored instead of alphabetical order:

Crangonyctoid: Gammaridans of the hypothetical superfamily Crangonyctoidea.
Crangonyctid: Crangonyctoids of the hypothetical family Crangonyctidae.
Gammaridean: Amphipods of the suborder Gammaridea.
Gammaridan: Gammarideans of the hypothetical section Gammarida (=old Gammaridae sensu lato).
Gammaroid: Gammaridans of the hypothetical superfamily Gammaroidea.
Gammarid: Gammaroids of the family Gammaridae.

Antenna 1: "Gammarus-form," article 2 of peduncle more than half as long as article 1, primary flagellum much longer than peduncle, accessory flagellum variable. Figure 4:E1.
"Pontogammarus-form," article 2 of peduncle half or less as long as article 1, primary flagellum not greatly longer than peduncle, accessory flagellum less than half as long as primary flagellum. Figure 4:F1.
"Compactogammarus-form", like "Pontogammarus-form" but accessory flagellum more than half as long as primary flagellum. Figures 4:A1, 4:B1.

Antenna 2: "Pontogammarus-form", article 5 of peduncle easily distinguished, about as large as article 4 and significantly larger than first article of flagellum. Figure 4:A2.
"Stenogammarus-form", article 5 of peduncle much smaller than article 4 and scarcely larger than first article of flagellum, therefore being intermediate in size between articles on either side. Figure 4:C2.

Crawlout: A species or evolutionary line having emigrated from an immediate marine ancestor.

Gnathopod 1: "Melita-form", much smaller than gnathopod 2, mittenform, wrist elongate, hand almost rectangular, palm transverse, one or more articles with pubescence. Figures 13:B1, 13C1.
"Ceradocus-form", like Melita-form but palm oblique, hand not as fully rectangular, pubescence often absent. Figure 13:A1.

Gnathopod 2: "Hadzia-form of female", wrist weakly elongate, slightly bulging apically at joint between wrist and hand palm indistinct from posterior margin of hand, part of hand enclosed by dactyl bearing sparse groups of stiff, apically curved setae. Figure 15 C:female.

"Ceradocus form of male", wrist short, hand large, subrectangular, palm weakly oblique, usually sculptured, poorly setose and spinose. Figures 10:A2, 10:D2.

Gnathopods as a group: "Gammarus-form,"male, gnathopods moderately enlarged, hands almost identical in size, wrists not elongate, hand of gnathopod 1 almond-shaped, palm very oblique, hand of gnathopod 2 subrectangular, palm slightly oblique, palms of both pairs with one or more enlarged midpalmar spines, but spination uneven. Figure 10B.

"Acanthogammarus-form", gnathopods large, almost identical, wrists short, hands weakly almond shaped, palms very oblique, curved, lined with numerous evenly distributed spines or setules. Figure 37:B.

"Pontogammarus-form", like Gammarus-form but gnathopod 2 dominant, midpalmar spines often absent, palmar slopes variable. Figure 10:A.

"Eulimnogammarus-form", gnathopod 1 dominant, often like Gammarus gnathopod 1, but midpalmar spination variable, gnathopod 2 much smaller, wrist elongate, hand elongate, both strongly setose, rectangular, palm almost transverse or poorly spinose; or, alternatively, gnathopod 1 dominant without other qualifications. Figure 10:C.

"Niphargus form", hammer-like, resembling mittenform gnathopod 1, hands expanding apicalwards, palms dominant, often transverse but on occasion weakly oblique, in any event palms of both pairs identical in slope. Figure 14:C.

Mittenform, small mitten-like gnathopods as in Eriopisellids. Figure 14:E.

Gills, accessory: lobes or appendages of coxal gills.

Gills, coxal: gills attached to coxae. Figures 9:G, 9:K, 9:L.

Gills, sternal: gills attached to thoracic sternites medial to coxae. Figures 8:B, 9:G, 9:H, 9:I, 9:J.

Increment: a morphological step upward on an evolutionary tree.

Mandibular setae: the formula of Stock (1974c) shown in Figure 5A.

Number: in parentheses following name of genus indicates number of species.

Sternobranchiate: referring to sternal gills.

Uropod 3 is described in the following terms:

Dispariramous, outer and inner rami dissimilar; Figure 17E.

Aequiramous, outer and inner rami similar in length, shape and patterns of armament; Figure 17:C.

Magniramous, inner ramus extending as far as outer ramus; Figure 17:H.

Variramous, inner ramus not as long as outer ramus but medial margin with armaments; Figure 17:B.

Parviramous, inner ramus much shorter than outer ramus and lacking medial armaments, inner ramus usually very short and scale-like. Figures 17:O, 17:P.

The presence of a conspicuous article 2 on the outer ramus results in a classification of dispariramous; such uropod 3 can be magniramous, variramous or parviramous; an aequiramous uropod 3 is always magniramous but a magniramous uropod 3 can be either dispariramous or aequiramous.

Parsimonious: the least complicated; describing a progression, deployment or transition with the fewest steps.

Pygidization: reduction in mobility or diversity of the posterior body and its parts by fusion, loss or gross enlargement of segments, pleopods, uropods, peduncles, rami, and telson.

World biogeographic regions are cited as proper nouns: Holarctica, Palearctica, Nearctica, Paleotropica, Ethiopia, Notogaea, Nearctica (Udvardy, 1969:259-260, the Wallacean definition). Paleotropica is here expanded to include all IndoPacific tropical islands west of the Galapagos except for Madagascar and Australia.

The Primitive Amphipod

We propose that the hypothetical amphipod bears: a long accessory flagellum; chewing and biting mouthparts with 4-articulate palp on the maxilliped; extended coxae forming side plates; prehensile pereopods 1 and 2 (gnathopods); glands in pereopods 3-4 that exude amphipod silk for constructing abodes; freely articulate segments of thorax and abdomen; magniramous uropod 3 with biarticulate outer ramus; fleshy telson (thick, not laminar, uncleft, not movable as one unit).

Several fossils of amphipods dating from the Upper Eocene have been recorded (Hessler, 1969; Hurley, 1973), but no fossil record bearing on the origin of amphipods has been reported. The question as to what kind of organism could first be called an amphipod and what its functional niche might have been is open to discussion and no conclusions can be reached. One might argue that early amphipods were either nestlers, fossorials, domiciles, or pelagonts in predatorial mode. J.L Barnard (1969c:27) has argued for purposes of definition that the earliest amphipod must have had gnathopod 2 fully prehensile and probably was a nestler. We now believe that the Corophioid line is the most primitive and that early amphipods were therefore domiciliary. But imagination can give full vent to many alternative theories. Amphipods could easily have been constrained into pelagont or fossorial modes in their early existence if they originated during times when other orders of organisms excluded them from nestling habitats. There is very little concrete knowledge about functional morphology in amphipods. Only small changes are necessary in their morphology to adapt them to various roles or a mixture of roles. It is quite easy to pick the fossorial mode as primitive and construct evolutionary lines outward into the nestling and predatorial modes, or to commence with the pelagont mode and move into the nestling and fossorial modes. Evolutionary flow from a fossorial mode in the sea to a nestling mode with later invasion of freshwater might require the loss of fossorial adaptations such as heavy setal armament, streamlining of pereopods and improvement in prehensility of gnathopods. But a filtrative mode that mimics the fossorial mode is found in freshwater Echinogammarus and Sarothrogammarids and is then elaborated again in fossorial apomorphs of the PontoCaspian Basin. The predatorial pelagont mode requires extensive prehensile adaptations, elongation of appendages, strengthening of swimming and floating mechanisms, but in amphipods the extent of these could be reversed to provide the nestling mode. The predatorial pelagont mode occurs sporadically throughout the group in many families and the entire "suborder" Hyperiidea has this habit, at least superficially. The fossorial mode has arisen less frequently, perhaps 3 or 4 times (if the fossorial characters of Phoxocephalids, Pontoporeids and Pontogammarids are considered to be synapomorphic). Inquilinous amphipods are now known to have evolved in many families, so that the detritus-feeding nestler lacking any special adaptations or feeding positions is far less dominant in the Gammaridea than heretofore assumed.

Domicolous amphipods construct abodes spun into tubes or nests from silk exuded by pereopods 3 and 4. Domicolous amphipods differ in their most primitive aspect from nestlers only in the constraint to remain in the vicinity of their abodes, apparently for protection but also for functions assisted by tubal confinement (such as water current management). Nevertheless, many of the primitive forms crawl out of the abodes and feed somewhat similarly to nestling amphipods which have no fixed abode. Many domicolous amphipods apparently do not have a precise homing instinct as they use any available abode, even those constructed by other phyla. The early amphipods could easily have been domicolous and then have radiated into nestlers lacking the spinning glands used to weave the abode. The main domicolous group (Corophioidea) is characterized by fleshy telson, an attribute conducive to speculation about origins. Most other peracarid crustaceans have a fleshy or uncleft telson in contrast to the non-domicolous amphipods which carry a split and laminar telson.

The morphological parallels between primitive Corophioids and primitive Gammaroids are numerous. Article 2 on the outer ramus of uropod 3 is vestigial in the primitive Corophioids, and the rami of uropod 3 have the symmetrical appearance of the marine Gammaridan.

There is no doubt that wide discontiguities exist between many of the marine lines of evolution and their hypothetical ancestors. The links have been lost. For example, the link between Gammarus or Phreatogammarus and the Corophioidea is lost, although the basic morphology between the primitive Corophioid and Gammarus has many parallels (J.L. Barnard, 1969c:23). If one assumes that a fleshy telson and the presence of spinning glands are advancements, then Corophioids may have been derived from the basic Gammarus-like amphipods.

On the other hand, removal of Corophioids to a position plesiomorphic to the Gammaroids is a very attractive proposal (Graph 1). The fleshy, uncleft telson of Corophioids is much more a character of primitive aspect than is the laminar cleft telson typical of most Gammaroids. Fleshy, immovable telsons are a feature of many other Crustacea actually bearing telsons, whereas the laminar articulate telson is rarer.

Although no living Corophioid has an enlarged article 2 on the outer ramus of uropod 3, typical of several Gammaroids, a few genera of Corophioids actually bear a second article. An hypothetical ancestor to Gammaroids and other descendent groups would require the presence of this article. Its enlargement in several Gammaroids is less a difficulty than its creation would be from an ancestor lacking it.

The loss of spinning glands in sequences towards Gammaroids (and even within the Corophioids, Podocerids and Chelurids) would fit the normal simplification theory of Gammaridean evolution (see below). Simple Corophioids in other respects fit the primitive Gammaroid plan in the well developed and prehensile gnathopod 2, well developed accessory flagellum, fully developed chewing and biting mouthparts and lack of significant pygidization.

A few Corophioids are said to bear coxal gill 7 (Bousfield, 1973:193) but Gammaropsis, the most primitive appearing genus does not (but only two species at hand have been examined by us). Nevertheless, the presence of gill 7 in the group is of positive value to the plesiomorphic state of Corophioids.

A new classification of Amphipoda is shown in Graph 1. Amphipoda are divided into two main suborders, Corophiidea and Gammaridea, based on telson. The Corophiidea and Gammaridea contain subgroups, for example, the sections Corophiida and Caprellida in the Corophiidea and the Gammarida and Talitrida in the Gammaridea. Superfamilies, such as Gammaroidea and Urothoidea, are situated in the sections. Families, such as Ischyroceridae and Corophiidae, then fall below superfamilies. The Hyperiidea are retained as a token suborder possibly of polyphyletic descent from several Corophiidean ancestors; they are divisible into 2 superfamilies (Bowman and Gruner, 1973) as shown in Graph 1.

The Evolutionary Pattern

(Graphs 2-7)

The "simplification" evolutionary system in Amphipods is based on the proposals that (1) loss of an attribute in an evolutionary line of descent is irreversible and (2) wholesale transoceanic migrations of freshwater amphipods have not occurred. The absence of a significant early fossil record in the group prevents any support to these proposals.

Graphs 2-7 accompanying this section are meant to be self-explanatory and applicable to the entire essay. They generally conform to the text, appendices and keys but are meant to express generalities and to show minor alternate pathways of descent.

Two facts suggest that the origin of freshwater Amphipoda occurred during the time of Pangaea when the continents were coalesced: (1) Certain freshwater amphipods in widely separate regions, such as Palearctica and Notogaea, have coxal gill 7 present and some of these have sternal gills; (2) No living marine Gammaroid, bearing coxal gill 7 and sternal gills, with a common distribution between Palearctica and Notogaea, is extant. The term "Gammaroid", in this instance, excludes for example, such clearly constrained marine genera as *Anisogammarus* and such clearly disjunct genera as *Megaluropus* (the *Cheirocratus* case is explained in the accompanying box below). *Anisogammarus* and its allies are narrowly confined to boreal waters and *Megaluropus* has lost the prehensility of gnathopods, a characteristic presumed to be irreversible in a short sequence of evolution. If any prehensile Gammaroid distributed in both hemispheres has ever existed there is no evidence of that remaining in the sea today. Marine waters around Australia today are populated with highly advanced subtropical Gammaroids largely confined to very shallow waters, while the primitive Gammaroids living in the boreal seas adjacent to Eurasia are so poorly adapted to the marine environment that dispersal southward is severely blocked by subtropical climates. Obvious marine dispersions between the hemispheres were made in past eons but connections have been lost except in the Cheirocratids. There remains no evidence of a marine connection across wide tropical seas between Palearctic and Notogean freshwater amphipods. There is, however, evidence and presumption that oscillation between freshwater and marine habitats has occurred in the Palearctic realm.

The *Cheirocratus* Case

Cheirocratus has recently been discovered (1974) from Australia by M.M. Drummond and J.L. Barnard and their report on that discovery may not reach print before this work. As far as is known, *Cheirocratus* is the only marine genus that occurs only in the North Atlantic and Australia. A species from Madagascar formerly placed in *Cheirocratus* is now considered to be apomorphic and has been transferred to *Incratella*. *Cheirocratus* and its north Atlantic allies, *Cheirocratella* and *Casco*, have close affinities to tropical genera such as *Hornellia* and *Megaluropus* which are believed to be apomorphic. Although there is a possibility that a species of *Cheirocratus* has been transferred by humans from Britain to Tasmania, we find no difficulty in accepting its presence in both places as a result of continental drift. What does support the human interference theory is the lack of dozens of other Atlantic taxa not found in Tasmania. What does not support the human interference theory is the strong specific distinction of the two known species in Tasmania, a speciation which would have had to occur in 200 years.

The extraordinarily close morphotypy of Palearctic Gammaridans and Notogean Gammaridans suggests that they had a common ancestor, which indicates that they were dispersed from Notogaea to Palearctica or vice-versa in the time of Pangaea. Many Gammaroids but not Crangonyctoids have halinity tolerances sufficient to suggest that some degree of dispersal could have occurred after continental drift had commenced while the gulfs between continental segments were narrow and of brackish character.

The antipathy of freshwater Gammaroids to torrid climate indicates that this wide dispersal would require a continuous cool-temperate climate along the pathway from Gondwana to Laurasia. Today, freshwater Gammaroids (sensu stricto, excluding certain marine crawlouts) are extinct in the Ethiopian regime, except for the warm-temperate outpost of South Africa. They apparently do not occur in the tropics of northern Australia.

Freshwater Gammaridans are entirely absent in Neotropica, except hypothetically for the Bogidiellids, here believed to be asternobranchiate descendents of Crangonyctoids. Despite geological evidence to the contrary (Dietz and Holden, 1970), South America appears superficially to have been excluded from Gammaroid invasion by its remoteness from the remainder of Gondwanaland, yet a pathway between Palearctica and Australia-Africa was extant. Alternatively, most of the Gammaroids of South America may have become extinct and replaced by Hyalellids. The latter group of Talitroideans has a tropical distribution and is widespread through warm freshwaters of South America but it has also adapted to the cold waters of alpine Lake Titicaca. The lack of widespread generic diversification in Hyalellids in South America indicates that they are either relatively more recent in origin compared to Gammaroids or are evolutionarily stagnant. This is supported by the apomorphy of the group relative to Gammaroids but it does not necessarily suggest that Talitroids were not already in existence at the time of Pangaea. It does suggest that they are less viable as a group than are freshwater Gammaroids and, en masse, would offer no severe competitive stress to Gammaroids, especially in the cooler parts of South America. These suppositions could indicate that the major dispersal of freshwater Gammaroids took place at a time when a temperate pathway existed between Gondwanaland and Palearctica but that South America was barred, in some way, from this radiation.

Notogean and south Ethiopian Gammaridans are extremely close morphologically to most Palearctic Gammarids. In plesiomorphic states they differ in only two consistent features, the presence of sternal gills or osmotic organs in Notogean Gammaroids and the clustering of urosomal spines and setae away from the posterior margins in Palearctic Gammaroids.

Each group has otherwise undergone many similar evolutionary events, although Notogean Gammaridans have been so constrained by the relatively small habitat and drifting of Australia into unfavorable climes that their environmental space is severely reduced and the geographic divisibility has been narrowed. Much extinction has probably occurred in Australia. The wide separation of South Africa and Australia has not diminished the close similarity between the truncated faunas.

The northern hemisphere also has Gammaridans with sternal gills. These are divided into three groups, the widespread Crangonyctids throughout much of Holarctica but dominantly Nearctic, the Pseudocrangonyctids confined to east Asia and the "Sternomoera" group confined to Japan. These are presumptively Notogean in affinity. Their only morphological marker is the sternal gills. The urosomal setation pattern has decayed but this has occurred so widely throughout Notogean Gammaroids that its loss is only of negative value in suggesting any alternative conclusion as to the origin of northern sternobranchials. Sternal gills also occur in the South American Hyalellids in the remote superfamily Talitroidea, so that such gills are known to have arisen twice in Amphipoda. If Japanese Sternomoeras, with sternal gills, are apomorphs of the greater Crangonyctoid group, then presumption of a third origin of sternal gills may be false. The alternative to a Notogean origin for northern Crangonyctoids is a strict descent from sympatric Gammaroids with separate origin of sternal gills. This alternative is less parsimonious than the former alternative.

Nearctic Crangonyctoids often lose their sternal gills intragenerically and there are a few Notogean taxa (Austrogammarids) that do also (W.D. Williams, in litt.). Coxal gill 7 is retained plesiomorphically in Holarctic and Notogean-Ethiopian Crangonyctoids but is often lost in Holarctic species and has been lost in part of the New Zealand Phreatogammarus. Some of the complications in classification of Gammaroids result from this loss of a morphological marker.

Our proposal that Crangonyctids represent a Pangaenic dispersal relict is supported by evidence from other Peracarida. Schram (1974, 1977) supports the thesis that many crustacean groups arose in the Laurentian (northern cool or tropical) continental system before Pangaea. When the continents coalesced, these marine crustaceans became distributed throughout Pangaea and invaded freshwaters. After Triassic times, the continents drifted apart but the old Permo-Triassic marine fauna of Pangaea was replaced in the ocean with a modern, post Triassic fauna, and only Notogean freshwaters retained remnants of the Permo-Triassic crustacean groups. For other peracarids, Holarctic freshwaters now also contain modern crustaceans whereas we propose that Holarctica retains PermoTriassic amphipods in the form of Crangonyctids. In Asia they have almost been extirpated by later Gammaroids (Gammarus, Echinogammarus) and Niphargids. In Nearctica where Niphargids never extended and where the Gammarus-Echinogammarus radiation has been notably unsuccessful for unknown reasons, Crangonyctoids have been widely preserved and are the dominant fauna. The competitive stress between Crangonyctids and Gammarids may be very delicately balanced, so closely that replacement of one group by the other is not revolutionary. The noticeable differences are extremely subtle except for sternal gills, which themselves are lost several times in apomorphic Crangonyctids of different evolutionary lines (for example, western Stygobromus, apomorphic species of Austrogammarus and Neoniphargus and one or two species of Phreatogammarus).

If one adheres rigidly to the thesis that the presence of an attribute such as sternal gills is primitive then the Crangonyctoids would be considered to be the most primitive of the Gammaridans. On the other hand, the dispersed armament on the urosome in Holarctic Gammaroids would have to be considered a specialization, even though such an attribute has the appearance of complexity and the trend throughout Gammaroids is the loss of that armament.

The distribution of Crangonyctoids also suggests that they are primitive. To a certain extent they can be considered to have a relict distribution. They dominate Notogaea and South Africa in parallel with many other relict groups of organisms, but in Holarctica they dominate only Nearctica and may have been largely replaced in Palearctica by a wide diversity of more advanced Gammaroid genera. The sparsity of Nearctic

Gammaroids, sensu stricto, suggests that dispersal to North America from Palearctica took place late in the breakup of Laurasia and that the environmental pathway for Gammaroids was very tenuous. The strength of Crangonyctoids in Nearctica indicates an earlier invasion but also complements the loss of sternal gills.

Sternal gills probably increase the respiratory capability of an amphipod in oxygen-poor freshwater (Bousfield, 1977:285), but they may also be mainly osmotic organs (F.H. Drummond, in litt.). Many freshwater amphipods lack sternal gills, suggesting that those species lacking gills have an increased tolerance for low oxygen levels. There is virtually no other visible morphological difference between sternobranchiate species and those lacking sternal gills. The suggestion is made therefore that the balance between a need for those gills and the viability without those gills is so narrow that in Crangonyctoids they formed only a reserve of evolutionary "strategy"* not necessary to the survival of the group. They may be a superfluous holdover adapted to some function other than the original. The loss of those gills could be coupled with an immigration of Crangonyctoids into an oxygen rich environment, such as the shallow sea. In morphotypical terms this suggests that the Holarctic Gammaroid (marine Gammarus for example) is simply a Notogaean Crangonyctoid lacking gills but supplied with a richer diversity of urosomal spination. This move into a brackish Sinus Borealis (Map 2, northernmost gulf) may have been the trigger event that was correlated with loss of gills; more importantly, the loss did not impede later reinvasion of freshwaters. The survival value of those gills was so low that small physiologic adjustments not affecting the general morphology of amphipods had equal survival value. The need for gills was so low that later groups (Niphargids) lost coxal gill 7 and yet became hypogean and highly diversified.

Invasion of the sea by freshwater Holarctic Gammaroids is today marked by the tenuous hold of a few species of Gammarus and Echinogammarus along the narrowest margins of the sea in Holarctica or in special environments, such as meltwaters under Arctic pack ice. These Gammaroids appear to be very poorly adapted to fully marine environments, perhaps either because they lack the polyhalinic facility or because they have been constrained by more advanced marine amphipods. The latter supposition holds little merit because of the generally low diversity of primitive marine Amphipods in Holarctica compared with other areas of the world (see later discussion). These marine Gammaruses are mostly confined to the upper few meters of marine waters where some dilution nearshore may occur most of the time. They are joined by the Anisogammaruses, which also retain coxal gill 7 in the sea but have replaced the sternal gills with accessory lobes on the coxal gills. The Anisogammaruses are confined to the North Pacific Basin, also hug shorelines and, like Gammarus, have "reinvaded" freshwaters along the continental margins. Gammarus has "reinvaded" Palearctica much more deeply than Anisogammarus. The only extension of Gammaroids into deeper waters is seen in the abyssal Bathyceradocus, a relict genus of uncertain origin, but possibly with affinities to Anisogammarus.

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* Because this objectionable word implies conscious planning by animals to influence their evolutionary future we place it inside quotation marks.

Gammarellus and Weyprechtia form an incipient familial grouping (Gammarellids) that also bear coxal gill 7 and occur in the sea. They are characterized by the partial to full loss of prehensility on one or more gnathopods and presumably would be considered in earlier times as poor ancestral forms to the strict Gammaroid groups. However, the two genera make very important potential intergrades between Corophiideans and Gammarideans because their uncleft telson, though laminar, could be construed to be an intergrade between the fleshy uncleft and laminar cleft telson of typical Gammaridans; and because the poorly prehensile gnathopods, especially of Weyprechtia, fit the model of Prof. Stock who suggested (in litt.) that amphipod legs 1 and 2 originally were simple and then became prehensile. To use these Gammarellids as models for evolutionary schemes requires the salt-loving Gammarellus to be a model for the marine precursor to both Crangonyctids and Gammarids, the Crangonyctids for some reason going on to develop sternal gills, the Gammarids simply developing cleft telsons and complicated gnathopods. In this scenario it yet may be possible, but it isn't very parsimonious (meaning uncomplicated), to retain the fresh-to-salt-to-fresh cycle as part of the selective process for descent between Crangonyctoids and Gammaroids while sternal gills are lost. To invoke this model means that a major ancestral form (Gammarellus) remains alive in brackish arctic regions. The improbability of the scenario lies in the proposal that the Arctic is said to be a fairly late development on Earth (Dunbar, 1972:121) and a hypothetically close sibling (Cheirocratus) remains alive in Tasmanian seas. Because they would be considered to be plesiomorphs to the modern Gammaroids, Gammarellids could be called relicts. This makes them very attractive as possible ancestral models and they should be kept in mind as the other evolutionary sequences are developed in this essay.

All other marine amphipods of the Gammaroid facies that bear gill 7 (at least in their primitive genera) are apomorphic forms with apparent origins in highly derived Gammaroids. These include the Melphidippids, Megaluropids, Cheirocratids, Phoxocephalids, Pontoporeids, Urothoids and Haustoriids.

The sparsity of Gammaroids bearing gill 7 in world seas suggests that the most primitive living Gammaroids are those in freshwater. Although gill 7 apparently has survival value in the marine Melphidippids and Phoxocephalids, its presence cannot be valued in a fashion similar to Gammaroids. Those other marine groups occupy entirely different categories of niche than marine nestlers and the gill may have other functional adaptations.

We presume, in summary, that Crangonyctoids widely populated Holarctica but, after Laurasia commenced its breakup, the Gammaroids appeared as descendents from Crangonyctoids within the Palearctic fragment. The evolutionary cycle took place in the ocean and a few Gammaruses were thus able to reach Nearctica. In Palearctica they also reinvaded freshwaters and diversified enormously into the Metohias, Echinogammaruses, Sarothogammaruses, Dikerogammaruses, and Pontogammaruses. These groups and others, such as Niphargids, which later invaded freshwaters from the sea, almost fully extirpated the Palearctic Crangonyctoids. Such a domination did not develop in Nearctica where the Gammaruses may be of fairly late arrival or poor adaptability.

Coxal gill 7 is presumed not to have arisen separately in a marine Gammaroid invading freshwaters. If the earliest amphipods resembled Gammaroids and had a marine origin then they would have had that gill; but the earliest amphipods have been replaced by worldwide genera lacking the gill. Freshwater amphipods and their derivatives retaining the gill would therefore be considered as relicts. Apomorphic marine amphipods retaining the gill can therefore be traced back to groups bearing the gill, and apart from plesiomorphic groups, such as Pontoporeiids and Anisogammaruses the largest group bearing the gill resides in freshwater. Without geological evidence no conclusion can be made as to whether or not amphipods originated in freshwater and spread to the marine world, but the possibility of this cannot be dismissed.

Article 2 on the outer ramus of uropod 3 is another good marker. Its presence in well developed condition suggests affinity among groups but its absence has little monophyletic value because it has been lost apomorphically within so many tightly knit groups. One presumes that the plesiomorphic members of one group bearing article 2 must have their origins in the plesiomorphic members of a similar group. The presence of article 2 is confined mostly to freshwater taxa or their obvious derivatives, such as Phoxocephalids. In the sea, two main groups, the Melitids and the Eriopisellids, retain article 2 in well developed form, with immense enlargement in the Eriopisellids. These groups, therefore, appear to have a stronger relationship to freshwater Gammarids than do their sympatriots in the sea, the Ceradocids. The latter group is characterized by the loss or severe reduction of article 2 on the outer ramus and the aequiramous condition of uropod 3. This group also retains the fully magniramous uropod 3 of the supposed primitive amphipod, whereas most of the freshwater groups have variramous or parviramous uropod 3 with the inner ramus reduced in varying degree. Even in magniramous freshwater amphipods the inner ramus differs in shape and setosity from the outer ramus. The symmetrical (aequiramous) magniramous uropod 3 of marine Ceradocids is potentially a good marker of affinity but it is difficult to determine whether or not it has arisen more than once in several evolutionary sequences. Because of its simplicity, it has the appearance of being more primitive than the freshwater magniramous uropod 3. A transformation from the marine form to the freshwater form would require the addition of article 2 on the outer ramus and the loss of symmetry in the rami. The freshwater form of the uropod bears striking resemblance to that of certain Syncarida, a possible phyletic partner of the Amphipoda. Except for pelagic taxa, the majority of marine Gammaridea (the suborder) is characterized by decreasing size and complexity of uropod 3 so that the Ceradocid uropod 3 would fit between the freshwater form and the general situation in other amphipods.

The freshwater uropod 3 has been exchanged for the marine kind in the freshwater genus Phreatogammarus in New Zealand. Coxal gill 7 has been lost but sternal gills partly remain. The Ceradocids may, therefore, have their origin in the Notogean Crangonyctoids from ancestors common to Phreatogammarus (or the evolutionary flow could be reversed if hypothetical stages are intercalated).

Kergueleniola and the Bogidiellids also have a similar uropod 3 with stable and symmetrical rami. But this kind of uropod 3 is not sufficiently distinctive to accord the Ceradocids and Bogidiellids a remote ancestry because this form of uropod 3 has intergradations in such antiboreal marine genera as Ceradocopsis (=Maeracunha), where the outer ramus retains a tiny second article. The second article is also carried along in various Ceradocids as a minute vestige (Elasmopus). Hence, the freshwater kind of uropod 3 is still considered the more primitive, although many of the evolutionary events in the transformation to the marine uropod 3 appear to have occurred in the southern hemisphere (or are retained there in relict form).

The reduction of the inner ramus on uropod 3 is a dominant feature of both Holarctic and Notogaean Gammaridans. When the ramus is fully reduced to a small scale lacking any medial setae, the condition is known as parviramous. Loss of article 2 on the outer ramus is common. Further reduction in size of rami is the trend and, occasionally, the inner ramus is completely lost and the outer severely reduced. This is an especially strange feature of Nearctic Crangonyctoids which have become hypogean, because the feature contrasts so strongly with that of the Palearctic Niphargids, which are also hypogean. The Niphargid uropod 3 has reversed the trend and is enlarged, the outer ramus often becoming almost as long as the body of the amphipod, with article 2 as long as article 1. Most Niphargids have a parviramous uropod 3 but one plesiomorphic genus, Pontoniphargus, retains a variramous uropod 3 with partially elongate inner ramus. Descent into phreatic waters, therefore, lacks correlation of morphology in uropod 3. One might presume that the elongate uropod 3 of Niphargids could be used as a posterior sense organ to assist in guidance backwards through tight spaces. This might be a characteristic of predators, yet this uropod is unavailable to Crangonyctids living in the same environment. Biologists reject Niphargids as predators.

The marine Melitids and Ceradocids may have had distinct origins as based on uropod 3 mentioned above in connection with Phreatogammarus. The Melitids have the freshwater form and the Ceradocids have the marine (Phreatogammarus) form. Some of the Melitids maintain an association with diluted waters near the sea margin, although many have departed dilute waters fully. The plesiomorphic Ceradocids are fully marine but they probably represent the ancestors of Weckeliids, which have largely reinvaded freshwaters in subtropical and tropical regions. The Niphargids, which also have reentered freshwaters in Palearctica appear also to have a marine origin from the Melitids. Niphargids can be derived in several steps from various antecedent groups but the most parsimonious derivation passes through Melitids. Vandel (1965:135) holds that all hypogean amphipods are of marine origin but we now propose that this does not apply to Nearctic Crangonyctids, which have no clear links to marine Amphipods but have links to Notogean freshwater Amphipods. The Austroniphargids of Madagascar are a difficult case but appear as easily derivable from marine ancestors as from freshwater, though they are most likely apomorphic Crangonyctoids. On the other hand, the interstitial seashore Sarothrogammarids clearly have a freshwater origin from Echinogammarus-like ancestors.

These suggested sequences reinforce the proposal that the most primitive Gammaridan Amphipods are Notogean Crangonyctoids, that Gammaroids underwent a brackish water cycle in losing sternal gills, reinvaded Palearctica, but formed the ancestors to marine Melitids, from which the Nipharfgids were derived. The latter reinvaded Palearctica to replace most

Crangonyctoids. The setting for the brackish water cycle was confined to Palearctica and the Niphargids arose too late to reach Nearctica before it moved away from Palearctia. The Niphargids may have arisen so late that they have not had time to spread eastward througout Asia so as to reach a Bering landbridge, whereas Crangonyctids, apparently, have passed across that landbridge eastward (Holsinger, 1974c:4). However, the main evolutionary flow of Nearctic Crangonyctids extends from southwest to northwest. The oculate epigean species with well developed uropod 3 occur in the southeast USA, whereas groups to the northwest have progressively smaller uropod 3, greater loss of sternal gills and greater descent into hypogean environments. The supposition is made, therefore, that the group reached Nearctica from the east.

The Tethyan pattern of distribution in Hadziids does not negate the general theory of Pangaenic origin for amphipods. Because Hadziids are very advanced taxa, with marine ancestors in Ceradocids or Melitids, their Tethyan pattern of distribution suggests that they existed also in Laurasian times and had a common ground of dispersal through that Seaway when its western part in Nearctica closely abutted the Palearctic part. Notogean Crangonyctoids would have had to have entered the sea and undergone their considerable deployment through Melitids to Hadziids so as to provide this segment of the fauna. The Tethyan distribution, however, is probably coincidental with environmental favorability to Hadziids rather than to phyletic constraint owing to geographny. Hadziids are strongly dispersive, as they have reached Hawaii and occur in Micronesian atolls. Unlike Niphargids, which have penetrated deeply into Eurasia, Hadziids and Weckeliids are confined to seaside or insular aquifers within 200 km of the sea. They have diversified greatly at generic level in the western Tethys (Caribbean, Gulf of Mexico), but only a few species have reachedthe Mediterranean region. There may have been a degree of extinction in Mediterranean Hadziids during Pliocene drying of that sea but the Sarothrogammarids, another group; with a severely restricted seaside habitat, survived that catastrophe on Trans-Gibralter shores and then reinvaded the Mediterreanean. The greater diversity of Hadziids in the western Tethys, of course, can be correlated with the larger supply of isolating mechanisms involving troglobitic habitats of numerous, widely separated islands and continental fragments. Added to this is the absence of the Gammarid diversity seen in Palearctica, as represented by the Sarothrogammarids, Metohiids, _Typhlogammarus_, _Pseudoniphargus_, _Metacrangonyx_, and Salentinellids, all of which coexist to a certain extent in seaside aquifers or in limestones within a few kilometers of the sea. The absence of stronger Gammarid elements in the western Tethys is well demonstrated by Holsinger and Longley (1980), who found in a single South Texas aquifer a host of amphipods of at least three family nuclei (Crangonyctids, Bogidiellids, Sebids), one of which, the latter, is clearly of marine origin. Hadziids have penetrated much farther inland in Mexico than in the Mediterranean region.

A closely parallel group, the Weckeliids, has been removed from the Hadziids (J.L. Barnard, 1976b) and proposed as descendents of Ceradocoids. The Weckeliids are confined, as far as is known, to the western Tethys, mainly Caribbean Islands on shores and inland aquifers along the Gulf of Mexico. The group differs from Hadziids mostly in the retention of a distinctly subchelate gnathopod 2 in the female bearing small, evenly dispersed palmar spines but the definitive difference is the absence of article 2 on uropod 3. Uropod 3 is magniramous and almost aequiramous. In contrast, most Hadziids have a different female gnathopod 2 lacking distinction between palm and margin of hand and bearing stiff, apically bent setae, not only on the hand margin but also on the palm. Similar setae are found in Melitids, such as Psammoniphargus; but in Melitids the palm remains distinct and the special setae have not penetrated the palmar margin. Hadziids, therefore, have the appearance of apomorphic Melitids, whereas Weckeliids have very close affinities to Ceradocids, such as Paraweckelia. Nevertheless, little imagination is needed to visualize the transformation of an Hadziid uropod 3 (plesiomorphically seen in Psammogammarus, including longiramus) into a Weckeliid. The morphological and ecological convergence of Hadziids and Weckeliids is striking. They have close sea connections but mainly have moved landward along subtropical or tropical seashores with aquifers in limestone.

The ultimate question concerning Niphargids is their origin. They have occasionally been considered to be parallel but not phyletically homologous to Eriopisellids (Ruffo, 1953c:33) but there appear to be few taxonomists (Chevreux, 1920:8; Schellenberg, 1933a:406) convinced of our belief in their evolutionary congruence. All Niphargids are of freshwater occurrence and the suggestion that Niphargids might have a marine ancestry from Eriopisas has not been acceptable in the past. One could, of course suggest that the line of descent flows through such salt-pool forms as Psammogammarus or Pseudoniphargus, which themselves may have then emerged into the sea. There is little difference other than in gnathopods among Eriopisellids and Niphargids and those groups differ from the Eriopisids only in reduced maxillary setation. Most Niphargids have enlarged hammer-like gnathopods of close similarity to each other but of diverse shapes in various genera, or of diverse enlargement, some species groups having rather poorly enlarged gnathopods even though both may be the same size. This recalls the mitten-shaped situation in Eriopisellids where the gnathopods actually form small hammers.

The marine origin of Niphargids might explain the lack of coxal gill 7, the loss of maxillary setation, the possible but remote connection to Austroniphargids in Madagascar, and the lateness of their appearance might suggest why Niphargids (sensu stricto) did not reach the Western Hemisphere. However, a closely parallel but very constrained group, Allocrangonyx, did reach America possibly through the Pseudoniphargus-like morphology (but see below), and possibly through a marine Tethyan pathway, but the Crangonyctoid affinities remain convincing. Pseudoniphargus is an anchialine and interstitial group which may have readily formed the necessary linkage (or its ancestors might have). The authors believe that Austroniphargus has Crangonyctoid ancestors.

Ecological distinctions between fully phreatic Crangonyctids and Niphargids are intriguing. Crangonyctids dominate North America whereas Niphargids, except in the analogous form of Allocrangonyx, are missing there. In Eurasia, Niphargids dominate and Crangonyctids are very poorly diversified. Crangonyctids in North America have both epigean and subterranean species and Gammaruses are rather poorly diverse, whereas in Eurasia Crangonyctids are rare and epigean habitats are packed with Gammarus and Echinogammarus. Subterranean habitats of Eurasia are dominated greatly by Niphargids but they are poorly epigean, apparently being emergent from phreatic waters in small epigean areas. Niphargids have strongly hammer-like gnathopods whereas Eurasian Crangonyctids do not, while in America some Crangonyctids and Allocrangonyx have gnathopods approaching the hammer-like form. Niphargids are characterized by immensely elongate uropod 3, while most American subterranean Crangonyctids have uropod 3 severely reduced. Only Allocrangonyx, with 2 species, has enlarged uropod 3 in America. Most Crangonyctids have many more gills than do Niphargids. The latter have 5 pairs of coxal gills, whereas many Crangonyctids have 6 pairs of coxal plus several sternal gills.

These differences plus many others (for example palmar spines of Crangonyctids and Allocrangonyx) suggest either that the habitats of America and Eurasia are distinctive or that the happenstance of evolution has brought differing dominance to the two continents. Why have the Niphargids with gigantic uropod 3 in Eurasia speciated so strongly and the similar Allocrangonyx in America not? Why have the Crangonyctids with tiny uropod 3 diversified in America but remain so constrained in Eurasia? Niphargids appear to be well adapted in the predatorial mode requiring rapid movement, whereas Crangonyctids do not bear such evidence morphologically. However Niphargids are said to be detritus feeders only. Perhaps they use rapid movements or rearward sensing by uropod 3 as an escape mechanism. If differing dominance is mainly an evolutionary happenstance on the two continents then a host of niches may remain open in both areas. If the kind of morphology in Niphargids has resulted in their domination over Crangonyctids, then one might expect the Allocrangonyx kind of amphipod to become predominant in America in coming geological ages, given the regular events necessary for dispersal and speciation. However, the Allocrangonyx morph is strangely constricted to mid-United States as if its test of fitness against Crangonyctids or physical factors had restricted it to a very narrow regime; however, there is the possibility that it became isolated from sea encroachment prior to Oligocene times and may be confined to an underground basin province isolated from surrounding regions by differing chemical habitats or lack of underground stream capture. This isolation theory is contradicted by the presence of Stygobromus in the same area. Comparison of functional morphology among the groups and between continents may produce some ideas on the various adaptations these groups express in their morphology.

To support the contention made above that Notogean ancestors emerged into western Palearctic seas (to wit, the embryonic Atlantic Ocean or even Sinus Borealis), lost their sternal gills, but in their strict Gammaridan form were forever confined tightly to a diluted medium, and then reinvaded freshwaters to form the great Palearctic fauna with its many offshoots, requires exposition on the modern marine fauna. One must demonstrate the level of impoverishment and degree of apomorphy remaining in the North Atlantic embayment. At least one student of marine Amphipoda views the North Atlantic of today as relatively youthful (J. L. Barnard, 1958a:150, 1960:289). This means that the marine fauna has certain kinds of taxal impoverishment suggesting that the North Atlantic has been isolated from the remaining seas by barriers of various sorts, but it also means that the bulk of North Atlantic Amphipoda are highly derived forms. Despite the barriers to certain groups, those taxa, which have indeed arrived in the

North Atlantic by overcoming these barriers, are very advanced or specialized. Non-tropical groups that are absent or impoverished in the North Atlantic are Exoedicerotidae, Phoxocephalidae, Acanthonotozomatidae, Dexaminidae, Dogielinotidae, Eophliantidae and Paracalliopiidae, but these impoverishments are amply replaced by rich development of Pleustidae, Cressidae (endemic), Podoceridae, Oedicerotidae and Eusiridae (J.L. Barnard, 1972a:12; 1974:2, and J.L.Barnard and Drummond, 1978:37). Virtually every marine group has its most specialized members in the North Atlantic if it has any representation there at all. For example, the Phoxocephalidae, an impoverished group in the North Atlantic, have only 4 genera in the northeast and 4 (partly overlapping) in the west. Three of the N.E. genera are represented by the most simplified (= specialized) species in those otherwise widely distributed genera and the fourth genus, Harpinia, well diversified, is the most specialized genus of its subfamily. Sexual dimorphism by size alone in antenna 2 flagella has been lost and replaced with setular diversity. Harpinia is the dominant genus in shallow waters and yet is blind. It has been traced by Barnard and Drummond (1978:33) through a bathyal pathway as the only way in which such blind, cool-loving Phoxocephalids can reach the North Atlantic easily past the tropical barrier.

The sublittoral, warm-loving, western Atlantic Phoxocephalids, for the most part, appear to have entered the area through mid-American isthmuses.

The impoverished Dexaminids of the north Atlantic are the most specialized (simplified) of the group, with antecedents possibly arriving through a Tethyan pathway from Australia. All North Atlantic Oedicerotids belong to the apomorphic groups. Many other examples can be stated.

The North Atlantic is therefore characterized by the late arrival of marine taxa or the extinction of any plesiomorphs outside of Gammaridans. In almost every fully marine familial group the highest degree of apomorphy occurs in the North Atlantic, if the group has reached there at all. This suggests that the Gammaruses occurring on the seamargins have not always been severely constrained by fully adapted marine amphipods and had their opportunity to expand outward, to radiate. If they did, they have now been constrained tightly to the shoreline, but no remnants of any Atlantic advance by the Gammarids remain. By this is meant that the kind of diversification in Holarctic Gammaroids, as expressed in freshwater, never occurred in the sea. More distantly related groups, such as Pontoporeiids, apparently were spawned by Gammarids but perhaps not in the medium of the North Atlantic. One might therefore imagine that the Gammaruses now living in the North Atlantic have emerged from freshwater or represent the remnants of a cycle in brackish water when the embryonic Atlantic was a rift valley partially influenced by the sea.

Incursions of Gammarids into the sea spawned the Arctic-Atlantic Gammarelluses and the North Pacific Anisogammaruses but these never became strong marine groups either. Hence, the Neogenic Gammarus-like taxa are very poorly adapted to marine waters, have never spread out of their localized marine areas and cannot be considered ever to have been fully marine and primitive amphipods which invaded freshwaters in a direct marine to freshwater cycle. The Gammarelluses may be ancestors of the Cheirocratids, another group rather closely confined to boreal shores and Tasmania. The only groups to have escaped fully to the sea were the

Hornellias, the Megaluropuses and the Melphidippids. Bathyceradocus may have descended from an Anisogammarid ancestry.

On the other hand, the deployment of Gammarids through the Ponto-Caspian Basin during the eons when it fluctuated in salinity and in its Tethyan connections (Sarmatian Sea, Lac Mer) may have spawned important groups of marine fossorial amphipods. Again, the flow of evolution, as marked by morphology, moves outward from primitive freshwater taxa into genera adapted to polyhalinic waters of the PontoCaspian Basin. That basin today is now confined to the Caspian Sea, the Azov Sea, the Aral Sea, and the Black Sea where numerous Gammaroid fossorial taxa are preserved. Fossorial amphipods burrow into the benthos and have developed adaptations for this function. No Gammaroid fossorial lives today outside of that ancient basin except for the escapees to Lake Baikal and into rivers or across canals (Jazdzjewski, 1980). The Dardanelles have not provided egress for Pontogammarids into the Mediterranean but the Mediterranean has a Phoxocephalid-Haustorioid fauna so impoverished that it could not possibly prevent the emergence of Pontogammarids through competitive stress. Pontogammarids today therefore must have a severe salinity barrier. However, they are so close morphologically to Phoxocephalidae that one must at least explore the suggestion that the latter group has its origins remotely in Pontogammarids. Phoxocephalids have been found by Barnard and Drummond (1978:36) to have undergone their major radiation in Australia (or the remnants of that radiation are now confined to that region). Phoxocephalids may have descended from nearby freshwater Crangonyctoids of Australia but if so the environmental milieu as well as the morphological remnants have long become extinct. From a morphological focus, a parsimonious view is that PontoCaspian Gammaroids escaped by halophilic adaptation to the sea and through fortuitous circumstances reached the favorable Australian-like environment (in whatever position that continent or a neighbor might have been). There they radiated and commenced dispersal back into the northern hemisphere. But that dispersal has been so restrained that they have scarcely been able to reach the North Atlantic Ocean and probably are still in the dispersive and speciational process owing to the presence of open niches outside of Australia. This proposal has no support from ecological and geographical foci.

Pontoporeiids, another group of marine, but rather tightly constrained, fossorial amphipods may also have emerged from the Lac Mer phase of the PontoCaspian Basin, possibly into Arctic Seas through glacial lakes (Segerstrale, 1957b, 1976). The group has remained mostly in the North Atlantic Ocean tightly held to boreal waters and very partial to diluted waters.

Haustorioids, yet another fossorial group outside the Gammaroidea, are mainly confined to the Atlantic Basin and may have been a product of the interplay of Gammaruses in the embryonic Atlantic Ocean if that sea underwent phases similar to the PontoCaspian. They are tightly constrained to nearshore sand bottoms. Some have escaped to the North Pacific probably by an Arctic pathway but others have now been described in Magellan and Australian regions (Barnard and Drummond, 1982). The southern members retain primitive mouthparts but support highly specialized and complex uropods that are not thought to have any primitive status despite their complexity because they are so unusual in Gammaridea. The north Atlantic component retains somewhat primitive and ordinary uropods, whereas the mouthparts have become extremely complex and specialized. Another Haustorioid group, the Zobrachoids, retains the more primitive kind of gnathopods (fully subchelate) and also live in the southern hemisphere. Still another Haustorioid group, the Urothoids, are widely spread except for poor representation in the North Atlantic Ocean, and have so many similarities to Phoxocephalids that they may also have been a product of the TethyanPontoCaspian cycle and escaped to southern seas before undergoing a weak reinvasion of the north. Again, of course, they could have been entirely antipodeal in origin. They are under intensive study in the Australian region (Barnard and Drummond, 1982).

Lake Baikal, in Siberia north of Mongolia, contains almost 20 percent of the world Gammaroids. The origin of these 45+ genera remains speculative. Amphipoda in other parts of the world have so many lines of parallelism and convergence that a single origin for Baikalian amphipods could be proposed. Baikal could be treated as an entirely closed microcosm with a single founder species. The lines of adaptive radiation outward from a primitive Heterogammarus ancestral form are as easy to trace as they are in parallel groups outside of Baikal. The lake contains primitive nestling groups (Heterogammarus, Eulimnogammarus), ordinary fossorial groups (Micruropus), discoid fossorial groups (Hyalellopsis) and pelagic groups (Abyssogammarus) with very well developed predatorial gnathopods (Acanthogammarus) suggesting demersality. One mysidiform pelagic genus is also represented (Macrohectopus). Unlike the PontoCaspian Basin, where fossorial groups dominate the broad shallows, Baikal is dominated by nestling and pelagic groups. Baikal is so deep that the ratio of water volume to bottom area is high compared with the PontoCaspian Basin. Many students (Segerstrale, 1956a-62, Holmquist in Illies, 1967, Hutchinson, 1967) believe that Baikal has straddled several migratory pathways for amphipods and that the fauna is polyphyletic. Kozhov (1963:291) cites 4-5 founder species for the amphipod fauna. Stock (1969a:70), and Pinkster and Stock (1970a:205) identified a Baikalian genus as far away as Iberia (Eulimnogammarus). This might suggest that the genus was widespread through Eurasia but blossomed in Baikal and receded elsewhere. But G.S. Karaman (in litt.) has found that Eulimnogammarus is characterized by reduced coxa 1 and this is not characteristic of the Iberian species which must revert to Echinogammarus. The Baikalian Acanthogammarus and the Arctic marine, glacial-lake Gammaracanthus are clearly aequimorphic, though Gammaracanthus is probably an escapee from Baikal. There are broad analogies between Baikal and the PontoCaspian Basin in the protofossorial and fossorial groups such as Gmelina to Gmelinoides, Lobogammarus to Iphigenella (reversal), Obesogammarus to Homocerisca, and Micruropus to Obesogammarus (reversal). This implies that several connections based simply on morphology in the nonfossorial groups are not coincidental but may indicate common ancestry.

Glacial Relicts

Three of the eight classic glacial relicts of northern Europe are Gammarideans, Pontoporeia affinis, Gammaracanthus lacustris and Pallasiola quadrispinosa. The other five are Mysis relicta (mysid), *Mesidotea entomon* (isopod), *Myocephalus quadricornis* (fish), *Limnocalanus grimaldii macrurus* (copepod) and *Pusa hispida* (seal).

Except for *Pallasiola* (formerly *Pallasea*), these amphipods live in very dilute arctic seawater and tolerate freshwater so as to live in arctic lakes. By reason of altitude, of distance from nearest dilute seawater or of drainage patterns, these arctic relicts today have no extant environmental pathway between the freshwater of the lakes and the dilute saltwaters of the ocean. The glacial relicts are therefore species with disjunct distributions and because one assumes they originated in the ocean, their inhabitation of certain lakes today is considered relict.

For five decades Segerstrale has been the resident expert on the amphipods involved in this story of relicts originally propounded by Loven in the mid-19th Century. A vast literature may be opened by consulting Segerstrale (1962, 1976).

The lacustrine relicts are presumed to have been sluiced up from dilute seawaters, pushed ahead of advancing glacier fronts and left behind as residual occupants of ponds and lakes when the ice margins retreated (Kvasov, 1979:7). Because several ice ages occurred in varying extents the resultant distributions are complex, owing no doubt to the many vagaries which could occur during such revolutions.

Perhaps the most amazing part of the relict situation is how close nature came to losing the entire modern record of this event, as only a few species on earth are adapted adequately to live both in freshwater lakes and dilute arctic seawater and then be able to survive sluicing. Of course, sluicing is actually a very slow, plastic event. Dilute arctic seas hold many other species, especially of amphipods, which did not participate in the proglacial movement. For example, no species of *Gammarus* occurs as a relict and no species of *Pseudalibrotus* (=*Onisimus*) is today found in true glacial lakes. On the other hand, a species of *Pseudalibrotus*, apparently reached the PontoCaspian Basin and today survives as *P. caspius* and coincidentally, *Gammaracanthus caspius*, a sibling of *G. loricatus-lacustris* today lives in the PontoCaspian Basin. One may therefore argue that the PontoCaspian Basin is a glacial relict itself. A great ice lake apparently was pushed south far enough to make connection with drainage into the PontoCaspian basin (Segerstrale, 1976).

This conclusion is amplified by *Pallasiola quadrispinosa*, a partial relict. This species has its closest affinities to *Pallasea kessleri* of Lake Baikal and may have emerged from the Baikalian region into an ice lake system and then penetrated from the PontoCaspian Basin, while also being left behind by the retreating ice front in the FinnoBaltic glacial lakes. *Pallasiola quadrispinosa* does not tolerate salty waters, and thus, was not anble to survive in arctic sea where it also must have been carried by down sluicing at the terminations of the several glaciations.

The Baikalian connection opens a much wider door of inquiry as to whether or not a major connection between PontoCaspian and Baikalian areas could have occurred through the Wurm icelake. Such a connection might explain some of the amazingly coincidental morphologies occurring in the two bodies of water.

Probably, glacial relicts, apart from *Pallasiola*, lived in dilute salty waters prior to glaciation; otherwise, our conclusion that Gammaroids in general had a freshwater origin makes the return of glacial relicts from a dilute salty medium back into their original freshwater home an unremarkable feat.

Distribution of Gammaridans (See Table 2)

This section summarizes the biogeography of freshwater Gammaridans amphipods in condensed format. A short version of the generic content and diversity on the several continents draws together all of the evolutionary lines and places them into a geographic context. The more diverse genera and several of the less diverse but widespread genera are amplified in their proper geographic regimes.

Each genus is listed in Table 2 in geographic format and has separate distribution map numbers appended. Distribution maps for all widespread genera were made in March 1979 and though additional species may have been added to generic lists in the appendices of this monograph, the maps were fixed inalterably at that time.

The contents of each map are generally listed on the map, though names of species are often referred to by numbers or symbols found in the species lists in the appendices.

A full exposition of the evolutionary and geographic pattern starts in the chapter entitled "Freshwater Gammaridan Groups."

Holarctica

Few freshwater amphipod taxa are pandemic in this region. Gammarus, the major genus of freshwater amphipod, is confined to Holarctica; it has freshwater, brackish, and marine species and a few are found in the upper reaches of caves but none is fully phreatic. One species, G. lacustris, occurs throughout the colder parts of freshwater Holarctica. Most of the other freshwater species of Gammarus are found in Palearctica (102) while about 12 occur in Nearctica. Marine species (14) are confined to the North Atlantic Ocean and arctic waters but apparently are constrained from dispersing southward into the Pacific Ocean by the richly dominant Anisogammarids. A few species of marine Gammarus occur on both sides of the Atlantic Ocean.

Crangonyx reflects a mirror image of the Gammarus distribution in that its major diversity occurs in Nearctica (21), while only four species occur in Palearctica. This genus is both epigean and hypogean.

Echinogammarus has mostly freshwater species in Palearctica (37) and only 3 marine species in Nearctica (total marine species = 7).

Bogidiellids occur in both Nearctica and Palearctica though no genera are pandemic. Bogidiella itself, found in Palearctica (14) is found in the western hemisphere only in Neotropica (8). The same can be said for the true Hadziids, whereas Weckeliids (if indeed separated from Hadziids) are found only in Neotropica.

Palearctica (January, 1979)

The major non-lacustrine genera are Gammarus, Echinogammarus and Niphargus but a few species of each genus are also lake dwellers. The minor pandemic genera are Crangonyx and Stygobromus which are much more prevalent in Nearctica than in Palearctica. All other genera are confined to smaller regions such as western, middle and eastern Palearctica. The western section has about 20 minor genera, among which taxa are 5 small genera of the *Niphargus* group (such as *Niphargellus*), 5 genera of the *Sarothrogammarus* group (such as *Neogammarus*), 5 genera of the *Metohia* group (such as *Ilvanella*), 2 genera of the *Salentinella* group, 2 genera of the *Hadzia* group, 2 genera of the *Bogidiella* group, 2 of the *Metacrangonyx* group, 2 of the Eriopisellid group and one uncertain genus, *Bathyonyx*, and *Pseudoniphargus*. So-called glacial relict genera are *Gammaracanthus*, *Pallasiola* and *Pontoporeia*.

Middle Asia contains 3 genera of the *Sarothrogammarus* group, 3 genera of the *Metohia* group (*Anopogammarus*, *Tadzocrangonyx* and *Zenkevitchia*).

East Asia contains 2 genera of the *Pseudocrangonyx* group, plus *Eoniphargus*. Many freshwater habitats also are occupied by the Anisogammarid genera.

Invasive marine genera are *Psammogammarus* (in reality the old *Eriopisa*) and *Microniphargus* in western Europe.

Major lacustrine genera are those of Lake Baikal and the Ponto-Caspian seas (Black, Caspian, Azov and Aral). The Baikalian fauna contains 45 genera and 262 species (conservative estimate); some of the large or familiar genera are *Eulimnogammarus* and allies (50+), *Heterogammarus* (5), *Poekilogammarus* (18), *Pallasea* (15+), *Abyssogammarus* (3), *Ceratogammarus* (3), *Garjajewia* (3), *Acanthogammarus* (13), *Carinurus* (6), *Micruropus* (37), *Crypturopus* (5), *Hyalellopsis* (16), plus the famous mysidiform *Macrohectopus* (1).

The intrinsic PontoCaspian fauna contains 30 endemic genera, 4 exotic genera and 83 species; large or familiar genera include *Amathillina* (5), *Gmelina* (2), *Axelboeckia* (1), *Dikerogammarus* (7), *Pontogammarus* (6), *Pandorites* (1), *Stenogammarus* (7), *Niphargoides* (3), and *Cardiophilus* (2).

In addition middle Asia has a lacustrine genus, *Issykogammarus*, in Lake Issykul, with affinities to Baikalian genera.

To amplify, *Gammarus* in Palearctica (102 species) is divided into the following groups: marine = 14; freshwater = pan-Palearctic (*lacustris* and *pulex*); east and north Asia (7); mid-Asia (Tadzhikistan region) (8); mid-Asian lakes (7); west Palearctica (west Asia and Europe) (8); Caucausus (6); Asia Minor (8); mid-East (2); Asia Minor plus Balkans (4); Balkans (15); Iberia (1); west Europe (2); remaining Europe (4); North Africa (4). [The remaining 13 species of the genus are Nearctic for a total of 115; many others are dubious or extinct].

Those classes are also analyzed for *Echinogammarus* (48 species as of January, 1979): marine = 7; freshwater = pan-Palearctic (0); east and north Asia (0); mid-Asia (Tadzhikistan region) (0); mid-Asian lakes; west Palearctica (west Asia and Europe) (*thoni*); Caucausus (0); Asia Minor (0); mid-East (0); Asia Minor plus Balkans (0); Balkans (2); Iberia (16); west Europe (4); remaining Europe (all southern) (11); North Africa (3). [The remaining 5 species of the genus are PontoCaspian for a total of 48; some of the marine species are amphi-Atlantic.

Niphargus is a subterranean genus with 140 species wholly confined to Palearctica as follows: west Palearctica (1), west Asia (7), Caucausus (9), Asia Minor (2), widespread Europe (5), central and east Europe (20), Balkans (50), southern Europe (17), Iberia (1), west Europe and Britain (13), middle East (2), Europe to W. Asia (5) and southwest Europe (8).

Satellites of Niphargus are Pontoniphargus from Rumania (1), Haploginglymus from Portugal (1), Niphargopsis, midsouthern and eastern Europe (2), Niphargellus, central Europe (2), and Carinurella, the Balkans (1).

The Metohiids closely related to Gammarus include cave dwelling or hypogean Metohia, Yugoslavia (1), Anopogammarus, Caucausus (2), Ilvanella, Elba Island (1), Accubogammarus, Yugoslavia (1), possibly Typhlogammarus, Balkans (1), Zenkevitchia, Caucausus (1), Tadzocrangonyx, Middle Asia (2), and the epigean Fontogammarus, Yugoslavia (2). Probably the epigean Tadzhikistania, Middle Asia (2) belongs nearby and is a bridge from the Sarothrogammarids, to follow.

The closely related Sarothrogammarids include the high altitude epigean Sarothrogammarus, middle Asia (5), Comatogammarus, middle Asia (1), and the sea margin cobble-brackish genera: Neogammarus, Mediterranean (3), Lusigammarus, Lusitanian (2), Pectenogammarus, east Atlantic (1), Longigammarus, Mediterranean (1) and Rhipidogammarus, Mediterranean (2).

The southern Palearctic, including north Mediterranean shores and North Africa, contain all hypogean Metacrangonyx (3), Pygocrangonyx (1), Pseudoniphargus (1), Hadzia (3), Metahadzia (2), Salentinella (2), Parasalentinella (1), and Psammogammarus (1).

Eastern Asia (Manchuria to Japan) has only 3 endemic genera, all epigean: Eoniphargus(1), Pseudocrangonyx (9) and Procrangonyx (1).

To summarize, in early 1979 Palearctic Gammaridans totaled 117 genera and 765 species of which 45 genera and 262 species occur in Baikal, 30 genera and 83 species occur in the PontoCaspian fauna, 3 genera and 11 species are special east Asian hypogean taxa, 1 genus and 1 species are special mid-Asian lacustrine taxa, 28 endemic and 2 exotic genera and 231 species are mainly hypogean taxa mostly in western Eurasia and 9 endemic and one exotic genera and 175 species are mainly epigean taxa mostly in western Eurasia (western China westward), and 1 genus and 2 species are east Palearctic epigean marine ingressors (Anisogammarids). Overlaps result in lowered totals in the above numbers.

Nearctica

The diversity of freshwater genera in Nearctica is much lower than in Palearctica and the number of species somewhat fewer. Of course, major new discoveries continue to be made in Nearctica (especially by Holsinger) so that the outline of the fauna is incomplete.

The major genera are Stygobromus (96), Crangonyx (21) and Gammarus (13). The minor genera are Allocrangonyx (2) and Bactrurus (3), confined to the middle United States and 9 genera of Bogidiellids and Weckeliids in the Texas-Edwards-San Marcos-Yucatan fauna.

Only 10 or so species of freshwater Gammarus occur in Nearctica. As in Palearctica G. lacustris covers most of the habitable environment south to 45*N and in much of the western United States south to 40* N or more. This is the only Palearctic Gammarus in America. The next most widespread species is G. fasciatus across the Great Lakes and southward along the Atlantic piedmont. The third is G. pseudolimnaeus which also extends across the Great Lakes but turns southward at its western terminus into Arkansas, forming a reverse dogbone to G. fasciatus. The fourth, G. minus, occupies an interrupted distribution from Oklahoma northeastward to eastern Pennsylvania. All of the other species have very limited distributions, mostly scattering westward and southward through Texas and New Mexico from the Mississippi Valley.

All of the southeastern United States is therefore devoid of *Gammarus* and is replaced by *Crangonyx*. The distributional perimeters of these species are much smaller than perimeters of the top four species of *Gammarus* but a greater diversity of species is present. The top few species would appear to be *serratus*, *antennatus*, *setodactylus*, *minor*, *forbesi*, *pseudogracilis*, *obliquus*, and *?gracilis* (the latter not clarified). Many species of *Crangonyx* range well into *Gammarus* territory, thus overlapping and presumably to some degree utilizing the same resources as *Gammarus*.

In Nearctica *Stygobromus* is the habitat counterpart of Palearctic *Niphargus*, though we doubt that the two genera occupy precisely the same class of niches. Both are mainly hypogean but the two genera have radical morphological divergence, especially in uropod 3.

As to be expected, *Stygobromus*, like *Niphargus*, is very diverse because of the hypogean habit. One presumes that barriers to distribution are very numerous in aquifers. Given time, successful adaptation and lack of radical competition, one would expect *Stygobromus* and *Niphargus* to have become widely spread and diversified in their separate parts of Holarctica.

Both *Crangonyx* and *Stygobromus* appear to have radiated evolutionarily from the east or southeast of the United States westward and northward across the Rocky Mountains onto the Pacific slope. This is reflected in the morphological simplifications that progress westward in the many taxa. The major barrier, the central plains, like the Steppes of Russia, marks attenuation of diversity and, for the most part, delimits the western species of *Stygobromus*, most of which lack sternal gills and have very reduced uropod 3. At the moment, it does not appear likely that evolutionary progression from *Crangonyx* to *Stygobromus* occurred more than once; most of the morphological increments appear in the southeast, whereas in the northwest the two genera are much more distinctive morphologically than in the southeast. They moved westward on different paths, epigean and hypogean.

Bactrurus is a genus of 3 hypogean species apparently divergent from *Crangonyx* and occupying a small rectangle stretching from the western shore of Lake Erie to the eastern parts of Oklahoma and Arkansas. This is known as *Bactrurus* territory and is accorded a special number in our geographical scheme. *Bactrurus* is not as morphologically simplified as *Stygobromus* and one species, *B. mucronatus*, diverges from both *Crangonyx* and *Stygobromus* in the greatly elongate male telson. These subterranean species have not been swamped out by *Stygobromus* and must be studied intensively to determine their special niche adaptations.

Allocrangonyx is another minor genus of 2 species found only in the Arbuckle Mountains of Oklahoma and the Ozark Plateau of Missouri. This is the only subterranean genus of Nearctica that mimics *Niphargus* closely in the morphology of uropod 3. It has strange morphological coincidences with African *Pseudoniphargus* but Holsinger (1971:320) thinks it does not have

Niphargid affinities. Both Bactrurus and Allocrangonyx lie north and west of the Eocene embayment line and may be very old remnants of diverse taxa long ago expunged by marine incursions. Only Crangonyx and Stygobromus managed to reinvade the Mississipian plain after reemergence of land, and Gammarus has also been largely barred from regions of that embayment.

The San Marcos Well near San Antonio dominates the remainder of the Nearctic freshwater fauna (Holsinger and Longley, 1980). This well lies to the north and east of the Edwards Plateau in the Balcones Fault Zone. Together these two areas contain 7 genera and 15 species of hypogean amphipods, the well itself having discharged 9 species alone. Nine species of Stygobromus and 6 species in the Bogidiellid and Weckeliid genera of Artesia, Parabogidiella, Texiweckelica, Allotexiweckelia, (Texiweckeliopsis and Holsingerius), have been found in this area, which for all practical purposes is probably better classified in the Neotropical region rather than the Nearctic. However, this area forms the counterpart to the southern European limestones of Yugoslavia, Iberia, and Italy, where so many species of Hadziids, Bogidiellids and oddities in the Metohiid and Sarothrogammarid groups are found. In place of Metohiids and Sarothrogammarids a diversity of Bogidiellids and Weckeliids has evolved and one clearly marine import, Seborgia, from San Marcos Well, has become fully adapted to the subterranean world.

The Hadziid-Weckeliid-Bogidiellid fauna continues throughout Mexico, being especially well developed in karstic areas such as the Yucatan (sensu lato). Here 5 species occur in: Mayaweckelia, Mexiweckelia, and Paramexiweckelia.

South of Guatemala, well into the true Neotropical zone, exploration for freshwater amphipods on the continent is sparse to absent; until one reaches Brazil the only known freshwater amphipods yet discovered belong to Hyalella.

Neotropics

Apparently all but one genus of Neotropic Gammaridans are hypogean and blind. Ten genera and 25 species were known in January 1979. The area is here taken to include the Caribbean islands (cave and hypogean), which are dominated by Hadziids and Weckeliids of the genera Metaniphargus (8), Saliweckelia (2) and 3 other monotypic genera (Alloweckelia, Paraweckelia, Weckelia). The other diverse genus of the Neotropics is Bogidiella, which ranges throughout Central and South America, sometimes in caves, often in artesian waters.

Pseudingolfiella (1) is isolated on the western side of the cordillera in Chile and has a second species in remote Kerguelen. The Galapagos Islands have 2 marine imports, from the Paleotropics, Galapsiellus and Anchialella.

Falklandella (2) in the Falklands Islands has to be placed here but is really an import from the Ethiopian province by way of plate tectonics.

Ethiopian

This region contains only 5 genera because the Red Sea and Somalian regions are included in Palearctica. Hence, the Ethiopian region has amphipods only in South Africa and Madagascar owing to the sterility of the

African rift lakes. All but one genus (Paramoerella) are classified as Crangonyctoids. Paramelita, mainly epigean, is the most diverse genus (12) and almost identical to Austrogammarus from Notogaea. The apomorph of Paramelita is Sternophysinx (3) which probably was in the ancestral pool of the Falkland Islands Falklandella. The two small genera, Austroniphargus and Sandro on Madagascar, are considered to be apomorphic Crangonyctoids. Paramoerella is one of the Bogidiiellids, which themselves are probable apomorphs of the Crangonyctoids.

Notogaea

Australia has 7 genera of freshwater Gammaridans, all of which, except Giniphargus, are believed to be Crangonyctoids. Giniphargus (1) is a presumed marine ingressor. The largest genus is Neoniphargus (10) which may have to be subdivided. The next is Austrogammarus (6) which also may be divisible. Uroctena (3) and Perthia (2) are the only other genera with more than one species.

All taxa are probably hypogean except for most species of Austrogammarus and perhaps a few of Neoniphargus.

New Zealand

This satellite of Notogaea has a very primitive group of 2 genera, Phreatogammarus (3) and Paraleptamphopus (2), which have little but remote plesiomorphic relationship to Australian taxa but which have probably advanced very strongly in their own microcosm from now extinct ancestors. Paracrangonyx (1) probably is a Bogidiellid import. The species in New Zealand are divided among epigean and hypogean habitats.

Kerguelen

This remote island, in the Indian Ocean subantarctic, apparently has adequate environmental diversity to support 2 freshwater genera, Kergueleniola, an apparent Bogidiellid, and a second species of Pseudingolfiella, the first being known from Chile. How these species have managed to be distributed across thousands of miles of open ocean is a tantalizing mystery.

Paleotropica

Despite being the oldest or steadiest environment on earth (excluding India), the Paleotropics (Oriental) are devoid, as far as known, of Gammaroid and Crangonyctoid taxa but have been sparsely populated by marine ingressors primarily in the Melitid and Eriopisellid lines. To some extent these connect across the Pacific to the Neotropical Galapagan taxa, which indicates only that such taxa probably are easily distributed throughout marine pathways. Seven genera with 10 species comprise this weak fauna.

Definition of Gammaridans

(Figure 1)

Rostrum if present not visor-like, head neither galeate, globular, proboscoid nor elongate; article 1 of primary flagellum not greatly elongate, accessory flagellum present; mouthpart field not conical; mandibular palp usually present (if absent then accessory flagellum always 2+ articulate), outer lobes of lower lip only weakly separated and never tilted; maxillipedal palp 3+ articulate, plates well developed; if anterior coxae acuminate then accessory flagellum always 2+ articulate, coxa 1 well developed, coxa 4 as large as or larger than coxa 3; gnathopod 1 present and well developed; article 3 of gnathopod 2 not elongate; gnathopods neither chelate nor carpochelate; pereopods 3-4 not glandular, lacking dactylar meatuses; if pereopods fossorial then gnathopods subchelate, not enfeebled; when pereopod 7 distinctive from pereopod 6 then articles 3-7 together combined not significantly shorter than on pereopod 6; telson laminar; urosomites either free or all coalesced together, never 2-3 coalesced together alone.

If accessory flagellum 1-2 articulate then gnathopods never Acanthogammarid or simple.

Exclusions.--Taxa with mandibular molar simple and telson with narrow apices notched (example, Liljeborgiids); taxa with large visor rostrum (Phoxocephalidae) or with facially spinose articles on pereopod 5 or taxa derived from such ancestors (Haustorioids in general but see Priscillina in Pontoporeids); taxa with accessory flagella 1-articulate or 0-articulate except in clearly apomorphic cases; taxa with fleshy telsons (Corophioids); taxa without mandibular palps except in clearly apomorphic cases (example, Talitroidea); taxa with Lysianassid gnathopod 2.

Freshwater Gammaridan Groups (or Gill 7 present)

Groups with Sternal Gills (Notogaean, Ethiopian, and Holarctic)

About 20 world genera of Gammaridans have sternal gills (or osmotic appendages). They are called Crangonyctoids. This group of genera is one of the most poorly studied groups and even the Crangonyctids (a subgroup), though well described, are in a state of flux recently owing to widespread synonymies (Holsinger, 1974c:3; G.S. Karaman, 1974e:105).

Sternal gills generally occur on the thorax in the middle or posterior part, generally on segments 2-7 (or fewer) and occur in bilateral pairs attached to the sternum of the thorax (rarely abdomen) slightly inside the attachment of the coxa or occasionally they are midventral (item V in Figures 8B, 9GHIJ, 14G). Sternal gills are either simple, bifid, or fimbriate. The term "accessory gill" used in this paper refers to additional coxal gills or branchings (Figure 38C) and not to sternal gills.

Three morphogeographic groups occur. All groups have at least a few calceoliferous members. The calceoli are paddle-shaped (Figure 33A). The Holarctic Crangonyctids are characterized by the presence of bifid spines on the palms of the gnathopods (Figure 14J). The east Palearctic Pseudocrangonyx group has palmar spines but they are apparently not bifid. The Notogean-Neotropical-Ethiopian ("southern") group either lacks densely packed palmar spines or, in one exception, *Phreatogammarus*, the spines are simple and in the other, *Neoniphargus* the bifid spines occur on neotenic gnathopods. The Crangonyctids have virtually no dorsal setation on the urosome whereas the plesiomorphic southern genera have dense dorsal setation primarily aligned transversely but occasionally and strongly longitudinal (W.D. Williams, in litt.). The *Pseudocrangonyx* group has setae weakly developed. In the southern genera the setation decays rapidly in the evolutionary lines. The *Pseudocrangonyx* genera have apparently lost coxal gill 7 and so has *Phreatogammarus*; this gill is also lost occasionally in the Crangonyctids, especially in the western members of *Stygobromus* (Holsinger, 1974c:4, key), so that its absence does not necessarily have any strong taxonomic meaning. This gill is definitely absent in some of the southern genera. Several new genera must be constructed from the known species and others are in process of description (W.D. Williams, in litt.).

Sternal gills also occur in several groups outside the Gammaridans (Hyalellidae, *Sternomoera*, noting that the latter may actually be descendent from Crangonyctoids). If sternal gills mark a common ancestry in the immediate Crangonyctoids then the lineage must be extended backward in time to a place in Pangaea when these organisms could be dispersed among the several continents, such as Eurasia, Africa, Australia and South America. Marine linkages are unlikely though not completely dismissed. The modern distribution of Crangonyctoids suggests that they have been severely constrained in the southern hemisphere by the modern continental positions of Australia and Africa. Gammaridan Amphipods are not adapted to the tropics nor to jungles but, instead are temperate in distribution and are either epigean or hypogean. In Australia and southern Africa their antitropical position has put them into somewhat arid modern climates so that one would suspect that a great degree of extinction has occurred. They have not radiated as widely in New Zealand as might be expected, because New Zealand has several other freshwater amphipodans presumably of marine ancestry which suggest that open niches have occurred since the arrival of *Phreatogammarus*. New Zealand, indeed, probably has more freshwater amphipods of non-Gammaridan ancestry that have evolved in situ, per square kilometer of area, than any other place in the world. South America proper is devoid, as far as known, of Gammaridan taxa with sternal gills; it is devoid of most freshwater Gammaridean amphipods except Hyalellidae and Bogidiellids. It appears to have been out of contact with other continents during the dispersion of freshwater Gammaridans or has undergone total extinction since Pangaea. The remnant, *Falklandella*, in the Falkland Islands, is enigmatical but suggests that a close time correlation of events in the breakup of Pangaea might be useful to pinpoint the arrival of sternobranchiate forms in the vicinity of South America. Perhaps the Falkland Islands lagged sufficiently to maintain connection with Africa for a long time.

If the sternobranchial forms are monophyletic they have undergone much of the same degree of diversity in morphological developments found in other microcosms, such as Baikal or Europe, but of much less extent than in the PontoCaspian microcosm. The normal trends have occurred: parviramous modification of uropod 3, loss of dorsal armaments on the usosome, mittenform modification of gnathopods, fusion of telsonic lobes, development of vermiform bodies, descent into hypogean environments with loss of eyes and pigment, posteroventral lobation of article 2 on pereopods 5-7 (weak), various axial reversals in gnathopods, and loss of medial setation on maxillae. Fully fossorial types have not developed as far as is known. Any great and persistent inland seas or lakes of southern continents apart from South America and east Africa, which may have developed since the early Mesozoic, are now extinct. The east African rift lakes are said to be devoid of amphipods and Lake Titicaca in South America is dominantly Hyalellid. Inquilinous species do not occur.

In Palearctica the hypogean Crangonyctids have been largely replaced by Niphargids. East temperate Asia is dominated by Pseudocrangonyx and Procrangonyx, perhaps as an outpost of survival by an ancient group never fully excluded by Niphargids. In Nearctica the Crangonyctids have diversified very widely. Formerly, they were divided into half a dozen genera but G.S. Karaman (1974e) has found reason to synonymize most of them into two main genera, Crangonyx and Stygobromus. Stygobromus may actually be a gradational genus with several ancestors in Crangonyx. The wide dispersal and lack of clear disjunction among most of the species groups has the appearance of youth but may actually be the result of low competition from other freshwater amphipod groups (which in Nearctica outside the Edwards aquifer are very sparse). Despite orogenic and glacial events in North America, Crangonyctids carry their specificity everywhere. The lack of competition is reflected in the great diversity of characters expressed in the group, as if the group filled completely open niche categories while biotic selection (competition) remained at a virtual standstill. For example, Crangonyctids have species with almost complete loss of uropod 3, bifurcate sternal gills, expanded basis of pereopod 7 with ventral lobation, or division of the basis into gross teeth, partial development of Eulimnogammarin-like gnathopods in females, intrageneric losses of medial setation on maxillae, great aberrancies in telson, such as vast elongation, all of which suggest the kind of diversity explosion known for youthful or biocompetitively unconstrained groups reaching new archipelagoes.

To a great extent the same can be said for the Niphargids, which are confined to Palearctica and which hugely dominate the few Crangonyctids present in Eurasia. Again, Eurasian taxonomists find intergradation among the species groups of Niphargus so broad as to deny the existence of subgenera, and a few taxonomists believe that most of the few and poorly disjunct genera that remain segregated from Niphargus could be synonymized.

Ecologists have suggested that the development of sternal gills formed a surviving selective response of a genosome to oxygen deficient waters (Bousfield, 1977:285). The theory could actually be expanded more subtly to point out, that if known Gammaridans with sternal gills are monophyletic, this development of sternal gills is a survival mechanism of a group initially less well adapted to oxygen deficient waters than other amphipods. For example, Niphargids not ony lack sternal gills, but also lack coxal gill 7. An inherent physiological distinction in oxygen metabolism or osmotic properties may therefore be worth studying in the several groups. The situation is not confined just to hypogean taxa. The alternative absurdity is that Palearctic freshwaters are richer in oxygen than those of Nearctica and Notogaea.

Phreatogammarus, from New Zealand, is the least consistent of the taxa bearing sternal gills At least one species lacks coxal gill 7 and has a cylindrical third uropod (Figure 18A) that is completely foreign to the Gammaroid facies. Uropod 3 is much more similar to the kind found in plesiomorphic Weckeliids or Ceradocids or Corophioids. It, therefore, has more of the appearance of a truly marine uropod 3. The genus may have crawled ashore in situ but more plausibly *Phreatogammarus* is a relict of the ancient dawn-gammarids (Corophioids) in which uropod 3 had two equally extending rami, the outer with secondary segmentation now lost in *Phreatogammarus*. This common type of amphipod could have been widespread in freshwater but was replaced by the incipiently variramous kind now much more predominant, in which, also, the rami have become flattened. The loss of coxal gill 7 could then be coincident in *Phreatogammarus* and New Zealand could be the outpost necessary to preserve the early type. As said before, New Zealand is so remote from the ordinary freshwater Gammaridan dispersal that other marine types have now fully invaded its freshwaters. Australia and South America are secondarily so remote from the original dispersal that they also have freshwater amphipods of clear marine origin (*Paracorophium*). In Palearctica, of course, marine genera, e.g., *Corophium*, occur which appear to be invading freshwater (in a geological time sense) so that our attribution is not very strong.

Sternal gills have also been found in at least one of the species of *Sternomoera* in freshwaters of Japan and its satellite islands. *Sternomoera yezoensis* (Ueno, 1933a), bears coxal gill 7 and sternal gills on pereonites 2-7. Compared to *Eoniphargus*, *S. yezoensis* differs in the magniramous uropod 3 and reduction of spination on the telson, while *Eoniphargus* has pediculate and 2-articulate coxal gills (Figure 9L), plus distinctive calceoli (Figure 33G). The convergence is otherwise striking *Sternmoera yezoensis* has the accessory flagellum reduced to one article, whereas it is multiarticulate in *Eoniphargus*. Owing to the configuration of pereopod 7, with weakly expanded and ventrally lobate article 2, no tightly parsimonious ancestor for *S. yezoensis* can be found in living Nearctic Gammaroids. Owing to the multiarticulate accessory flagellum, *Eoniphargus* does not appear to be a marine import from a known *Paramoera*-like line. Sternal gills and coxal gill 7 are presumed to be absent in *Eoniphargus* and its marine origin is thereby suggested, especially in light of the otherwise pediculate coxal gills (like Figure 9K). Without further information available one must suggest that *Sternomoera yezoensis* also has a marine origin from a *Paramoera* stock with independent development of sternal gills. But there is little to refute our suggestion that *S. yezoensis* is another kind of Crangonyctoid.

New Zealand (*Phreatogammarus*)

New Zealand is considered to be a satellite of Notogaea and because it may have been appressed to Australia in the Triassic, there exists a possible connection between lacustrine and phreatic faunas of the two island systems. According to Smith and Briden (1976), New Zealand broke away from Australia in the Eocene period. *Phreatogammarus* (3), and *Paracrangonyx* (1), are the only known genera in New Zealand of supposed non-marine origin. A third genus, *Paraleptamphopus*, is debatable and discussed below.

Phreatogammarus is an amazing antiboreal morphological counterpart of the Holarctic Crangonyctids. The two groups especially share similarities in gnathopods. Like the Crangoynctids, Phreatogammarus has spines on the gnathopodal palms but they are not as strongly bifid (they have subapical triggers only, observation confirmed by us) nor apparently are they ever trifid as in most (northern) Crangonyctids. Crangonyctids have a variety of sizes and shapes in gnathopods but the hypogean species (especially Stygobromus for example) often have both pairs enlarged similar to the type-species of Phreatogammarus. However, gnathopods are strongly reduced in another species of Phreatogammarus and gnathopod 1 in the female of a third species is of Melitid form (Hurley, 1954b). Trends of this kind also occur in Crangonyctids but never as markedly as in Phreatogammarus.

In other ways Phreatogammarids are very distinctive. They have elongate magniramous third uropods with elongate peduncle; the rami are aequiramous, almost cylindrical, and the outer ramus is uniarticulate; to some extent they resemble uropod 3 of primitive Weckeliids. Phreatogammarus retains strongly setose maxillae as in most Crangonyctids, though in the latter an occasional species has these setae rather severely reduced (Crangonyx richmondensis).

Phreatogammarus lacks inner lobes on the lower lip, has reduced coxal lengths and therefore approaches a vermiform appearance, and retains dense posterior spines on the urosomites. The mandibular palp maintains B-setae (Figure 5A), an unusual feature. The accessory flagellum is elongate in contrast to Crangonyctids. The gnathopodal dactyls are serrate, uropod 1 bears a basofacial spine and one or two enlarged apical spines on the peduncle. The telson is fully cleft though the lobes are appressed. Phreatogammarus lacks coxal gill 7 but one species, P. fragilis, bears a simple sternal gill on segments anterior to 7 (observation confirmed by our examination).

The broadly expanded brood plates in Phreatogammarus negate an immediate marine origin for the group. The presence of dorsal urosomal spines also tends to confirm this. The distribution of these elements resembles that in Austrogammarus. To some extent uropod 3 is more primitive than in Austrogammarus because of the aequiramous condition.

The species of Phreatogammarus bear and lack eyes and occur in streams near the sea, in wells and in mountain pools. Gnathopods are extremely diverse. In P. helmsi, occurring mostly in lowland streams near the sea, eyes are present, the male has large raptorial gnathopods but the female has very small and thin nonraptorial gnathopods. In P. propinquus, from a mountain pool (854 m high), the eyes are present, but only the female is known and she bears large raptorial-second gnathopods and small Melitid first gnathopods. In P. fragilis, from wells in the Canterbury region, the eyes are absent; only the female is known and both gnathopods are fully enlarged and raptorial. The sequence apparently progresses from "epigean sexual dimorphism with one sex bearing weak gnathopods" to "subterranean loss of sexual dimorphism" (one would not expect P. fragilis male to have distinctive gnathopods) and development of raptorial capacity. This suggests that such potential ancestors as Austrogammarids could give rise to the Australian raptorial forms.

The raptorial Australian forms (not Austrogammarus) and Phreatogammarus share certain similarities, such as supernumerary dactylar spination on the pereopods, but otherwise have numerous distinctions.

Phreatogammarus is characterized by aequiramous uropod 3 (the rami said to be cylindrical and lacking article 2 on the outer ramus), and by the serrate dactyls of the gnathopods, but like the the most primitive Austrogammarids, the maxillae are fully setose and the telson fully cleft.

Paraleptamphopus is an apparent apomorph from ancestors like *Phreatogammarus*. The single species of *Paraleptamphopus* resembles the three species of *Phreatogammarus* in having at least one large pair of gnathopods with short wrist in one sex, the magniramous, almost aequiramous uropod 3 with elongate peduncle, the general body shape, similarities in coxae, antennae, pereopods and gross items of mouthparts. *Paraleptamphopus* differs from *Phreatogammmarus* in the reduction of the accessory flagellum to one article and the coalescence of the telsonic lobes; *Paraleptamphopus* has heretofore been placed in the Calliopiidae because of its uncleft telson but can be derived from *Phreatogammarus* by assuming the changes in accessory flagellum and telson. Though radical and heretofore of familial importance, this kind of change probably occurred just in this minor spoke of the New Zealand microcosm and, therefore, uncleft telson has probably arisen many times in the other taxa heretofore placed in Calliopiidae. That classification is abandoned by us.

Paracrangonyx is the only other freshwater Gammaridan of New Zealand. The other freshwater genus, *Paracalliope*, is a Calliopiid-like amphipod, requiring creation of a distinctive family in the vicinity of primitive Oedicerotidae (Barnard and Karaman, 1982). *Paracrangonyx* is a vermiform genus with semiraptorial gnathopods and uniramous pleopods and somewhat resembles the Australian raptorial genera. Owing to the elongate uncleft telson, reduced pleopods and extremely shortened coxae, the relationship is very remote. *Paracrangonyx* may be closer to a Weckeliid or Bogidiellid ancestry than to the Austrogammarid group. However, the equality of gnathopods suggests a Crangonyctoid origin, because this condition is nonexistent in Melitids, Hadziids and their allies. For the moment *Paracrangonyx* is placed in the cluster of Bogidiellids.

Australia

The Australian fauna of freshwater Gammaridans consists of about 25 species and 7 genera. Many more species remain to be described (W.D. Williams, in litt.) and new genera must be erected to cover the diversity known at present. The origin of Australian Gammaridans attracts great interest. Are their ancestors of marine occurrence or did they come directly from freshwater ancestors during continental aggregation?

The group with closest similarities to Eurasian *Gammarus* is the Austrogammarid group composed of 7 species, *australis*, *haasei*, *antipodeus*, *mortoni*, *ripensis*, *barringtonensis* and ?*niger*. The similarities to Holarctic Gammaruses lie in the magniramous uropod 3 of several species, development of dorsal setation on the urosome (but also weakly on the pleosome), the fully to partially developed medial setation on the maxillae, the well developed accessory flagella and, in at least one species, the presence of coxal gills on pereonite 7. *Austrogammarus* is distinguished by the weakness of slope on the palm of male gnathopod 1, the similar palmar slopes on all gnathopods in both sexes, the lack of special midpalmar spines, the shortness of the wrist on male gnathopods and its elongation on female gnathopods, the presence of strong posteroventral spination on anterior coxae, the lack of organized spine clusters on the urosome (only an occasional spine and many setae are present), the presence on the telson of only thin setae, the presence in at least one species of sternal gills, the stronger setosity of anterior coxae, to some degree the pediculation of coxal gills, and the broader, more rounded telsonic lobes lacking basolateral spines but bearing dorsal setae.

The gnathopodal situation in Austrogammarus therefore does not closely approximate the familiar Holarctic Gammarus, but is slightly more like other Holarctic groups, very vaguely some of the Caspian and Baikalian genera. However, no Holarctic Gammaroid known to us has precisely the kind of shapes and differences seen in the two sexes of Austrogammarus.

Austrogammaruses share with Holarctic Crangonyctids the presence of sternal gills, coxal gill 7 and calceoli, but lack the dense bifid palmar spines on the gnathopods of Crangonyctids and plesiomorphically bear the special urosomal armaments. The paddle shaped calceoli of the two groups are very similar. Crangonyctids have the broadly rounded apices on the telson but, of course, the lobes are mostly fused basally. Austrogammaruses appear to have a stronger sexual dimorphism in gnathopods than do Crangonyctids and have lost the albeit weak inner lobes on the lower lip. No Crangonyctid has magniramous uropod 3.

Austrogammarus australis and A. haasei represent the magniramous form of uropod 3, whereas barringtonensis, mortoni, antipodeus and ripensis have parviramous uropod 3. Article 2 on the outer ramus is reduced in ripensis and lost in mortoni and antipodeus.

No living marine Gammaroid in the vicinity of Australia can be hypothesized as an ancestor to this morphotype. The marine Gammaroids would have to redevelop gill 7, redevelop strong urosomal setation and undergo changes in uropod 3 to match the Austrogammarid. If one discounts a worldwide hypothetical marine ancestor now extinct, and for which there is contradictory evidence, the most parsimonius conclusion is that Austrogammarids and Crangonyctids reached a pandemic distribution via Africa, Antarctica and Australia during aggregation of the continents and obviously during a cool climate period. Antipathy to the modern tropics by freshwater Gammaridans is strong.

The Austrogammarid group, once probably widespread and very diverse when Australia lay farther south and west, is now confined to the southeastern wetlands and montane regions of New South Wales, Victoria and Tasmania, reaching altitudes of 1400 m. The northward and eastward movement plus the low degree of late mountain building has driven the continent partly into the tropics where freshwater amphipods fare poorly and mostly into the warm-temperate desert doldrums where water supply is low except in high altitudes. Mountainous areas, mainly southeastern and Tasmanian, are only moderately developed in Australia. The southwestern corner of Australia enjoys sufficient wetness to have freshwater amphipods and may have a considerable number of subterranean species in the limestones of that region.

The dominant genus of Australia is Neoniphargus with 10 species; it appears to be divisible into several genera based at least on the presence or absence of medial setae on the maxillae, and on the presence or absence of article 2 on the outer ramus of uropod 3. Neoniphargids are characterized by the reduction of the gnathopods to a hammer-like form approximating a mitten: small, equal and not sexually dimorphic. The wrists are lobate or not but short, the hands are short, the palms are almost transverse, and armed with bifid spines as in Crangonyctids. Pubescence occurs frequently on a hyaline lobe projecting from the palm posteriorly along the hand. The lobes of the telson are fused basally so that the cleft is reduced but not less than halfway. Occasional species have supernumerary spination on the pereopodal dactyls and if the indications hold true, the group is characterized by fimbriate sternal gills (Figure 9J) and calceoli. The *Neoniphargus* group is especially characterized by its distribution in high tarns, pools, streams and springs in southeastern Australia and Tasmania, generally between 700 and 1200 meters of altitude.

A progression of species moves from fully epigean to those with reduced eyes and very superficially finds its final expression in *Giniphargus pulchellus*, the fully hypogean vermiform kind. The basic *Neoniphargus* is not vermiform but *Giniphargus pulchellus* otherwise can be related to Eriopisellids and is a presumed crawlout.

Neoniphargus yuli has medial maxillary setation, whereas the type of *Neoniphargus*, *N. thomsoni* does not; *N. wellingtoni* and *N. niger* lack article 2 on the outer ramus of uropod 3; *N. yuli* appears to have stronger posterior lobes on the fifth articles of the gnathopods than several other species; *N. niger* (also put in *Austrogammarus*) has an elongate wrist on the gnathopods. Undoubtedly, several genera must be distinguished.

Protocrangonyx, a monotypic genus from springs in southwestern Australia, also is blind and almost vermiform. The gnathopods are fairly small, uniform and almost mitten-shaped but hammer-like, resembling Niphargids. The genus is characterized by the uncleft short telson, the reduction of uropod 3, especially the length of the outer ramus; article 2 is absent and the inner ramus is very small. The maxillae are poorly setose but the 2-articulate accessory flagellum is unusually large. This genus could be derived through a series of steps from the *Neoniphargus* group but the distance is great. *Protocrangonyx* also has sternal gills and is discussed with the Bogidiellid group.

Hurleya (monotypic, from a well in Western Australia), *Uroctena* (4 species from creeks) and *Perthia* (2 species from lakes and brooks) are characterized by enlarged and almost Acanthogammarid gnathopod 2, with long sloping palm and short, lobate wrist. These are termed raptorial gnathopods. In *Uroctena* gnathopod 1 is small and Melitid, with weakly to moderately sloping palm, the telson is of ordinary length, well cleft and spinose and uropod 3 is somewhat reduced, stout, has a very thick but short article 2 and in the male has the basolateral margin of the outer ramus serrate and setose. In *Hurleya* gnathopod 1 is small but somewhat similar to gnathopod 2, with long sloping palm and well developed palmar spination. Only the female is known, so that sexual dimorphism is undetermined. Uropod 3 is normally parviramous but the telson is short and cleft only halfway. *Perthia* has fully raptorial gnathopods with Eusirid connections between wrists and hands and long thin lobes on the wrists. The lower lip has the widely spaced outer lobes separated by inner lobes frequently, seen in supposedly predatorial amphipods. Uropod 3 is normally parviramous, the telson is elongate and deeply cleft and like *Hurleya* and *Uroctena* the pereopodal dactyls have supernumerary spination and the maxillary setation is reduced.

Gill formulas are unknown on Hurleya. It otherwise resembles Hadziids so closely that it could be placed in the vicinity of that group but it differs in the non-Melitid gnathopod 1. It bears close comparison with Psammoniphargus.

Perthia is the only other known Australian genus with almost magniramous uropod 3. The type-species has a parviramous uropod 3 but P. acutitelson has an almost magniramous uropod 3. The genus is otherwise characterized by loss of medial maxillary setation, loss of most B setae on the mandibular palp, and great narrowing of brood plates. Calceoli and sternal gills are present. Coxal gill 7 is unknown. Some of the urosomal spination is retained.

Uroctena is characterized by strong sexual dimorphism in gnathopods, antenna 2 and uropod 3. Male antenna 2 is almost as pediform as in Corophium. Male gnathopod 2 is very large with expanded hand, oblique and often sculptured palm and short wrist whereas gnathopod 2 of the female is a much smaller version with less oblique or shorter or better defined palm. Gnathopod 1 of the female is almost Melitid but the hand is stouter in the male. Uropod 3 is parviramous and a large article 2 remains on the outer ramus. Unbranched sternal gills occur, and the telson is cleft more than halfway but is less ballooned than in the Austrogammaruses.

Giniphargus pulchellus, from a freshwater pool in Thorpdale, Gippsland, Victoria, has most of the Niphargid characteristics: vermiform body, severely reduced coxae, hammer-like gnathopods, elongate uropod 3 with elongate article 2 on the outer ramus, and inner lobes on the lower lip; but it differs in the medially setose maxillae. Even though the gnathopods are severely reduced to a mittenform state and the inner ramus of uropod 3 is absent, Giniphargus does not lie outside known Palearctic Niphargids on those counts. The elongation of article 5 on gnathopod 2 is, however, aberrant. Like Niphargus the wrists lack lobes. Giniphargus may be another product, like Austroniphargus and Niphargids, of the tightly littoral taxa in Eriopisids and has progressed evolutionarily in gnathopods to the same degree as have the Eriopisellids. Unlike Eriopisellids, however, it retains medial setation on the maxillae. Giniphargus is probably interstitial though it was found in freshwater runnels.

The Australian fauna, in summary, is composed of 3 groups, the Austrogammarid group with sexually diverse gnathopods of fairly ordinary form somewhat resembling the Pontogammarid form, a second group with poorly diverse gnathopods approaching the condition of mitten-shaped (Neoniphargus, Protocrangonyx and Giniphargus), and the raptorial group composed of Uroctena, Hurleya and Perthia. The possibility that the raptorial group and the mitten-handed group could descend from the Austrogammarid group should be entertained (see below). Presumably, many more species and genera will be discovered that may provide a solution to the problem. The raptorial group could be derived from contiguous marine amphipods in a hypothetical sequence but some of the species in the mitten-handed group have well developed maxillary setation and would have to be drawn from a proto-Eriopisellid line of descent. A parsimonious viewpoint would suggest that the Neoniphargid group descended from the Austrogammarids, as there are many similarities and apparently several species showing the stepped intergradation between the groups (niger, for example). This would reduce the probable founders of the known Australian fauna to 3 (Austrogammarid, raptorial, and Giniphargus).

South Africa

Paramelita is a diverse, mostly epigean genus of 12 species from South Africa. To a great extent its Palearctic counterpart is Echinogammarus but it differs from that group of genera in the significantly reduced gnathopod 1, strongly reduced medial setation on the maxillae, domination on uropod 3 of spines and unplumose setae, the uniformity of dorsal setation on urosomites (which in Echinogammarus is composed of both setae and spines in groups, some of which do not run parallel to the posterodorsal margin of the segment), the presence of stiff fully dorsal setae on the telson (at least plesiomorphically) and the absence of basolateral telsonic spines (which are plesiomorphic in Echinogammarus and Chaetogammarus but which are lost in highly derived species).

Gnathopod 1 in several species of Paramelita is so strongly Melitid that one might suspect a marine origin but this is contradicted by the presence of coxal gill 7. Paramelita also has simple sternal gills.

Paramelita and the Austrogammarus have many characters in common: coxal gill 7, sternal gills, special dorsal setation on the telson, very similar setation on the urosome, non-Gammarus gnathopods, but in Austrogammarus gnathopod 1 is as large as gnathopod 2, and the hands of both are more elongate and regularly rectangular.

Sternophysinx has 3 hypogean species in South Africa. Among southern sternobranchiate forms, only this genus and Falklandella from the Falkland Islands have gnathopod 1 larger than 2. This gives it the aspect of Bogidiellids. Sternophysinx retains the urosomal setation (and spination) typical of the southern plesiomorph, has simple sternal gills (really ventral blisters), poor palms on the gnathopods, fully parviramous uropod 3, bears weak inner lobes on the lower lip, has biramous pleopods, a poorly cleft or entire telson and fully reduced medial setation on maxilla 1 but retention of a few of the setae in the oblique row on maxilla 2. The coxal gills are pedunculate.

Falkland Islands

Falklandella (2) was first found in a small stream 200 m from the sea shore in the Falkland Islands. It has coxal gill 7 and bifid sternal gills but differs from Australian forms in the slightly enlarged gnathopod 2 and the mittenform gnathopod 1 with lobate and somewhat Eriopisellid article 5. Perhaps the gnathopods have been axially reversed. Uropod 3 is very small, with the outer ramus very short and lacking article 2, as if it were derived from a parviramous uropod 3; the inner ramus has the parviramous appearance, except that it has a medial seta and is almost half as long as the outer ramus.

Male pereopod 3 is prehensile. The telson is very short and broad and scarcely excavate posteriorly. The accessory flagellum is reduced to one article.

Falklandella differs from Sternophysinx of South Africa in the fleshiness and bifidation of the sternal gills, the mitten-like gnathopod 2 with poorly oblique palm and extended, broad posterior lobe on article 5, the very short outer ramus of uropod 3 and the prehensile pereopod 3 in the male.

Sternophysinx and Falklandella have the facies of Bogidiellids in body and gnathopods but this facies is also characteristic of many Holarctic Crangonyctids and the evolutionary connection between Bogidiellids and Crangonyctids need not pass through these two genera. Falklandella is, therefore, presumed to be an outlier of South African origin situated on an island group dragged across on the Fuegian tectonic plate away from earlier contiguity with Africa.

Holarctica

The Crangonyctidae were defined by Bousfield (1973) to include Bactrurus, Allocrangonyx, Crangonyx, and Stygobromus (now including Stygonectes, Synurella, and Synpleonia). Allocrangonyx is discussed in its own section where Holsinger (1971:320) believes it should be isolated but the definition of Crangonyctidae could easily be broadened to include Allocrangonyx. The evolutionary descent would require the loss of medial maxillary setation, the loss of coxal gill 7, the bilobation of coxal gill 2, the loss of sternal gills, the development of a basofacial spine on uropod 1 (confirmed by examination of A. hubrichti), the development of outer spines on the dactyls of the posterior pereopods, the slight strengthening of the gnathopods so as to approach the hammer-like condition of Niphargus, the size reduction and loss of one row of notched spines on gnathopodal palms, the full development of fleshy inner lobes on the lower lip and the development of sexual dimorphism in uropod 3. The main similarity between Crangonyctids and Allocrangonyx is the presence of notched spines on the palms of the gnathopods, a condition not found in Niphargids. Although Crangonyctids and Niphargids are sympatric in Palearctica, the Niphargids are absent in Nearctica where Allocrangonyx is represented by 2 species confined to a very small area of midwestern United States. Nearctic Crangonyctids are far more diverse than those of Palearctica and are the only group of the Neogene in reasonably close contact with Allocrangonyx and therefore a potential evolutionary source of that genus. The Crangonyctidae can be much more tightly defined if Allocrangonyx is removed to a separate position (see below).

The fossil genus Paleogammarus, composed of three poorly known species preserved in Baltic amber, probably is a synonym of one of the Crangonyctid genera. So far, the species have not been sufficiently described to warrant the validity of the genus.

Crangonyctids in primitive state have a parviramous uropod 3 lacking article 2 on the outer ramus but the evolutionary trend rapidly progresses towards reduction and loss of the inner ramus and the reduction of the outer ramus to a small vestige. The telson is cleft about halfway in some of the primitive epigean taxa but becomes solid in most other taxa although it remains cleft about halfway even in some of the subterranean species, such as Crangonyx packardi, and in the mackini group of Stygobromus (Holsinger, 1978:60).

Strong medial setation on maxillae is retained in Crangonyctids, although a few species, such as Crangonyx subterraneus from Europe, have the medial setae on maxilla 2 severely reduced. Coxal gill 7 is present but many species a also have sternal gills mostly towards the posterior end of the thorax; the loss of these gills in many taxa (especially western Stygobromus) is considered to be derivative and not primitive in the

TABLE 3.--Long Distance Distribution of Species in Crangonyx (C) and Stygobromus (S), Top Few in Rank

Map	Species Number	Species	Distribution
13	5 (S)	ambulans	W. Italy to Oka River
13	24 (C)	subterraneus	S. England to mid-Czechoslovakia
13	57 (S)	intermedia	Yugoslavia to N.W. Carpathians
11	19 (C)	richmondensis	Wisconsin to Quebec
12	18 (C)	pseudogracilis	Wisconsin to N. Carolina
15	3 (S)	alabamensis	Oklahoma to Alabama
11	21 (C)	serratus	N. Florida to Maryland
16	14 (S)	bifurca	Texas to Alabama
15	108 (S)	tenuis	Virginia to Connecticut
15	20 (S)	chamberlaini	S. Carolina to Maryland

Neogenic fauna, as this loss is associated with other advancements. Some of the coxal gills are pedunculate and 2-articulate as in Hadziids and Weckeliids. The palms of the gnathopods are tightly packed with small notched spines also found in reduced form on Allocrangonyx and to some extent in Weckeliids, where the notching is less pronounced. Inner lobes on the lower lip are definitely present though, not as well developed as in Allocrangonyx nor in most Melitids.

If the Crangonyctids have a phylogeny common to the Hadziids, the presence of gill 7 and inner lobes on the lower lip would require their branching at a point of ancestry earlier than expressed by any living amphipod. Each group is highly remote from that ancestor, however, as the Crangonyctids have a derived uropod 3, while Hadziids have lost gill 7. Numerically, Allocrangonyx shares more characters with Hadziids than with Crangonyctids and may be a relict of ancient Hadziid penetration of middle North America curing Cretaceous sea encroachment, though this is not the most parsimonious view.

Crangonyx contains 21 species in Nearctica and 2 species in west Palearctica, plus one introduced from America (pseudogracilis). About 25 more species in North America are said to be undescribed (Holsinger, 1972:28). In North America, the genus contains oculate and anoculate species occurring in lakes, rivers, streams, springs, caves and swamps; the genus extends into southern Canada especially into the southeastern part but is excluded from the arid southwestern United States. Only 3 species are known as yet from west of the Rocky Mountains. Long distance and areal distribution statements are found in Tables 3 and 4.

In Europe, only 3 species occur; all are subterranean and range through middle Europe to southern England, with the eastern boundary near the Oder River and the southern boundary near the Drava River. However, C. chlebnikovi is isolated far to the east in the Ural Mountains.

Crangonyx arsenjevi is so poorly described that its systematic position cannot be determined (see Holsinger, 1977b:254). It comes from the Ussurian Basin in East Siberia.

TABLE 4.--Widespread (Bulk in Contrast to Long Distance) Areal Distribution of Species in Crangonyx (C) and Stygobromus (S), Top Few in Rank.

Map	Species Number	Species	Distribution
13	5 (S)	ambulans	W. Italy to N. Germany to S. Turkey to Oka River
13	24 (C)	subterraneus	S. England to mid-Czechslovakia
13	57 (S)	intermedia	Yugoslavia to N.W. Carpathians, N.E. Rumania
11	19 (C)	richmondensis	Wisconsin to Quebec to S. of Great Lakes
15	3 (S)	alabamensis	Alabama to Oklahoma to Missouri
11	21 (C)	serratus	Florida to Maryland
16	14 (S)	bifurca	Texas to Missouri to Alabama

Crangonyx schizurus from Tadzhikhistan was removed by G.S. Karaman and Barnard (1979:143) to Tadzocrangonyx of the Metohia group near Ilvanella. Crangonyx setiferus from Tian-Shan Springs likewise is not a Crangonyx and also placed in Tadzocrangonyx. Crangonyx shimizui should be transferred to Melita. Stygobromus pusillus from Teletzkoye Lake in Siberia has not been clarified (Holsinger, 1974c).

Apocrangonyx, Synpleonia and Stygonectes have now been synonymized with Stygobromus by Holsinger (1966, 1973, 1974c, 1978) and G.S. Karaman (1974e) to form a large genus of over 115 species in the Nearctic region. About 60 species remain to be described (Holsinger, 1974c:1 and in litt.).

Stygobromus differs from Crangonyx in the loss of the inner ramus on uropod 3 and the outer ramus is either shorter than the peduncle or absent. The telson is entire or weakly incised and the epimera are usually rounded posteroventrally. Urosomites are often free but in many species groups they become fused together. There is a great deal of variation within the limits described above and additionally in the relative sizes of gnathopods, posterior pereopods, lateral telsonic spination, the reduction or loss of inner lobes on the lower lip, size of coxa 4 and the development of a posteroventral lobe on article 2 of pereopod 7, among many other character variables.

Stygobromus occupies in Nearctica the same gross ecological position as does Niphargus in Palearctica (Holsinger, 1967a:124, G.S. Karaman 1974e:105), living in wells, caves and springs. In eastern North America it has about the same distribution as Crangonyx except that it has not been found in southeastern Canada and in the west it is much more widespread and diverse than Crangonyx. Long distance and areal distribution statements are found in Tables 3-4.

Synurella, Diasynurella, Eosynurella, and Lyurella are believed by G.S. Karaman (1974a:85, 1974e:104) to be potential synonyms of Stygobromus.

This action is consummated here to elevate to 115 the total species in the genus. Synurellas are characterized by paddleshaped calceoli in males. This adds 4 epigean Nearctic and 15 epigean and subterranean Palearctic species to the 65 known and 60 undescribed species in *Stygobromus* (potential species = 175). To a great extent, *Synurella* bridges the morphological gap between *Crangonyx* and *Stygobromus* in that the epimera are produced and/or acuminate (Holsinger, 1967a: table 2) and the telson is usually deeply incised as in *Crangonyx* but, like *Stygobromus*, uropod 3 is severely reduced. A few species of *Synurella* have eyes and, therefore, are not fully adapted for subterranean life. The North American species are epigean but some of the Palearctic species are blind and subterranean. One species of *Synurella* occurs in Alaska and forms a geographic interconnection between mid-North American and Siberian species. The other three American species are confined to the southeastern United States from about Missouri eastward and southward. In Eurasia *Lyurella* is a monotypic genus from springs around the southern Caspian Sea and is believed by G.S. Karaman (1974e:97) to be a taxon intermediate between *Stygobromus* and *Synurella*. *Diasynurella* is Transcaucasian. Ruffo (1953c) shows the distribution of *Synurella* in Eurasia to be confined to the Kolyma-Koni region of east Siberia, the Lena River Delta in north Siberia and in a large area of east and central Europe with a clockwise polygon reading W. Pomerania to Riga to the Volga Upland, across to the Black Sea, across southern Yugoslavia to Trieste and northward again to West Pomerania with a weak westward bulge in the Alps. Greece and most of Italy are excluded. The genus may be more widespread in Asia than now known. Our latest view of the distribution is shown in Map 64.

Bactrurus is composed of 3 described and one undescribed species (Holsinger, 1972:73) in middle western United States from Lake Erie southwestward to Kansas and Oklahoma. The genus differs from *Crangonyx* in the short outer ramus of uropod 3 and the poorly cleft telson but, unlike *Stygobromus* and *Synurella*, bears an inner ramus. The genus is largely interstitial and blind.

If *Synurella* becomes a synonym of *Stygobromus* (Appendix VI) the incipient division into subgenera should be retained for evolutionary purposes. Taxonomists for years have recognized that a *Stygonectes* group occurred in the United States east of the Rocky Mountains and that the weakly diverse Synurellas in the southeastern United States were among the most primitive of the genus. West of the Rocky Mountains *Synurella* was absent, except for southwestern Alaska where the affinities are with Siberia. Holsinger (1974c) has shown how widespread and moderately diverse *Stygobromus* is west of the Rockies, perhaps more diverse than the sensu stricto *Stygobromus* east of the Rockies. Isolation and concomitant selection never reached the stage that species groups became divided or consolidated, except for the western *hubbsi* group of 15 species lacking the sternal gills. However, *Bactrurus*, a genus representing a morphological intergrade between *Crangonyx* and the *Synurella-Stygobromus* groups, did develop but has since become sympatric with the others. One might presume that the southeastern United States oculate species of *Synurella* with free urosomites are the ancestors of *Stygobromus* in North America, the main morphological changes being loss of paddle-calceoli and eyes. In some way one species of *Stygobromus* crossed the Bering Land Bridge and reached Lake Teletzkoye (if indeed *S. pusillus* belongs to *Stygobromus*) and one species of Asian *Synurella* crossed in the opposite direction to reach southwestern Alaska. *Synurella chamberlaini* especially fits this model ancestor because of its exceptionally long ramus on uropod 3, presence of eyes and free urosomites. The Eurasian Synurellas progressed to some extent down the same path to *Stygobromus* in the shortening of the ramus on uropod 3, the loss of eyes and the reduction in cleft of the telson. Those features imitate *Stygobromus* but the loss of paddle-shaped calceoli did not occur and the epimera never became as "rounded" as in *Stygobromus*.

Allocrangonyx

Allocrangonyx, with 2 species, is the Nearctic analogue of *Niphargus* in Palearctica. The similarity occurs mainly in the hammer-like gnathopods but Holsinger (1971:320) points out numerous differences of *Allocrangonyx*, such as the bifid gill 2, the presence of small notched spines on the inner margins of the palms of the gnathopods, the absence of serrations on the main spines of maxilla 1 and the presence of supernumerary spines on the dactyls of the posterior pereopods, not only on the anterior (inner) margin as in *Niphargus*, but on the posterior (outer) margin as well.

The spinose palms of the gnathopods suggest affinities of *Allocrangonyx* with the Crangonyctidae where Schellenberg (1937c:33) implied it should be assigned. However, Holsinger (1971:319) believes that *Allocrangonyx* has fewer affinities with Crangonyctidae than with the Niphargids. Many of the differences between *Allocrangonyx* and Crangonyctidae, however, are the same as between Niphargids and *Allocrangonyx*: bifid gill 2, posterior spines on dactyls of pereopods, broadened and apically truncate outer plate of maxilla 2 bearing 2 kinds of setae (similar to *Pseudoniphargus*), and absence of serrations on maxillary spines. In addition, one might note that *Allocrangonyx* has the fully reduced medial setation on the inner plates of maxillae, whereas in most Crangonyctids that setation is fully developed. The inner lobes on the lower lip are much fleshier than in most Crangonyctids. Most Crangonyctids appear to have pedunculate and 2-articulate coxal gills and most species have sternal gills.

Males and females of *Allocrangonyx* bear a minute second article on the outer ramus of uropod 3 but males also have the basal article highly elongated and segmented secondarily. This recalls the parallel in *Pseudoniphargus* where the male has the fully developed and elongate article 2 but females lack article 2. The telson of *Allocrangonyx* is closer to the average poorly cleft condition of Crangonyctids than to the well-cleft Niphargid telson. The hammer-like gnathopods appear less similar to Niphargids when compared to such Crangonyctids as *Synurella ambulans*. A special significance is seen in the resemblance between *Allocrangonyx* and *Synurella* of the weak posterior lobation of article 5 on gnathopod 2, quite in contrast to *Niphargus*. As noted in the Eriopisellid section (Appendix VII), this kind of gnathopod is found also in *Pseudoniphargus* (hypogean on Mediterranean coasts).

If *Allocrangonyx* and *Pseudoniphargus* have no direct relationship, the convergence between the two genera is striking. Many characters of *Pseudoniphargus* require description, but gill 7 is absent (Holsinger, in litt.). One should note that *Allocrangonyx* lacks gill 7 (personal examination of *A. hubrichti*).

Gills of Pseudoniphargus are of Hadziid form and gill 2 is not bifid.

The two known species of Allocrangonyx have very restricted ranges in two regions, the Ozark Plateau and the Arbuckle Mountains of Oklahoma; they are separated by a distance of 520 km. They appear to be restricted to caves and solution channels and are not interstitial. To some extent this ecology also appears to be true of the circum-Mediterranean Pseudoniphargus but the two genera are so isolated as to deny a former contiguity except in extremely remote eras.

East Asia

Pseudocrangonyx (=Niphargonyx) and Procrangonyx (= Eocrangonyx) form a pair of freshwater genera of familial magnitude from Japan, Manchuria and Kamchatka. Procrangonyx (monotypic) differs from Pseudocrangonyx (9) only in the absence of article 2 on the single ramus (outer) of uropod 3. Both genera are characterized by the Niphargid body facies, blind, but with extremely short coxae which are almost discontiguous posteriorly. Uropod 3 lacks the inner ramus but the outer ramus is elongate. Gnathopod 1 is larger than gnathopod 2 and each is spiny. The resemblance to Bogidiellids is so striking, except in uropod 3, that one might suggest the two groups have a common ancestor. The Pseudocrangonyx group resembles the males of many species of Bogidiellids in the significant shortness of the outer ramus on uropods 1-2, in the pedunculate coxal gills and in the gnathopods. A stronger lobe occurs on the wrist of gnathopod 1 in Bogidiella and Procrangonyx than in Pseudocrangonyx. The telson is poorly cleft or entire in both groups but in Pseudocrangonyctids it is elongate. Maxillary setation is partially reduced in both groups but the apical setation and curvilinear aspect of the mandibular palp on Pseudocrangonyctids are reduced in Bogidiellids. The latter retain an elongate inner ramus on uropod 3 but have lost article 2 on the outer ramus, as in Procrangonyx. Many Bogidiellids have reduced pleopods but Pseudocrangonyctids have fully developed biramous pleopods. Both groups have weakly developed inner lobes on the lower lips, and weakly or non-triturative molars.

The Pseudocrangonyctids may be apomorphic Crangonyctids, in which coxal gill 7 has been lost but sternal gills retained. The retention of a basofacial spine on uropod 1 and the retention of article 2 on the outer ramus of uropod 3 in Pseudocrangonyx (but not its sibling Procrangonyx) are plesiomorphic, whereas the loss of the inner ramus on uropod 3 and the elongate, almost entire telson, are apomorphic characters.

These disjunctions suggest that the Pseudocrangonyx group must stand apart from the central Crangonyctids and from Eoniphargus. The latter genus, clearly Gammaroid, has diverged strongly in gnathopods and has lost the inner lobes on the lower lip (which are retained in Pseudocrangonyx), maintains full maxillary setation, almost normal Gammarus-like telson (but weakly fused basally) and has a large parviramous uropod 3 with article 2 marked by notches but otherwise fused to article 1. Whether or not Eoniphargus retains the basofacial spine on uropod 1 is unknown, and coxal gill 7 and sternal gills, if present, have not been studied.

Madagascar

The Austroniphargus group comprises two genera of apparent interstitial amphipods on Madagascar. The second genus, Sandro, is based on A. starmuhlneri. It is more primitive than Austroniphargus because it bears inner lobes on the lower lip, well developed pleopods with equal rami, and an elongate almost fully cleft telson. But it is not a precise ancestor to Austroniphargus bryophilus, because it has a peduncular process on uropod 3 and has only one article on the accessory flagellum, whereas A. bryophilus bears two of those articles.

Although the Austroniphargids have similarities to Eriopisa and Eriopisella and might have crawled out of the sea onto Madagascar, a somewhat more parsimonious morphological relationship focuses on the Palearctic Niphargid group composed of Niphargus, Niphargellus, Pseudoniphargus and other genera.

The Austroniphargids resemble the Niphargids in the enlarged gnathopods, reduced maxillary setation, densely spinose apices of the telson but differ in 2 important characters: the fully fused urosomites and the strongly lobate wrists of the gnathopods. Such urosomal fusion is also found in the Niphargid, Carinurella, but not to the full degree expressed in Austroniphargids.

The Austroniphargids comprise a microcosm of evolution showing the easy transformation from starmuhlneri to bryophilus in the loss of inner lobes on the lower lip, loss of D setae on the mandibular palp (also a feature of Niphargellus in comparison to Niphargus) and reduction in pleopods. Austroniphargids also lack palmar combs on the gnathopods and supernumerary setae on pereopodal dactyls but these trends are already complete in various Palearctic species.

The size equality of gnathopods is foreign to any marine Melitoid ancestor that could be hypothesized, thereby leaving the impression that Austroniphargids might be descendents of Crangonyctoids, where such gnathopodal morphology is more frequently found. But Austroniphargids have lost all three of the Crangonyctoid markers: sternal gills, densely packed bifid palmar spines on the gnathopods and coxal gill 7, so that their affinities must be sought in more sophisticated studies. For the moment we ask that the group be proved not to have Crangonyctoid affinities.

Neotropica (With Connections to Palearctica)

Bogidiella Group, with Vermiform Bodies and Reduced Pleopods

Six genera, Bogidiella, Afridiella, Bollegidia, Paracrangonyx, Kergueleniola (=Kerguelenella, homonym) and Pseudingolfiella are characterized by a reduction in pleopods and the development of a vermiform body. Some Niphargids also have a vermiform body but maintain well developed pleopods. The general structure of gnathopods and uropod 3 in Bogidiella, Bollegidia and Kergueleniola is so reminiscent of Phreatogammarids or certain Weckeliids that one might suspect Bogidiellids of being a very advanced group descendent from these sources. However, Corophioid affinities can also be suggested by the general Melitid appearance of gnathopod 2, with medial pubescence, then replicated on gnathopod 1, the elongate Phreatogammarid-like uropod 3, Hertzog organs, brood plate setosity; and the presence of wide inner lobes on the lower lip. But setation on the maxillae is reduced and the inner lobes on the lower lip of at least Bogidiella are well developed in contradistinction to Phreatogammarids, Weckeliids and Niphargids. The coxae are greatly reduced in size and the telson is essentially entire or scarcely emarginate, while uropod 3 remains very large, with equal rami and lacking article 2 on the outer ramus. Kergueleniola retains 2 weakly developed rami on the pleopods but Bogidiella and Bollegidia have evanescent inner rami. These three genera have at least 25 species with several more remaining to be described.

Bogidiella Hertzog (= Jugocrangonyx S. Karaman) comprises a group of over 20 blind species of widely diverse habitat, ranging from shallow marine gravels to mesopsammic, interstitial and troglobitic habitats in freshwaters. In the western hemisphere the species are confined to tropical regions but in the eastern hemisphere they have penetrated as far north as 53* and occur as far east as Turkestan. They have not been found, as yet, in eastern Asia, Indonesia, Australia, or western Africa. The only cave dwellers are in Central America. The low level of exploration suggests these facts will be changed significantly in the future.

Bogidiella is characterized by strongly reduced and often discontiguous coxae, loss or vestigiality of the inner ramus on the pleopods, the development of a vermiform body, the reduction of gills to 3 pairs of pedunculate and biarticulate members (pereonites 4-6), the loss of eyes, thin poorly setose pereopods, the fusion of the telsonic lobes to form a short, solid or weakly emarginate plate, and the reduction of medial setae on the maxillae. But Bogidiellids retain the ordinary Gammaroid antennae, albeit poorly setose, and the accessory flagellum is reduced to 2-3 articles. They retain a huge primitive uropod 3 of magniramous form and have large gnathopods, with gnathopod 1 slightly larger than gnathopod 2. The outer lobes of the lower lip are widely spread by the intercalation of two short but broad inner lobes. The mandibular molar remains well developed, weakly to strongly triturative and often bears an enlarged spine or plusetule plus a projecting articulate and toothed plate, suggesting Corophioid ancestry. The mandibular palp remains relatively powerful although setation of article 3 is confined apically.

Many species of Bogidiella are reported to bear lenticular Hertzog organs, each composed of a sphere set basally in article 2 of pereopods 3-7 or 5-7. The female brood lamellae appear to have their marginal setae dense and confined apically. Gnathopod 1, especially, has article 5 highly shortened and lobate posteriorly. Occasional species, such as Afridiella somala, have somewhat broadened article 2 of pereopods 5-7 and increased pereopodal setation. Afridiella is a monotypic offshoot of Bogidiella with grossly callused mandibular incisors and living in Somalia.

Bollegidia (1) from South African emergent intertidal aquifers, differs from Bogidiella in the uniarticulate palp of maxilla 1, the even more reduced pleopods, with sexual dimorphism, and the presence of 4 pairs (versus 3) of coxal gills.

Ruffo (1973:74) has suggested that Pseudingolfiella Noodt (Chile, Kerguelen, anchialine, interstitial), Kergueleniola Ruffo (= Kerguelenella Ruffo) (homonym, Kerguelen, freshwater fish stomach) and Paracrangonyx Stebbing (New Zealand, wells) might belong to the Bogidiella group. To these might be added Protocrangonyx (W. Australia, hypogean with sternal gills). In many ways Paracrangonyx (monotypic) qualifies best in this assertion but it differs from Bogidiella in the parviramous uropod 3 bearing a second article on the outer ramus, has more widely spread setae on the female brood lamellae, a strongly setose mandibular palp, rather well spinose uropods 1-2, an elongate telson (though solid and emarginate) and the coxae are contiguous though short. The wrist of gnathopod 1 is not as strongly lobate as in most species of Bogidiella but the gnathopods otherwise have the same gross context found in Bogidiellids. Lenticular organs and gills are unstudied as yet. These facts suggest a distinct origin, although the mandibular molar is rather strongly acetabularian in shape, somewhat similar to the lesser development found in the Bogidiellids. Gnathopod 1 has article 5 much less strongly lobate than in the Bogidiellids but (only female known) gnathopod 1 probably dominates gnathopod 2 as it does generally in the Bogidiellids. Again, the maxillary setation is reduced, the lower lip bears inner lobes, the maxillipedal dactyl bears a nail but as far as known the pereopodal dactyls lack supernumerary setation and one presumes that pereonite 5 lacks coxal gills as in the Bogidiellids. The latter group bears apical spination on the rami of uropods 1-2, whereas Paracrangonyx lacks that spination and has dorsal spines on the rami.

Lenticular organs (Hertzog organs) are not reported in Paracrangonyx (and may have been overlooked if they do occur). However, the distinctions among the other characters suggest that Paracrangonyx has a completely distinctive ancestry from that of Bogidiellids. Could Hertzog organs be parasites?

Kergueleniola has reduced pleopods but both rami are present in subequal size, having lost their segmentation almost completely and with their setae all confined apically except for one seta on pleopod 1. The retinacula are severely reduced in form. Though short, the telson is deeply cleft and poorly spinose, the spines being represented be thin setules. Mandibular palp article 3 is well setose, containing A, D and E setae. The mandibular molar remains powerful but tintinnabulate. Article 5 of gnathopod 1 is poorly lobate and somewhat lengthened. Hertzog's organs are not reported. Coxal gill pairs are present on pereonites 2-6. The accessory flagellum is reduced to one article.

Pseudingolfiella (Chile, Kerguelen, anchialine, interstitial) is the most vermiform of the Gammarida. It strongly resembles those members of the suborder Ingolfiellidea which strikingly resemble tanaids. Originally Pseudingolfiella chilensis, the type-species, was described as an Ingolfiellidean but it differs from that suborder in the relatively normal gnathopods. Ingolfiellideans have article 5 of the gnathopods dominant and articles 6 and 7 joined together to form a false dactyl closing on article 5. Pseudingolfiella has article 6 dominant, with article 7 forming the dactyl but it bears a significantly enlarged apical nail suggesting a twin articulation. The pleopods are severely reduced. They consist mainly of the peduncles but either or both of pleopods 2-3 may bear a vestigial one-articulate ramus. Uropod 3 is reduced and lacks both the inner ramus and the second article on the outer ramus. Gnathopods 1-2 are virtually alike, small, with reduced wrists, with palms defined from the hand only by spines. The dactyls have become differentiated by the enlargement of the apical nail and its attendant basal setules even more so than in species like Bogidiella neotropica. The telson is elongate but solid and apically trifid, palp article 1 of maxilla 1 is elongate (or article 2 is reduced), and the plates of the maxilliped are reduced in size and setation. The lower lip is unknown. Lenticular organs are not reported. Gills appear to be uniarticulate and nonpeduncular. Uropods 1 and 2 are sexually dimorphic, the male bearing hyaline outer rami, the female often lacking rami. Uropod 1 has commenced the Ingolfiellidean trend where it is shortened and hangs ventrally from urosomite 1, much as does a pleopod. Coxal gills are absent on pereonite 7.

A degree of sexual dimorphism in uropod 1 is found in Bogidiella holsingeri Ruffo and Vigna-Taglianti (1973) from Central America.

There is, of course, great need for further studies and explorations to deduce the similarities in gnathopods between Bogidiella neotropica and Pseudingolfiella, to discover the many undescribed species that probably exist, to search for linkages among the taxa, and probably to divide Bogidiella itself into distinctive groups.

Until now Pseudingolfiella chilensis has been found only in seaside interstitial waters in Chile. It bears a morphological intergradation between the Tethyan Bogidiellids and the much more widespread Ingolfiellideans that have been found in most interstitial environments imaginable, from the marine abyssal to troglobitic. The occurrence of a freshwater amphipod in South America, is of course, always something of great interest because only Paracorophium, Hyalellids, Bogidiellids and Pseudingolfiellids are known to occur on that continent. Whether or not Pseudingolfiella would prove to be a relict preserved on an otherwise impoverished continent has been disproved by the discovery of the second species on Kerguelen Island.

A strong resemblance occurs between the Bogidiellids and the Pseudocrangonyx group in vermiform body, coxae, and the similar and subequal enlargement of the gnathopods. Pseudocrangonyx, however, has 5 pairs of coxal gills, "often" bears sternal gills, maintains a well-developed sickle-shaped article 3 on the mandibular palp, has completely lost the inner ramus of uropod 3 (although the outer remains elongate as in Bogidiella), and has the setae well spread proximally on the brood lamellae.

There is also a weak similarity of Bogidiellids to Austroniphargus especially in the lobate article 5 of gnathopod 1 in Bogidiella (on both gnathopods in Austroniphargus).

Because of their many parallels, Pseudocrangonyx and Pseudingolfiella could be visualized to lie on the same ancestral line. Pseudocrangonyx is more primitive in the sense that its body is less vermiform, its coxae larger, its gnathopods are better developed and more strongly diverse and have the Crangonyctid palmar spination, its pleopods are better developed, the telson is cleft and the maxillae are setose. The two genera share the uniramous uropod 3 and replicated gnathopods with short wrists. Uropod 2 has a weak trend for spinal modification in Pseudocrangonyx whereas in Pseudingolfiella male uropod 1 has developed an oddly naked membranous outer ramus.

Protocrangonyx (1, Australia) is characterized by the reduced parviramous uropod 3, the presence of sternal gills and coxal gills 2-6, has stunted gnathopods, lacks inner lobes on the lower lip, but retains small biramous pleopods. In the classificatory scheme this genus is placed near other Australian Crangonyctoids because it retains sternal gills unlike various Bogidielloids. As there is simply no reason to honor a Bogidiellid group by formal nomenclature there should be no objection to this kind of schizoid classification until more study can be undertaken.

Artesia (1) and Parabogidiella (1) are recently described taxa (Holsinger and Longley, 1980), from the famous San Marcos Well or its aquifer in Texas, north of the Edwards Plateau. They appear to intergrade Spelaeogammarus (to follow) and other Bogidiellids in the retention of medium sized coxae on several segments. In Artesia, coxae 5 and 6 are so large that they cover coxa 7.

Both rami of the pleopods in Artesia are multiarticulate and Parabogidiella retains the normal five sets of coxal gills. These intergradations of conditions between Crangonyctids and Bogidiellids, superimposed on vermiform bodies of subterranean taxa, should firmly demolish the independence of Bogidiellids.

Most Bogidiellid genera bear in common the reduced coxae, the nondominance of gnathopod 2, reduced pleopods and maxillae in varying degrees and all bear a weakly to strongly abnormal mandibular molar.

These characters do not appear to be of sufficient unifying value at this time to suggest a common origin for the several taxa owing to the wide variability in so many other features, especially the finer structure of telson, pereopods, and gnathopods or the counts and shapes of gills, setation of brood lamellae, and the wide range of conditions in uropod 3, accessory flagellum (1-3 articulate) and mandibular palp.

Nevertheless, the aequiramous uropod 3 and replicated gnathopods of Bogidiellids and Kergueleniola point to ancestry in the Phreatogammarid Crangonyctoids (or better in Corophioids) and those two groups might better be placed immediately before the orthodox Crangonyctoids. For want of a better phyletic position, Pseudingolfiella is also appended but one must remember that its geographic discontiguity from living Gondwanan Crangonyctoids is strong. However, Pseudingolfiella has much in common with Bogidiellids and the exploration of South American aquifers and southern freshwaters is so embryonic that a connection might yet be discovered between Spaeleogammarus and Pseudingolfiella through other Bogidiellids. South American aquifers are so poorly studied that surprises may be forthcoming. Recently, Andres (1975:127) found a species of Paracorophium (otherwise Notogean) in Chilean freshwaters, a discovery equivalent to finding Araucarian pines both in Tierra del Fuego and Norfolk Island.

Spelaeogammarus

Spelaeogammarus (1), from a cave in Brazil, is a supposed Bogidiellid but its only good marker attributes are the reduction of the coxal gills to 3 pairs and the partial reduction of the pleopods (the rami being short, the outer with 4 articles, the inner elongate but uniarticulate). Otherwise, the body is not vermiform, the anterior coxae are elongate and the peduncle of uropod 1 bears multiple facial spination. The antennae are elongate, the accessory flagellum 3-articulate, the mandibular molar is of medium size but poorly triturative, palp article 3 is slightly shorter than article 2 and bears one apical seta, the maxillae are not medially setose and the outer plate of the maxillipeds is slightly reduced. The gnathopods are large, subchelate, the palm is very oblique and furnished with large (?simple) spines, and gnathopod 1 is much larger than gnathopod 2. The wrist of gnathopod 1 is short and deeply lobate, whereas the wrist of gnathopod 2 is more elongate and poorly lobed. The telson is almost entire and spiny. Sternal gills are not mentioned and the characteristic setation found in many Bogidiellids on the female brood lamellae is also not mentioned.

This genus makes a very good ancestral form to Bogidiella but is so strongly plesiomorphic in body form, coxae and pleopods that a wide gap should be maintained between the genera.

Spelaeogammarus has a mixture of characters so diverse that its ancestry is difficult to trace; this aspect is also seen in Phreatogammarus, the "universal" Crangonyctid of New Zealand. The gnathopods resemble those of other Crangonyctids and reinforce the proposal that Bogidiellids are of Crangonyctid ancestry rather than descendents from Corophioids.

In summary the Bogidiella group is likely to be polyphyletic and, therefore, we have not wanted to discuss it in the logical evolutionary order shown in the appropriate keys and phyletic scheme (Graph 3). If indeed these genera show an evolutionary connection a good arrangement of descent is: Spelaeogammarus, Artesia, Parabogidiella, Bogidiella, Afridiella, Bollegidia, ?Protocrangonyx, Paracrangonyx, Kergueleniola and Pseudingolfiella in terms of gradistics, the gradual conversion from an ordinary looking gammaridean to a vermiform one with obsolescent coxae, pygidization and reduced pleopods.

Evolutionary Pattern in Holarctic Gammaroids

This section introduces the Gammaroids of Eurasia, including Baikalian, PontoCaspian, and other freshwater and marine emigrants. The group lacks sternal gills, bears coxal gill 7 but lacks notched spines packed on the palms of the gnathopods. It thus excludes the Niphargids, Crangonyctids, the Hadzioids (Melitoids) and Bogidiellids and the groups lacking palms on the gnathopods.

The Holarctic Gammaroids are confined to section III of the Check List of Genera (Appendix IV) and contain almost 85 genera and about 450 species. They are divided into about 20 groups, some of which have strong familial integrity but others of which are much less distinctive and grade into each other by web-like patterns. In general, the later in the list the stronger the groupings become. For example, the Eoniphargus, Hyalellopsis, Micruropus, Compactogammarus, Pontogammarus, Sarothrogammarus, Cardiophilus, Iphigenella, Dikerogammarus and Metohia groups are reasonably well defined and mostly disjunct from earlier groups, such as the Gammaridae, Echinogammarus, Fluviogammarus, Acanthogammaridae and Gmelina groups. The evolutionary flow through the earlier groups outward to the later groups could be construed easily as monophyletic but the flow outward from Gammaridae through the Gmelina group is suspected to be so broad and polyphyletic that this entire section should be coalesced at familial level. It could then be divided into subsections much more finely than now undertaken by phenetic clustering methods. We conclude that the following characters have arisen more than once, perhaps many times: shortened inner ramus of uropod 3, posteroventral protrusion of article 2 on pereopod 7, predatorial (Acanthogammarid) gnathopods and expanded bases of pereopods 5-

7. Unweighted phenetic methods may, therefore, be more useful in finding clusters than weighted methods (e.g., assuming single origins for each character).

The linkages between the *Echinogammarus* to *Pontogammarus* and *Gmelina* to *Pontogammarus* groups are also very clearly expressed in such intermediate genera as *Baikalogammarus* or *Macropereiopus*, and *Obesogammarus*, so that the *Pontogammarus*-like antenna 1 is not a characteristic well segregated by extinction of intermediate taxa. It may have arisen separately in the PontoCaspian and Baikalian provinces but this point should be studied more thoroughly. On the other hand, the *Compactogammarus* antenna 1 is almost fully distinctive and is confined to the PontoCaspian basin, except in the marine *Priscillina*.

No single set of characters distinguishes the Baikalian fauna. That group is characterized in a dominant way by various trends, such as development of dorsal body teeth, a significant percentage of raptorial gnathopods, diminution of fossorial characters in those genera considered to be fossorial (such as loss of setae or reduction of accessory flagellum), the high degree of speciation in genera with Eulimnogammarid gnathopods (propodus of gnathopod 2 slightly to greatly smaller than gnathopod 1), the predatorial or nektonic adaptations through increased lengths of appendages, development of cuspidate coxae and cephalic processes, frequent loss of article 2 on outer ramus of uropod 3, and the moderate (against absence) development of setation on uropods 1-2. All of these characters, however, have their rudiments in taxa occurring outside Baikal. This is not to suggest that the Palearctic Gammaroids constitute an organic whole, a great pool of taxa intermingling throughout the continent. On the contrary, the Baikalian Gammaroids do not necessarily have the marks of a single ancestor and, therefore, may have had several origins. Because most of the kinds of characters found in Baikal have also evolved outside the lake, one could in the extreme, hypothesize a single ancestor that underwent, in microcosm, all of the parallels found elsewhere. A better suggestion is that at least 2 ancestors, a Gammarid (*Heterogammarus*) and a fossorial taxon (*Micruropus*) comprised at least a minimum input to Baikal. This would leave *Macrohectopus*, the most aberrant Baikalian genus, as descendent from the Gammarid ancestor. Owing to the loss of palms on gnathopods, there is the faintest suggestion that *Macrohectopus* is an immigrant from the *Gammarellus* group, now confined to Arctic shores and the Caspian Sea. The group is characterized by loss or reduction of true palms on the gnathopods but *Macrohectopus* is otherwise so mysidiform that its origins are disguised. Such a supposition would increase the probable ancestors to at least 3. But there is great likelihood that the immigrants into Baikal well exceeded that figure as the predatorial (Acanthogammarid) kind of gnathopod occurs outside Baikal both in the Arctic Sea, Caspian Sea and in Balkan cave dwellers. This trait may have therefore been more widespread and not directly attributable to a Baikalian origin. This would increase ancestors to 4, with the predatorial gnathopods reaching full bloom in Baikal but apparently also decaying towards the *Gammarus*-like gnathopodal situation to such an extent that it is difficult to sort out or to find a full disjunction between the Acanthogammarid gnathopod and other kinds of gnathopods in Baikal. A way to make this distinction by studying loss of palmar spines (present in *Gammarus*), loss of lobation on wrists (present in *Acanthogammarus*), loss of palmar homogeneity (present in *Acanthogammarus*) should be of first priority in the study of Baikalian fauna so as to determine whether or not a well defined Acanthogammaridae can be established. If this were possible then Baikal might be seen to be characterized by Acanthogammarids, Gammarids, Micruropids (fossorial) and the two small odd groups, the Hyalellopsids and the Macrohectopid. The first two groups would show convergence in the development of body processes. The Hyalellopsid group has no immediate counterpart outside Baikal but may be derivative from the fossorial taxa. Kozhov (1963:291) believes in 4-5 ancestors.

The absence in Baikal of such widespread and successful groups, especially in western Eurasia, as *Gammarus* and *Echinogammarus*, must be pondered. Many Baikalian species were formerly placed in *Gammarus* and *Echinogammarus* but have been removed to the closely similar *Heterogammarus* and *Eulimnogammarus*. Apparent true species of non-endemic *Gammarus* live in the ultimate reaches of the outflowing tributaries of Baikal and, to improve fish food, have been introduced by humans into the very shallow fringes of the lake. True species of *Gammarus* or allies have reached eastward in Asia across to Japan and through the great central Asian mountain chain, but, for some reason have not persisted in depths of Baikal greater than a few cm. They have not speciated therein either. Why they should be so widespread elsewhere but missing from most of Baikal is mysterious. Although *Eulimnogammarus* was identified from Spain (Stock, 1969a, Pinkster and Stock, 1970a), G.S. Karaman (in litt.) finds that an erroneous conclusion. He finds that true Baikalian *Eulimnogammarus* is characterized by short coxa 1 and that the Iberian species is really a member of *Echinogammarus.* *Eulimnogammarus* is immensely diverse in Baikal (if one accepts all of the subgenera) and might be construed to be a descendant of the most primitive living Gammarid, formerly of widespread provenance but now limited to Baikal. If so, then *Gammarus* could be construed as a second descendent group having penetrated westward, southward and then eastward of Baikal but not having viability in the Baikal region. Besides the odd coxa 1, *Eulimnogammarus* is characterized by a smaller propodus on gnathopod 2 which Prof. Stock (personal discussion) believes is a more primitive state than that propounded by J.L. Barnard 1969c:27). The latter person believed that primitive Gammarideans must be characterized by full development of a prehensile appendage on free somite 2, whereas any reductions in dominance or change in morphology and functions are the result of derived conditions evolutionarily. Neither student, of course, is propounding that either *Gammarus* or *Eulimnogammarus-Heterogammarus* is the earliest Gammarid. Much history has been lost in the poorly extant fossil record. Corophioids are just as llikely to be primordial. Nevertheless, Stock's implication that reduced gnathopod 2 of *Heterogammarus-Eulimnogammarus* is more basic, or was more widespread, than the *Gammarus* form, has merit and is confirmed to some degree by the discovery of the same kind of gnathopod 2 on a species of *Echinogammarus* in western Europe. If comparison of European and Baikalian species, despite differing coxa 1, confirms a sibling identity, then one might propound the theory that Gammaroids reached Baikal in the Eulimnogammarid form, whereas the Gammarid form has either (1) been extinguished there, or (2) never reached the area, or (3) is in some way excluded by functional intolerances. *Gammarus* is generally confined to streams and has little success in lakes, at least in the eastern hemisphere.

Echinogammarus (specifically its plesiomorphic state represented by *Chaetogammarus*) lives in lakes, rivers and brackish seas in the western part of the PontoCaspian basin but apparently also is now excluded from Baikal. The sensu stricto *Echinogammarus*, as defined by Stock (1971:98) the diverse European genus of calcium-rich streams, is also excluded. Except in Iberia, both genera have gnathopod 2 unreduced. The reduction of gnathopod 2 in many species of *Heterogammarus-Eulimnogammarus* is so weak as to be barely perceptible. The Baikalian genera need to be established on a firmer basis than is now apparent in the literature. Because many species have had only a few figures or descriptive remarks published, greater attention to minute differences in shapes, proportions and armaments of various appendages in non-Baikalian Gammaroids is required.

Taxonomic problems in *Gammarus*, sensu lato, have not been adequately settled. During the 3 decades between 1940 and 1970 the genus was divisible into 3 groups, *Gammarus* (marine and freshwater), *Rivulogammarus* (streams) and *Marinogammarus* (sea margins and brackish waters). These groups (or subgenera) were distinguished on shapes of cephalic lobes, the shortness of the inner ramus of uropod 3 (*Marinogammarus*) and in the presence of a weak posteroventral proturusion on article 2 of pereopod 6 (*Rivulogammarus*). First (in retrospect), Stock (1969b) found that the type-species of *Rivulogammarus* was the same as that of *Gammarus* and sank *Rivulogammarus*, and further concluded that *Rivulogammarus* was of no generic value in any event and did not need a new name. Then, Stock (1968:17) found that *Marinogammarus* was a junior subjective synonym of *Chaetogammarus*, a primarily PontoCaspian genus not theretofore adequately compared with *Marinogammarus*. He concluded that the shortness of the inner ramus on uropod 3 did have value generically so as to segregate *Chaetogammarus* from *Gammarus*. Stock's work (especially 1968), involving extensive analysis of *Echinogammarus*, demonstrated that *Chaetogammarus* and *Echinogammarus* could be maintained separately by a complex definition of setosity found in *Echinogammarus* but more poorly expressed in *Chaetogammarus*. Presumably, this same definition of setosity applies to distinctions of *Echinogammarus* from most non-Baikalian Gammarids, so that *Gammarus*, *Chaetogammarus* and *Echinogammarus* became the familiar genera of the group west of Central Asia. However, Sket (1971b) described *Lagunogammarus* to distinguish yet another group of the classic *Gammarus* on the basis of shape in oostegites, sharp points on the cephalic lobes and weakly produced posteroventral corners on the bases of pereopods 5-7. This group included only a few of the old *Rivulogammarus* group. Then Tzvetkova (1975a) reinstated *Marinogammarus* and segregated it from *Chaetogammarus* on the presence of the sharp ocular lobes and the short spiny telson of *Chaetogammarus*. Parenthetically, one must note that Bousfield (1969) had already determined that at least three species (but the type-species not examined) are distinguished from other Gammaruses by the accessory coxal gills on some thoracic segments (see Bousfield's, 1969 key). G.S. Karaman and we have examined those species but cannot find the stated accessory gills. Tzvetkova (1975a) also used *Pephredo* Rafinesque (1817) formally in a taxonomic sense after Bousfield and Holthuis (1969:105) had extracted this old name from obscure literature and suggested its abolishment. Tzvetkova's (1975a:29) result was a classification maintaining *Gammarus*, (*Pephredo?*), (*Lagunogammarus*), *Marinogammarus*, *Chaetogammarus* (and by inference), *Echinogammarus* by utilizing the inner ramus of uropod 3, the acuity or roundness, the concavity or noncavity and the slope of the cephalic lobe, and setation patterns on the mandibular palp so as to distinguish these groups. Bousfield (in 1977) has informed us that he will segregate even further by pulling away several American Gammaruses into distinctive genera. J.L. Barnard and Gray (1968) had also described the subgenus Mucrogammarus, which after further reflection and extensive study by us, is seen to be characterized only by the development of dorsal body teeth, a characteristic discounted by Stock (and other European experts, such as Pinkster and G.S. Karaman, personal discussion). The gnathopodal characters elucidated by Barnard and Gray (1968:220) are a misconception and overemphasis now revealed by personal examination of pertinent European species, such as Gammarus roeselii. Nevertheless, the Gammarus situation remains completely unclear. Most species must be redescribed at least for gills, brood plates, gnathopods, pereopods, and mandibular palps (and they might as well be fully illustrated for everything else) so as to determine what kind of clustering can be effected. The value of the characters must be tested (ultimately against the logic of evolutionary flow, the low degree of absurdity in biogeographic relationships, the definite disjunction and, the disproof of morphological oscillations). J.M.C. Holmes (1975b) selected 13 familiar species of Gammarus and Marinogammarus and subjected them to a variety of analyses in numerical taxonomy. The largest discontiguity continued to be the distinction between species of Gammarus and Marinogammarus (= Echinogammarus) and presumably much of this is weighted by the parviramous uropod 3 of Echinogammarus. Gammarus lacustris and G. pulex were commented on as being very closely clustered (something we use as an example of taxonomic difficulty, see index, "Taxonomy, subtle") but discontiguous from other species of Gammarus; this shows nicely in most of the clustering and graphic techniques presented. Of course, after 5 species of Marinogammarus are removed, and one subspecies thrown out, the techniques are being applied only to 6 species, so when 100 species of Gammarus are subjected to the techniques in the future the discontiguity level will be most intriguing.

One must presume that a reduction of the inner ramus of uropod 3 to the level found in Echinogammarus (= Marinogammarus and Chaetogammarus) is not reversible in evolution and, therefore, the remaining genera of Section III.A., the Gammaridae, are placed close to that primitive form even though this results in a very widespread geographic distribution of the group and may be objectionable to those believing that Baikal is a separate microcosm. The genera are characterized by magniramous or variramous uropod 3. The classification, however, follows the views of many taxonomists who discount dorsal body processes as evolutionarily significant because it aligns such processiferous genera as Pallasea with Gammarus rather than drawing them outwards from a complex Baikalian evolution.

Sowinskya (Caspian) was returned to Chaetogammarus by Birstein and Romanova (1968) but its uropod 3 is unknown and the great elongation of article 3 on antenna 1 is a strong disjunction, reminiscent of Baikalian tendencies. Admittedly, it has the loss of dominance on gnathopod 1 so characteristic of Caspian genera, and which, in itself may be found to signify a different clustering than provided here.

Derzhavinella (Caspian) also has the increased dominance of gnathopod 2 and the odd article 3 of antenna 2. Not much weight is given gnathopodal dominance in attempts to segregate Caspian from Baikalian and then from Eurasian genera, even though a majority of Caspian genera has gnathopod 2 dominant, a majority of Baikalian genera has gnathopod 2 equal to or dominated by gnathopod 2 and most other Eurasian genera have no significant differences. There are sufficient exceptions in Caspian and Baikalian faunas to suggest that more subtle analyses will be required to untangle any potential clustering using this simple semanticism of size dominance. Gnathopods undoubtedly are as vitally important secondary (if not primary) sexual characters to amphipods as are the reproductive organs of plants or other organisms but they also have other functions than in amplexy or sperm transferral and non-sexual adaptations of gnathopods may override their sexual functions. Even though the functions of these widely varying appendages are not well understood, there is already a plethora of taxonomic value outside the Gammaroids. Until gnathopods can be clarified by functional morphologists, they can be used to make only the grossest taxonomic groupings above generic level.

Our classification (III.A., Appendix VII), therefore, implies that there is close connection (or convergence) between the Gammarus-like genera of Baikal and TransUralia, between Baikal and the Caspian, and between the Caspian and TransPontian faunas; but the specializations found in Baikal and the Caspian imply an inward move of extrinsic taxa, with very little escape (Pallasiola) from the confined basins. This same conclusion results from most of the remaining sections of the classification; for example, the outward escape or interchange of Acanthogammarids in sections III.E. and F. is confined to Issykogammarus, Gammaracanthus and, doubtfully, Typhlogammarus. Indeed, one must hypothesize a degree of parallel evolution or convergence in the Typhlogammarus case, because of the great ecological barriers to widescale migration involved with the cave-dwelling Balkanian Typhlogammarus.

The occurrence of dorsal body processes ("ornamentation") is not abandoned as a good taxonomic mark of distinction but it is not accorded any more value than any other character. This character (or complex of characters) appears to operate in a system of evolutionary flow and appears to be just as useful taxonomically as are such characters as the progressively shortened inner ramus of uropod 3, the progressively expanded or produced article 2 of pereopod 7, the progressive changes in gnathopods (mentioned two paragraphs above), the progressive increase of setation in coxae or any other character found by taxonomists. The fact that we can only surmise the functions of body processes is no reason to abandon them as good characters. There is no evidence that body processes arose just once and thereafter diversified within a monophyletic group, else we would have to pull North American Mucrogammarus into a pool of Baikalian genera (where they used to be placed). At the other extreme, however, there is no more reason to synonymize Carinurus with Gammarus by discounting dorsal body processes, than there is to unite Dikerogammarus with Echinogammarus by discounting the expansion of article 2 on pereopod 7 and invoking the intermediate conditions of E. pauxillus or E. warpachowskyi.

There is also no reason to suggest that every genus with dorsal processes has arisen separately from some smooth bodied genus, just because obvious generic clusters do occur in the group, for example, the duo of

Brandtia and *Spinacanthus*. These genera share so many unusual similarities in dorsal body processes that one can scarcely doubt their sibling origin, yet one genus bears expanded article 2 on pereopod 7 and the other does not. The expansion of pereopod 7 is also not a monophyletic character by this example and many others, so that groupings III. A.-F. within the Palearctic Gammarids must be much more finely divided than we have attempted in order to find affinities by clustering methods. These actions must await a much firmer descriptive base than now available.

Gammarus and *Echinogammarus* (November, 1978)

Gammarus and *Echinogammarus* are two of the largest epigean freshwater genera of amphipods in the world. The other great Palearctic genus, *Niphargus*, is mainly hypogean and *Crangonyx* and *Stygobromus* are mainly Nearctic.

Contrary to the opinions of all experts on these two genera, we regard the first 2 as poorly distinct and slightly overlapping, with the possibility that *Echinogammarus*, the apomorphic state of the "supergenus," is polyphyletic. Recently Stock (1978a:90) also entertained doubt about uropod 3. *Gammarus* bears so-called magniramous uropod 3 and *Echinogammarus* bears parviramous uropod 3 but the overlap is very broad, there being species with the inner ramus of uropod 3 reaching 25 or 30 or 37 or 45 or 55 or 75 or 95 percent as far as article 1 on the outer ramus of uropod 3. *Echinogammarus* is composed of those species generally below (shorter than) 31 percent. That a long inner ramus can spawn a short inner ramus in a cycle of evolution appears no better represented than in the pair of species *roeselii* and *annandalei*. *Gammarus roeselii* is a widespread carinate species of Eurasia with long inner ramus on uropod 3, and *Echinogammarus annandalei* is the perfect replica in North Africa with a much shortened inner ramus on uropod 3.

The list of species in *Gammarus* (Handbook, Appendix VI) is padded with many obscure names, and therefore only about 110 valid species of *Gammarus* are known. In November, 1978, Table 5, with 110 species, was constructed to analyze the biogeography of the genus. About one fifth of the species are marine, which mainly indicates they have a slight tolerance for saltwater. Most live close to shore in diluted seawaters, largely in the uppermost meter, rarely as deep as 30 meters below water surface. Most experts believe the marine species are relicts of a former era in which *Gammarus*, a basic genus, formed a rootstock and invaded freshwaters. To the contrary, we propose that the marine species have emerged from freshwater into the sea in response to the impoverishment and youth of North Atlantic seas but will be slowly extinguished in future eons as more well adapted marine amphipods move into the North Atlantic from other oceans.

The present freshwater members of *Gammarus* (and *Echinogammarus*) may lie closer to the ancestral Gammarid than do the marine members and the genus may have evolved completely in freshwater, probably from a Crangonyctoid ancestor. This evolutionary cycle may have taken place partly in salt water (or in water of low salinity) if it was catalyzed by the opening of narrow continental brackish gulfs with the breakup of Pangaea. *Gammarus* and *Echinogammarus* never became fully adapted to the sea; there is no living evidence of any further generic deployment in the sea from this

TABLE 5.--Geographic distribution of species in *Gammarus* and *Echinogammarus* (November 1978)

	Gammarus	*Echinogammarus*
Marine	(20)	(10)
AmphiAtlantic	2	3
Moved by mankind across Atlantic (*tigrinus*)	1	0
CircumArctic	2	0
Northern Europe	5	5
Mediterranean	4	2
America (East Coast)	6	0
Freshwater	(90)	(43)
Holarctic (*lacustris*)	1	0
Palearctic (*pulex*)	1	0
America	11	0
Eurasian, widespread east to Caucausus	9	4
Iberia	0	12
Europe, others (+Britain)	6	13
Balkans	14	4
North Africa	4	3
Asia Minor and Mideast	13	0
North Africa and Spain together	1	2
Caucausus	7	0
W. Siberia, Crimea, Lakes	13	1
Asia Minor to Turkestan	2	0
Turkestan	3	0
Orient (+Japan)	5	0
PontoCaspian Mudbottom Endemics	0	4
	110	53

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root, except remotely in the deep sea genera *Bathyceradocus* and *Metaceradocoides*. This fact, of course, could be interpreted to mean that any apomorphs from the *Gammarus* stock have since been extirpated by negative selection against other amphipods but we enforce our opinion with the knowledge that *Gammarus* and *Echinogammarus* are very weak when compared to such strong genera as *Melita, Ampelisca, Corophium, Monoculodes* (and many others). We maintain that if they had made a great marine success their marine remnants would occur outside Holarctica. Instead, *Gammarus* and *Echinogammarus* have remained in Holarctica where continental morphology and climate preserve many places in which dilute seawaters hug the shores and from which fully adapted marine taxa are repelled. Fully adapted marine taxa have had to come north, especially into the north Atlantic, through fully saline tropical seas and, therefore, any southern mixohaline species are effectively kept out of the area.

TABLE 6.--Long distance and widespread areal distribution of major marine species in *Gammarus*; A = recommenced ranking in America.

Map	Species Number	Species	Distribution
25,36	116	*wilkitzkii*	Circumarctic
25,33 34,35	95	*setosus*	Circumarctic south to boreal edge
31,34 35,37	79	*oceanicus*	Labrador and New England to Novaya Zemlya and Normandy
29,30 33,37	32	*duebeni*	Labrador and New England to White Sea and Brittany
28	107	*tigrinus*	North America, introduced western Europe
23	117	*zaddachi*	Ireland to White Sea and all Baltic, Normandy
30	65	*locusta*	Iceland to Cadiz and Gulf of Bothnia
30	49	*insensibilis*	Ireland to Black Sea
29	94	*salinus*	Ireland to Gulf of Finland
30	29	*crinicornis*	Ireland to Morocco
30	100	*subtypicus*	Mediterranean and Black Sea
30	5	*aequicaudus*	Mediterranean and Black Sea
30	26	*chevreuxi*	Ireland to Portugal
A 37	10	*annulatus*	New Jersey to New Hampshire
34	63	*lawrencius*	Long Island to N. Labrador
33	72	*mucronatus*	Gulf of St. Lawrence to North Mexico; introduced Salton Sea
34	83	*palustris*	S. Maine to N. Florida

Southward records of penetration by marine species in *Gammarus* appear to belong in the western hemisphere to *G. mucronatus*, a species which is estuarine or lagoonal and which is known from at least as far south as the border between Mexico and the United States of America. The tolerance of this species makes it good material for transplantation and it has been introduced successfully into the Salton Sea in California, a salty artificial lake (Barnard and Gray, 1968). In the eastern Atlantic the southward record probably belongs to *G. crinicornis*, reported from south of the Spanish Sahara, near Faux Cap Blanco, 35-50 m (Stock, 1967a:32) where, apparently, it has submerged to find cool waters.

TABLE 7.--Widespread areal distribution of major species in freshwater Gammarus; A = ranking recommences with American species.

Map	Species Number	Species	Distribution
23,26, 33	61	lacustris	Holarctic
25,27,	90	pulex	Palearctic
30,32	92	roeselii	Oise and Rhone to E. Turkey
29	38	fossarum	Pyrenees to mid Balkans and ?Turkey
24,28	14	balcanicus	N. Italy through Balkans and Turkey to Tien Shan
24,29	56	komareki	Greece to Syria
30	108	triacanthus	E. Czechoslovakia to Greece
32	54	kischinefensis	N.W. Carpathians to Ukraine and E. Turkey
30	40	gautieri	N. Spain to Tunisia
31	12	arduus	Balkans
26,31	89	pseudosyricus	Lebanon to N. Afghanistan
31	113	varsoviensis	Poland and White Russian SSR
25,30	102	syriacus	Egypt to Tadzhikistan
34	35	fasciatus	Wisconsin to Quebec, Connecticut to North Carolina
33	88	pseudolimnaeus	Oklahoma to Quebec
33	69	minus	Arkansas to E. Pennsylvania

Early in the history of study on Gammarus, the common marine species, G. locusta, from the eastern Atlantic Ocean, was considered to be a highly variable species with formae or morphs restricted to differing salinity regimes. Through a long and arduous history of critical work, mainly since 1940, experts such as Sexton, Segerstrale, Spooner, Kinne, Stock, Pinkster, A.L. Roux, Meijering and Goedmakers have determined that the original locusta was a complex of at least 7 species now recognized to have constancy in their characters of recognition. Instead of morphs or phenotypes responding to differences in halinity by changes in setation, and proportions of appendages, the populations were found to be definable species with highly discrete but complexly overlapping tolerances to environmental variables (Stock, 1967a, in part). Some species have wider tolerances and higher prodigality than others and this has resulted in the Gammarus catastrophe of Europe with the introduction of the scourge, Gammarus tigrinis, from North America. This species has caused the great

TABLE 8.--Long distance distribution of species in *Echinogammarus*, marine (M) and Freshwater (F), top few in rank.

Map	Species Number	Species	Distribution
42,44	18 (M)	*finmarchicus*	N.W. Atlantic to White Sea, Iceland, Channel
42,43	29 (M)	*obtusatus*	N.W. Atlantic to White Sea, Brittany
42,44	47 (M)	*stoerensis*	N.W. Atlantic to Barents Sea, Baltic to Gotland
42,43	27 (M)	*marinus*	Iceland to Kattegat, Cape Finisterre
40,42	37 (F)	*pungens*	N. Spain to Syria
39	51 (F)	*thoni*	Riviera to S. Turkey
39	36 (F)	*placidus*	Caspian to E. Balkans, ?also escapee
41,42	55 (F)	*veneris*	N.W. Italy to Israel
41	43 (F)	*sowinsky*	PontoCaspian and escapee
40	57 (F)	*warpachowskyi*	PontoCaspian and escapee
39	9 (F)	*berilloni*	N. Spain to Mid-Germany
39	45 (F)	*stammeri*	Nice to Greece
40	21 (F)	*klaptoczi*	Balearics to Libya

constriction and near extinction of lesser adapted species, *G. pulex*, *G. duebeni* and *G. zaddachi*, each with much smaller reproductive powers (Dieleman and Pinkster, 1977; Pinkster, Smit and Brandse-de-Jong, 1977).

Four marine species of *Gammarus* penetrated into the Black Sea (Stock, 1967a). Two others have been recorded there but may be early misidentifications of the species Stock clearly verifies. Unlike several species of the *Chaetogammarus* section in *Echinogammarus*, no species of salt adapted *Gammarus* is endemic to any part of the PontoCaspian basin. There are, of course, many freshwater species of *Gammarus* in PontoCaspian tributaries. Species widely transported by humans are discussed by Jazdzewsky (1980) who, besides analyzing many PontoCaspian transplants, discusses *G. tigrinus*, *G. roeselii* and *G. varsoviensis*. His fascinating article presents the history of river connections by canals and transplantations of amphipods as food for fishes to improve freshwater pisciculture, especially in the Soviet Union. Some of his maps are reproduced here (Maps 47, 48).

Gammarus chevreuxi is the species used by Sexton (1913-35; and Sexton and Clark, 1936; and Sexton and Matthews, 1913) in her pioneering work on growth and development of amphipods and is clearly a very useful laboratory animal, although many Gammarids are expected to be easy to culture. The giant Arctic *G. wilkitzkii* is one of the two main surface-dwelling

TABLE 9.--Widespread (bulk in contrast to long distance) areal distribution of species in Echinogammarus, top few in rank. Species 18, 29, 47, 27, see Long Distance, Table 8, marine species.

Map	Species Number	Species	Distribution
39	9	berilloni	N. Spain to mid Germany
40,42	37	pungens	N. Spain to Syria, to mid France, N. Africa, N. Italy
41,42	55	veneris	N.W. Italy to Balkans to Israel to Egypt
39	45	stammeri	Nice to Greece
41	43	sowinskyi	PontoCaspian, tributaries and escapee
39	36	placidus	PontoCaspian, to east Balkans and escapee
40	57	warpachowskyi	PontoCaspian and escapee
39	23	longisetosus	N. Spain
39	51	thoni	Riviera to Balkans to S. Turkey

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amphipods in the polar basin. Individuals occur in moderate abundance just below the ice canopy in the inverted benthos of that environment and may be one of the main producers of tissue in the polar sea (J.L. Barnard, 1959d:116).

Subdivisions within Gammarus remain unclear. No one has subjected all the species to phenetic analysis to find groups and possible evolutionary clusters, nor has anyone done any kind of cladistic synthesis. We are told by experts that marine species, for the most part, form a systematic cluster and the literature confirms that taxonomists detect a locusta group (Stock, 1967a) and a pulex group (G.S. Karaman and Pinkster, 1977a). The latter authors point out that the mixohaline (our "marine") species clustered by Sket (1971b) into the genus Lagunogammarus are intermediated by G. duebeni and doubt is cast on efficacy of that clustering.

Long distance and widespread areal distributions of major species in Gammarus are given in Tables 6 and 7. These are grouped into marine and freshwater species and within such groups are classed as Eurasian and American. Most of the major species are in Eurasia.

The distribution of the 53 known species of Echinogammarus (November 1978) in Table 5 among the geographic categories differs greatly from Gammarus, especially in the freshwater areas. First, in the marine biome there are no circumarctic or endemic American species, the bulk of species being north European or amphi-Atlantic. Long distance and widespread distributions are found in Tables 8-9.

In the freshwater biome, the representation of Echinogammarus in Asia is confined just to the western part and then very poorly. The genus is absent in freshwater America but, unlike Gammarus, is concentrated in western Europe, especially Iberia, where it appears to have captured the environment from *Gammarus*. The apomorphy of the species suggests they evolved later than species of *Gammarus* but, of course, this statement can be applied only to the extent that all species of *Echinogammarus* are but one increment of evoluton removed from the single ancestral species of *Gammarus*. For example, one could envision all species of *Echinogammarus* unfolding before any but the first species of *Gammarus* had differentiated. Nevertheless, the distribution pattern suggests a major radiation confined to western Europe and a secondary radiation confined to the PontoCaspian basin, where *Echinogammarus* (in its *Chaetogammarus* cluster) has invaded the salty lacustrine parts of the basin, unlike *Gammarus*. All of this suggests we are faced with cryptic physiological diversity within the genera, cryptic to the extent that we see no discontiguous morphological correlations as yet.

Until now, regardless of taxonomic appellation, these genera have been interpreted as having originated in the sea and then having invaded freshwaters. *Gammarus* came first, evolved into *Echinogammarus* (apomorphic uropod 3) and then each invaded freshwaters, while *Echinogammarus* got around to the PontoCaspian basin either through the Mediterranean-Dardanelles seaway or through the proglacial Wurm ice lake. *Gammarus* reached America in strength sufficient to invade freshwaters but has never been greatly successful there. *Echinogammarus* has reached America only through amphi-Atlantic marine species none of which has either become endemic nor invaded American freshwaters.

In our opinion *Gammarus* and *Echinogammarus* are products of freshwater ancestry, possibly cycled weakly in the first evolutionary increment through polyhaline continental clefts of Pangaea but descending from purely freshwater ancestors and then invading the sea secondarily. They could invade the sea and survive only in the North Atlantic where other well adapted marine amphipods from the Pangaenic world ocean had not yet reached and which continue to be barred by the highly saline and very warm Atlantic tropics or by the low salinity and great cold of arctic pathways. Amphipods, no doubt, are cold-adapted but, if we accept the Bruun-Menzies thesis that cold polar and abyssal waters of 4* C or lower came into being after the Oligocene, then the cold adaptation we see in amphipods really is centered in the 4-10*C range (Bruun, 1957; Menzies, Imbrie, and Heezen, 1961). The margins of the North Atlantic are therefore a regime of 4-10*C slightly diluted waters, which world ocean amphipods have difficulty in reaching. The North Atlantic therefore is an isolated gulf in terms of amphipod invasion. This is apparently why so many strange taxonomic components occur in the marine Atlantic: blind or nearly blind groups, such as *Harpinia* and Haustoriidae which have had to come into the North Atlantic along a bathyal pathway; or various highly apomorphic and greatly filtered taxa which immigrated from the IndoPacific through the Red Sea-Suez-Mediterranean pathway (*Dexamine*) or hosts of filtered taxa moving eastward through the Panamanian isthmus and then northward (various *Ampelisca* and Phoxocephalidae). Virtually every endemic marine amphipod in the North Atlantic is the most highly apomorphic of its generic cluster, genus or family (for example, amphipods in the taxa *Harpinia*, Haustoriidae, *Phoxocephalus*, *Metaphoxus*, *Eriopisa*, *Melita*, *Dexamine*, genera of *Podoceridae*, Corophiidae). Apomorphy is youth.

For the most part in *Gammarus* and *Echinogammarus*, there is a coupling between high setosity and freshwater in contrast to low setosity and saltwater. This was especially noticeable to taxonomists in the recent past who distinguished *Chaetogammarus* from *Echinogammarus* by a formula of lowered setosity (Stock, 1968). For a short period, the definable *Chaetogammarus* was confined to the PontoCaspian basin, then quickly synonymized with the marine *Marinogammarus* but finally incorporated into the theretofore freshwater *Echinogammarus* on the lack of complete discontiguity in the setosity formulas. One could now propound the idea that *Echinogammarus* (as *Marinogammarus*) surrounded Europe and invaded the PontoCaspian basin during its marine or Tethyan phases. By an evolutionary cycle of increased setosity and broadening and lobation of article 2 on pereopod 7 (seen rudimentarily in *E. warpachowskyi*), *Echinogammarus* became the founder of the great fossorial Ponto-Gammarid Swarm. The theory follows from the idea that *Echinogammarus* (as *Marinogammarus*) invaded west European freshwaters also and formed the highly setose inhabitants of calcium-rich streams.

The distributional pattern described in the hypothesis under discussion is almost perfectly parsimonious. In our opinion, however, *Gammarus*, as we know it today, had a freshwater ancestry. Whether or not *Echinogammarus* was spawned in freshwater or dilute seawater cannot be determined as we are yet uncertain as to whether or not it is monophyletic or whether or not it may have had several ancestors in *Gammarus*. One crucial fact in the story is that some of the most rapaciously advancing migrants in freshwaters of PontoCaspian tributaries and highly successful humanly transplanted species are *Chaetogammarus sowinskyi* and *C. warpachowskyi* (Jazdzewsky, 1980). This suggests that certain species with lowered setosity are not correlated with salinity and that indeed setosity has a very complex function responding to many evolutionary stimuli. Almost all of the Pontogammarids actually living in the lake parts of the PontoCaspian Basin today are heavily setose fossorials. It is therefore no surprise that some of the river and stream species are of the *Chaetogammarus* morphology, as one cannot imagine fossorial amphipods finding much success upriver, except in slow, wide rivers with fine and stable bottom sediments. This is not to say that several fossorials have not also migrated far upstream (see "Human interference" in Index). The exercise here is to try to find evidence bearing on the origin of *Echinogammarus* and the Pontogammarids and more remotely on the freshwater history of *Gammarus*. Philosophers may argue for ages as to apomorphy or plesiomorphy of setosity; it is after all useful both to filtrative nestlers and fossorials.

Only 14 species of marine Gammaruses from northeastern America have been described, though others are known to be undescribed (Bousfield, 1969). Three of these belong to *Echinogammarus* and 11 to *Gammarus*.

Only 12 purely freshwater species of *Gammarus* have been described from North America (if *G. elki* and *G. breviramus* are synonyms of *G. minus*) (see Holsinger, 1972). Apparently a few other species from west Texas and New Mexico remain to be described. The most widely distributed species is the Holarctic *G. lacustris*, which spans the continent from 45* N to the Arctic and extends southward along the continental divide to 35* N, well into New Mexico, and west of the Rocky Mountains to 38* N, but is absent from the Pacific coastal mountain chain south of Canada. *Gammarus fasciatus* is widespread through the Great Lakes region and extends southward along the

Atlantic piedmont to the southern Carolinas. *Gammarus pseudolimnaeus* occurs through the Great Lakes region and St. Lawrence seaway region, then extends southward through the Mississippi river valley and spreads latitudinally from Kentucky to Oklahoma. *Gammarus minus* extends through the Appalachian Mountains westward through Kentucky and Tennessee and then in patches to western Arkansas and Missouri. The other eight species have distributions restricted to small areas. Except for *G. fasciatus*, the genus is absent in the part of the southeastern United States encroached by the Eocene Sea. *Gammarus fasciatus* occurs in parts of the small area between Chesapeake Bay and Long Island also encroached by the early sea.

This absence of freshwater *Gammarus* from southeastern USA coupled with the absence of *Stygobromus* (= *Stygonectes*, = *Apocrangonyx*), suggests that the region has never recovered faunistically from that incursion by marine waters. Apparently the more adaptable *Crangonyx* and *Synurella* captured the region after the Eocene. By comparing distributional maps in Holsinger (1972, 1974c), one may note the close fit of the modern distribution of *Synurella bifurca* and the *Crangonyx obliquus-richmondensis* complex to the old Eocene shoreline, the two species now occupying large parts of the old seabed in the Mississippi Valley region.

The taxonomy of species in *Gammarus* and *Echinogammarus* and indeed in many other Amphipodan genera is becoming very highly refined and subtle. To make a reliable identification requires the services of an expert who is well practiced in recognition of minor character states. Words often cannot convey the image of shape and proportion necessary to identify the material.

For example, two of the most common species of *Gammarus*, *G. pulex pulex* and *G. lacustris* differ in the following ways (stated for *lacustris*): (1) flagellum of antenna 2 slender, composed of unthickened articles; (2) dactyls of pereopods slender (very subtly); (3) antennae slightly shortened; (4) each tooth on epimera 2-3 slightly more extended and pointed.

Within *pulex* the following subspecies differ from *pulex pulex*, some in greater degree from *pulex pulex* than does *lacustris*:

G. pulex araurensis, setules on flagellum of antenna 2 reduced, segments of this flagellum not flattened.

G. pulex gallicus, flagellum of antenna 2 less swollen, less setose, urosomites somewhat elevated.

G. pulex polonensis, eyes absent (strong character), flagellum of antenna 2 poorly setiferous but calceoliferous; pereopods 3-4 with long curled setae; pereopods 5-7 with anterior setae unusually sparse.

There is no way to evaluate character combinations as to whether or not they stand at specific or subspecific level except by cross-breeding tests which are undertaken when consistently distinct demes are discovered or by geographic analysis. Cross breeding of *pulex* subspecies with parent *pulex* usually results in *pulex*-like offspring. Crossbreeding attempts with other true species results in failure, thus confirming the specific status. Subspecies have distinct and narrow geographic ranges and consistent morphology maintained by some kind of ecologic barrier, either geographic or chemical. To breed with a spawned subspecies the parent subspecies would have to cross dry land or cross chemically unsuitable waters.

Unfortunately, the experts who can identify species so readily from long experience and practice are busy researchers in pure science unwilling to forego the challenges of research to engage in technical services which would provide consistent identifications for nontaxonomists. These researchers move in and out of the field of study according to their scientific pursuits, so that an expert on *Gammarus* today may five years from now have largely abandoned the practice and expertise for some other genus, such as *Niphargus*, or some other area of biology. To maintain continuity and make science a replicable technology would require a supported laboratory where technicians trained by the passing experts can be supported eternally for the purpose of providing identifications. Of course, refinements will occur and must be assimilated as time goes by. Stagnation must be avoided. One would now expect our level of knowledge to have accreted sufficiently that an identification center could be supported for a wide array of organisms, among them many freshwater genera of amphipods. This, of course, would have to be a joint world effort.

The complexity of the expertise can be measured by the knowledge that G.S. Karaman and Pinkster (1977a) had to examine and fully identify 2800 samples of *G. pulex pulex* alone while in the process of untangling the taxonomy of the *pulex*-group. Ultimately, they found 34 valid species and subspecies in many additional samples throughout Palearctica but for which they found 25 additional names in the literature which had to be altered either by synonymization or transfer as subspecies from one umbrellar species to another. In this process they created, from 1971 to 1977, either together or separately (often with third authors), 19 new names (out of the 34 ultimately valid names). All of this was then brought together in the coauthored 1977 paper. This monumental effort required thousands of hours of intense, often tedious research, all of which became compressed into 97 large pages and 38 pages of figures. The simple act of assembling the samples from a host of sources would drown the average person. They had very little help from any technical assistants, because taxonomists these days cannot enlist such luxuries. The point to be made is that advances in this field of endeavor will depend on stability of funding over several decades.

Mediterranean-Tadzhikistan Filtrators

(*Sarothrogammarus* Group)

According to Stock (1971) the *Sarothrogammarus* group comprises 8 genera (3 since added) with affinities based on the occurrence of either semifossorial pereopod 3 ("interstitial" or "filtrative") or reduced uropod 1. The genera are *Rhipidogammarus*, *Longigammarus*, *Neogammarus*, *Comatogammarus*, *Sarothrogammarus*, *Pectenogammarus*, *Tadzhikistania* and *Lusigammarus*. The first 3 are characterized by a reduction in both size and spination of uropod 1 and all but *Neogammarus* have pereopod 3 specially setose in the male. Stock (1971:96) terms this a "modified" pereopod 3 which bears 10 or more transverse rows of long setae on the merus and carpus; this slightly exceeds the condition in several species of *Echinogammarus*, which have 9 or fewer and 6 or fewer on these articles respectively. Male gnathopod 1 is never larger than gnathopod 2 in the *Sarothrogammarus* group. Stock proceeds to include definitions of long setae on the propodus of pereopod 3 but we abandon that definition so as to include *Pectenogammarus* (1) in this complex; it lacks long setae on the propodus of pereopod 3 and unlike the other genera has heavily setose bases on pereopods 5-7, heavily setose coxae 1-4 and strong tufts of setae on the distal articles of pereopods 5-7. To some extent, *Pectenogammarus* resembles the Pontogammarids in the setation of article 2 on pereopods 5-7 but that article is not as strongly expanded as in the Pontogammarids nor is it posteroventrally lobate. *Pectenogammarus* occurs as far north and west as the British Isles.

Pereopod 3 of females is variable and pereopod 4 of both males and females is variable in this group of genera; some genera have pereopod 3 of the interstitial form in females and others do not; pereopod 4 reflects the form of pereopod 3 or not and occasionally is smaller than pereopod 3.

These variables plus the absence of the interstitial mode of pereopod 3 in *Neogammarus* make this a loosely interwoven group, perhaps of polyphyletic descent from the *Echinogammarus* group, and which G.S. Karaman and Ruffo (1977) heavily synonymize (see below). *Neogammarus* can be detected only by its reduced uropod 1 lacking dorsal ramal spines, which Karaman and Ruffo throw out as a generic character. The genera are divisible into 2 groups: (1) mountains of middle Asia, *Sarothrogammarus*, *Tadzhikistania*, and *Comatogammarus*; (2) Mediterranean and Lusitanean cobble-beach brackish water genera, *Neogammarus*, *Rhipidogammarus*, *Longigammarus*, *Pectenogammarus* and *Lusigammarus*.

An evolutionary deployment of the Sarothrogammarid group, based on reversing the key to the group in Appendix V would have ancestry in *Echinogammarus*. The first offshoot, *Sarothrogammarus* (6) differs only in the loss of pigment and the strongly filtrative form of male pereopod 3. The next two genera, *Tadzhikistania* (2) and *Lusigammarus* (2), differ in the loss of midpalmar spines on gnathopod 2 and the loss of apical telsonic setae; *Lusigammarus* differs from *Tadzhikistania* in the retention of a well developed article 2 on the outer ramus of uropod 3. *Pectenogammarus* (1) is simply an excessively setose *Echinogammarus*, especially on article 2 of pereopods 5-7. *Comatogammarus* (1) has pereopod 4, as well as 3, filtrative. *Rhipidogammarus*, *Neogammarus*, and *Longigammarus* have lost the dorsal spines on the rami of uropod 1. *Longigammarus* (1) diverges in the broadened plates of maxilla 2 and the maxilliped. *Neogammarus* (3) departs from *Rhipidogammarus* (3) in the complete loss of dorsal spination on the urosome. *Sarothrogammarus*, with 6 species, is the most diverse genus. All of its species occur in freshwater of the Afghanistanian and Turkestanian mountains in torrent streams at altitudes as high as 3000 m and in high springs and caves. Two similar species formerly in *Sarothrogammarus*, *Lusigammarus guernei* and *L. madeirensis*, occur in the Azores and Madeira and have a strongly excavate palm on gnathopod 2 lacking a midspine, in weak contrast to the other species and which we recognize at generic level by removing to *Lusigammarus*. The geographic disjunction is quite extreme between greater Turkestan and the Atlantic islands. The single species in the Azores has been found in stream torrents or a spring, the Madeiran species has been found in an environment we call the "seashore brackish cobble" habitat and in which most of the other western Sarothrogammarids are found. This is an apparent interstitial habitat in beach gravels and cobbles where emergent or offrunning freshwater is diluting the sea.

Another 2 species formerly placed in *Sarothrogammarus*, *S. shadini* Birstein and *S. ruffoi* G.S. Karaman were rejected from that genus by Stock

(1971:95). They have fewer than the appropriate number of setal rows on pereopod 3 but have normal uropod 1 and, therefore, lie somewhat closer to *Echinogammarus* (= *Chaetogammarus*) than they do to the *Sarothrogammarus* group. Nevertheless, they stand between the groups because they lack basal telsonic spines typical of the *Chaetogammarus* group, lack elongate setae on uropod 3, have a poorly spinose urosome and article 2 on the outer ramus of uropod 3 is severely reduced. The two species occur either in Tadzhikistan or Afghanistan respectively and may descend from the stock of Chaetogammaruses ancestral to the *Sarothrogammarus* group. They are here described as *Tadzhikistania*.

According to G.S. Karaman (1977a:118) and G.S. Karaman and Ruffo (1977:163) the *Sarothrogammarus* group is much less diverse generically than shown by Stock. Karaman synonymizes *Neogammarus*, *Pectenogammarus* and *Rhipidogammarus* with *Echinogammarus*. Karaman (1977a:figs. 1-2) shows that there is considerable variability in the size of uropod 1 in Neogammaruses and notes that *Echinogammarus catacumbae* G.S. Karaman and Ruffo (1977:176) has shortened uropod 1 intermediate between typical *Echinogammarus* and *Neogammarus*. He goes on to mention the variability in filtrative form of pereopods 3-4, in epimera, coxae, gnathopodal hands, and setosity of uropod 3 but our analysis of these characters shows that the mentioned distinctions continue to fit the species clusters formerly divided by Stock (1971). The major problem is *Echinogammarus catacumbae*, which indeed has a shortened uropod 1 and epimeral plates intermediate between the pointed kind of *Echinogammarus* and the rounded kind of *Neogammarus* or the weakly pointed kind of other Sarothrogammarids. However, *E. catacumbae* retains the normal dorsal spines on the rami of uropod 1 and the normal dorsal spinosity of the urosome typical of *Echinogammarus*. Actually, the epimera of *E. catacumbae* scarcely differ from those of the *E. foxi* group as indeed shown by G.S. Karaman (1977a:fig. 3) and that attribute is therefore a poor character in the *Echinogammarus* to *Neogammarus* sequence. We continue to separate *Neogammarus* and *Rhipidogammarus* from *Echinogammarus* on the absence of dorsal spines on the rami of uropod 1. There is no doubt that *Rhipidogammarus* intermediates *Echinogammarus* (strong dorsal spines of urosome) and *Neogammarus* (no dorsal spines on urosome) in the small and sparse spines of the urosome but again the condition is easily recognized and remains useful as a taxonomic character.

G.S. Karaman (1977a:112) removes the Lusitanean members of *Sarothrogammarus* from that Asiatic genus and returns them to *Echinogammarus*. Instead, we prefer to describe a new genus, *Lusigammarus*, to recognize this group for the absence of palmar spines on male gnathopod 2, the absence of apical setae (but retention of spines) on the telson and to distinguish the genus from *Echinogammarus* on the achromatic condition and lack of dimorphic sexual characters.

Pectenogammarus continues to be distinguished from *Echinogammarus* on the same achromatism and sexual monomorphism plus the strong setosity of pereopods 5-7 and the presence of strong setae on the peduncle of uropod 1. Karaman (1977c:73) justifiably calls this genus a simple variant of setal density but we believe the odd cobble-brackish environment it lives in signals caution on such evaluation.

Karaman and Ruffo (1977:165) continue to maintain *Longigammarus* on the unusual breadth of the plates on maxilla 2.

The disjunction in the distribution of this group between eastern Adriatic shores and Afghanistan is extreme but may be filled in with further exploration. The adaptability of the group is well expressed by Rhipidogammarus rhipidiophorus, which is widespread on the seashores of the western Mediterranean in marine cobbles, wells, ponds, springs and grottos to altitudes of 100 m and as far as 130 km inland in Tunisia, fitting the ancient marine incursions shown by Thienemann (1950).

The present distribution of the group suggests it might be a relict from Lac Mer or the Pontian Sea and that its continuity was severely disrupted by the drying of the Mediterranean 7 million years ago (Hsu, 1972). The seaside refuge would have been the eastern Atlantic outside Gibraltar but the group is so weak that it appears to have been maintained in the narrower and warmer confines of the eastern Atlantic, only one species having penetrated as far north as the British Isles. In contradistinction, the strength of the group is reflected by its occurrence in the oceanic Lusitanian islands. This disjunction might be explained as marking the remnants of continental drift or alternatively the success of rafting. The Sarothrogammarid group has undoubted biogeographic importance because so many unanswered questions can be asked about the group. The puzzles are manifold and should form a strong focus for functional biologists to help unravel. One might suggest that the group began a Miocene radiation that was truncated by drying of the Mediterranean and concomitant radiation by Pontogammarids. Subsequent drying and disjunction of the Pontian Sea left remnants of the group in the open eastern Atlantic and in the orogenic zone east of Lac Mer. Evolutionary stagnation occurred. Why did the group fail to survive in the deltas of the Black Sea and Caspian Sea? The group is anchialine-adapted but not marine adapted and thereore cannot radiate in the sea. The group is interstitially adapted but, apparently, is very marginal because it has not moved into those habitats where Niphargids and Crangonyctids dominate. Its apparent morphological ancestors, the Echinogammarids, remain in possession of any other possible habitats. If it is a relict group, it also has the Neogenic aspect of a group pressing farther into the interstitial habitat; but it has not yet attained the ability to survive in anoculate form. The group, therefore, remains in a category with a low level of biocompetition squeezed into the interstitial brackish anchialine habitat or in the orogenic frontier far removed from the mainstream of the Niphargid radiation.

Ultimately the Sarothrogammarids are such a weak cluster that they could never be segregated even at subfamily or supergeneric level. They clearly have their roots in Echinogammarus or similar ancestors and probably one or more genera are polyphyletic. Lumpers will clearly want to put most of these genera together and lessen the remarkable geographic disjuncion by attributing the morphological adaptations at geographic extremes to coincidence or parallel evolution. They will point to the apparent "edge" effect, the confinement of the Sarothrogammarids to the outer margins of the Echinogammarid distribution. We tend also to this viewpoint and hold the Sarothrogammarids together only to alert functional biologists to the many interesting aspects of the group.

The Metohiids

At least 7 genera outside of Baikal, *Tadzocrangonyx*, *Metohia*, *Accubogammarus*, *Zenkevitchia*, *Anopogammarus*, *Fontogammarus* and *Ilvanella* belong to this special group of apparently interstitial blind Gammarids. *Typhlogammarus* is excluded but discussed in the context of the group. The 7 genera are characterized by the homogeneity of the bases of pereopods 5-7 on which article 2 is weakly expanded, bears a softly angular but projecting posteroventral lobe, and has a posterior setosity of intermediate grade. Setae on the anterior coxae also occur, for the most part, in an intermediate grade between setose and glabrous. Apparently all species occur interstitially. Owing to the almost fully parviramous uropod 3 and similarities in almost all other characters, one may hypothesize that this group had its origins in the *Echinogammarus-Chaetogammarus* group. *Metohia*, *Anopogammarus* and *Accubogammarus* retain rather well developed *Gammarus* gnathopods with midpalmar spine but *Ilvanella* and *Zenkevitchia* have less oblique palms lacking midspines, and *Tadzocrangonyx* has oblique palms without midspines. The condition in *Fontogammarus* is unknown. *Accubogammarus* maintains reasonably well developed facial setae on the bases of pereopods 5-7, *Metohia* has these reduced to single setules and they are apparently absent in *Ilvanella*, *Zenkevitchia*, and the others.

Metohia (1), from caves in Yugoslavia, appears to be the most primitive of the group because of its almost normal spination of maxilla 1, plesiomorphic uropod 3, relatively ordinary cephalic lobes, and fully developed urosomal spination, although pereopodal setation has decreased. *Accubogammarus* (1), also from a cave in Yugoslavia, and the type-species of *Anopogammarus* from Transcaucasus, has the projecting cephalic lobe typical of *Zenkevitchia* but has more primitive pereopods 3-7 than does *Metohia*. *Accubogammarus* lacks article 2 on the outer ramus of uropod 3 in contrast to *Anopogammarus*. *Fontogammarus*, with 2 stream subspecies in Dalmatia, differs from *Accubogammarus* and *Tadzocrangonyx* simply in the blade-like (not pectinate) lateral spines on the outer plate of maxilla 1. *Tadzocrangonyx* (2) from Tadzhikistan and the Tjan-Shan, is probably the least specialized of the subgroup, characterized by symmetrical maxillary palps, in that the outer plate of maxilla 1 bears the normal numbers and shapes of spines and uropod 3 is not reduced.

In summary of morphology the least specialized taxon appears to be *Metohia* because of primitive uropod 3, then *Ilvanella* with parviramous uropod 3, then *Tadzocrangonyx* because of primitive maxilla 1 (but uropod 3, inner ramus is apomorphic), then *Accubogammarus* (shortened uropod 3 but more or less normal maxilla 2), then *Anopogammarus* (more or less normal maxilla 1 but palps asymmetrical, uropod 3 elongate but parviramous), then *Fontogammarus* with slightly modified outer spines on maxilla 1, then the divergent *Typhlogammarus* with greatly modified coxae and gnathopods and finally *Zenkvitchia* with immensely modified maxilla 1.

The type-species of *Zenkevitchia*, *Z. admirabilis*, bears an immensely developed outer plate of maxilla 1, similar to that of *Niphargopsis*, on which are set numerous finely serrate spines forming a raker comb. This kind of maxilla 1 has also been found by Holsinger and Longley (1980:17) on *Texiweckelia* from a well in Texas and by Cole and Watkins (1977:175) on a new species of *Hyalella* from a well in Arizona. Its incipient state is signaled in *Accubogammarus* and *Anopogammarus*, where the normal 11 spines are much more finely serrate than in other Gammarids. The second species, *Zenkevitchia revasi*, was transferred to *Anopogammarus* by Karaman and Barnard (1979) so as to magnify the importance of that raker comb as a generic character.

Zenkevitchia admirabilis, from caves in Abkhazia, is also the most specialized of the group in lateral cephalic lobe, relative loss of dorsal urosomal setation (but maintenance of posterior dorsal setal tufts on the pleosome), loss of facial setae on pereopods 5-7 and probably in the gnathopods which, though from a female, are very small and have almost transverse palms. Its companion species, *Anopogammarus revasi*, from a cave in West Georgia, USSR, retains well developed male gnathopods, although gnathopod 1 is palpably smaller than gnathopod 2 and lacks the midpalmar spine, gnathopod 2 retaining that spine. The spines on the outer plate are finely serrate as in *Accubogammarus*. *Ilvanella*, from interstitial waters of a stream on Elba Island, has essentially normal maxilla 1 with coarsely serrate spines. Male gnathopod 1 is divergent from Gammarids in the weaker slope of the palm lacking a middle spine and in its tendency to be much smaller than gnathopod 2, which also lacks the fully set midspine. However, the lateral cephalic lobe projects well, though not as strongly as in *Zenkevitchia*. Dorsal urosomal spines are poorly developed as in all taxa except *Metohia*. Males of both *Metohia* and *Ilvanella* retain basal or lateral telsonic spines, though in *Ilvanella* they have migrated rather distad.

At present, the evolutionary flow of this group appears centered on the western side of the Dinaric Alps with a line towards the Transcaucasus and another westward towards western Italy (Elba). Undoubtedly much more information will result from increased exploration of interstitial habitats. Apparently the group must have a slightly different habitat from that of Niphargids, because in the vast explorations for that group rather few Metohiids have been captured. *Tadzocrangonyx* is so far away in Tadzhikistan that it could be considered to have an origin from Echinogammarus ancestors separate from the western Metohiids.

Typhlogammarus (1) from Yugoslavian caves has been compared by G.S. Karaman (1974b:43) to *Metohia* and *Accubogammarus*. The strongest resemblance occurs in the fine serrations on the spines of the first maxillae and there is a weak resemblance of the coxae between *Typhlogammarus* and *Accubogammarus*. *Typhlogammarus* otherwise is very distinctive in its normally shaped *Gammarus*-like pereopods 5-7 with narrow second articles bearing sinuous posterior margins and lacking expansion ventrally. The gnathopods of *Typhlogammarus* are strongly Acanthogammarid in character, gnathopod 1 being slightly smaller than gnathopod 2 but of similar enlarged condition bearing undefined oblique raptorial palms and short wrists with faint posterior lobes. This is admittedly somewhat transcended by the gnathopods in *Accubogammarus*, yet known only for the female. The two genera also share the short telson atypical of *Metohia*. Pereopods 5-7 in *Typhlogammarus* are supplied with tuftlets of posterior setae on article 2. *Typhlogammarus* has about as many similarities as it does significant differences from the *Metohia* group and must be evaluated as a Metohiid only by suppressing the importance of its prehensile adaptations that so closely resemble the *Acanthogammarus*-*Issykogammarus* cluster.

PontoCaspian Basin

Taxonomy (see temporary key to follow)

The PontoCaspian Gammaroids comprise 33 genera and 77 species (Table 10). Besides these, eight species of *Corophium*, two species of *Pseudalibrotus* (=*Onisimus*), one species of *Caspicola* (=*Caspiella*), and one of *Pontoporeia* represent the non-Gammaroids directly in the Caspian Sea itself. One species each of *Gammaracanthus* and *Gammarellus*, though Gammaroids, are considered as aliens. *Corophium* is a world-wide marine genus with the propensity to enter non-marine habitats, not only because some species are euryhaline but because some have a low level of biocompetition in the fully marine biome. *Onisimus* is an arctic genus of low diversity and mainly confined to habitats with a degree of dilution. As a marginal Gammaroid, *Pontoporeia* has only 3 species, all of which are associated with diluted waters and one of which is widely spread in glacial lakes of northern Eurasia. The population in the Caspian Sea is considered to be a subspecies of *P. affinis*. *Caspicola* is a unique Caspian Sea endemic of unknown origin, though it has features of Stenothoidae and Nihotungidae.

In the Caspian Sea 28 genera and 60 species comprise the main Gammaroid facies. *Axelboeckia* and *Gammaracanthus* (a genus not called PontoCaspian) have direct relationship to Baikalian taxa and may have entered the PontoCaspian basin during the widespread freshwater period of Lac Mer; *Gammaracanthus*, however, and *Gammarellus* of the Black Sea, also occur in the Arctic marine waters, are euryhaline, and may have arrived in PontoCaspian waters via a marine Arctic connection.

Axelboeckia is of special interest because the 3 species of Lake Baikal formerly placed in that genus belong to *Boeckaxelia* but this was overlooked by Bazikalova (1945) and J.L. Barnard (1958c). *Axelboeckia*, therefore, is a monotypic genus endemic to the Caspian Sea. *Axelboeckia* differs from *Boeckaxelia* in the reduced gnathopods of non-Acanthogammarid form, in the large anteroventral cephalic cusp, the vestigial accessory flagellum, the reduced inner ramus of uropod 3 and the distinctive body ornaments combining the features of *Carinurus* and *Coniurus*. On a numerical comparison of character similarities, *Axelboeckia* appears as close to *Brandtia* as to any other Baikalian genus but again is so remote that no line of descent can be presumed. One of the features of *Axelboeckia* is the close approach of antenna 1 to the *Pontogammarus* condition and in other respects, especially the gnathopods, *Axelboeckia* appears close to *Amathillina*, but ultimately is allied to *Gmelinopsis*.

The Caspian Sea Gammaroids, those which are believed to have evolved and selected within the basin, are divisible into the following groups:

Antenna 1 of *Gammarus* form
Article 2 of pereopod 7 not expanded
Accessory flagellum well developed. . . *Echinogammarus*-group
Accessory flagellum 1-articulate. . . . .*Gmelina*-group
Article 2 of pereopod 7 expanded, usually lobate. . . . . .
. . . . *Dikerogammarus*-group
Antenna 1 of *Pontogammarus* form (article 2 of pereopod 7 usually lobate)

One of mouthparts simplified. . . . .
. . . .(polyphyletic) Cardiophilus-group
Mouthparts ordinary
Primary flagellum of antenna 1 elongate. .Pontogammarus-group
Primary flagellum of antenna 1 short...Compactogammarus-group

Key to Gammaridan Genera in PontoCaspian Basin

[Alternative Key in Karaman & Barnard, 1979]

1. Gnathopods chelate (not gammarid). . . . . .Caspicola
Gnathopods subchelate or simple. 2
2. Telson entire or poorly cleft. 3
Telson cleft 4
3. Gnathopods of Eusirid form, telson long and cleft. . . . . Gammaracanthus
Gnathopods of ordinary form, telson short and emarginate . . . . .Gammarellus
4. Article 2 of pereopod 7 unlobate 5
Article 2 of pereopod 7 lobate 13
5. Article 3 of antenna 2 keeled ventrally. . . . . . . .Derzhavinella
Article 3 of antenna 2 unkeeled ventrally. 6
6. Article 3 of antenna 1 as long as or longer than article 1 or article 2. . . . . Sowinskya
Article 3 of antenna 1 much shorter than articles 1 and 2. 7
7. Accessory flagellum 2+ articulate. . . . . Echinogammarus
Accessory flagellum 1-articulate 8
8. Uropod 3 magniramous 9
Uropod 3 parviramous 10
9. Pereonal pleura smooth . . . . Andrussovia†
Pereonal pleura humped . . . . Praegmelina†
10. Body unkeeled. . . . . .Yogmelina
Body keeled or knobbed 11
11. Body with carination only medial, head lacking wing tooth . . . . Gmelina
Body with lateral teeth (median teeth present or absent), head with wing tooth (sometimes weak) 12
12. Body humps in bilateral dorsal lines, head tooth vestigial . . . . Kuzmelina
Body humps both bilateral and median, head tooth giant . . . . .Axelboeckia
13. Body keeled anterior to urosome. 14
Body unkeeled anterior to urosome. 15
14. Gnathopod 1 enlarged strongly. . . . . .Gmelinopsis
Gnathopod 1 not greatly enlarged (minutely). . . . . . . .Amathillina
15. Gnathopod 1 enlarged 16
Gnathopod 1 not enlarged 18
16. Pereopods 3-7 prehensile . . . . .Iphigenella
Pereopods 3-7 simple 17

17. Female gnathopod 2 large, antennae short, epimeron 3 with strong tooth . . . . *Baku*
Female gnathopod 2 small, antennae long, epimeron 3 with weak tooth . . . . *Lanceogammarus*
18. Urosome with dorsal knobs. 19
Urosome without knobs. 22
19. Pereopod 6 elongate . . . .*Pontoporeia*
Pereopod 6 not elongate. 20
20. Coxae 1-4 and article 2 of pereopod 7 strongly setose. . . . .*Turcogammarus*
Coxae 1-4 and article 2 of pereopod 7 poorly setose or glabrous.. 21
21. Head ordinary. . . . . *Dikerogammarus*
Head giant . . . .*Cephalogammarus*
22. Antenna 1 of *Gammarus* form, article 2 more than half as long as article 1 23
Antenna 1 of *Pontogammarus* form, article 2 half or less as long as article 1 25
23. Accessory flagellum 1-articulate . . . . *Jugogammarus*
Accessory flagellum 2+ articulate. 24
24. Article 2 of pereopod 6 lobate . . . .*Shablogammarus**
Article 2 of pereopod 6 not lobate . . . .*Akerogammarus*

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*and see *Stenogammarus macrurus* of Carausu, 1943

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25. Article 2 of pereopods 5-7 alike, mouthparts with reduced or aberrant morphology (either dactyl of maxilliped reduced or setae of maxillae inner plates reduced or palp articles 1-2 of maxilla 1 equal in length) 26
Article 2 of pereopods 5-7 diverse, maxillae strongly setose medially and all other mouthparts ordinary 28
26. Article 2 of pereopods 5-7 narrow and scarcely lobate, coxa 4 poorly lobate. . . . . *Cardiophilus*
Article 2 of pereopods 5-7 broadly lobate, coxa 4 lobate 27
27. Article 2 of pereopods 5-7 hatchet-shaped, coxa 1 not expanded distally . . . . *Behningiella*
Article 2 of pereopods 5-7 ovate, coxa 1 expanded distally . . . . *Zernovia*
28. Primary flagellum of antenna 1 about as long as peduncle, accessory flagellum shorter than half of primary flagellum. . 29
Primary flagellum of antenna 1 much shorter than peduncle (almost always shorter than article 1 of peduncle), accessory flagellum longer than half of primary flagellum . . 33
29. Coxa 4 with lobe vestigial . . . . *Pandorites*
Coxa 4 strongly lobate 30
30. Article 2 on outer ramus of uropod 3 "elongate" (15+ percent of article 1), first 2 flagellar articles of antenna 2 together more than 95 percent as long as article 5 of peduncle . . . .*Stenogammarus*
Article 2 on outer ramus of uropod 3 short (less than 12 percent of article 1), first 2 flagellar articles of antenna 2 together less than 80 percent as long as article 5 of peduncle 31

31. Posterior setae on article 4 of pereopod 4 divided into groups. . . . .*Obesogammarus*
    Posterior setae on article 4 of pereopod 4 in continuous fan . . 32
32. Inner ramus of uropod 3 about half as long as outer ramus . . . .*Euxinia*
    Inner ramus of uropod 3 about one third as long as outer ramus . . . .*Pontogammarus*
33. Epimeron 3 with posteroventral fan of setae on face. 34
    Epimeron 3 without setal fan on face 36
34. Inner ramus of uropod 3 more than half as long as outer ramus . . . . *Uroniphargoides*
    Inner ramus of uropod 3 about one third as long as outer ramus . 35
35. Mandibular palp with D-setae, article 2 of pereopod 5 unlobed . . . . *Niphargoides*
    Mandibular palp without D-setae, article 2 of pereopod 5 with posteroventral lobe. . . . . *Compactogammarus*
36. Mandibular palp lacking D-setae, article 2 on outer ramus of uropod 3 elongate, articles 4-5 of antenna 2 each about as long as article 3 (scarcely longer) . . . . *Niphargogammarus*
    Mandibular palp with D-setae, article 2 on outer ramus of uropod 3 not elongate, articles 4-5 of antenna 2 significantly longer than article 3 . . . . . *Paraniphargoides*

Echinogammarids

The first group of this section is limited to *Echinogammarus* (=*Chaetogammarus*), *Sowinskya*, and the satellite, *Derzhavinella*. The primitive gnathopodal state resembles that of the *Gammarus* group, in which gnathopod 1 is weakly dominant or at least not dominated by gnathopod 2 and in which palmar spines are present; the palmar slope is greater on gnathopod 2. The bases of pereopods 5-7 are unexpanded and therefore *Gammarus*-like.

Probably the most primitive genus of this subdominant Caspian group is *Echinogammarus*, which is represented by 5 marine species of the *Chaetogammarus* (as *Marinogammarus*) facies whose other members are distributed along the shores of Eurasia: *finmarchicus*, *pirloti*, *marinus* and *olivii*, etc.

At one time *Chaetogammarus* and *Echinogammarus* were construed to be sibling genera, the latter genus not being represented in the Caspian Sea but being widely distributed throughout freshwaters of Europe. As defined by Stock (1968) (but reversed in connotation for our purpose here), *Chaetogammarus* differed from *Echinogammarus* mainly in the shorter or fewer setae on one of the following parts: dorsal urosome, coxae 1-4, ventral epimera, and posterior pereopods, especially on article 2 of pereopod 7. The greater diversity and wider distribution of *Echinogammarus* would suggest that it is the founder genus and that *Chaetogammarus* is the derived genus. This would appear to correlate with the general scheme that simplification is the evolutionary direction in Amphipods but, in this case, one may argue the opposite by examining the biogeographic and ecologic data. The poorly setose *Chaetogammarus* is dominantly Caspian (ignoring the marine species) but can be construed, by proximity, to be the ancestral stock of the *Dikerogammarus* group, characterizd by increased width of article 2 on pereopod 7. In the derivative *Pontogammarus* and *Compactogammarus* groups an increase in setation of pereopods occurs. This increase is also seen in the groups supposed to be derived from *Echinogammarus* stock, for example the non-Caspian *Sarothrogammarus* group. Hence the *Chaetogammarus* group of species appears to represent a stock ancestral to the PontoCaspian fossorial groups and to the *Echinogammarus-Sarothrogammarus* group, some of which have semifossorial or filtrative adaptations.

Birstein and Romanova (1968) synonymized *Sowinskya* with *Chaetogammarus*, but the unique type-species, *S. macrocera*, differs markedly in the elongation of article 3 on antenna 1 and should be segregated from *Chaetogammarus*. The bases of pereopods 5-7 are especially thin.

The final but enigmatic genus of the Echinogammarids is *Derzhavinella* (1). The bases of pereopods 5-7 are thin, the gnathopods are large, with gnathopod 2 extremely enlarged and dominant, antenna 2 is thick, heavily setose, and article 3 is especially large and bears a stout ventral tooth. The inner ramus of uropod 3 is not fully parviramous as it is somewhat elongate and has a strong brush of apical and subapical setae; of course, uropod 3 overall is reduced so that the largeness of the inner ramus is also a function of the reduction in the outer ramus. The telson has brushes of long apical setae. The presence of strong defining spines on the gnathopods and the presence of a palmar spine on gnathopod 2, albeit very close to the dactylar hinge, suggest that this genus has its origins close to the Gammarid (*Chaetogammarus*) stock. It would branch away at a level ancestral to *Dikerogammarus*. It has diverged very strongly in the shortness and weak lobation of the gnathopodal wrists and has faint resemblance to Acanthogammarids.

A pelagic predatory fossil genus, *Hellenis*† has been found in PontoCaspian Miocene sediments. It has some of the mysidiform character of the Baikalian *Macrohectopus* but the coxae are obsolescent and the pleosome is neither greatly enlarged nor bears a tooth. It is not a fossorial genus so must be isolated at this position before the narrative launches into the PontoCaspian fossorials.

Gmelinids

The *Gmelina* group is composed strictly of taxa marked by the reduction of the accessory flagellum to one article: *Andrussovia*†, *Praegmelina*†, *Yogmelina*, *Gmelina*, *Kuzmelina* and *Axelboeckia*, all of which also lack fossorial adaptation on pereopod 7 but which have broad connections outward both from *Gammarus* or *Echinogammarus* and from fossorial taxa such as *Amathillina* and *Gmelinopsis*. Because so many similarities in body form, teeth, and head tooth are widely mixed, it is difficult to determine whether or not the *Gmelina* group is retrogressive. Although the evolutionary diagram (Graph 5) shows some connection between *Echinogammarus* and *Yogmelina*, we hypothesize that an evolutionary flow might have come from *Amathillina* across to *Gmelina*, and then through loss of body teeth, into the neotenic *Yogmelina* but this requires the loss of fossorial adaptation on pereopod 7 rather immediately. Another pathway for *Axelboeckia* could come from *Echinogammarus* through fossorialized *Akerogammarus* and the *Baku* group, in which gnathopod 1 is enlarged. *Axelboeckia* retains this enlargement in neotenic form.

These conclusions are based only on living taxa, whereas Derzhavin (1927a:187) has shown that a fossil ancestral form of *Gmelina* is easily conceived in *Praegmelina*† which, remarkably, is said to have magniramous uropod 3. Two well preserved but imprinted species of *Praegmelina*† occur in Upper Sarmatian marly clay rich in organic matter. The magniramous uropod 3 presumably requires *Praegmelina*† (and its companion genus *Andrussovia*†) to be shifted backward to a position on the plesiomorphic side of *Echinogammarus*. This indicates that the two fossil genera lie much closer to *Gammarus* and various magniramous genera of Baikal than does *Echinogammarus*. The remarkable similarity in many characters of *Praegmelina*† and the modern *Gmelina*, *Kuzmelina* and *Yogmelina* suggests an origin of this group independent of *Echinogammarus*.

Derzhavin (1927a:190) also suggests that *Andrussovia*†, with 2 distinctive species, may be ancestral to *Amathillina* but the connection is not quite as good as in the other case because *Amathillina* has a well developed accessory flagellum and therefore cannot be directly descendent from *Andrussovia*†. The two genera could however, have a common ancestor. *Amathillina* has the broadly expanded and lobate article 2 of pereopod 7, and parviramous uropod 3, unlike *Andrussovia*†, so that Derzhavin's presumption is probably based greatly on body shape and dorsal cuspidation rather than on antennal, pereopodal and uropodal similarities. *Amathillina* is therefore much more remote from *Andrussovia*† than *Gmelina* is from *Praegmelina*†, and indeed we would put *Praegmelina*† and *Andrussovia*† very close together, and antecedent to the Gmelinas and the Amathillinas.

Yogmelina, *Gmelina*, *Kuzmelina* and *Axelboeckia* are arranged in the PontoCaspian key (above) in order of increasing ornamental complexity. *Yogmelina* (5) is ornamentally simple, whereas *Gmelina* (2) has medial body carinations, *Kuzmelina* (1) has body humps in bilateral dorsal lines and bears a vestigial cephalic tooth, while finally, *Axelboeckia* (1) has both bilateral and median body humps plus a large cephalic tooth.

Two other genera, *Amathillina* (5) and *Gmelinopsis*, (2) are placed in the *Gmelina* group which again demonstrates the multiple evolutionary pathways in Gammaroids. Those two genera have article 2 of pereopod 7 distinctly lobate as in the Dikerogammarids and in this discussion are appended to that group but clearly they have ornamental affinities to the Gmelinids. They have either dorsal body cuspidation or cephalic teeth. They demonstrate the high probability that lobation of article 2 on pereopod 7 has occurred more than once and therefore is not a monophyletic basis for a general Pontogammarid family.

Dikerogammarids

The next descendent group is named for *Dikerogammarus* and contains species with *Gammarus*-like antenna 1 combined with expanded and lobate article 2 of pereopod 7, but the accessory flagellum is multiarticulate. Because gnathopodal dominance is ignored, genera such as *Baku* and *Lanceogammarus* are included in the group. Otherwise, gnathopods decrease in their Gammarid appearance by loss of palmar spination and humps though they are better represented as truly Gammarid in the *Pontogammarus* group than they are in some of those genera with normal antenna 1. Several of the genera actually have gnathopods of great similarity to the Baikalian Acanthogammarid kind with shortened and lobate article 5, and unspecialized palms.

The typical Caspian genus is *Dikerogammarus* (8) bearing the fully broadened article 2 of pereopod 7 and characteristic urosomal knobs. *Dikerogammarus* is also known from the Black Sea and Azov Sea and penetrates into rivers and lakes in the AraloPontian basin. *Turcogammarus*, represented by 2 exotic species in the mountains of Greece and TurkoCaucasus, also bears urosomal knobs but the two species are far more setose on the anterior coxae than are species of *Dikerogammarus* and have antenna 1 somewhat reduced as in the *Pontogammarus* mode. A third probable species lives in the Aral Sea. A side issue is *Cephalogammarus* (1), which is simply a *Dikerogammarus* with enlarged head.

Dikerogammarus retains the normal *Gammarus*-like antenna 1 but differs from (*Chaetogammarus*) in the loss of dominance or equality in gnathopod 1, which becomes smaller than gnathopod 2 and loses the palmar spination typical of (*Chaetogammarus*). An intermediate stage is actually seen in (*Chaetogammarus*) *warpachowskyi*, which maintains the *Gammarus* gnathopods but has article 2 of pereopod 7 broadened. That species may need removal to a new subgenus intermediate between *Echinogammarus* and *Dikerogammarus*. The next stage is formed by *Akerogammarus* (3) including *subnudus*, formerly in *Shablogammarus*, in which the antennae become shorter and article 2 of antenna 1 becomes shorter. In one evolutionary direction this leads to *Shablogammarus*, a monotypic genus, of Lac Sabla (in anchialine position to the Black Sea), on which article 2 of all pereopods 5-7 becomes expanded.

We maintain the distinction between *Shablogammarus* and *Akerogammarus* (3) the latter with article 2 of pereopod 6 unexpanded. *Shablogammarus* thus becomes restricted to one species inhabiting Lac Sabla. Though *Shablogammarus* is not of Caspian occurrence, it appears to be in ancestral position to the unusual *Zernovia* and *Behningiella* characterized by homogeneous and expanded bases of pereopods 5-7.

In another evolutionary direction, *Akerogammarus* leads to *Jugogammarus* (1), which is a middle Danube species characterized by reduction of the accessory flagellum to 1 article. *Jugogammarus* joins *Turcogammarus* as the only other PontoCaspian genus not directly connected to, adjoining or living in the basins themselves.

Like *Iphigenella*, the old *Pontogammarus* *paradoxus* is an exceptional Caspian Pontogammarid in the dominance of gnathopod 1. It is relegated to *Baku* and because of antenna 1, is put into the Dikerogammarids. Stock (1974c:83) notes the close similarity of this species to the Baikalian *Pachyschesis*. Whereas dominance by gnathopod 2 is the prevailing trend in the Caspian genera, dominance by gnathopod 1 prevails in non-Acanthogammarid Baikalian genera. Despite the odd gnathopods of *B. paradoxa*, the further affinities appear to lie close to *Stenogammarus* in the Caspian Sea. The diversity of article 2 on pereopods 5-6 resembles that of *Stenogammarus* but is contrasted to *Pachyschesis* and *Shablogammarus* where article 2 of pereopods 5-7 is identical. The Stenogammarid antenna 2 is well developed in *B. paradoxus* and *Stenogammarus*, but *Pachyschesis* appears to have a normal antenna 2, or only weakly Stenogammarid. *Pachyschesis* is characterized by weakly prehensile pereopods 3-7. Both *B.*

paradoxa and *Stenogammarus* have ventrally lobate article 2 on pereopod 7 in contrast to *Pachyschesis*.

Baku paradoxa differs from *Stenogammarus* in the dominance of gnathopod 1, the unusually short wrists on both gnathopods and the shortness of article 2 on the outer ramus of uropod 3. The maxillipedal dactyl is not described, so that only the thinness of body in *B. paradoxa* may give some indication of affinity to the *Cardiophilus*-*Behningiella* group.

The occurrence of *Lanceogammarus* (1), another Caspian genus with Baikalian gnathopods, in Caspian waters suggests (apart from faunal mixture) that dominance by gnathopod 1 in Baikalian genera is an adaptive feature of polyphyletic background rather than a mark of homology and that *Pachyschesis* could therefore have direct affinity to the Caspian Cardiophilids. *Lanceogammarus* differs from *Baku* in the unenlarged female gnathopod 2.

Iphigenella completes the triad of genera with enlarged gnathopod 1. *Iphigenella* is unique in the group for the prehensile pereopods. The single species is a commensal on Decapoda in the Caspian and Black Seas and their tributaries, especially on the crayfish, *Astacus leptodactylus*.

Pontogammarids

In another evolutionary deployment, *Akerogammarus* and *Turcogammarus* appear to bridge *Dikerogammarus* and the greater *Pontogammarus* group, whose least specialized member is *Pandorites*, which lacks the fully setose condition of pereopod 7 and the epimera. Genera with fully fossorial antenna 1 are the *Pontogammarus* kind in which articles 2-3 are considerably shortened and articles 1-2 are often strongly setose on the ventral margin. Antenna 1 becomes dominated by article 1, the flagella are shortened but the accessory flagellum remains less than half as long as the primary flagellum. One or more species of *Obesogammarus* are somewhat intermediate in this development. Five genera, *Obesogammarus*, *Euxinia*, *Pandorites*, *Pontogammarus* and *Stenogammarus* form the *Pontogammarus* group. *Pandorites* (1) splits away to form a branch in which coxa 4 is shortened and mostly excavate posteriorly, whereas *Obesogammarus* (6) and *Pontogammarus* (3) have a normal coxa 4 with the excavation and posterior margin distinct in equal degree. *Pontogammarus* differs from *Obesogammarus* by the coalescence of all posterior setae on article 4 of pereopods 3-4 into a single even row, whereas *Obesogammarus* has the ordinary and primitive condition of setal tufts. These genera also are characterized by facial tufts of setae on the bases of pereopods 5-7, in contrast to *Pandorites*.

The genus *Euxinia*, accidentally conceived by Tucolesco (1933) who apparently was not aware of *Pontogammarus*, is now revived by G.S. Karaman and Barnard (1979:125) because the small difference in length of the inner ramus on uropod 3 must be honored if the whole Gammarid classification system is to maintain its integrity. *Euxinia* (3) retains the more plesiomorphic longer inner ramus in contrast to the parviramous *Pontogammarus*.

Stenogammarus (7) belongs to the *Pontogammarus* group but antenna 2 is heavily modified so that article 5 of the peduncle is difficult to pick out rapidly as it is somewhat intermediate in size between article 4 of the peduncle and article 1 of the flagellum. Karaman and Barnard (1979:119) find this much less workable as a generic character than did Stock

(1974c:85) but they maintain Stenogammarus mostly on the elongate article 2 of the outer ramus on uropod 3.

Overlapping and convergence are strong in this scheme, so that opinions may vary as to the classification of certain species.

Stenogammarus is divisible into two subgenera, the second subgenus (Wolgagammarus) (one species) being distinguished from the nominate subgenus in the presence of lateral plumose setae on uropod 3 and the elongate wrist of gnathopod 2. (Wolgagammarus) lives in lakes along the Volga River.

Compactogammarids

This "Niphargoides" group created by Stock (1974:77,81) has antenna 1 much more reduced, so that the peduncle is much more dominant, the primary flagellum much shorter than in Pontogammarids and the accessory flagellum is longer than half the primary flagellum. Stock (1974c:77) terms this a "Niphargoides antenna 1" but we prefer to rename it "Compactogammarus antenna 1" to avoid confusion with various non-Pontian genera with similar nomenclatural roots (Niphargus, Niphargellus, etc.). Compactogammarus, Niphargogammarus and Uroniphargoides differ from Niphargoides and Paraniphargoides in the reduction or loss of D setae on the mandibular palp. Niphargoides (3) appears to be one of the primitive genera of this group but Paraniphargoides (3) obviously has diverged from the hypothetical ancestor because of vestigial dactyls on the pereopods. Niphargoides has a setal fan on epimeron 3. Both genera have the Stenogammarid antenna 2, whereas the other 3 genera of the Compactogammarus group have the "normal" Pontogammarid antenna 2. Niphargogammarus (4 species, 3 in Caspian) forms a branch in which article 2 on the outer ramus of uropod 3 becomes elongate, whereas it is short in the monotypic genera, Compactogammarus and Uroniphargoides. The latter two genera also have a fan on epimeron 3 similar to Niphargoides. Uroniphargoides has the inner ramus of uropod 3 aberrantly elongate or secondarily swollen.

Paraniphargoides grimmi is transferred to Niphargoides where, though it is transitional between the two genera, it fits better. Niphargogammarus borodini and N. intermedius have Pontogammarid setation on pereopods 3 or 4, suggesting they should be distinguished from their congeners.

Cardiophilids

Cardiophilus (2 species, one in Caspian) has small and thin gnathopods and the body is so poorly expanded that one cannot connect the genus to the other Caspian species characterized by the expansion of pereopod 7. On that basis, Cardiophilus might be an extension of the true Gmelina, which also has the expansion reduced. At least one species of Cardiophilus is inquilinous, being found in the mantle cavities of Cardium.

The monotypic genera Behningiella and Zernovia (Volga Delta) also have very short antennae. Behningiella has the incipiently vermiform body of Cardiophilus. Both genera are characterized by homogeneity in the expansion of articles 2 and 4 on pereopods 5-7; the shapes are, however, distinctive between the two genera. Gnathopod 2 is dominant and article 5 is short and triangular, weakly lobate.

Cardiophilus, *Behningiella* and *Zernovia* have the maxillipedal dactyl reduced as if all genera occur in an inquilinous habitat. This is probably an adaptive attribute rather than of monophyletic origin but the genera are grouped together here until their true affinities are discovered in the *Dikerogammarus-Pontogammarus* ancestry.

A similar taxon, *Pachyschesis* (3) occurs in Baikal. Its maxillipedal dactyl is not elaborated but the genus resembles the Caspian taxa in the degree of similarity on article 2 among pereopods 5-7. Article 2 is evenly expanded on all 3 pereopods in the several genera, though to different degrees and shapes in each. *Pachyschesis* also resembles the Caspian taxa in the reduction of medial setae on the maxillae, the somewhat inflated article 1 of antenna 2 but varies in the degree of setation on anterior coxae and the posterior margins of article 2 on pereopods 5-7. The three species of *Pachyschesis* are known to inhabit the marsupia of larger species of amphipods or to occur in the incipient brood space of males of other species. The weakly prehensile pereopods suggest this parasitic existence, and this fits the apparent inquilinous pattern of the *Cardiophilus* group. *Pachyschesis* differs from the Caspian genera in the dominance of gnathopod 1, a Baikalian feature. The prevalence of that condition in Baikalian taxa suggests a common ancestry, in which case *Pachyschesis* would form a remarkable convergent almost indistinguishable in its adaptive features from otherwise similar Caspian genera.

Pontoporeids

The final topic of the Caspian group is *Pontoporeia*, a genus with many morphological similarities to PontoCaspian Gammarids but which for nearly a century has been allocated to a distinct family. At first this genus was relegated to a family Pontoporeiidae (1882) later made synonymous with a junior synonym, Haustoriidae (Stebbing, 1906), but which we are reviving and transferring into the evolutionary vicinity of Gammaridans. *Pontoporeia* is very close to *Turcogammarus*, *Dikerogammarus* and *Obesogammarus*. Some of the species share the dorsal knobs on the urosome of *Turcogammarus* and *Dikerogammarus*, the strong setosity of *Obesogammarus*, the general *Pontogammarus* antenna 1, and well setose maxillae. *Pontoporeia* is, however, characterized by the following items: (1) short but magniramous uropod 3, outer ramus 1-articulate; (2) diverse and distinctive pereopods 5-7, with pereopod 6 elongate, pereopod 7 short; (3) diverse and distinctive but feeble gnathopods, gnathopod 1 larger than 2, wrist lobate and more or less elongate, gnathopod 2 parachelate; (4) lower lip especially fleshy; (5) maxillipedal dactyl reduced.

Three other genera are grouped with *Pontoporeia*. They are much more strongly oceanic than *Pontoporeia*. This entire group is characterized by their feeble gnathopods. A monotypic genus from the arctic sublittoral, *Priscillina*, differs from *Pontoporeia* in the unlobate wrist of gnathopod 1, pointed anterior coxae, diverse gnathopods and Compactogammarrid-like antenna 1.

Amphiporeia (3) is an Atlantic American genus, which has a geniculate antenna 1, and similar gnathopods with poorly expanded article 2 of pereopod 7. *Bathyporeia* (13) is a circumboreal genus with representation in the marine part of the Black Sea. This genus may descend from *Amphiporeia* and has diverse gnathopods, the second pair with the dactyl having been lost or reduced, and uropod 3 having progressed fully to the parviramous condition.

Evolution of Fossorial Gammaroids

PontoCaspian Gammaroid groups, except Echinogammarids, are characterized by weak to strong fossorial adaptation. Several of the species are nestlers and not burrowers but the nestlers were apparently preadapted to evolve into burrowers. One presumes that the vast reaches of level bottom in the ancient Carpathian Sea, with continuation into the Neogene of the Caspian shallows and available parts of the Aral, Azov and Black Seas, favored the development of a rich fossorial fauna. Fossorial amphipods are marked by one or more of the following characters: the reduction in length of antennae, with extreme reduction especially in articles 2-3 of the peduncle and the flagella of antenna 1 and their supposed increase in strength relative to size; the reduction of peduncle and flagellum on antenna 2 with increased ventral setation, a small degree of facial setation, especially on article 3 (but not as heavily spinose as in Phoxocephalids); the broadening of articles 4-5 on pereopods 3-4 with great increase of posterior setation; the broadening of one or more bases (article 2) on pereopods 5-7, especially pereopod 7, the development of posterior and facial setae on those articles; the shortening of those appendages resulting in increased strength; the addition of supernumerary setae or spines, the setae and spines often becoming thicker or stronger by various means; and the broadening of the body. Not all amphipods with fossorial adaptations are burrowers, so that one must use caution in ascribing the fossorial mode to amphipods with apparent fossorial adaptations. Hence, one may not state that reduction in uropod 3, fusion of telsonic lobes, increase or extreme reduction of uropodal spines or similar adaptations are always the marks of the fossorial mode.

Nevertheless, the recognition of these adaptations, for whatever function they have, appears to mark an evolutionary significance in the sense that we can detect an evolutionary flow outward from amphipods lacking such adaptations towards amphipods that are most fully enriched with such fossorial characteristics.

Apparently the most primitive Pontian fossorials comprise genera, such as Dikerogammarus, Shablogammarus, Amathillina, Axelboeckia, and Gmelina, in which antennae 1-2 remain somewhat similar to those of the ordinary Gammarid ("Gammarus" type, Stock, 1974c) and in which article 2 of only pereopod 7 is broadened (Gmelina). In the other genera, pereopod 7 bears the (?vestige) rudiment (Axelboeckia) or full development (Amathillina) of a downthrust posteroventral lobe. A slight increase in length of posterior setules is found in Amathillina and Gmelinopsis. Otherwise, setae have rarely been pertinent to the fossorial process in this context because increase and elongation of anterior coxal setae are poorly developed in most genera. Exceptionally, setae are better developed to a small extent in Axelboeckia, Dikerogammarus and Gmelinopsis and to a great extent only in Turcogammarus.

For some unknown reason, the basal and lateral spination of the telson deteriorates in PontoCaspian Gammaroids, so that only Amathillina and Shablogammarus maintain weak remnants of this spination, whereas terminal spination also decreases largely throughout the group. Article 2 on the outer ramus of uropod 3 usually remains of ordinary length but occasionally is severely shortened or totally lost (Axelboeckia).

Within these primitive fossorials, distinguished by normal Gammarus antenna 1, are two sub-groups more or less distinguished by the dominance of gnathopods. The first of these, named again for Gmelina, has gnathopods of equal size or with increasing dominance by gnathopod 1. Gnathopod 2 becomes smaller or thinner and has elongate articles. This resembles the Eulimnogammarus group of Baikal. The Gmelina gnathopodal subgroup contains nine Caspian genera, Gmelina, Amathillina, Iphigenella, Gmelinopsis, Kuzmelina, Lanceogammarus, Baku, Axelboeckia and the transitional genus Yogmelina. The latter differs from Gmelina in the development of posterior setae on article 2 of pereopods 5-7 and in the presence of facial setae on pereopod 7, as well as the better development of uropodal spines and the absence of dorsal body teeth.

If derived from Baikalian ancestors, the primitive mode of this group would be the "Eulimnogammarus" kind of gnathopodal configuration, in which gnathopod 1 is large and retains the Gammarid spination of the palm but in which gnathopod 2 is much thinner and more elongate, the wrist especially being elongate. This primitive mode is best seen in Iphigenella (1), which otherwise is not the best kind of primitive representative because of the prehensile pereopods. Its plesiomorphic non-prehensile "ancestor" might be Baku (one Caspian species) except that antenna 1 is reduced. Stock (1974c) has removed the other member of Iphigenella, I. andrussowi, to the Baikalian genus Lobogammarus but G.S. Karaman and Barnard (1979:134) described Lanceogammarus to receive it.

Iphigenella is characterized by the lobate article 2 of pereopod 7 as in the Pontogammarus-Compactogammarus group but retains the Dikerogammarus antenna 1. The expansion of article 2 on both pereopods 5 and 6 suggests affinities with Shablogammarus. That locus would be the place to derive Iphigenella from a Chaetogammarus ancestry within the Aralo-Caspian fauna; but the Eulimnogammarus system will be treated elsewhere (see the "Heterogammarus Group" under "The Evolutionary Pattern"). The remaining genera have diverse article 2 on pereopods 5-7. Amathillina (5) bears gnathopods so weakly Eulimnogammarid that the genus is attributed to this group mainly on its resemblance to Gmelina, Gmelinopsis and Axelboeckia in dorsal tooth pattern. Nevertheless, one or more species have gnathopod 1 weakly dominant. Unlike other genera of the group, article 2 of pereopod 7 is deeply lobate ventrally. Amathillina therefore forms a bridge to the Dikerogammarus group, where several species of Dikerogammarus share similar dorsal humps on the urosomites. Amathillina has a short uropod 3 in contrast to Dikerogammarus. Stock (1974c:80) placed Amathillina and Dikerogammarus together as partner genera on the basis that the propodus of gnathopod 1 is not larger than that of gnathopod 2, though a weak tendency for enlargement of gnathopod 1 is apparent in figures of the literature.

The great difficulty in judging the proportions between gnathopods 1 and 2 in so many cases throughout the Gammaroids (even within genera such as Heterogammarus and Eulimnogammarus, where the typical Eulimnogammarid gnathopods are supposed to be present), indicates that a more substantial character alternative at familial level or even at generic level should be employed. Amathillina might therefore be placed more firmly in the vicinity of Dikerogammarus because of ventral lobation on article 2 of pereopod 7. In so doing one must admit that the differences between

Gmelinids and Dikerogammarids are weak, because degree of ventral lobation throughout Gammaroids is no more discontiguously graded than gnathopodal size.

The remaining 5 genera have a much shortened antenna 1 with reduced accessory flagellum. *Yogmelina* (5) retains the Eulimnogammarid gnathopods in miniature form, while article 2 of pereopod 7 is expanded and setose. The true *Gmelina* subgroup (2 genera with 3 species, 2 in Caspian) has the expansion of pereopod 7 severely reduced and dorsal body ornaments are developed. *Kuzmelina* (one species) differs from *Gmelina* (2) in the doubling of the carina, the protruding cephalic lobes, the rudimentary cephalic wing, the marginal eyes and short telson.

Gmelinopsis, resembling *Gmelina* and *Kuzmelina* superficially, has gnathopod 1 enlarged but gnathopod 2, though significantly smaller, does not have the Eulimnogammarid form; rather, the wrist is short and almost lobate. Article 2 of pereopod 7 is expanded and setose and article 2 of pereopods 5-6 is pyriform. *Gmelinopsis* (2) in those characters, therefore, has more affinity with *Amathillina* than with the other genera in this discussion but otherwise has the congruent head. One species of *Gmelinopsis* has the telsonic lobes basally fused.

Axelboeckia (1) would appear to be an apomorph of *Gmelinopsis* in which the gnathopods are dwarfed and becoming mittenform. Like *Gmelinopsis* the head bears a tooth anteroventrally and similar dorsal body cuspidation is found. Article 2 on the outer ramus of uropod 3 has been lost.

Many fossorial genera are characterized by the presence of tufts of facial setae on the bases of pereopods 5-7 and the extreme setosity of the posterior margins of pereopods 3-4. In *Pontogammarus* and a few other taxa, the setae on article 4 become very dense and aligned serially rather than being divided into tufts.

Antenna 2 develops strong ventral setation on the peduncle (Pontogammarid) but antenna 2 in *Stenogammarus* and a few other taxa becomes "Stenogammarid" with article 5 losing dominance. Several taxa develop facial spination on antenna 2 while article 3 notably bears strong facial setation. Article 2 of pereopod 7 becomes broader and more heavily setose. All of these characters typify fossorial amphipods of similar families. Barnard and Drummond (1978) have found that primitive Australian Phoxocephalidae have these characters and suggest the possibility that the PontoCaspian *Uroniphargoides* is the closest morphotype to Phoxocephalidae. In its primitive state the latter family differs from the PontoCaspian model in the acetabularian mandibular molar and the presence of a large visor-like rostrum, but the medial setation of the maxillae is also reduced and the wrist of gnathopod 2 becomes cryptic. The morphological similarities involve the Compactogammarid antenna 1, the general Pontogammarid antenna 2 (short and powerful), the Pontogammarid pereopod 7 bearing an expanded and lobate article 2 with long posterior and facial setae. Some of the facial setae occur in bundles and thereby form a link between Pontogammarids and the primitive *Pontharpinia* of the Phoxocephalidae. Almost all Phoxocephalidae have a variramous or parviramous uropod 3, at least in the female, the males usually bearing a fully magniramous uropod 3. All PontoCaspian Gammaroids have a variramous or parviramous uropod 3, or at least the inner ramus is much shorter than half the outer ramus in all genera except *Uroniphargoides*. The primitive Phoxocephalids have a magniramous uropod 3, which deteriorates to the parviramous condition in the females of the most advanced genera. This disjunction suggests that a link has been lost between the PontoCaspian Gammaroids and the Phoxocephalidae, if there ever was one. Uronipharqoides might be a good ancestral link, not only because of its elongate inner ramus, but because antenna 2 is of the Stenogammarid form in which article 4 of the peduncle dominates article 5, the latter becoming thinner and shorter and in the most extreme cases assuming the appearance of a first flagellar article. In Phoxocephalidae the extreme case never occurs but article 4 distinctly dominates article 5 and in several advanced Phoxocephalid genera the latter becomes quite short and thin.

Phoxocephalids overall differ from Gammaroids in the combination of any 2 of the following three characters: (1) the presence of a distinct, visor-like, dorsoventrally flattened rostrum; (2) the fully developed Phoxocephalid pereopod 7 bearing a broad shield-like article 2 extending as a broad lobe ventrally, the overall appendage being much shorter and of entirely different form than pereopod 6; and (3) the presence of spine clusters on the lateral face of article 4 on antenna 2. Only 5 of the 55 genera of Phoxocephalids have a triturative mandibular molar, all others having some degree of loss in structure of the molar. The molar of the 5 primitive genera is unlike that of any known Gammaroid in its acetabularian or crown-like appearance of teeth surrounding a central depression. Only the males of a very few primitive species bear D-setae on the mandibular palp. All genera have lost the oblique facial row of setae on the inner plate of maxilla 1 and all but the most primitive genus, Pontharpinia, have lost all but 4 (or fewer) setae on the inner plate of maxilla 1. That inner plate has become enlarged and broadened in Phoxocephalids. All Phoxocephalids have well developed fleshy inner lobes on the lower lip. The most primitive Phoxocephalids have article 5 of gnathopod 2 severely reduced in length to the point that the posterior margin of the article is "cryptic", e.g., hidden posteriorly from the environment by the abutment of articles 4 and 6.

Niphargogammarus is extremely close to a conceptual ancestor of the Phoxocephalidae. It lacks only the well developed rostrum and the fully developed pereopod 7 to prevent its assignment to Phoxocephalidae. A weak rostrum is rudimentarily expressed but article 2 of pereopod 7 is insufficiently extended ventrally and articles 4-6 are not shortened relative to article 2 and to the size of pereopod 6 as in Phoxocephalidae. But Niphargogammarus bears enlarged articles 1 and 3 of antenna 2, bears heavy ventral, almost facial setation on article 3, bears the rudiments or even full development of facial spines on article 4, bears the Stenogammarid-Phoxocephalid article 5 which in Niphargogammarus carries facial spines as in Phoxocephalids (these become reduced in the majority of Phoxocephalids), has lost all but 4 setae on the inner plate of maxilla 2, bears the rudiments of fleshy inner lobes on the lower lip, lacks D-setae on the mandibular palp, has only one or two setae on the oblique facial row of maxilla 2, has extremely shortened fifth articles on the gnathopods, albeit with posterior lobes unlike Phoxocephalids, has pereopods 4-5 almost identical to those of Phoxocephalids (except that Phoxocephalids lose the Pontogammarid eveness of posterior setae on article 4 in favor of the Obesogammarus clustering), bears the facial setae in clusters on article 2 of pereopods 5-7 (one or more represented) as in primitive Phoxocephalids (but soon lost) and has the rudimentary traces of continuous dorsal spination on some rami of uropods 1-2 typical of primitive Phoxocephalids (but soon lost). Dozens of other more minor similarities exist but sufficient dissimilarities occur to counteract the suggestion that *Niphargogammarus* is the perfect ancestor to *Pontharpinia*.

Unfortunately, mandibular molars have not been well reported in PontoCaspian Gammaroids so that any potential similarities between the molar of Gammaroids and Phoxocephalids remain unknown.

If one genus of PontoCaspian Gammaroids does not contain all morphological elements expressed in Phoxocephalids, the combination of the known species forms a pool of characterrs showing the potential for evolutionary flow between the groups. For example, *Niphargoides boltovskoyoi* bears the posteroventral tooth and facial setae of epimeron 3 characteristic of primitive Phoxocephalids and has the setal reduction on article 2 of antenna 1 even though it lacks many of the other Phoxocephalid characters such as facial spines on antenna 2.

A close analogue to the PontoCaspian fossorial Gammaroid is *Pontoporeia*, the type-genus of the Pontoporeiidae. One species of *Pontoporeia* occurs in the Caspian Sea but the genus and the family consist primarily of shallow water fossorial species in the boreal Atlantic and seas surrounding western Eurasia. *Pontoporeia* also occurs in glacial lakes of the far north and is, therefore, adapted to low salinites (Segerstrale, 1957a:781). Pontoporeiids have a wide variety of adaptations but the group as a whole scarcely differs from PontoCaspian Gammarids. The main differences seem to be the very feeble gnathopods and the strong sexual dimorphism in the flagellum of antenna 2. Barnard and Drummond (1982) in their reappraisal of Haustorioids remove Pontoporeiids to the Gammaroids.

If Pontogammarids have been the ancestors of the fully marine Phoxocephalidae and of the weakly marine Pontoporeiidae, they have otherwise expanded very little into non-Pontian environments. Many have gone up rivers and through human interference have escaped through canals and transplantation into exotic environments but otherwise only 5 species in *Turcogammarus*, *Jugogammarus* and *Pontogammarus* live in rivers or lakes somewhat disjunct from the modern PontoCaspian basin. Even *Jugogammarus* is in a subtributary of the Black Sea.

On the other hand, the development of the PontoCaspian fauna occurred long before the present basin configuration because very few taxa are endemic to the Caspian Sea itself and some of these may actually be relicts and not speciated just since regional uplift and constraint of the Caspian Sea. Only the following 8 genera with 10 species are endemic to the Caspian Sea: *Akerogammarus*, *Axelboeckia*, *Baku*, *Behningiella*, *Cephalogammarus*, *Derzhavinella*, *Sowinskya* and *Zernovia*.

The other 25 genera, with 67 species have 26 of those species confined to the Caspian but 41 species are found in the Aral, Azov, Black Seas and their tributaries or adjacent areas. To state all of this in yet another way, the Caspian Sea, with 60 species has 33 endemic species, of which 10 belong to endemic genera; a total of 28 genera is found, of which 8 are endemic. All but 5 PontoCaspian genera are found in the Caspian Sea, these being *Andrussovia*†, *Jugogammarus*, *Praegmelina*†, *Shablogammarus* and *Turcogammarus*.

Caspian Ecology

Influence by non-Gammaroid marine Amphipoda on the Caspian Sea is minimal. Caspicola is an unknown quantity assumed to have a marine origin. The species of Corophium and Onisimus (=Pseudalibrotus) indicate that a marine connection has been present. But Onisimus is so weakly marine it might be a brackish water genus. Nevertheless, its ancestors are clearly marine; the family Lysianassidae is otherwise a very strong marine family with only occasional penetration into anchialine environments, such as the salines of the Lesser Antilles (Stephensen, 1933a,c). Corophium has many fully marine species, such as C. baconi, but a majority of the species appears to be associated with abnormal marine conditions and many are inhabitants of heavily polluted marine harbors or occur near brackish water sources. The remote evolutionary origins of Corophium are definitely marine but the closest gnathopodal morphotype of the genus, Paracorophium, is also associated with brackish waters in the southern hemisphere. The evolutionary connection between the two genera is unknown though believed to be remote, and the further origin of either is unknown except to the extent that they belong to a large group (60+) of mainly marine genera, known as the Corophioidea (J.L. Barnard, 1973).

Gammaracanthus belongs to the Acanthogammarids which are dominantly Baikalian. Although a few species, such as that found in the Caspian Sea, have escaped from the Baikalian regime, one of those penetrated the Arctic Sea. Pontoporeia belongs to a dominantly brackish to freshwater group. Its marine relatives appear to be more advanced evolutionarily than Pontoporeia.

Gammaracanthus, Pontoporeia and Onisimus (=Pseudalibrotus) belong to a relict group of Amphipods thought to have been sluiced up from Arctic seas by advancing ice fronts, and pushed southward in a proglacial lake until impingement with the PontoCaspian watershed occurred. This Hogben theory of up-sluicing is thoroughly covered by Segerstrale (1957, 1976). A species of Pallasiola also was distributed by this proglacial lake system but Pallasiola quadrispinosa probably originated from Pallasea kessleri, which resides in Baikal and its drainage system (Yenisei and Angara Rivers). Pallasiola quadrispinosa is not adaptable to salty waters and thus does not survive in PontoCaspian tributaries and Arctic seas, though it is widely spread today in upheaved glacial lakes.

Pontoporeia affinis occurs both in the Caspian Sea and glacial lakes and is believed to have evolved from the arctic species, Pontoporeia femorata, which lives in somewhat diluted marine waters. On the other hand taxonomists have recognized three subspecies or forms of Gammaracanthus, G. l. loricatus (= G. l. typicus) in arctic seas, G. l. lacustris in glacial lakes and G. l. caspius in the Caspian Sea. The main distinctions of these taxa occur in the dorsal body carina, which is anteriorly well developed and sharp in the ocean, humped or rounded in the Caspian Sea and absent in freshwater. This indicates to Segerstrale (1957b:105) that the Caspian form spent less time in the proglacial lake system before reaching salty Caspian waters than did the freshwater form, which must be the ultimate product of the great ice lake.

Contiguous marine relatives of the dominant Pontogammarid group of the Caspian Sea are found in the "Marinogammarus" section of Echinogammarus, a group thought by Stock (1968) to be synonymous with Chaetogammarus, and now confirmed by other workers. "Marinogammarus" marinus is found in the Black Sea and the Azov Sea. The extrinsic distribution of "Marinogammarus" lies on both sides of the Atlantic Ocean and in Mediterranean waters outside of the Black Sea. The various species in the group appear to be closely tied to sea dilution or to hug shorelines very closely. They may have reached the PontoCaspian basin through favorable environmental pathways afforded by salinity changes in Lac Mer and the Sarmatian Sea or they may actually be a product of the Sarmatian basin and then have escaped to the Atlantic in a Carpathian pathway rather than through the Mediterranean. (The later geology and climate are found in Kvavsov, 1979.) In any event, the species would have been extirpated in the Mediterranean during Pliocene drying. The group is poorly adapted to the fully marine world, but like the Sarthrogammarids has repenetrated the Mediterranean despite the small amount of runoff into that sea.

Only a few species of Gammarus live in the ocean and they are poorly adapted to that regime. They hug the coastlines, scarcely occurring below mean low tide level and have not spread outside the circum-Arctic seas or the boreal Atlantic Ocean. Many have a clear affinity for diluted seawater. One species, G. wilkitzkii, lives under mid-Arctic pack-ice but also is inhabiting an environment near meltwater and an environment grossly devoid of other amphipods (J.L. Barnard, 1959d). Its main companion is a species of Pseudalibrotus (=Onisimus). If Gammarus (sensu lato) ever had a fully developed, widely sublittoral marine ancestor, that ancestor is not now extant.

All evolutionary flow in Caspian Gammaroids is retrospective from the Gammarus form, whether directly through the Marinogammarus-Chaetogammarus-Echinogammarus-Dikerogammarus line or indirectly through the Gmelinid group (Heterogammarus ancestry?) with Baikalian affinities. Though one may conclude that the Caspian Gammaroids have a connection with a species group today living in salty waters (Marinogammarus), the ultimate thesis would remain that the gross affinities lie with organisms earlier adapted to freshwaters, or those with a dominantly freshwater ancestry. One cannot, therefore, visualize a PontoTethyan basin of primarily marine value providing the ancestry to Caspian genera. The Mediterranean-like extremes of that body of water, whether of earlier times, or today, do not foster a viable nursery ground for Caspian Gammaroids. Instead, the best that can be said, is that the Caspian Gammarids would have a brackish water affinity. The ancestry from freshwater Gammaroids appears so strong that one might also hypothesize that "Marinogammarus" itself may be a product of the PontoSarmatian dilution.

Hutchinson (1967:217,225) already points out that the invasion of surrounding freshwaters by Caspian Gammaroids is "not great". He notes from the work of Behning (1924a) that eight of the 25 Amphipoda then known to live in the Delta Region of the Volga River (emptying into the Caspian Sea) penetrate at least 1000 km up the Volga River. We must digress here to explain some human contribution to the distribution of PontoCaspian amphipods. The eight species mentioned by Behning included Compactogammarus compactus, Dikerogammarus haemobaphes, Obesogammarus obesus, Pontogammarus abbreviatus, Stenogammarus macrurus, Echinogammarus ischnus, E. platycheir and Euxinia sarsi. As pointed out by Jazdzewski (1980:90-99), even by 1924 many Pontogammarids had been transported to far places either by saltation through manmade canals or by active transplantation into lakes and reservoirs to provide food for commercial and game fishes. Jazdzewski particularly discusses *Echinogammarus sowinskyi* (which probably was what Behning and other authors have called *Chaetogammarus ischnus*), *Obesogammarus crassus*, *Pontogammarus robustoides*, and *Dikerogammarus haemobaphes* as being transported by man and adds to the now widely distributed species thought by Behning to occur only as far as the Volga Delta the following: *Amathillina cristata*, *Echinogammarus warpachowskyi*, and *Yogmelina pusilla*. Parenthetically, Jazdzewski also discusses *Gammarus roeselii* and *G. varsoviensis* as being widely moved about but those species are not PontoCaspian.

The data presented by Jazdzewski seem to confirm that the widely distributed PontoCaspian species do best in large rivers and lakes-reservoirs.

Dikerogammarids and Pontogammarids are also known from Lac Sabla, and from freshwaters of western Greece and Turkey. Poor repenetration of PontoCaspian Gammarids into freshwater would argue against their freshwater ancestry and point to a marine origin, except for the fact that in the majority they are fossorial and thereore unsuited for riparian habitats. In any event, they would meet stiff competition from *Gammarus* and *Echinogammarus* in stream systems outside the PontoCaspian basin or the main river drainage.

Our conclusion is therefore supported that Neogenic Gammaroids have their origins in what is now a primarily freshwater stock; the most primitive members of that freshwater stock do have a few weakly marine species but they are so poorly adapted to the sea and so narrowly constrained in their distribution that one must suspect the marine representative also had a freshwater origin. In light of this opinion the PontoCaspian basin, or the old Pontian and Sarmatian Seas, and Lac Mer, would represent nursery grounds where adaptability to increasing salinity was naturally selected during incursions of marine waters. This is not to say that marine amphipods in general have had a late origin and that the pathway outwards from freshwater was through the PontoCaspian Basin into an arm of a Tethyan Sea. The weak fossil record indicates that amphipods were well developed as early as upper Paleocene, and Crangonyctid distribution suggests a late Paleozoic origin. The opinion is favorable that the Pontian Seas may have formed a nursery ground for at least one marine group, the Pontoporeiidae; but the theory that the Ponto-Tethyan sea arm might have been a nursery ground for the Phoxocephalidae, some members of which escaped to a favorable warm-temperate marine environment (today represented by southern Australia where the group is predominant), the remainder of which were caught in the diminishing Caspian basin to be preserved as relicts of a widely spread fossorial and Tethyan fauna (Barnard and Drummond, 1978:36), has no grounds of support. Even though the Mediterranean dried to extinction in the Pliocene, the remnants of such a hypothetical Phoxocephalid fauna should exist outside Gibraltar but do not. Whereas the evolutionary flow in the Pontogammarid group proceeds outward from *Chaetogammarus* through *Uroniphargoides*, the advanced or derived members are PontoCaspian. The IndoPacific tropics are almost devoid of Phoxocephalids. The present and impoverished Phoxocephalid fauna of the Mediterranean and eastern Atlantic is clearly derivative from the Australian focus. Any escape (or better the interconnection) would have had to have taken place directly into the Indian Ocean, well divorced from the Mediterranean part of the Tethyan sea in a nontropical environment.

In retrospect, the Caspian fauna today is a residue of a more widespread fauna that occurred when the PontoAraloCaspian Basin was much more extensive and which occasionally had a marine connection (Zenkevich, 1957:891). But the Caspian fauna evolved and was confined almost always to the greater basin. The marine group Pontoporeiidae, may have evolved or had ancestors within that regime and escaped towards more saline waters. The evolutionary flow aims toward adaptability to saline waters and not from saline toward freshwaters. The connection to any hypothetical ancestor is remote and occurs through what today are mainly freshwater amphipods. The few amphipods in the Caspian Sea today with obvious marine ancestors come from some of the most advanced marine groups (Lysianassidae and apomorphic sections of Corophioidea). Almost all of the purely marine amphipods of the eastern Atlantic, the Mediterranean Sea and the arctic shores of Europe are highly advanced or derived forms; most of these groups are represented in their primitive form in some other part of the world. The Atlantic-Mediterranean fauna, therefore, has the attributes of youth.

The views of various students (see discussion, pp. 193-198, Banarescu, 1970 [1975:193,198, English translation]), that Gammaroid species in the basins of the Don, Dnieper, Dniester, Volga and Danube Rivers have a relict origin can be supported only to the extent that the ancestors might have been weakly "marine." Because the PontoCaspian Gammaroids remain so close to their freshwater origin and there is so little evidence that any of them ever were fully marine, one must modify this precept that the lacustrine relicts are marine. Instead, they are brackish Pontian, for all practical purposes always confined to that basin, never having had any existence in a purely marine world. There is no morphological evidence in the evolutionary flow that any of the riparian species are discontiguous from the Pontian brackish water genera and, therefore, an egress into the sea and a disjunct leap into freshwaters has not occurred. The egress and ingress to and from freshwater and brackish water must have played a part in the Pontogammarid evolutionary system. The whole Neogenic PontoCaspian Gammaroid fauna could therefore be considered a relict, today divided into several parts owing to aridity and uplift. It is a relict in the sense that it was much more widely distributed at some time in the past but its distribution was confined to the same kinds of environments present today. The Pontogammarid fauna was not captured from the sea but evolved into the basin from freshwaters. Parts of the fauna may have entered the sea and there may have been numerous genera associated with greater salinities than now present that have since gone extinct; and the environment was definitely invaded by marine amphipods of high morphological advancement. But when the sea connection was interrupted and salinity dropped, most of the marine groups became extinct and what survives today are the very few polyhaline, oligohaline and freshwater species of direct marine origin (<u>Corophium</u>, <u>Onisimus</u>) and the broadly eurytopic Pontogammarid group with taxa adapted to every degree of halinity below the polyhaline limit. They are relicts because many of their congeners and many of their compatriots died but they are not outside of their places of origin. Their evolution is probably continuing today because of habitat changes affecting a magnificent gene pool which may again result in natural selection. Some of the purely freshwater species appear to be in the process of moving upriver and extending their ranges (Mordukhai-Boltovskoi, 1960, 1969, Banarescu, 1970). Unfortunately, human interference with tributaries could result in isolation that might select for further speciation. The lacustrine species are therefore not out of contact with their congeners or ancestors.

Mordukhai-Boltovskoi (1960, 1964, see Banarescu, 1970:9, bibliography) points out that the presence of old Pontian (strictly Caspian of Neogene) elements in the Black Sea actually represent relicts of the NeoEuxine transgression (during the Wurm glaciation), which reconnected Caspian and Black Sea faunas. This occurred after the first incursion of Mediterranean salines into the Black Sea. One must note that none of these Pontian amphipods has subsequently moved outward into the Mediterranean and that they are far less diverse than the fauna remaining in the Caspian Sea. They lack any viability in the marine macrocosm and this further supports the supposition that the PontoCaspian taxa basically have a background in freshwater adaptabilities, whether or not these include both halinity and biocompetitive tolerances. The Caspian environment is a definite relict in the sense that it no longer has contact with or is a part of the former great body of freshwater called Lac Mer, nor is it in contact with or a part of the former great Tethyan Sea. It contains a small part of the salt from earlier times but is also accumulating salt from normal runoff. The salt becomes concentrated because of evaporation and relative stability of sea level (and lately by more human interference in building dams against freshwater influx). Saline gradients occur because of the smallness of the sea in proportion to the volume of freshwater input (prior to alterations by mankind). Even in times when the basin was an arm of the Tethyan Sea, there must have been salinity gradients, as represented at the least by estuaries, so as to preserve the oligo-polyhalinic components of the fauna during the saltier period. The sea connection must have been minimal, at least for the part of the fauna today restricted to polyhaline waters. In no place of the open sea today are there any close relatives of the Pontogammarid genera; the closest morphotypes appear to be in Pontoporeiids and Phoxocephalids. If the sea connection were relatively recent (Pliocene), then any marine relatives were extirpated catastrophically. If the sea connection were primarily pre-Oligocene, then the normal processes of marine evolution and extinction have wiped out all traces of the marine connection. Ipso facto, time has nothing to do with the problem; the temporal statements simply establish a framework of sequence. The few Pontogammarids in the Black Sea are not penetrating into the Mediterranean; they remain confined to polyhaline or fresher waters. This indicates that the PontoCaspian basin remained polyhaline or fresher until relatively late geological time and that the Bosphoric connection occurred after Pliocene drying of the Mediterranean. The lack of metasaline sea waters in the PontoCaspian Basin would form a barrier against encroachment of polyhaline salinities, resulting in extinction of marine species. Although the Mediterranean is today impoverished of species compared to the rich faunas of undisturbed Australia, it nevertheless has over 400 species of fully marine amphipods which could form a competitive barrier against PontoCaspian elements emerging from the Black Sea. However, there is a degree of mystery in this situation because the Mediterranean is extremely impoverished of fossorial amphipods, whereas the majority of Pontogammarids is fossorial. There may be a biological demand in the Mediterranean for fossorial species. One must therefore suggest that the Pontogammarids are stenohalinic below the polyhaline limit or that biocompetitive stress

TABLE 10*.--Deployment of PontoSarmatian Gammaroids, including *Echinogammarus* (=*Chaetogammarus*) (species only) and *Pontoporeia*. Other taxa are included in lower right extension of table. See Appendix II for lists of taxa and sources (June 1979).

	Species	Genera		
Total World	77	33 (not including *Echinogammarus*)		
Endemic Caspian	36	8		
Azov	1	0		
Black (including Azov)	14	2		
Aral	1	0		
Outside these basins	8	2		
Joint				
Caspian-Azov	18	12		
Caspian-Aral	0	0		
Caspian-Black	23	15	Other amphipod taxa, mostly marine incursants.	
Black-Azov	22	13		
Caspian-Azov-Black	23	15		
Total in each basin			Species	Genera
Caspian	60	28	12	4
Azov	23	13	11	9
Black	37	21	74	37
Aral	1	1	0	0
Lac Sabla	1**	1**	?	?
Escapees outside Ponto-Caspian Basin.	8	2	0	0

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*Left 2 columns of table excluding *Gammaracanthus*, *Gammarellus*, *Corophium*, *Pseudalibrotus* and *Caspicola*.
**Counted also in Black Sea.

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prevents the emergence of fossorial Pontogammarids. This situation would also suggest that in every instance when the PontoCaspian Basin came into marine contact, there was not necessarily any emergence of PontoCaspian elements and that the Ponto-Caspian environment was not a good nursery ground for prototypical marine elements. Perhaps only in the case of the Pontoporeiids (?and Phoxocephalids) was there a successful emergence. The Phoxocephalidae appear to be an otherwise dead end in evolution so that they cannot be regarded as the link to more advanced amphipods. Their modern distributional pattern (Barnard and Drummond, 1978:36) suggests that they are not relatively youthful but are Gondwanal in age, and expanding outward very slowly from their Australian-Fuegian center, but are severely hampered by the tropical frontier against which they are poorly adapted.

This statement may be taken as a good argument against a PontoCaspian origin and, because of tropical antipathy, much of the evolutionary development in Amphipoda appears to be enmeshed in a framework of northern to southern hemispherical isolation.

The timing of evolutionary events contains anomalies. Gondwana much preceded PontoCaspia. If the Phoxocephalidae had a SarmatoTethyan origin, they must have escaped when the sea was open to the east (much later than Gondwanal eras). At that time the sea was also open to the west into the Mediterranean part of the Tethyan Sea but no modern Phoxocephalid evidence of this connection now exists. The drying of the Mediterranean is insignificant because the faunal elements would have been able to survive outside Gibraltar. This seems to be confirmed by the Sarothrogammarids which today form two relict groups in Afghanistan-Tadzhikistan and in insular Lusitania and the Mediterranean. One would presume this group reinvaded the newly filled Mediterranean from a trans-Gibraltar source. This group would appear to have been drowned by a saline PontoCaspian basin and today is confined to the east and to the west of that old basin. But no Pontogammarids and no primitive Phoxocephalids live in the Mediterranean basin except for a species of Turcogammarus in the freshwaters of Greece. The western marine connection to the PontoCaspian existed much later than the eastern connection. This would suggest, therefore, that the Pontogammarids are closely stenohaline and have been so since the eastern connection was open. While the PontoCaspian basin was in its Euxinic (freshwater) phases, these species must have been confined to special environments, branches or isolated saline lakes only to reinvade the basin during Sarmatian phases. If any preadapted species emerged into marine waters of the Mediterranean or Indian seas, then their extinction through rapid and progressive selection has been complete; the links have disappeared. We therefore conclude Phoxocephalids had an independent origin but convergence from later Pontogammarids in grade of morphology.

The sudden inrush of Atlantic water to fill the Mediterranean Basin in 100 years (which happened several times in the Pliocene) could have impounded the Pontogammarids severely; one might presume the initial filling was in each case hypersaline because of dissolution of salty sediments in the process. Hence, the Pontogammarids may have been subjected to a series of harsh environmental events on their western flank which, for all practical purposes, could have been halogenic disasters to any species almost fully adapted to marine waters but now subjected to hypersalinities. This condition would presume that Pontogammarids were confined by some kind of geologic barrier near the Bosphorus and that hypersalinities prevented emergence of the PontoCaspian fauna, while the marine fauna trailed inward through Gibraltar as the strait rapidly deepened. A hypersaline pool in the Aegean Sea could have formed a barrier until most of the Mediterranean had been occupied by marine species. One would presume that a wet Mediterranean would immediately increase rainfall well to the north in the tributary sources of the Sarmatian, thus increasing its level so as to spill across the Bosphorus and permit faunistic intermingling. If so, polyhalinic Pontogammarids would retreat into the Black Sea.

Black Sea

The Gammaridea of the Black Sea consist of 58 genera and 111 species (Miloslawskaja and Pauli, 1931; Carausu, 1943, Carausu et alia, 1955. Greze, 1977b, see Table 10 and Appendix I). Three genera and 5 species represent incursional beachhoppers. Gammarus crinicornis and G. subtypicus probably are to be included with the weak "marine" invaders which total 37 genera and 74 species. Thirteen species of Corophium occur in the region, about half in limans (lagoons); seven of these also occur in the Caspian Sea. Gammarellus carinatus may have reached the Black Sea from an arctic seaway.

The remaining 21 genera and 37 species are PontoSarmatian. All but 2 species occur exclusively in the limans and all but 14 species occur in the Caspian Sea and 22 of these species occur in the limans of the Azov Sea. Euxinia maeotica occurs in both limans and the open sea. Cardiophilus marisnigrae, considered to be a synonym of C. baeri by Carausu (1943:193) occurs only in the open part of the sea and, therefore, appears to be the only recorded PontoSarmatian amphipod extending toward marine salines.

Only two fossorial marine amphipods occur in the open sea, Bathyporeia guilliamsoniana and Perioculodes longimanus. Despite this poverty, none of the fully fossorial PontoSarmatian species has emerged from the limans into the open sea. The Sarmatian (PontoCaspian or purely Caspian) element in the Black Sea fauna is said to have accumulated very recently (post-Pleistocene), when the Black and Caspian basins were connected through the Manych depression (Caspers, 1957:805). Only a few of these Sarmatian elements are said to be endemic to the Black Sea, the remainder being identical with or, at best, races of the Caspian taxa. Strangely, these Sarmatian elements in the Caspian Sea live in higher salinities, mainly 12-13 ‰ while in the Black-Azov Sea they live in salinities down to 3 ‰. However, such taxa as Pontogammarus maeoticus (now in the genus Euxinia) have spread rapidly in the last 50 years along the more southerly Black Sea coast into higher salinities than found near the northern limans.

Taxonomic difficulties remain to be clarified in light of the above remarks as Karaman and Barnard (1979:130, 136, 139) have extracted several non-conforming identifications of G.O. Sars' Caspian species in the Black Sea by Carausu (1943). In the past 80 years Russian fishing interests and canal connections have caused the transfer of so many amphipod species from one basin to the other, or from the tributary systems of one basin to the other (Jazdzewski, 1980), that modern collections cannot be relied on to solve the question as to which species lived where prior to man's interference.

Azov Sea

The Gammaridea of the Azov Sea consist of 21 genera and 39 species (Miloslawskaja and Pauli, 1931; Mordukhai-Boltovskoi, 1972). Ten genera and 17 species represent late marine invaders from the Black Sea, including one beachhopper. The fully marine species are excluded from the limans. Two species of Gammarus are common freshwater taxa distributed through river systems. Six species of Corophium occur in the region, mostly in limans (not included in Appendix I but added to statistics here). Five of these also occur in the Black Sea and 4 occur in the Caspian Sea.

The remaining 8 genera and 15 species are PontoSarmatian. All but 7 of these species also occur in the Caspian Sea and 14 occur in the Black Sea. All but one species, *Euxinia maeotica*, are confined strictly to limans. The lone species found only in the Azov Sea is *Dikerogammarus bispinosus*.

Lake Baikal

Lake Baikal contains 45 genera with more than 260 species of Amphipoda. In addition to these species almost 80 additional subspecies or varieties have been described. Some of these are probably good species because one would have to demonstrate complete geographic isolation to admit subspeciation as a taxonomic practice in the Baikalian fauna (this problem is discussed later). The Baikalian fauna has a compact literature concentrated chronologically in the works of Dybowsky, Garjajeff, Sowinsky, Dorogostaisky, Bazikalova, and G.S. Karaman (after 1976) with Stebbing (1899c, 1906) having described many of the genera. Almost all of the processiferous Gammaroids of the world are concentrateed in Baikal. Just over half of the genera are conspicuously noted for dorsal body or cephalic projections but only 91 of the 245 species (of 1973) occur in these genera so that Baikal is actually dominated by smooth bodied species. Many of these, of course, bear dorsal spination on the body.

The Baikalian species are very large, often larger than 40 mm long in adult stages and occasionally reaching 80 mm in body length. Their colors are often very striking, "blood-red, green, violet, brown, pink" (Kozhov, 1963:110), mottled and variegated. Their body form is strongly diversified because of the wide range in presence and size of teeth on the body and appendages, in the degree of lateral body compression, the length of major body appendages, and the inflation or discoid appearance of various appendages (bases of pereopods 5-7 or hands of gnathopods).

On first examination the Baikalian amphipods can be divided into 10 groups as follows: (1) The *Heterogammarus* group with extremely close resemblance to *Gammarus-Echinogammarus* group; (2) The *Fluviogammarus* group, like *Gammarus* but article 2 of pereopod 7 bearing a small, sharp posteroventral lobe; (3) The *Acanthogammarus* group, like *Gammarus* but with dorsal body teeth and often with predatorial gnathopods; (4) The *Brandtia* group, like *Gammarus* but antenna 1 shortened and article 2 of pereopod 7 expanded and the body bearing dorsal teeth; (5) The *Baikalogammarus* group, like *Gammarus* but article 2 of pereopod 7 fully expanded and bearing a posteroventral lobe; (6) The *Macropereiopus* group, with articles 2-3 of the peduncle on antenna 1 shortened as in *Pontogammarus*, with article 2 on pereopod 7 expanded, the accessory flagellum remaining more than 2-articulate; (7) The *Micruropus* group, like group 6 but the accessory flagellum reduced to one article; (8) The *Pachyschesis* group, like *Micruropus* but some pereopods prehensile; (9) The *Hyalellopsis* group, like *Micruropus* but with uropod 3 severely reduced and body and pereopod 7 generally expanded and discoid; and (10) The *Macrohectopus* group, body mysidiform and the gnathopods simple, possibly with affinities to the superfamilial group characterized by *Gammarellus*.

In earlier times Baikalian taxonomists have valued patterns of dorsal body ornamentation more highly than now accepted by modern taxonomists. Many of the ornamental species appear to be nektonic or demersal.

Usefulness of ornamentation in identifying and interrelating Baikalian amphipods was extended to the maximum by Bazikalova (1945) in her key to the Baikalian genera (see translation, to follow).

There are several Baikalian clusters of genera sharing such similar body ornamentation that one might suspect close genetic connection among the several taxa (for example, *Spinacanthus* and *Brandtia*, whereas *Garjajewia*, with superficially similar ornamentation, is so radically different in pereopod 7 and antenna 1 that one might suspect simple convergence in ornamentation). Schellenberg (1937b et alia) began a trend towards discounting dorsal ornamenation as a primary attribution in finding taxal clusters, an opinion generally accepted by most freshwater students (personal communications). We believe that such abandonment may have gone too far because many other similar attributes of amphipods are well accepted as useful characters; for example, expansion and protrusion of article 2 on pereopods 5-7, slight size differences in gnathopods subject to almost unclassifiable degrees of transition between one state and another, and degrees and states of setation on various appendages. There is little reason to believe that one or another kind of character is any more conservative than another, or more likely to be subject to processes of mutation and selection, or to be of greater or lesser functional use to the organism. The main objection to use of dorsal ornamentaton as a taxonomic character may be our lack of knowledge about its function and the bad connotation of the term "ornamentation."

Key to the Gammaridan Genera of Lake Baikal

(Translated but semantically modernized, from Bazikalova, 1945)

(Brackets indicate our changes)

(See modern key in Appendix V.B.)

1 (20) Accessory flagellum uniarticulate or absent.
2 (3) Antenna 1 many times thicker than filiform antenna 2. Body thin, weak, highly elongate. Accessory flagellum absent . . . . .23. *Macrohectopus* Stebb.
3 (2) Antenna 1 of same thickness as antenna 2, or only slightly thicker or thinner.
4 (7) Uropod 3 vestigial, one or both rami absent or rarely both rami present and rudimentary. Telson short, entire.
5 (6) Uropod 3 with 2 vestigial rami on inner side of peduncle. Article 2 of pereopod 7 overdeveloped and extending to end of body . . . . 9. *Gammarosphaera* Baz.
6 (5) Uropod 3 composed of peduncle or peduncle and outer ramus, or sometimes both outer and inner rami located at apex of peduncle. Article 2 of pereopod 7 not reaching end of body . . . . 8. *Hyalellopsis* Sow.
7 (4) Uropod 3 with 2 rami, sometimes more or less reduced, not vestigial. Telson cleft.
8 (9) Head with strong erectly bent rostrum, frequently spinose. Body wide, with strong middle and marginal keels, usually spinose on meso and metasome . . . . 7. *Brandtia* Bate.

9 (8) Body smooth or with slight eminences, not spinose.

10 (11) Meso and metasome with slightly rounded, medial and marginal tubercles. . 6. Gmelinoides [Bazikalova].

11 (10) Meso and metasome without marginal tubercles.

12 (15) Anterior body highly expanded. Main peduncular articles of antenna 1 short, swollen.

13 (14) Eyes present. Body length over 6 mm. . . . 1. Crypturopus Sow.

14 (13) Eyes absent. Body length not over 5-6 mm. . . . . .2. Homocerisca [Bazikalova].

15 (12) Anterior body slightly expanded or cylindrical. Main peduncular articles of antenna 1 not swollen.

16 (17) Peduncles of antenna 2 twice as long as peduncles of antenna 1, articles 4-5 of antenna 2 thin, bent. Eyes very large, black reniform . . 4. Baicalogammarus Stebb.

17 (16) Peduncles of antenna 2 less than twice as long as peduncles of antenna 1, articles 4-5 not bent.

18 (19) Uropod 3 armed with strong spines; very occasionally with pinnate setae; in latter case median keels present . . . . .5. Echiuropus Sow

19 (18) Armament of uropod 3 consisting of setae or of setae and spines jointly, never spines alone. . . .3. Micruropus Stebb.

20 (1) Accessory flagellum 2+ articulate*.

21 (22) Article 5 of peduncle on antenna 2 apically swollen, flagellum thin, sharply distinct from peduncle 5 in thickness. . . . . . . 19. Plesiogammarus Stebb.

22 (21) Article 5 of peduncle of antenna 2 not swollen, flagellum almost of similar thickness.

23 (24) Inferolateral angle of head extended as sharp tooth or short rounded lobe. Eyes narrow, elongate, slightly convex, cross set. . . . . . 25. Ceratogammarus Sow.

24 (23) Head and eyes of different construction.

25 (50) Body smooth or with only vaguely marked transverse ribs and marginal tubercles.

26 (27) Rami of uropod 3 of similar or almost similar length, outer ramus 1-articulate, both rami armed with pinnate setae on both margins . . .22. Poekilogammarus Stebb.

27 (26) Uropod 3 of different structure.

28 (29) Lateral margins of mesosome extended downward or outward as teeth. Head extremely convex with downturned rostrum extended as triangular appendages with lateral lobes. . . . . 21. Hakonboeckia Stebb.

29 (28) Lateral margins of mesosome not extended as teeth.

30 (33) Eyes atypical, with excavate posterior margin.

31 (32) Urosomites spinose posteriorly. Forehead high, dropping steeply down. Uropods 1-2 spinose.. 35. Ommatogammarus Stebb.

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*The same group should include Pallasea dybowskii, having a uniarticulate adventitious flagellum.

32 (31) Meta and urosomites spinose posteriorly. Forehead low, gently sloping. Uropods 1-2 with pinnate setae . . . . 18. Leptostenus [Bazikalova].
33 (30) Eyes not posteriorly excavate.
34 (35) Posterior margins of article 2 on pereopods 5-7 produced into powerful spine. . . . . 34. Odontogammarus Stebb.
35 (34) Posterior margins of article 2 on pereopods 5-7 not produced into powerful spines.
36 (37) Flagella of antennae 1-2 calceoliferous. All body segments spinose . . . . 26. Polyacanthisca Baz.
37 (36) Calceoli present only on antenna 2 or absent.
38 (39) Telson divided by gaping notch. Body with vague transverse ribs on boundary of segments . . . . .17. Paragarjajewia [Bazikalova].
39 (38) Telson cleft to base, sometimes to 3/4 only. Body smooth.
40 (41) Palp of maxilliped with vestigial dactyl, outer plate very short, reaching 1/3 - 1/4 length of inner plate. Length of antenna 1 exceeding body length.. . . 31. Abyssogammarus Sow.
41 (40) Palp of maxilliped with normal dactyl, outer plate extending beyond 1/3 length of inner plate.
42 (45) Article 2 of pereopods 5-7 with long and more or less dense setae along posterior margins.
43 (44) Eyes absent . . . . 36. Macropereiopus Sow.
44 (43) Eyes present, sometimes absent; in latter case antennal cone extending to more than half length of article 4 on peduncle of antenna 2. . . . . .33. Pachyschesis [Bazikalova].
45 (42) Article 2 of pereopods 5-7 with spikes or very short single setae along posterior margin.
46 (47) Head with anteriorly protruding lateral lobes. Article 2 of pereopods 5-7 wide, on pair 7 forming narrow lobe exceeding next article. . . . . .32. Lobogammarus [Bazikalova].
47 (46) Lateral cephalic lobes not protruding or only slightly protruding forward. Article 2 of pereopod 7 unlobed or lobe not exceeding next article.
48 (49) Body massive, very compact, extremities thick, shortened. Article 2 of pereopods 6-7 short, pyriform or with incision along posterior margin. . . . . . .37. Fluviogammarus (Dor.).
49 (48) Body less compact, extremities normally built. Article 2 of pereopods 6-7 longer, pyriform, shaft-like or rounded, without incision along posterior margin . . . . .30. Eulimnogammarus [Bazikalova]
50 (25) Body segments with various types of armaments.
51 (56) Body armament consisting only of middorsal keels.
52 (53) Median eminences keel-like, laterally compressed, forming continuous crest when body extended. . . . . 27. Eucarinogammarus Sow.
53 (52) Median eminences forming low triangular or rounded tubercles.
54 (55) Hands of gnathopod 1 almond-shaped, of 2 beaker-shaped. . . . . 28. Carinogammarus Stebb.
55 (54) Hands of gnathopods 1-2 distally extended. . . . . .29. Cheirogammarus Sow.

56 (51) Body with lateral or marginal rows of eminences besides median row.

57 (60) Median eminences weak or absent.

58 (59) Median eminences absent, lateral rows formed of spurs or keels, marginal rows formed of swellings . . 24. Parapallasea Stebb.

59 (58) Median eminences formed of faint tubercles, lateral and marginal rows formed of sharp cusps, sometimes of square plates, occasionally median and lateral rows absent. .20. Pallasea Bate.

60 (57) Eminences of median row most strongly developed.

61 (64) Eminences of one or more rows with secondary spines.

62 (63) Flagellum of antenna 2 flattened, medial margin crenate. Eyes absent . . . . .16. Garjajewia Sow

63 (62) Flagellum of antenna 2 cylindrical, not crenate. Eyes large and dark. . . . . 15. Spinacanthus Dor.

64 (61) Eminences of all three rows lacking secondary spines.

65 (70) Eminences of median row more or less uniformly developed on meso and metasome.

66 (67) Median row of eminences on mesosome and metasome represented by strong sharp spurs or high sharp keels. Coxa 1 not covering head . . . . .13. Acanthogammarus Stebb.

67 (66) Median row of eminences on mesosome and metasome represented by low saddle-shaped, triangular or rounded keels. Coxa 1 strongly developed, directed forward and covering half of head.

68 (69) Article 2 of pereopods 5-7 long, narrow. Gnathopods 1-2 with large hands expanded distally . . . . 11. [Boeckaxelia Schellenberg]*

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*Not Axelboeckia Stebb. which is a Caspian genus.

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69 (68) Article 2 of pereopods 5-7 broad, hands of gnathopods slight, in pair 1 almond-shaped, in 2 beaker-shaped. . . . . 10. Dorogammarus [Bazikalova]

70 (65) Keels of median row of eminences more intensely developed on metasome or urosome; mesosome smooth or with low tubercles and transverse ribs.

71 (72) Keels on median row of body more highly developed on urosomites 1-2. Head smooth . . . . 14. Coniurus Sow.

72 (71) Keels on median row of body best developed on metasome. Head with longitudinal keels . . . . .12. Carinurus Sow.

We do not wholly abandon the use of configurations in teeth, humps, and spination patterns, though in this presentation of Baikalian taxonomy ornamentation is used in lesser degree than by Bazikalova.

Classification of Baikalian amphipods is rendered difficult not only by the complications of ornamentation but also by the varying degrees of other pelagic adaptations, such as predatorial gnathopods and great elongation of appendages. In the marine biome predatorial gnathopods are best illustrated in the Eusirids where the hands are inflated, the palms have become simplified and elongate, the dactyls have become much more powerful and flexibility of the appendage has been increased through narrowing of the connection between the hand and the wrist. Both pairs of Eusirid gnathopods are often identical. In Baikal this kind of gnathopod is best seen in Acanthogammarus but varying degrees of development are seen in similarly cuspidate genera. No sharp line of demarcation occurs between the Acanthogammarid gnathopod and gnathopods of the Gammarus form, suggesting that various species occupy transitional niches that are neither fully predatorial and nektonic nor fully passive and benthonic.

An occasional marine raptorial scud has piercing and sucking mouthparts but as far as known no Baikalian amphipod has these mouthparts. Another fraction of toothed Baikalian amphipods has clearly nektonic adaptations, such as elongate appendages, but most toothed Baikalian amphipods do not appear to be in this ecological category. Hence, the function of dorsal processes in the majority of cases is unknown. The precise habitats of Baikalian amphipods are insufficiently recorded to make any approximation as to whether or not most toothed species are nektonic; one might suspect that this is the case but, at least, the species are epibenthic or demersal. This habit would fit the environment: a body of water with a high ratio of water volume to bottom area. The processes themselves may have some survival value in maintaining nektonic positions through storage of oil or increase in body surface to counteract sinking rates or as defense mechanisms. This opposes the supposition that the species might require streamlining for swift predatorial motions. Heavy chitinization occurs in many of the genera with strong lateral protuberances on the pereon, suggesting that body weights are high and that many species are rather cumbersome. Several species appear as overspecialized as do the edaphosaurians.

The special Baikalian form of nonpredatorial gnathopod is noted by Stock (1969a:68, 1974c:83) in which the male propodus of gnathopod 1 is larger than that of gnathopod 2. The ordinary Gammarus-form has both propodi of subequal, almost identical size. Most Caspian fossorial genera have the propodus of gnathopod 2 much larger than gnathopod 1. In Baikal the larger first gnathopod dominates the nonpredatorial fauna. In the most extreme cases, male gnathopod 1 is quite large, whereas gnathopod 2 assumes a female form. The propodus (article 6) of male gnathopod 1 is large, almond shaped or becoming ovatorectangular, with very oblique palm becoming more transverse, with normal Gammarus-like midpalmar spines often reduced in more apomorphic forms. Gnathopod 2 is very slender, with elongate wrist and hand, the hand thin and rectangular, with short, scarcely oblique palm having reduced spination. This gnathopodal configuration is termed "Eulimnogammarid" after the genus in which it was first picked out as an important attribute.

Two schools of opinion differ as to the taxonomic importance and evolutionary background of this kind of gnathopod as a contrast to the normal "Gammarid" gnathopods or the Caspian "Pontogammarid" gnathopods. One school suggests that the Eulimnogammarid configuration is monophyletic and primitive, whereas the other school believes that the Eulimnogammarid state is polyphyletic and apomorphic. In the former belief one could then trace extrinsic Baikalian amphipods with Eulimnogammarid gnathopods, to a Baikalian ancestry (or at least predominantly so). It could be useful as a character at familial level. The opposite school draws on the numerous marine cases where axial reversal in dominance occurs within families (J.L.

Barnard, 1973) and between Eulimnogammarid and Gammarid gnathopods, even within the Baikalian fauna and even intragenerically in *Heterogammarus* or *Eulimnogammarus*. The predominance of Eulimnogammarid gnathopods in Baikalian genera may have selective advantage in that very special environment. Gnathopods are so poorly studied morphofunctionally that little is known, though much is speculated, about small advantages in the numerous states of those appendages. Amphipoda are often so widely omnivorous and opportunistic that taxa which otherwise appear to be benthic nestlers or even partly fossorial may function as part-time predators or large-carcass scavengers. Because Baikal is a dominantly pelagic environment, many benthic or nestling Amphipoda there may actually be ecological opportunists.

Everywhere in Palearctic taxonomy the size of the inner ramus on uropod 3 is highly valued as a taxonomic marker. Outside of Baikal the short inner ramus marks *Echinogammarus* (= *Marinogammarus*, = *Chaetogammarus*) from *Gammarus* and in Baikal the short inner ramus is used to distinguish *Eulimnogammarus* and its allies from *Heterogammarus* and its allies. This is another character where no precise discontiguity can be recognized. Because the majority of Gammaroids has the shortened form of inner ramus, one must suppose it has a selective advantage but the function is unknown.

The development of posteroventral protrusions on article 2 of pereopods 5-7 also marks groups of Palearctic Gammaroids, some of which are otherwise very close to the *Gammarus* and *Heterogammarus* ancestral forms and others of which may be far more remote. The ultimately developed expansions and dense setosities of these articles appear to mark fossorial amphipods.

The Evolutionary Pattern

There is clearly a progression from simple to complex in many Baikalian characters and, in contrast, several cases of simplification (such as pygidization in the *Hyalellopsis* group); but no straight-line evolution can be perceived. Several groups, such as those characterized by *Hyalellopsis* and *Macrohectopus*, are quite distinctive because their transitional ancestors have become extinct; but, for example, there is no evidence that all toothed genera have a common ancestor, nor those genera with expanded article 2 on pereopod 7. No good evidence exists that the *Pontogammarus*-like Baikalian genera have had a common ancestor and there is some difficulty distinguishing between *Pontogammarus*-like and *Gammarus*-like antennae because there are several intergradational genera (such as *Baikalogammarus*). Baikalian amphipods are not as strongly dominated by fossorial forms as are the PontoCaspian faunas and the Baikalian fossorial forms are themselves more weakly developed, with the exception of *Micruropus*. The antennae and pereopods are rarely as well adapted as in PontoCaspian genera, although heavy setation on uropods 1-2 is more widespread in Baikal than in PontoCaspia. About 14 of the 45 Baikalian genera (1979) (including the subgenera we have treated as genera) have a degree of fossorial adaptation. This comprises about 30 percent of the genera and 30 percent of the species (74 out of 245) (counted in 1974). But one must suspect that some of these so called fossorial taxa actually are engaged in other functions, for which fossorial adaptations are also well suited. Baikal lacks vast areal expanses of even or flat benthos, unlike the PontoCaspian basins, but is steeply sloped and very deep. Flat bottom is largely confined to the Sors (lagoons) at several river mouths. One would expect Baikal to be dominated by epifaunal and nektonic amphipods, as is the case. The weakness of the fossorial mode in morphology of the Baikalian taxa therefore reduces the actual fossorial index to some much lower percentage than 30.

1. *Heterogammarus* group.

This cluster of genera has the basic and primitive characters typical of *Gammarus*, with elongate peduncle on antenna 1, not of the *Pontogammarus* form, unexpanded or otherwise normal article 2 of pereopods 5-7, normal uropods and telson, glabrous anterior coxae, and the body lacks dorsal teeth, though articulate spines occur on the pleon.

The genus apparently most similar to *Gammarus* is *Leptostenus* (1), which differs from *Gammarus* mainly in the presence of dorsal spination on pleonites 1-3 and in the irregular posterior and dorsal outline of the eye. *Leptostenus* and *Abyssogammarus* (3) (see also group 2) resemble *Gammarus* in the magniramous uropod 3 but *Abyssogammarus* is characterized by hugely elongate uropods, pereopods and antennae, especially article 3 of antenna 1, and elongate wrist of gnathopod 2. *Ceratogammarus* (see group 2) may belong to this group because of its magniramous uropod 3 but the genus is often characterized by a large cephalic cusp, pereopodal cusps, and the presence of sets of dorsolateral spines on the pleon and posterior pereon. Gnathopod 2 is distinctly smaller than gnathopod 1 and both are somwhat modified toward the Acanthogammarid form. Like so many Baikalian Gammarids article 3 of antenna 1 is elongate.

The type-species of *Heterogammarus* (3) differs from *Gammarus* in the elongate peduncle of antenna 1.

Poekilogammarus (18) differs from *Heterogammarus* in the loss of article 2 on the outer ramus of uropod 3. Article 3 of antenna 1 is elongate. The genus is divided into 5 subgenera, of which (*Gymnogammarus*) is noted for the reduction of the inner ramus on uropod 3, (*Rostrogammarus*) and (*Bathygammarus*) have elongate setae on uropods 1-2 but differ between themselves in the short-broad or long-narrow article 2 of pereopods 5-7, and (*Onychogammarus*) differs from (*Poekilogammarus*) in the smooth body (lacking knobs) and the elongate peduncle of antenna 2. Although *Carinogammarus* (1) is placed later in this scheme, one must note that it is simply *Heterogammarus* with median carina. *Eucarinogammarus* (1) then deploys outward from *Carinogammarus* by development of dorsal vertebral body teeth. *Baikalogammarus* (1) is simply *Heterogammarus* with accessory flagellum reduced to 1 article. In the Handbook [Appendix VI] these genera are arranged differently than in the text to show some of the possible permutations. The remaining 2 uncuspidate genera of this group differ from *Gammarus* in the shortened inner ramus of uropod 3 but differ from similar non-Baikalian *Echinogammarus* and (*Chaetogammarus*) in the rounded anterodorsal corner of the cephalic lobe and shortened coxa 1. They closely resemble (*Marinogammarus*) but have dorsal spination on the pleosome unlike *Gammarus*. In this respect they resemble the non-Baikalian *Echinogammarus* but lack the setation of various body parts as outlined by Stock (1968:19) in his differentiation between (*Chaetogammarus*) and *Echinogammarus*. The 2 genera are *Eulimnogammarus*, sensu stricto (11), and *Corophiomorphus* (11).

Eulimnogammarus appears to be composed of 5 groups of species, one of which is *Heterogammarus* and mistakenly put into the junior genus *Eulimnogammarus* by Bazikalova (1945). That genus is removed and continues to represent the most primitive of the Baikalian genera. The following key shows the division of *Eulimnogammarus* and *Heterogammarus* into components, albeit poorly distinguished:

Key to the *Heterogammarus* Generic Cluster

1. Article 2 of pereopods 5-7 ordinary 2
   Article 2 of pereopods 5-7 with produced posteroventral corner
   (or one or more of pereopods with this lobe). 4
2. Article 2 on outer ramus of uropod 3 absent . . . .*Eulimnogammarus*
   Article 2 on outer ramus of uropod 3 present. 3
3. Inner ramus of uropod 3 about 50 percent or more as
   long as outer ramus . . . . *Heterogammarus*
   Inner ramus of uropod 3 40 percent or less as long
   as outer ramus . . . . *Corophiomorphus*
4. Inner ramus of uropod 3 40 or more percent as long
   as outer ramus . . . . *Eurybiogammarus*
   Inner ramus of uropod 3 33 or less percent as long
   as outer ramus . . . . *Philolimnogammarus*

The two genera of couplet 4 are put into the *Fluviogammarus* section of the Baikalian fauna because of the modified article 2 on one or more of pereopods 5-7.

The next grade of evolution concerns genera resembling *Gammarus* but with the development of dorsal body teeth. These genera are termed the *Pallasea* subgroup.

Metapallasea (1) is the first of 2 genera in the subgroup with well developed article 2 on the outer ramus of uropod 3, but uropod 3 is fully parviramous, a condition rarely encountered elsewhere in this subgroup. The dorsal teeth of *Metapallasea* are poorly developed and mainly confined to bilateral humps on pereonite 7 and pleonite 1. Coxa 5 has a slightly extended anteroventral lobe. The dactyls of the posterior pereopods are elongate.

Palicarinus, new genus (1) (Appendix VI) also bears well developed article 2 on the outer ramus of uropod 3 but the dorsal teeth of the body are very complex, each pereonite and pleosomite being divided into a dorsal compartment with concave margin, with 2 lateral compartments at right angles to the dorsal, the separation effected by a low pair of alate outwardly directed lateral carinae. Uropod 3 is variramous.

Finally, *Pallasea* (14) and *Parapallasea* (3) are characterized in ornamentation by the fact that at least one body segment has a pair of bilaterally disposed dorsolateral teeth. The telson is highly variable in the genus, ranging from partly cleft to entire; uropod 3 varies between magniramous almost to parviramous; and article 2 of pereopod 7, like that of *Boeckaxelia* and *Carinurus* may bear moderately developed posterior setation. Parapallasea differs from Pallasea in the absence of a median carina on the pereosome and pleosome and this leaves non-Baikalian species like Pallasea quadrispinosa somewhat difficult to place because of the vestigial median carina. For this reason and because of the loss of major spines on the gnathopodal palms and the reduction of the accessory flagellum to 2 articles, the famous species of Arctic seas and lakes, quadrispinosa (= laevis) is removed to a new genus, Pallasiola (1) (Appendix VI).

The Heterogammarus group of Baikal forms a tight complex of genera so closely related to the Gammarus (Echinogammarus-Marinogammarus-Chaetogammarus) group, that one cannot find an organic break between the Baikalian and non-Baikalian genera that would narrow the ancestry for the Baikalian group to a single isolate. The connection from inner to outer Baikalian is broadly spectral.

2. The Fluviogammarus Group

This group is characterized by the retention of a sinuous posterior margin on article 2 of pereopod 7 but the posteroventral corner becomes weakly produced. There is no evidence these genera are monophyletic.

Spinacanthus (5) has the appropriate pereopod 7 for this group but is so grossly toothed and spined dorsally on the head and body that its further relationships are discussed with Brandtia in group 5.

Fluviogammarus (4) is characterized by weak pairs of teeth on urosomites 1-2 whereas all remaining genera possess only dorsal spination on the urosome.

Eurybiogammarus (29), formerly a subgenus of Eulimnogammarus, is very difficult to separate from Fluviogammarus. Eurybiogammarus has normal Gammarus-like gnathopods. Philolimnogammarus (13), Lobogammarus (1), and Paragarjejewia (1) have the Eulimnogammarid gnathopods, gnathopod 1 like Gammarus but gnathopod 2 very slender and elongate. Paragarjajewia is characterized by extremely elongate antenna 1. Lobogammarus has a strongly extended cephalic lobe.

Polyacanthisca (1) is very close to Eurybiogammarus not only in the fact that dorsal spination runs forward onto the pereon but also in the variramous uropod 3. However, the gnathopods of Polyacanthisca are modified in a thin version of Acanthogammarid form.

Hakonboeckia (1) has a sharp medium sized lobe on pereopod 7 but is toothed on the head, laterally on the pereosome and dorsally on the posterior pereosome and pleosome.

Odontogammarus (3) has a narrow, elongate and sharp posteroventral lobe on article 2 of pereopods 5-7 coupled with normal Gammarus-like antenna 1 and has a sharp anteroventral lobe on coxa 5.

Ceratogammarus (3) has an extended ocular lobe, articles 2-3 of antenna 1 are elongate, gnathopod 1 is strongly dominant and pereopods 3-4 are of weak filtrative form.

Abyssogammarus (3) is the ultimate pelagic form of this group with greatly elongate pereopods, uropods and antennae but lacks the characters mentioned for Ceratogammarus except the elongate antennal articles.

Koshovia (1) is a strange genus, recently described, which has many characteristics of Abyssogammarus, such as thin pereopods, but which has an uncleft, alate telson.

3. Acanthogammarus Group

This group contains genera with Acanthogammarid gnathopods and cuspidate bodies. In the Baikal fauna Acanthogammarid gnathopods are intergraded with those of the Gammarid form so broadly that a family based on this character alone would not be valid owing to lack of clear discontiguity. Article 2 on the outer ramus is absent or vestigial.

Acanthogammarus (12) is characterized by the large and equal predatorial gnathopods familiar to marine students of Gammaracanthus or Rhachotropis (Gammaracanthus is an assumed marine and relict escapee from Baikal, related to Acanthogammarus). The subgenus Brachyuropus has a reduced and parviramous uropod 3. Boeckaxelia (see group 4) has these gnathopods less fully developed and coxa 1 does not turn forward anteroventrally. Acanthogammarus has cuspidate anterior coxae whereas those of Boeckaxelia and Carinurus (group 4) are not cuspidate. The latter genus has very short antennae and characteristic domination by the dorsal tooth on pleonite 3 or the teeth of pleonites 1-3 and pereonite 7.

The Acanthogammarid gnathopods of Garjajewia (3) are somewhat reduced and some of the pleosomal segments bear spines on the teeth in contrast to Acanthogammarus. Article 5 of antenna 2 has a jagged margin. Article 2 of antenna 1 is very short but article 1 is so elongate that the genus cannot be placed with the Micruropids.

Eucarinogammarus (1) is otherwise very simple except that all pereonites and pleosomites are raised upward in columns similar to spinal processes in vertebrates. Antenna 1 is elongate. Plesiogammarus (3) has poorly developed dorsal processes all along the body, has ventrolateral pereosomal humps, has gnathopod 2 larger than gnathopod 1 and is characterized by a circlet of plumose setae on the thickened end of article 5 on antenna 2.

Cheirogammarus (1) is very similar to Carinogammarus (group 4) but has enlarged, almost Acanthogammarid gnathopods with definitely lobate article 5 on gnathopod 2. Pereopods 3-4 are as setose as in Echinogammarus.

4. Brandtia Group

This artificial group has article 2 of pereopod 7 expanded, and usually antenna 1 short, but article 2 slightly more than half as long as article 1, and the body is furnished with dorsal teeth or processes. A special key (M-3) to this group is found in Appendix V. Perhaps the least specialized of this group is Carinogammarus, in which uropod 3 is at least variramous, article 2 on the outer ramus is present, pereopod 7 is modified the least, the gnathopods remain Gammarus-like and even the antennae are very similar to Gammarus. In earlier days some of the species (but not the type) had moderately developed posterior setation on article 2 of pereopods 5-7 but these were removed to Echiuropus by Bazikalova (1975a).

Gmelinoides (2) closely resembles Gmelina and Gmelinopsis in the PontoSarmatian fauna. It appears to be closest to Gmelina but differs in the slightly larger gnathopods and the more strongly elevated urosomites. Article 2 on the outer ramus of uropod 3 is vestigial. It is absent on all following genera in this group.

Hakonboeckia (1) (see group 2) has a sharp posteroventral lobe on article 2 of pereopod 7 similar to *Odontogammarus* (group 2) but differs from that genus in the much shortened antennae, the loss of article 2 on the outer ramus of uropod 3 and in the rugosal body condition, with sharp ventrolateral pereonal points, a large rostrum and large anteroventral cephalic tooth. *Hakonboeckia* can also be visualized as a remote descendent of *Boeckaxelia*.

Coniurus (3) is characterized by the enlarged gnathopods with gnathopod 1 much larger than gnathopod 2, with article 5 of gnathopod 2 almost lobate, combined with magniramous uropod 3 and dorsal tooth domination on the urosome.

Boeckaxelia (3) is also characterized by enlarged gnathopods but they are of subequal size. Dorsal tooth domination does not occur on the urosome and, unlike *Coniurus*, article 2 on pereopods 5-7 is almost homogeneous.

Carinurus (10), *Brandtia* (1), and *Spinacanthus* (5) (also see group 2) have dorsal tooth domination elsewhere than on the urosome, have *Gammarus*-like gnathopods and usually have dorsal processes and spines on the head. *Spinacanthus* was placed in group 2 because of the weak but sharp posteroventral cusp on article 2 of pereopod 7 but *Brandtia* has that article widely expanded and unproduced ventrally. *Brandtia* differs from *Carinurus* in the reduced accessory flagellum.

Dorogammarus (1) is distinguished in this group by article 2 of antenna 2 being significantly shorter than article 1. In other respects it appears to match *Boeckaxelia* but has a larger hump on urosomite 1, more deeply cleft telson, smaller and unexpanded gnathopods.

5. *Baikalogammarus* Group

This section contains only *Baikalogammarus* (1), in which article 2 of pereopods 5-7 is expanded, deeply lobate ventrally and weakly setose posteriorly. Antenna 1 remains of the *Gammarus* form but has article 2 as long as article 1. *Baikalogammarus* appears to stand between *Carinogammarus* and the Micruropids, differing from *Carinogammarus* in the ventral lobes of the pereopods but not having attained the *Pontogammarus*-like antenna 1. The genus differs from similar Dikerogammarids in the PontoCaspian basin in the reduction of the accessory flagellum to one article, similar to Micruropids. Uropod 3 is maintained in well developed variramous condition unlike most PontoCaspian genera. Article 2 on the outer ramus is present, the peduncle is elongate, coxae 1-4 are glabrous, the male gnathopods are enlarged but *Gammarus*-like, the telson is ordinary and cleft more than halfway and pereopods 3-4 are not fossorial.

6. The *Macropereiopus* Group

This group is the Baikalian analogue of the Dikerogammarids. The genera differ from Dikerogammarids and *Baikalogammarus* in the dominance of male gnathopod 1 and the shortness of article 2 on antenna 1. Article 2 of pereopod 7 is expanded but the accessory flagellum remains 2+ articulate in contrast to Micruropids, to follow.

Macropereiopus (7) differs from *Ommatogammarus* (3) in the broader expansion of article 2 on pereopod 7, the setosity of that article and in the dissimilarity of article 2 among pereopods 5-7. In Ommatogammarus, article 2 on pereopods 5-7 is similarly expanded, though weaker than in Macropereiopus.

7. The Micruropus Group

This group is the Baikalian analogue of Pontogammarids in the Caspian Sea. Peduncular article 2 on antenna 1 is very short but unlike Pontogammarids the gnathopods take the common Baikalian form in which gnathopod 1 is as large as or larger than gnathopod 2, whereas in Pontogammarids gnathopod 1 is weakly to greatly smaller than gnathopod 2. The Micruropids also have the accessory flagellum reduced to one article. Setae on articles 4-5 of pereopods 3-4 are always tufted and generally far less densely furnished than in Pontogammarids. The primary flagellum of antenna 1 is generally more elongate than in Pontogammarids. Article 2 of pereopod 7 is widely expanded but scarcely lobate ventrally. Antenna 1 of Pontogammarids is somewhat more densely setose than in Micruropids but the setae of antenna 1 in Micruropids are the short stiff variety found in Pontogammarids.

Micruropids strongly resemble the Gmelinids and Pontogammarids of the PontoCaspian regime. The two former groups both have the accessory flagellum reduced to one article and many of their taxa have gnathopod 2 enlarged. Perhaps in these two groups are found the best cases of probable faunal mixture between Baikal and the PontoCaspian. Yogmelina and Gmelinoides differ mainly in body tuberculation of the latter genus and broader and more setose article on pereopod 7. Gmelinoides differs from Obesogammarus mainly in the 1-articulate accessory flagellum and tuberculate body.

Micruropus (30) typifies this group in that article 2 of pereopod 7 is fully expanded and setose posteriorly but it is not or scarcely produced ventrally. The genus has probably the best Baikalian development of the Pontogammarus antenna 1 as facial armament is dense on several species. Pereopods 3-4 are distinctly fossorial. Uropod 3 is either parviramous or variramous. Micruropus also differs from Pontogammarus in the clumped setation on article 4 of pereopod 4 and in the nonventral protrusion of article 2 on pereopod 7. The gnathopods in the many species are variable in proportions of size and shape to each other.

Micruropus has 4 subgenera. The typical subgenus has densely setose epimera and pereopods 3-4. The others do not. Microgammarus retains article 2 of the outer ramus on uropod 3 but the following 2 genera do not. Setogammarus has long plumose setae on uropods 1-2 whereas Gammarisca has only spines.

Pseudomicruropus (4) scarcely differs from Micruropus except in the mandibular palp (see key).

Echiuropus (13) resembles Micruropus but the setae on uropod 3 are not pinnate.

Crypturopus (5) scarcely differs from Micruropus and needs further elucidation. Bazikalova (1945) distinguished Crypturopus in her key on the broadened body anteriorly and on the broader article 1 of antenna 1. Article 3 of the peduncle and the accessory flagellum are very distinctive because they are greatly swollen and article 3 is as long as article 2.

Homocerisca (3) has the thickened article 1 of antenna 1 typical of *Crypturopus* but article 3 and the accessory flagellum are not swollen, the eyes are absent and antenna 2 has the form of *Stenogammarus*, in which article 5 of the peduncle and article 1 of the flagellum are so similar that the peduncle appears to merge with the flagellum imperceptibly. *Homocerisca* has the strongest ventral lobation on pereopod 7 seen in the family group.

8. The *Pachyschesis* Group

Pachyschesis (4) contains an aberrant group of species found only as commensals in the marsupia of other Baikalian amphipods. Article 2 of pereopods 5-7 is expanded but poorly setose, the anterior coxae are strongly setose and antenna 1 has the form but not the setosity of *Micruropus*, while the 5 sets of posterior pereopods are weakly prehensile apparently to grasp the host amphipod. The setation on the inner plates of the maxillae is strongly reduced as a fairly unique condition in the Baikalian fauna. See a discussion of this genus with the Cardiophilids in the Caspian Sea section.

9. The *Hyalellopsis* Group

This division is an extension of groups 4-7, in which article 2 of pereopod 7 is well expanded and ventrally lobate but in which antenna 1 is of the *Gammarus* form. The body is either smooth or dorsally rugose. The distinguishing feature of the group is the severe reduction of uropod 3 to a tiny peduncle bearing one ramus and the discoid expansion of the body and pereood 7. The telson is small and entire. *Gammarosphaera* (1) differs from *Hyalellopsis* (17) in the greater vestigiality of uropod 3 and the greater shield-forming capacity of pereopod 7.

10. The *Macrohectopus* Group

Macrohectopus (1) stands alone. It fits the group 2 concept in its *Gammarus*-like antenna 1 but with article 3 highly elongate, in the unexpanded article 2 of pereopods 5-7 and in the presence of dorsal body teeth but it has departed very radically from other Baikalian Gammaroids in the essentially simple gnathopods, lacking definite palms but with weakly expanded hands. The body is mysidiform and has the pleosome enlarged and dorsally toothed; pereopods 6-7 are highly elongate, 6 the longer; the antennae and uropods are also highly elongate, whereas pereopods 5-7 are very small. It may belong with the *Gammarellus* superfamilial group.

A fossil PontoCaspian genus, *Hellenis*†, also has the thin bodied and long legged character of *Macrohectopus*, but the coxae are obsolescent and the body lacks a giant tooth.

Baikalian Escapee

Issykogammarus (1) from Lake Issykul in Central Asia, has many parallels with *Typhlogammarus* (see Metohiids) but is presumed to have affinities with Baikalian genera. *Issykogammarus* differs from *Typhlogammarus* in the lack of setal specialization on pereopods 5-7, in the more elongate telson, presence of article 2 on the outer ramus of uropod 3, the lesser irregularity of the anterior coxae, though coxa 4 bears an anteroventral cusp pointing laterally, in the much shorter peduncle of antenna 1 with article 2 only half as long as article 1 (like Pontogammarus but primary flagellum elongate) and in the weaker specialization of the male gnathopods. Instead of gnathopod 1 being slightly dominant, gnathopod 2 is slightly dominant and, being a blend of the Gammarus and Acanthogammarid forms, neither is as strongly Acanthogammarid as they are in Typhlogammarus. Issykogammarus has about as many or more characters in common with either Acanthogammarus or with Pallasea as with any other genus in Palearctica.

Baikalian Environment

Baikal is the deepest lake in the world and holds more water than any other lake. It may have as much as 20 percent of all freshwater on earth. The lake is elongate, slants northeast to southwest and is considered to be an embryonic tectonic rift between two future crustal plates (Dietz and Holden, 1970). Baikal is about 635 km long, has a maximum width of 75 km and is about 1742 m deep. Its bottom is divided into two large basins separated by a sill at the depth of 455-472 m (sources vary in this fact). Baikal probably has undergone much change in its morphology over the eons. Rocks around Baikal date from the Mesozoic but parts of the basin probably didn't come into existence until the early Tertiary, merging at the end of the Tertiary, the whole basin deepening no earlier than mid-Tertiary and perhaps not until the beginning of the Quarternary (Kozhov, 1963:268-272).

Besides amphipods, the lake has numerous species of mollusks and copepods, some of which are clearly of freshwater ancestry but the lake also contains marine elements, such as a seal. Kozhov believes in a mixed origin for the fauna, some from the marine world having immigrated by rivers, others having come from the Sarmatian-Maeotican-Pontian and Aralo-Caspian sources. One of the first theoreticians, Berg (1910), believed that Baikalian organisms had a freshwater origin in the widespread warm water Pliocene-Pleistocene fauna of Asia and Europe (the China fauna). Kozhov (1963:280), of course, points to the marine aspect of the fauna being steadied by the marine character of the lake, its magnitude and depth being of gigantic proportions. Both Dorogostaivsky (1923) and Taliev (1948) believe that most of the species are of Pliocene and Pleistocene character owing to rapid speciation late in the history of the lake (see Kozhov, 1963:282, 292, for those references). Kozhov believes in sympatric speciation, arguing that places for physical isolation are too few to permit allopatric speciation. The evolution of deepwater forms could not occur in any other means than sympatrically according to Kozhov. He implies that there is a great deal of variability in the species and may be implying that many of the so-called species are simply taxal morphs or phenotypes.

To a large extent the amphipodan composition in Baikal has remained undisturbed by transplantation experiments except for the massive injections of Gammarus lacustris through ice holes for winter fishing; this species now survives in the shallow fringes of the lake. Whether or not it lived in Baikal before mankind introduced it is unknown. During the 1960's the world press reported on massive Baikalian pollution from wood-pulp mills but in 1978 reports circulated that this has been ameliorated.

Bazikalova's Conclusions about Baikalian Gammarids

Bazikalova's (1945) monumental work on Baikalian Gammarids summarized her own views and those of her predecessors on the interrelationships and origin of the Amphipod fauna. She believes Baikal is a center distinct from the Caspian. She points out the very close relationship of the basic Baikalian genera *Eulimnogammarus* and *Eurybiogammarus* to *Echinogammarus* and *Gammarus*, though refusing to make any of the Baikalian genera synonymous with the latter two genera. At another point in her book she affirms the strength of their differences though these are not specified except to note that Baikalian taxa have distinctly enlarged gnathopod 1 and distinctive spination positions [we can scarcely find these distinctions].

Bazikalova extracts much value from Taliev's (1940) work on cross matching of sera among various species and by comparing them to *Gammarus*, she concludes that the most ancient (we rename them "basic") Baikalian genera are *Eulimnogammarus*, *Pallasea*, *Acanthogammarus*, *Crypturopus* and *Hyalellopsis* [here we have altered her order to proceed from generalized to specialized in our opinion]. We agree that these are satisfactory foci of evolutionary staging points but consider that the last mentioned genus is much too specialized to be considered as old as the others; and, as discussed elsewhere, we consider *Acanthogammarus* a possible ancestor of all freshwater Gammaridans in the contrapuntal predator-nestler ancestor problem.

The five basic genera mark 5 major groups of amphipods in the lake:

GROUP 1

Eulimnogammarus
[*Heterogammarus*]
Abyssogammarus
Pachyschesis
Lobogammarus
Odontogammarus
Ommatogammarus
Fluviogammarus
Polyacanthisca

GROUP 2

Pallasea
Parapallasea
Ceratogammarus
Hakonboeckia
Poekilogammarus
Macrohectopus

GROUP 3

Acanthogammarus
Carinurus
Coniurus
Spinacanthus
Garjajewia
Paragarjajewia
Plesiogammarus
Leptostenus

GROUP 4

Crypturopus
Homocerisca
Micruropus
Gmelinoides
Baikalogammarus
Echiuropus

GROUP 5

Hyalellopsis
Brandtia
Dorogammarus
Axelboeckia

Unknown: *Carinogammarus*, *Eucarinogammarus*, *Cheirogammarus*, *Macropereiopus*.

Bazikalova implies that evolutionary deployment proceeds from complex and highly ornamented ancestral types (such as those on the right of the above scheme, the order of which we have reversed from her presentation) to the left and upper where ornamentation and complexity are lost and the primordial Gammarus-like genus appears and, one presumes, escapes to the remainder of Palearctica.

Studies of osmotic pressure in the internal body fluids of Baikalian Gammarids suggest that Baikalian amphipods (Eulimnogammarus, Odontogammarus, Micruropus) are closer to marine forms than are such wide ranging Holarctic freshwater taxa as Gammarus lacustris (Kozhov, 1963:116). This implies a marine origin for the Baikalian Gammarids as well as the assumption that Baikal was the nursery ground for Palearctic Gammaroids. But Bazikalova does not organically reach that conclusion because she presents the alternative views of: (1) Berg, the founder of the proposal of a freshwater origin for the Baikalian fauna from an Upper Tertiary pandemic Palearctic fauna; (2) the Vereshchagin proposal of Cretaceous marine transgressions leaving behind basins in the Transbaikal, from which sweetwater Tertiary species evolved [we have misstated this viewpoint somewhat]; or (3) the Hoernes-Martynov-Taliev view that the fauna is a residual of an intracontinental Tertiary basin [presumably, in part, the Sarmatian-PontoCaspian-Lac Mer Basin] fluctuating between salt and sweet waters, with the species making their way into Baikal through various Siberian lakes and torrents. [But Taliev (1955) concludes that the northern seas provided the prime source of species in Baikal and Caspian faunas.]

Although Bazikalova points out some close serological relationships between Baikal and the Caspian Sea from Taliev's earlier work regarding the pairs of Micruropus-Pontogammarus, Crypturopus-Niphargoides, Gmelinoides-Gmelina [meaning Yogmelina], Hyalellopsis-Axelboeckia [she wrote Boeckia] and Gmelinoides-Pontogammarus, and between Acanthogammarus albus and Amathillina spinosa (among several other matches) she does not accept a Sarmatian origin for the Baikalian fauna, nor an origin from sweetwaters of the Transbaikal (the region east of Baikal). She does, however, note the obvious interchange with glacial lakes of the genus Pallasea [part of which we remove to Pallasiola]. Bazikalova concludes that the Baikalian fauna comes from an unknown ancient sea which underwent gradual desalinization, but which contained a rich amphipod fauna including the present Baikal faunal ancestors as well as the ancestors of Gammarus [the assumed ancestor of the greater Palearctic Gammaroid fauna]. A great deal of that conclusion is weighted by knowledge on the origin of other parts of the Baikal fauna used by Vereshchagin and to be found (in retrospect) in Kozhov (1963).

Bazikalova makes an evolutionary distinction between fossorial and nestling (or predatorial) kinds of amphipods which she terms respectively, "Pontogammarian" and "carnivorous". She notes such strong distinctions between the two groups of amphipods in Baikal that she assumes they had different ancestors. The roots of the amphipod fauna are very old but she believes that most of the species are quite young, meaning that the lake evolved slowly but that more rapid geomorphic events have occurred lately and thus more speciation has occurred in later times. She follows Vereshchagin in accepting: (1) straight line descent of the fauna over long duration; (2) slowness of ecological variations permitting adaptation to change by the organisms; (3) prolonged isolation. The latter preserves ancient faunas and allows them to diverge and speciate.

Evolution of the Baikalian Fauna

Between the alternatives of microcosmic evolution within the Baikalian fauna and extensive interconnection of the Baikalian fauna with that of the SarmatoPontoCaspian basins, we accept the view that congruencies among species in Baikal, the Caspian Basin and various lakes (such as Ohrid) result from the coincidence of parallel evolution. We agree that very little Sarmatian mixture needs to be invoked (though clearly a few taxa, such as *Axelboeckia* and *Brandtia*, seem almost too similar to be merely the happenstance of parallel evolution) and allow that such mixture could have taken place. The mechanism of rivers and glacial lakes is not yet adequate for our purposes, however.

One clearly cannot dismiss the sibling character of *Gammaracanthus* and *Acanthogammarus* nor can one dismiss the cross-identity of species of *Pallasea* and the *Pallasea*-group in general, all of which clearly shows that connections with PontoCaspia and glacial lakes of Europe did occur at some time, though these may have come late in the evolutionary cycle.

The bulk of the Baikal fauna is microcosmical though clearly with very similar if not identical ancestry in a generalized Palearctic fauna of the Mesozoic or earlier times.

Nearly 50 species have escaped Baikal into the Angara and 20 have made their way almost to the sea in conjunct river systems but otherwise farther escape is confined to *Pallasea* and *Gammaracanthus*. *Gammaracanthus* is also a good ancestral model in that its uropod 3 is magniramous and aequiramous, the telson is scarcely cleft and the gnathopods take the predatorial form.

One supposes the marine theory of origin requires the upstream invasion of Baikal from the Polar Sea by ancestors like *Gammaracanthus* or *Gammarus* and *Gammarellus*, all of which today live in the region. *Gammarus* would be a poor ancestral choice because its gnathopods and urosome are so much more specialized than those of many Baikalian forms. Nevertheless one may imagine a loss of structure in the descendents as a possible consequence of the lacustrine habitus. What also is probably implied by this theory is the supposition that *Gammarus* is an archaic marine genus and may be dimly perceived to be very primitive. We reject that hypothesis.

Baikalian osmotic and seral evidence contradicts the origin of the Baikalian fauna from a Bergian background of pandemic inherent freshwater Holarctic taxa and, therefore, also the Paleozoic pandemic Crangonyctoid sources at levels of immediate descent. What is suggested here is that Baikalian homeomorphs of *Gammarus* (such as *Heterogammarus* and *Eulimnogammarus*) are closer to marine relatives than is *Gammarus lacustris* and that this latter species underwent a long-term evolutionary descent with loss of salt-adaptation and then came back into Baikal or its vicinity at a much later time. One would have to invoke salt-water adaptation to Crangonyctoids as ancestors of Gammaroids, which we have suggested in other parts of this book, as a means that eliminated sternal gills from descendent Gammaroids. This very unparsimonious cycle requires pandemic freshwater Crangonyctoids to reenter brackish waters before an evolutionary descent to Gammaroids could occur. This complex theory does gain some support from the very poor outward expansion of Gammaroids into the sea. There are, of course, many Gammaridans in the sea but these simply lack any clear affinities with the dominant Baikalian-Caspian-general Holarctic freshwater Gammaroids. The Anisogammarids are the main link but again they behave like Gammaroids in their close ties with shallow and dilute coastal waters, so that they also appear to be late invaders of the sea.

Our supposition is that Crangonyctoids form the primitive Gammaridan stock and were archaically of freshwater habitus with an origin projected much farther back than middle Mesozoic (where the earliest Baikalian origin has been perceived at times). But this assumption does not negate the possibility that Baikalian amphipods did come from an initial marine incursion, though we would suggest those marine incursors had a Crangonyctoid ancestry. But if Crangonyctoids already existed throughout Eurasia in streams, torrents and lakes, a parsimonious viewpoint would opt for invasion of the embryonic Baikal from neighboring lakes and streams. Later, as the great rift deepened, the proper environment for pelagic, neritic, bathyal and abyssal, fossorial and nektonic forms could appear. Baikal could, therefore, have a mixed fauna, composed of Gammarus-like descendants (true Gammarus was excluded as the lake deepened and stronger lacustrine taxa evolved), marine incursors (Gammarellus perhaps as ancestor to Macrohectopus) and Acanthogammarids which themselves, because of their large gnathopods, may be disguised Crangonyctids.

In other words, the situation is so complex that no conclusion is possible. Our present knowledge of morphology and function is too weak and our ideas are too wide ranging for any harmony. The most vital point remains that Baikalian osmotic evidence contradicts the Crangonyctid sternal gill-tectonic theory coupled with the poorly developed marine Gammaridan situation in cold seas.

Japanese Phreatics

Eoniphargus Group

Eoniphargus (1), a phreatic genus from Japan, appears to form a group of its own. It lacks the inner lobes on the lower lip and thus is typical of Hadziids but differs from that group in the poorly Melitid gnathopod 1 apparently lacking pubescence and in the reduction of male gnathopod 2 to the Eulimnogammarid form; minute spines appear to occur on the palm of gnathopod 2 in resemblance to Weckeliids and Crangonyctids but the lower lip and gnathopods also do not fit the Crangonyctid scheme, where gnathopods 1-2 approach the hammer form seen in Niphargids (in the latter consistently gnathopod 2). But European Crangonyctids, such as C. vejdovskyi, have gnathopods weakly approaching the Eoniphargus condition. Uropod 3 is parviramous and has article 2 of the outer ramus fused to article 1. Article 3 of the mandibular palp is shorter than in Hadzia but in other respects the mouthparts and pedunculate gills fit the Hadziid form. The telsonic lobes are fused together broadly at the base as in Alloweckelia and Mexiweckelia but each lobe bears a subbasal pair of lateral spines as in primitive Gammaroids. The calceoli of male antenna 2 in Eoniphargus suggest the situation in Gammaroids but not in Crangonyctids and Hadzioids (Melitoids). Coxal gill 7 and accessory gills have not been confirmed in Eoniphrgus. Even if these are absent, the evolutionary ancestry of Eoniphargus superficially appears to lie in the vicinity of Gammarids. One should study the possibility that Eoniphargus comes from a remote ancestry near Eulimnogammarus.

The possible marine origin of *Eoniphargus*, lacking coxal gill 7 and bearing pediculate gills, places it near such forms as *Rotomelita* and *Dulzura*, but tympanic calceoli are absent in Melitoids. The tendency to have the reduced mitten-like gnathopods typical of Eriopisellids is also noteworthy but *Eoniphargus* differs from those genera, except *Bathyonyx*, in the strongly setose maxillae.

Oceanic Gammaroids

Mesogammarus group

Mesogammarus (1), a marine littoral taxon from the boreal to subarctic northwestern Pacific Ocean, appears to have Gammaroid affinities , because of the typical clustered spination on the urosome. But, apparently, coxal gill 7 is absent. Uropod 3 is magniramous, and though almost aequiramous it retains a well developed article 2 on the outer ramus. The telson is short, well spinose, weakly cleft and the lobes gape. The posterodorsal margins of the pleosomites are carved into large teeth running transversely. The maxillae are only moderately setose medially. The female gnathopods are strongly Eulimnogammarid. Because of the state of uropod 3 the genus may have ancient Crangonyctoid affinities, although the urosomal spine patterns are atypical of Crangonyctoids. No Melitoid has the combination of gnathopods and urosomites found in *Mesogammarus*. A close affinity to Anisogammarids (to follow) could be supposed, though the well developed palmar spines on gnathopod 1 are not peg-shaped and Anisogammarids bear coxal gill 7 plus accessory coxal gills here and there. The gnathopodal configuration otherwise fits that of several female Anisogammarids.

Paramesogammarus (1) differs from *Mesogammarus* in the lack of dorsal teeth on pleonites 1-3 and bears calceoli on antenna 2 in both sexes. Male gnathopod 1 is dominant whereas in *Mesogammarus* gnathopod 2 is dominant. So far, this intertidal genus is found only in southeastern Alaska on the outer coast near Sitka.

Gammaroporeia Group

The monotypic *Gammaroporeia* (Bousfield 1979), from littoral Alaska, appears as if it might be descendent from the *Anisogammarus* group in the slightly enlarged but stunted gnathopod 2 and the remnants of dense palmar spines on male gnathopod 2. It differs from the *Anisogammarus* group in the loss of both coxal gill 7 and the accessory lobes on other gills and in the broad expansion of article 2 on pereopod 7. Uropod 3 is strongly reduced and parviramous, the maxillae are medially setose, and the urosome has only scattered setae. Antenna 1 is almost of the Normal *Gammarus* form. Inner lobes on the lower lip are absent.

If one disregards the loss of gill 7, the genus approximates the gradal conditions of *Echinogammarus warpachowskyi* from the Caspian Sea. If one disregards the lack of ventral extension on article 2 of pereopod 7, then the genus approximates the gradal conditions of *Amathillina* and *Akerogammarus* but it can also be derived from the general ancestry of *Homocerisca*, *Pandorites* and *Micruropus* by various modifications which could occur in logical sequence. All of that is very mechanical and suggests that affinities should be sought with the Anisogammarus group.

A superficial similarity occurs between Gammaroporeia and Gammarella but the gnathopods differ strongly; Gammarella has Melitid gnathopods, whereas Gammaroporeia has stunted Anisogammarus-like gnathopods.

Anisogammarus Group

The Anisogammarids contain 10 genera of brackish, marine, freshwater, and anchialine species in the North Pacific basin. The group is characterized by retention of coxal gill 7 plus accessory coxal gills. Gnathopod 1 is usually slightly larger than gnathopod 2 and the palms of both pairs are furnished with dense rows of peg-like spines.

Anisogammarids have been divided into 10 genera by Tzvetkova (1975a) and Bousfield (1979). Only Anisogammarus (2) retains any semblance of magniramous uropod 3, although Barrowgammarus (1) has the inner ramus about 40 percent as long as the outer. Both of those genera seem otherwise to be apomorphic because they both have huge dorsal cusps on one or both of urosomites 1-2 and Barrowgammarus has lost the marginal spines on the rami of uropods 1-2. Otherwise uropod 3 is parviramous.

Eogammarus (10) has more of the central character of the whole group because of the ordinary uropods 1-2, ordinary urosome with Gammarid spination, though Ramellogammarus (4) has the Gammarid antenna 1 with articles 1-2 subequally long, and, unlike Eogammarus and Spinulogammarus (3), has only one accessory lobe on coxal gill 6 instead of 3 as in the former 2 genera. Jesogammarus (1) and Spasskogammarus (2) resemble Ramellogammarus in coxal gill 6 but have the somewhat shortened article 2 of antenna 1 and stronger urosomal spination. Carineogammarus (1) has the fewest accessory lobes on the coxal gills and thus seems plesiomorphic on first sight but it has dorsal pleonal carination and shortened uropods 1-2. Locustogammarus (4) also has shortened uropods 1-2 but more than one accessory lobe on coxal gills. Urosomal spine groups in Annanogammarus (1) are reduced to one spine each.

The presence or absence of dorsal spination on the pleonites (1-3) of Gammarus has been abandoned as a taxonomic device and Karaman and Barnard (1979) tried to eliminate it from Anisogammarids. Bousfield (1979) carried it forward but we have rewritten his key to genera (Appendix V) to avoid its use as a major character alternative. In that way we show herein that the generic pairs of Eogammarus-Spinulogammarus and Jesogammarus-Spasskogammarus are very weak, because one of their 2-3 intergeneric differences is reliance on this character.

To a great extent the genera reflect the evolutionary deployment as developed in our text and revised key. The basic taxon, Eogammarus, has the widest distribution, from South China to California through the cool north Pacific; it is joined by Locustogammarus. The next most widely distributed seems to be Spinulogammarus, from Kamchatka to British Columbia, and again it is a basic genus like Eogammarus. However, the genera with more plesiomorphic uropod 3, Anisogammarus and Barrowgammarus are found only from the American continent. They alone, however, have urosomal teeth and are otherwise apomorphic. Spasskogammarus and Carineogammarus are distributed from the Japan Sea region through the Aleutians. They are also apomorphic. The remaining genera are freshwater in occurrence. *Annanogammarus*, with one (or 2) strange species bearing apomorphic urosomal spination is confined to Asia. *Jesogammarus*, with morphology in the same grade as *Spasskogammarus*, is confined to Japan and *Ramellogammarus*, which, by another set of criteria, one might call plesiomorphic, is a diverse American genus.

If only modern taxa are considered (and not extinct hypothetical intergrades), then doubled accessory gill lobes are plesiomorphic, because the single lobes are coupled with apomorphic uropod 3 (no article 2 on outer ramus) in *Carineogammarus*. *Locustogammarus*, with reduced article 2 on uropod 3, has doubled gills, but like *Carineogammarus* has shortened uropods 1-2. They appear to form a cluster of apomorphs. *Annanogammarus* is unique for its odd spine pattern and is apparently apomorphic. *Anisogammarus* and *Barrowgammarus* are probably apomorphic because of urosomal teeth, despite their tendency towards plesiomorphic uropod 3. This leaves decisions to be made among 5 genera in 3 groups: *Ramellogammarus*, *Jeso-Spasskogammarus* and *Eo-Spinulogammarus*. If treble lobation on the gill of segment 6 is plesiomorphic then *Eo-Spinulogammarus* is the basic subgroup. But, if equally long articles 1-2 on antenna 1 are highly valued then *Ramellogammarus* could be plesiomorphic. *Jeso-Spasskogammarus* forms a more average condition than *Eo Spinulogammarus* as they have only one accessory lobe on gill 6 and slightly shortened article 2 on antenna 1; this may therefore be a better plesiomorphic model. If so, the basic group, *Jeso-Spasskogammarus* is composed of taxa distributed from Japan to the Aleutians in the Ocean but mainly represented in freshwater of Japan.

Bathyceradocus Group

Bathyceradocus, and possibly *Metaceradocoides*, are the only two taxa, each monotypic, and basically of the freshwater Gammaroid stock, that have fully entered the sea and have become completely divorced from freshwater influence. *Bathyceradocus stephenseni* occurs throughout the North Pacific abyssal and hadal zones from 1264-7250 m (confirmed minimal range). *Metaceradocoides vitjazi* occurs in the North Pacific hadal zone at a depth of 7210 m.

The mark of freshwater-primitive origin is the presence of coxal gills on pereonite 7. These are known to be in *Bathyceradocus* but are unstudied in *Metaceradocoides*. The two genera have in common the thin elongate gnathopod 2 of the female and elongate telson with narrowed but ragged apices. Males of *Bathyceradocus* have a slightly enlarged gnathopod 2 armed with peg spines on the palm. Males of *Metaceradocoides* are unknown.

Gnathopod 1 of *Bathyceradocus* is reminiscent of various species of *Melita* in its weak, mitten-shaped appearance, with transverse palm, but the presence of coxal gills on pereonite 7 divorces the genus from *Melita*. Both rami of uropod 3 are elongate and weakly paddle-shaped and the outer ramus lacks article 2. *Metaceradocoides*, on the other hand, has shorter, more lanceolate rami, with a second article on the outer ramus. In addition, *Metaceradocoides* bears inner lobes on the lower lip in contrast to *Bathyceradocus* which lacks inner lobes as in the freshwater Gammaroids.

Bathyceradocus resembles *Mesogammarus* to some extent in the dorsal toothing and serrations of the pleosome and retains a few spines on the urosome, adjacent to teeth not found in *Mesogammarus* but typical of the primitive freshwater Gammarids. *Mesogammarus* has a similar gnathopod 2 but gnathopod 1 is enlarged and Gammarid-like. This situation is weakly reflected in *Metaceradocoides* in the female, which bears a shorter somewhat stouter gnathopod, with much shortened hand and relatively elongate wrist. *Mesogammarus* apparently has weak inner lobes on the lower lip but *Metaceradocoides* has them very well developed though small.

The suggestion is not being made that either *Bathyceradocus* or *Metaceradocides* bear any affinity to *Mesogammarus* as the parallels are simply being drawn in order to dispose of the striking similarities. Too many factors are yet unknown, such as to whether or not *Mesogammarus* and *Metaceradocoides* bear gills on pereonite 7, and what the condition of male gnathopod 2 is in *Metaceradocoides*.

If one disregards gills of pereonite 7, the apparent affinities of *Bathyceradocus* lie in the Weckeliid line as based on lack of inner lobes on the lower lip, the weak gnathopod 2 and the condition of uropod 3. The closest counterparts might be *Alloweckelia* or *Paramexiweckelia* and these also share the elongate telson; both are North American interstitial genera and the ecological connection is absurd. Nevertheless, the convergence is striking in many fundamental features, although *Bathyceradocus* is very distinctive in its body carination, and elongate accessory flagellum. The spiny palm of gnathopod 2 in the male resembles both sexes of the Weckeliids but the peg-like condition is reminiscent of Anisogammarids. Gnathopod 1 of *Bathyceradocus* is otherwise distinctive because Anisogammarids have gnathopod 1 slightly larger than gnathopod 2 and of similar structure and also armed with peg spines. Anisogammarids have gills on pereonite 7 but some of the gills on several segments have accessory lobes.

Another possibility for *Bathyceradocus* is an origin from the early Gammarellid stock (*Gammarellus*-*Weyprechtia*) before the telson became fused in the modern descendents of that group. Of course, we can reverse the descent to suggest that *Gammarellus* is a good intergrade between Corophioids and Gammarioids and that the telson is becoming split rather than becoming fused. Gammarellids have weak gnathopods and magniramous uropod 3 lacking article 2 on the outer ramus.

When more is learned of *Metaceradocoides*, it should be compared with genera such as *Ceradocoides* (=*Maeracunha*) and *Ceradocopsis* from antiboreal regions.

One final note is the interesting similarity in the enlarged apical spines on the peduncle of uropod 2 in *Bathyceradocus*; they are severely constricted in the middle whereas those spines on *Metaceradocoides* are blunted and shortened as if the apical part of the spine in *Bathyceradocus* had been lost. If this is merely a convergent character, then its relationship with the abyssal habitat, where it is entirely confined, should have great interest to functional morphologists.

Gammarellus Group

The *Gammarellus* group is composed of two marine genera, *Gammarellus* (= *Pseudogammarellus*) and *Weyprechtia*. The basic genus, *Gammarellus* (3), has an aspect very similar to that of *Gammarus* but with the following modifications: loss of article 2 on the outer ramus of uropod 3, elongation of the telson and fusion of the telsonic lobes, with scarcely notable apical notch to mark the former lobation, thickening of antenna 1, slight broadening of the bases on pereopods 5-7 and the weakening of the gnathopods, with reduction of palms. Basal spination is lost on the telson.

Weyprechtia (2) is more specialized because coxa 4 becomes acuminate and the gnathopods become even smaller, very thin, with elongate wrists and hands bearing no palms at all. Dorsal spination on the urosome is lost but pereonite 5 retains coxal gills. Dorsal body carination is a tendency in this group.

The Gammarellid group contains four species. Three of those are marine and especially prevalent in the high arctic in depths of 0-200 m on coastal shelves but one species, *G. homari*, penetrates as far south as Antibes, France, in the Mediterranean Sea. A fifth species, *Gammarellus carinatus* is found in the Black Sea.

The Gammarellid group departs from the primitive Gammaroid model in the loss of article 2 on the outer ramus of uropod 3, the fusion of the telsonic lobes and the simplicity of the gnathopods and, therefore, cannot be a primitive marine group of immediate ancestral importance to freshwater groups, except possibly *Macrohectopus* (see Lake Baikal). Instead, this group would appear to be an invader of the sea, perhaps from the ancient Lac Mer.

Calliopius (2) is a remarkable boreal sublittorant that appears to be an apomorph of *Gammarellus*. *Calliopius* differs from *Gammarellus* in the loss of the accessory flagellum the retention of inner lobes on the lower lip and the loss of most of the medial maxillary setation. In earlier times, *Calliopius* has been the type of the family Calliopiidae but all of that classification is temporarily in disrepute until it can be reordered by more detailed study. Meanwhile we simply want to show the difficulties in the Gammaridea by temporarily appending *Calliopius* to the Gammarelluses.

An alternative theory, through interjection of hypothetical forms, gives an entirely different viewpoint to the Gammarellids. The telsonic form could be construed to represent an intermediate state between Corophioids and the remaining Gammaroids. Because gnathopodal prehensility is not completely lost in *Gammarellus* and because coxal gill 7 is present, *Gammarellus*, but not *Weyprechtia*, could be envisioned to have ancestry in the Corophioids and be in a stage between Corophioids and Gammaroids. As a model link, *Gammarellus* would approximate the ancestral grade both to Gammaroids and the Melphidippid groups. The uncleft telson characterizes *Gammarellus*, whereas the loss of prehensility in *Weyprechtia* signals the common denominator of the more advanced Melphidippid groups in which the telson has become secondarily cleft. But *Weyprechtia* would fit Stock's ideas about gnathopods being simple before they turn subchelate and *Weyprechtia* would thus be a good intergrade between a prototype with fleshy telson and simple gnathopods and Gammaroids which have cleft laminar telson and subchelate gnathopods. We are not trying to establish these genera as the actual intergrades, simply as models of the conditions being extrapolated.

If this idea of uncleft telson being a primitive stage antecedent to the clefted form is valid, then one must attempt to rearrange the so-called Calliopiids and Pontogeneiids with this in mind, that Calliopiids are simply Gammarellids with severely reduced accessory flagella (Barnard and Karaman, 1975). Clefting of telson, however, would become a polyphyletic development as it would have occurred repeatedly in Gammarids, Melphidippids, and Calliopiids, separately.

Melphidippoids

The Melphidippiods are characterized by loss of prehensility on gnathopod 1 and often gnathopod 2 and by the retention of coxal gill 7. The Gammarellids, already discussed, appear to be transitional between Gammaroids and Melphidippoids. The prehensility of gnathopods in *Gammarellus* is scarcely reduced but in *Weyprecthia* the gnathopods are fully simple. All other Melphidippids are characterized by dorsal crenulation on the pleonites, except a few apomorphic taxa such as *Incratella*.

The *Cheirocratus* group of the North Atlantic and cool Australian region are characterized by the retention of the short Gammaroid telson but the peduncle of uropod 3 has become elongate. Gnathopod 2 of both sexes is simple but gnathopod 2 of at least the male is weakly to strongly prehensile. Three genera, *Cheirocratus* (5), *Cheirocratella* (1) and *Casco* (1) are distributed from Arctic Seas to the Mediterranean Sea and in cool Australia but *Casco* is confined to western Atlantic where the other 2 genera are absent. *Cheirocratus* and allied taxa have been discovered in Tasmania recently (Barnard and Drummond, in prep.). *Incratella* (1) is composed of one advanced tropical taxon from Madagascar (Ledoyer's, 1967b: *Cheirocratus inermis*; this genus is like *Cheirocratus* but has lost the dorsal urosomal ornamentation).

The morphologic and geographic flow of evolution then proceeds tropicsward to the *Hornellia* group in which the peduncle of uropod 3 remains short but the telson is elongate. The species of *Hornellia* (2) and *Metaceradocus* (4) are found in the marine tropics and subtropics. *Maerella* and *Jerbarnia* are clearly apomorphs of *Hornellia* and extend into the Atlantic Ocean.

Maerella (2) from marine Mediterranean and *Jerbarnia* (1) from marine Micronesia are extremely cohesive genera characterized by elongate peduncle on uropod 3. They share similar body ornamentation dorsoposteriorly. *Jerbarnia* is much more specialized than *Maerella* in the reduction of maxillary setae, and in the male, the great elongation of coxa 2 and articles 2-3 of gnathopod 2. The appendage appears to flex under the body in such a way as to form a sled-runner or levator but predatorial uses could also be envisoned.

The Maerellids have so much in common with the *Metaceradocus*-*Hornellia* group that they must be studied further for possible interrelationships. The main difference between the two groups is the loss of prehensility in the gnathopods of Hornellias, but Hornelliids also do not have fully elongate peduncles of uropod 3 and retain primitive maxillae and telsons, as well as coxal gill 7. They otherwise conform in the unusual body ornamentation, most mouthparts and other appendages. Maerellids even show the rudiments of loss in prehensility on gnathopod 1.

The *Megaluropus* group contains 2 genera with abnormalities in anterior coxae, especially coxa 3 or coxa 2 being reduced in size. *Megaluropus* (7+) has flabellate rami and a short peduncle on uropod 3, whereas *Aurohornellia* (1) has an elongate peduncle and lanceolate rami with the outer ramus retaining article 2. These genera are tropical and subtropical marine.

Argissa (1) has so many characters in common with Megaluropus that a distant affinity must be supposed. The irregularity of coxa 3, coupled with short peduncle of uropod 3, expanded and lobate article 2 of pereopods 5-7, essentially simple gnathopods, and broadened plates of maxilla 2 suggest this affinity. The marine Argissa differs from Megaluropus in the lanceolate rami of uropod 3, the lack of transverse dorsal serrations on the pleon and the short setiferous dactyl of gnathopod 1. The eyes of oculate Argissids are composed of a wheel of 4 ommatidia.

The final group is composed of the Melphidippidae, sensu stricto. This group is characterized by elongate peduncle on uropod 3, lanceolate rami and great elongation of gnathopods and pereopods. The group appears to be demersal marine and is largely confined to north boreal waters as far as known. Three genera with 13 species are in this group, the genera being Melphidippa (10), Melphidippella (1) and Melphisana (2). So far they are mostly coldwater northern taxa in the high North Atlantic and Pacific but 2 species have been found in the southern hemisphere and more may have been overlooked.

An appendix here is Macrohectopus, the bizarre Baikalian mysidiform genus which in terms of body form, elongate appendages and simple gnathopods has the strong aspect of Melphidippoids in general. Otherwise that genus is discussed earlier in the Baikal fauna.

The Hadzioids (Melitoids)

The major marine Gammaridans and their derived groups, lacking coxal gill 7, many of which have invaded anchialine and freshwater habitats secondarily, are divisible into two large groups characterized by uropod 3. There is broad overlap within Hadzioids but further research may show the independent evolution of the subgroups. The Hadziid (Melitid) subgroup is characterized by dispariramous uropod 3, whereas the Ceradocid subgroup bears aequiramous third uropods. The dispariramous uropod 3 in its plesiomorphic condition carries elongate rami of strikingly different form. The inner ramus is simply an elongate triangle with sparse medial and apical setation, whereas the outer ramus bears a second article and has lateral spination. The fully magniramous form of the dispariramous uropod 3 is very rare, being found only in approximate form in Psammogammarus and Pontoniphargus. All other genera exist in the parviramous stage. This uropod is characteristic of the Gammaroid freshwater group. The aequiramous uropod 3, characteristic of Ceradocus and its allies, has 2 equally extending and equally armed rami, usually lanceolate. Article 2 on the outer ramus is vestigial or absent. This uropod is similar to that found in the Crangonyctoid, Phreatogammarus.

Whether or not either of these two kinds of uropod 3 can transform into the other through a series of evolutionary steps is unknown. The greatest concern lies in the Weckeliids where the aequiramous uropod 3 resembles that of Ceradocids, whereas Hadziids, with dispariramous uropod 3, resemble Melitids. Two kinds of special female gnathopod 2 occur in these 2 groups.

The Hadzioid group, less Weckeliids, comprises almost 50 genera. Only 12 of those genera lack any connection with anchialine, brackish or freshwater environments. Some of the genera, such as Melita, have many fully marine species but even Melita contains many species associated with diluted waters of sea margins. The Ceradocid group, with fewer than 20 genera has a stronger association with marine waters than the Hadzioids, as no genera are exclusively confined to nonmarine waters, although one genus, Quadrivisio, is found mostly in diluted nearshore waters. If the Weckeliids are added to the Ceradocids, ten genera would be added to the freshwater component.

The direct origins of Hadzioids (Melitoids) cannot be ascertained. They carry the dispariramous uropod 3 of either Crangonyctoids (not Phreatogammarus) or Gammaroids, thereby suggesting a freshwater origin for the group, but the loss of sternal gills, loss of coxal gill 7 and loss of strongly bifid spines densely lining the gnathopodal palms obfuscates their origin. The Ceradocids also lack those attributes, but uropod 3, being of magniramous and aequiramous form, closely resembles that of the Crangonyctoid, Phreatogammarus, thereby very remotely suggesting a Crangonyctoid origin for Ceradocids.

Greater Ceradocus Group

This group of 16 (and one dubious) genera retains a magniramous uropod 3 in contrast to Melitids, but has not developed the homogeneity of palmar spines on gnathopod 2 in contrast to Weckeliids. Most Ceradocids have some clear evidence of inner lobes on the lower lip unlike Hadziids, although a few genera have been reported as lacking inner lobes.

At least 6 clusters of genera may be found in the Ceradocids, although finer divisions would not be useful.

The Paraweckelia cluster is characterized by its antecedents to Weckeliids, especially in telsonic setule placement, and low level of sexual dimorphism. A second cluster, the Ceradocopsids, is characterized by conspicuous retention of article 2 on the outer ramus of uropod 3. The Paraceradocus group is characterized by leaf-like rami on uropod 3. The Gammarella (Nuuanu) group is characterized by plate-like article 2 of pereopod 7. Finally, all the other genera are arranged with Ceradocus as the basic group at the center and with extensions outward characterized by loss of maxillary setae, reduction of gnathopod 2 or further aberrancies, such as in Beaudettia, which has lost the mandibular palp, has an almost uncleft telson and has parviramous uropod 3. A satellite group is represented by Parapherusa for which a separate section is written to follow.

In Appendix IV, these genera are arranged in phyletic form as groups typified by Ceradocus, Paraceradocus, Maera and Parapherusa, with Paraweckelia appended to the Ceradocus group. Owing to narrative importance they are discussed in a different order in this text. Moreover, the former Maerella-Jerbarnia group is removed to the vicinity of the Hornellia group in the Melphidippids.

Ceradocus Group

This group characterized by Ceradocus is weakly divisible into several subgroups. Ceradocus (24) is a marine genus, as are all the remainder in this section and is widely distributed in the tropics but has a few species penetrating higher latitudes. Both pairs of maxillae are fully setose medially but Ceradocus appears to be more specialized than Anelasmopus and

Elasmopoides in the reduction of article 3 on the mandibular palp and the development of a tooth on article 1 of that palp.

Elasmopoides (1) occurs in South Africa, and Anelasmopus (1) in Brazil. The latter requires redescription. Ceradocides (1), from Antarctica, apparently is distinguished by the partial fusion of telsonic lobes.

Ceradocus, Ceradomaera (1, Madagascar), Ceradocoides and Paraweckelia (1) are placed in a subgroup characterized by shortened article 3 of mandibular palp (presumptive in Ceradocoides) to be distinguished from the primitive members of the Maera subgroup, Anelasmopus and Elasmopoides, with normal palp.

All of the remaining genera have lost the medial setae on the inner plate of maxilla 1. The two most diverse genera of this group are Elasmopus (58++) and Maera (59). Both are circumtropical and extend more (Maera) or less into higher latitudes or colder water. Elasmopus appears to be confined to shallow water almost entirely whereas Maera descends into upper bathyal depths. Maera has the linear, unmodified article 3 of the mandibular palp typical of all the remaining members of this group but Elasmopus has article 3 falcate and the D setae form a tight comb. Maera is rather more diverse in gross attributes than Elasmopus, because it has numerous variables in uropod 3, cephalic ornamentation, telson, epimera and various anterior appendages, whereas variation within Elasmopus is at a much finer level of detail. The taxonomist can generally distinguish the two genera just on the basis of facies so that they may be relatively remote from each other (facies meaning the more robust and pigmented bodies of Elasmopus with stouter pereopods).

Maeropsis (1) is simply a Maera-like genus with retention of medial setae on maxilla 2 and thus appears to be in a more primitive state than Maera. It occurs in the bathyal of the North Atlantic.

Meximaera (1), Pacific Mexico, appears to be a Maera with reduced male gnathopod 2 but the retention of medial setae on maxilla 2 suggests a closer relationship to Ceradocus.

Lupimaera (1) is an odd Californian littoral genus like Maera but in which article 2 of pereopods 5-7 is very small and article 2 of pereopod 5 is not longer than coxa 5. All of the spines on the rami of uropods 1-2 are shortened. This peculiar combination of characters is unique among the other 55 species of Maera. Actually, Lupimaera has some of the overall appearance of Ceradocus and may actually be a descendent of that genus, rather than directly from Maera. Lupimera is just another of the many Gammarideans with a manifold background almost impossible to trace without great advances in phyletic analysis. See the Handbook (Appendix VI) for all of the many other relationships that are struck for Lupimaera.

The Beaudettia subgroup contains Beaudettia, Ifalukia, Parelasmopus and Mallacoota. The entire group is confined to the IndoPacific tropics as far east as Hawaii and as far south as southern Australia. The Parelasmopus group is characterized by the presence of one of 2 attributes: bilateral dorsal carinae on urosomite 1 or a short second article on the mandibular palp. Apomorphy is widespread in the group, so that convergences toward Maera or the complete reduction of the mandibular palp have made its recognition difficult. Parelasmopus (6) is mainly confined to tropical waters, whereas Mallacoota (11) has many species confined to or extending into warm-temperate southern Australia.

Beaudettia (1), from Micronesia, appears to be a descendent of the Parelasmopus group in which the mandibular palp has been lost, the telsonic lobes have been fused and uropod 3 has become reduced and parviramous. It bears close comparison to Ifalukia (1), from Micronesia, with which it shares numerous other generalities. Ifalukia is clearly a descendent of the Parelasmopus group and differs from those genera in the loss of dorsal ornamentation on urosomite 1.

Beaudettia was formerly assigned to its own family by J.L. Barnard (1965a:514) who believed that it deserved familial status under Stebbing's (1906) classificatory scheme but recognized its affinities with Elasmopus. Now that the Parelasmopus-Mallacoota-Ifalukia sequence of taxa has been somewhat clarified (J.L. Barnard, 1972a), the affinities of Beaudettia can be tied to such cited group where reduction of mandibular palp is frequent. Mutant telsons of Elasmopus have been recorded by Shoemaker (1933a), so that the telsonic fusion is not as remarkable as heretofore believed. The mandibular molar has lost most of the triturative surface. The family name, Beaudettiidae, is available to cover the Ceradocids but we would suggest the use of a more appropriate name for the group and abolish Beaudettidae as a name conceived in an erroneous and outdated frame of reference to the old Stebbingian system of classification. The name might be applied to the Mallacoota subgroup.

Paraceradocus Group

Paraceradocus (1), from marine Antarctica, and Quadriviso (5), from marine tropics, are characterized by leaf-like rami on uropod 3. They may have no other than a gradational relationship but otherwise might be placed near Elasmopoides and Anelasmopus if uropod 3 were disregarded. Quadrivisio has the lateral eye divided into 2 parts by an hourglass-like constriction and, therefore, has 4 eyes in total. Antenna 2 of the genera dominates antenna 2. Articles 4-5 are elongate and slightly thickened.

Quadrivisio has been considered several times (for example Vandel, 1965) to be part of the Hadziid group and implied to be the marine ancestor to the group. It does have close resemblance to the Parawecklia group, which also is removed, herein, from the Hadziidae but which may itself be ancestral to Weckeliids. Paraweckelia is more primitive than Weckeliids because of the clear presence of inner lobes on the lower lip, the poorly developed spines on the palm of gnathopod 2, and the lack of Hadziid gnathopod 2 in the female but the link to Hadziids might be marked by the distal shift of lateral setule pairs on the telson. Quadrivisio cannot stand on a direct line to Hadziids or Paraweckelias because the mandibular palp is apomorphic (of the Maera-form), whereas plesiomorphic Hadziids have the well develped article 3 with several kinds of setae. Quadrivisio otherwise has the inner lobes on the lower lip as seen in Paraweckelia but the telsonic setules are not strongly shifted apically.

Parapherusa Group

Parapherusa is a strange, monotypic marine genus widely distributed in the littoral of antiboreal islands such as New Zealand, Tristan da Cunha and in southern Australia. The rather weak subchelation on gnathopod 1 and female gnathopod 2 suggest affinities with Gammarellids but male gnathopod

2 is fully Ceradocid in morphology. The telson is elongate and entire, thus resembling Gammarellids. The fully setose maxillae and the form of the other mouthparts could also be used to fit Parapherusa into the Gammarellids but Parapherusa differs from that group in the absence of coxal gill 7.

Uropod 3 is so severely reduced that its aequiramous condition cannot be reconstructed so that it could be allied either to Hadziids or specifically Ceradocids. The extremely fleshy inner lobes on the lower lip suggest Melitid ancestry but the Ceradocid gnathopod 2 of the male is foreign to that group. The rami of uropod 3 are of similar size and much shorter than the peduncle. Each is strongly spinose apically and the outer ramus bears an unusual rasp spine. Uropod 1 bears a wholly unique interramal tooth on the peduncle. The very elongate accessory flagellum is reminiscent of Paraceradocus.

Ceradocopsis Group

Ceradocopsis (= Maeracunha) is an antiboreal marine genus, with 3 primarily littoral species. Inner lobes on the lower lip are absent, though marks are present. Uropod 3 is miniaturized and of the parviramous form, though the outer ramus is so short that the inner ramus appears large. Mandibular palp article 3 is linear and varies from elongate to short. Gnathopod 2 is generally of the Melitid form closely approaching the Ceradocid condition. Gnathopod 1 is also of Ceradocid form so that Ceradocopsis may actually be a Ceradocid of evolutionary descent in the manner analogous to Beaudettia. The latter also has miniaturized uropod 3 but is certainly a Ceradocid, with a clear derivation from the Parelasmopus ancestry.

The outer ramus of uropod 3 bears a small article 2 in contrast to Beaudettia and to most Ceradocids (except Meximaera) but the relative size of this article may be a result of the overall reduction of uropod 3 without concomitant reduction in article 2. The stout, Elasmopus-like body and posterior pereopods suggest that Ceradocopsis has an ancestry in that group, where many species exhibit the rudimentary reduction of the inner ramus on uropod 3.

Metaceradocoides, the hadal Pacific genus, is another marine Gammaridan with Ceradocopsid uropod 3. That genus is discussed in relationship to Bathyceradocus elsewhere. The small and elongate female gnathopod 2 appears to remove Metaceradocoides from consideration here.

Gammarella Group (Nuuanuids)

The Nuuanuids form a group of 2 genera of tropical and Tethyan marine occurrence. Though otherwise greatly diverse, they are characterized by geniculation and excessive flexibility of antenna 1 combined with miniaturized parviramous uropod 3, notched cephalon, and short pereopods 5-7, with characteristic shield-like article 2 of pereopod 7. They lack inner lobes on the lower lip and lack gill 7. Most tropical species have large serrations on article 2 of pereopod 7 (and occasionally 5-6). At least one species, Gammarella amikai, has invaded anchialine waters of Hawaii. Most tropical species have reduced eyes and are poorly pigmented, suggesting that they are preadapted for entering cryptic environments.

A few years ago the four genera of Nuuanuids were Nuuanu (3), Gammarella (=Pherusa, =Pherusana) (1), Cottesloe (2) and Tabatzius (1). The latter genus is characterized by piercing maxillae. All the others have been synonymized with Gammarella by Karaman and Barnard (1979) who found a progression of character transformations too broad to permit generic divisions. Because of the inherent confusion with taxa of the genus Gammarellus, we are calling these organisms "Nuuanuids" here to distinguish them from Gammarellids of the genus Gammarellus.

The stout bodies resemble those of Elasmopuses but the morphology of the lower lip suggests an affinity with the Hadziids. The loss of inner lobes on the lower lip could be an advancement from the Melitidae. The reduction of the inner ramus of uropod 3 might be an outgrowth from the Ceradocopsids, but a relationship to the Elasmopus group would require enlargement of article 2 on the outer ramus of uropod 3 from its vestigial condition in Elasmopuses. As stated in the Ceradocopsid section, the relative size of article 2 may be a function of the overall miniaturization of uropod 3 without concomitant reduction in article 2.

Gnathopod 1 of Nuuanuids is of Melitid form, whereas that of Ceradocopsids is of Ceradocid form. The variability of this feature is also found in the Melitid, Eriopisa, so that little weight can be given to that characteristic.

Paraweckelia Group

Paraweckelia appears to be a Ceradocid with incipient Weckeliid characteristics. The genus is scarcely distinct from Ceradocus and Ceradomaera but, like Weckelia, it lives in a cave in Cuba. Uropod 3 is fully magniramous and aequiramous, although the outer ramus has a vestigial article 2. Gnathopod 2 of the female is of the Melitid form, with enlarged hand, oblique, unsculptured palm, short and lobate wrist. The palm is lined with tiny spines but the posterior margin of the hand lacks Hadziid setae. Like many Hadziids and Weckeliids the main pair of dorsolateral setules on each lobe is shifted towards the apex. The peduncle of antenna 2 is almost as elongate and thickened as in Quadrivisio. Gnathopod 1 is of the Melitid form and therefore is almost unique in the Ceradocids. To be derived from an ancestry near Psammogammarus, Paraweckllia would have to arise from a more primitive ancestral form because of the large anterior coxae and large Melitid female gnathopod 2. Paraweckllia would be unsuitable as an ancestor to Hadzia, though it could conceivably be ancestral to Weckeliids. Uropod 3, however, is far more streamlined than in Weckeliids and the oblique medial row of setae on maxilla 2 has been lost.

Paraweckelia, therefore, is placed near the Ceradocids and is considered to be remote from Weckeliids, despite the areas of convergence.

The Tethyan Stygobionts

Hadzia and Weckelia Groups

These two groups are discussed together, though they may have different ancestries. The Hadzia group (valid Hadziidae) may be close to the Melitids and the Weckeliids to the Ceradocids. They formerly were all considered a single, loosely knit group. Much taxonomy has been undertaken in the group lately, especially by Holsinger (1977a, b, 1980, and with his colleagues, Peck, 1968, and Minckley, 1971) and by Stock (1977). The two groups are very convergent. A few years ago they could be distinguished on female gnathopod 2, which in females of the Weckeliid group had distinct spines on the palm but which in the Hadziid group had long bent setae on the palm. This does not seem to be a workable diagnostic character.

The Hadziids differ from Weckliids in the presence of 2 articles on the outer ramus of uropod 3, whereas Weckeliids appear to be descendent from ancestors with aequiramous uropod 3, rather near to *Paraweckelia*, a monotypic genus of the Caribbean region which is rudimentarily a Weckeliid but also a Ceradocid (see above). Uropod 3 of Hadziids is dispariramous, the two rami being diverse, the outer of 2 articles and different in its armaments from the inner ramus, which may be long or short. Apparently, most Hadziids lack inner lobes on the lower lip whereas most Weckeliids have inner creases marking vestigial lobes.

Almost all Hadziids and Weckeliids are blind (except *Protohadzia*), and, except for *Protohadzia*, *Hadzia*, *Liagoceradocus* and *Dulzura*, most occur in subterranean situations. All Weckeliids occur in caves or wells or in aquifers of the Caribbean region, especially in the Antilles and southern Mexico. The Hadziids are circumtropical marine and freshwater taxa, in the marine world occupying apparently cryptic habitats in very shallow water but in Caribbean and Mediterranean waters penetrating into aquifers and caves near the sea. Only the Weckeliids penetrate far inland and then only in middle America.

Weckeliids

Paraweckelia (1, caves of Cuba), must be very close to the ancestry of Weckeliids but is clearly an apomorphic Ceradocid. It is so close to *Ceradocus* as to be almost indistinguishable except by its absence of eyes and weakness of maxillary setae. A very tiny article 2 occurs on the outer ramus of uropod 3 but otherwise the rami are aequiramous. Female gnathopod 2 is of the Ceradocid form and much larger than the Melitid gnathopod 1.

All other Weckeliids lack article 2 on the outer ramus of uropod 3 and also have reduced gnathopod 2 in both sexes, the palm being poorly defined and short, often with Hadziid setae, the wrist often elongate. Generally the maxillae are well setose medially.

The next stage of development appears to concern taxa which retain the posterior lobe on coxa 4. These include *Weckelia* (= *Neoweckelia*) (1, caves of Cuba) and *Alloweckelia* (1, caves of Puerto Rico). *Alloweckelia* retains a 3-articulate mandibular palp but has lost the inner lobes on the lower lip, whereas *Weckelia* has a reduced mandibular palp but retains inner lobes on the lower lip. *Alloweckelia* retains remnants of article 2 on the outer ramus of uropod 3 as marked by declivities. Sexual dimorphism in gnathopod 2 is weakly retained in *Alloweckelia* but more strongly so in *Mexiweckelia* (2, springs of Mexico). The latter genus and all following have lost the lobation on coxa 4.

In *Mexiweckelia* each ramus of uropod 3 bears apically an enlarged and elongate spine among shorter spines. This diminishes in *Paramexiweckelia* (1, Mexico, hypogean). The latter also lacks lobation on the gnathopodal wrists. *Mexiweckelia* resembles *Hadzia* less than other Caribbean phreatic genera, in that the wrist of male gnathopod 2 is scarcely elongate and gnathopod 1 has assumed some of the shape typical of gnathopod 2; these similarities involve the swollen hand and oblique palm of gnathopod 1. The female gnathopod 2, however, has the more elongate wrist. In Paramexiweckelia both male and female share similar gnathopods, with gnathopod 2, in this case, assuming the appearance of gnathopod 1, bearing rectangular hand, scarcely oblique palm much shorter than posterior margin of hand and with strongly overlapping dactyl. The palm remains spiny but the number of spines is reduced owing to the smallness of the palm.

Next in sequence is Mayaweckelia (2, Yucatan, hypogean), distinguished by the merochelate gnathopod 1. The medial margin of the outer plate on the maxilliped is setose and not spinose as in ordinary Weckeliids. Like many Weckeliids, the gills of Mayaweckelia are stalked and 2-articulate, while the oostegites remain narrow, a distinction from most freshwater epigean taxa in the Gammarida.

The final four genera are distinguished from other Weckeliids by the absence of the right lacinia mobilis and the enlargement of coxa 1 or reduction of coxa 2. Texiweckelia (1, San Marcos Well), typifies this condition and is the model taxon. Allotexiweckelia (1, Texas, hypogean) differs in the uniform gnathopods of the sexes, and in the strongly expanded and spinose article 2 of pereopods 3-4. In Texiweckelia the hand of gnathopod 1 differs from that of gnathopod 2 and is shorter than the wrist. The gnathopods of the sexes are distinct and article 2 of pereopods 3-4 is thin.

The final 2 genera are greatly modified in that the anterior mouthparts project strongly as far as article 2 of antenna 1. In Texiweckeliopsis (1, Texas, hypogean) the outer plate of maxilla 1 has 14 spines and the inner plate of the maxilliped is broadly expanded. The companion genus, Holsingerius (1, San Marcos Well), the outer plate of maxilla 1 has only 7 spines, the inner plate of the maxillipeds is ordinary, the inner plates of the maxillae are elongate and the dactyl of the maxilliped is short, with article 3 thin.

This group seems to exhibit an apomorphic trend in the direction away from Central America towards the Edwards plateau in Texas. The San Marcos aquifer now has 9 species of hypogean amphipods, among them several of these Weckeliids, some Crangonyctids and the non-Gammaridan Seborgia. Holsingerius and Texiweckeliopsis seem to have predatory adaptations in their mouthparts but the peculiarities need morphofunctional study.

Hadziids

Because they are blind (except Protohadzia), Hadziids appear to be a tightly knit group representing a cul-de-sac of evolution in the framework of the greater marine Gammaridan dispersal. Only a few other genera to be discussed later appear to have some relationship to Hadziids. Gnathopod 1 of Hadziids is of Melitid form: small, short, bearing rectangular hand and fully transverse or scarcely oblique palm with pubescence well developed especially on article 4. The maxillae are fully setose medially. The plesiomorphic mandibular palp is well developed but thin, bears a weakly elongate article 1 and a weakly sickle-shaped article 3 bearing D and E setae.

One may visualize the ancestry of both Hadziids and Weckeliids in taxa such as Psammoniphargus (1, Reunion, hypogean)*, where the inner ramus of uropod 3 is elongate but rudimentarily truncate apically, and spinose in fashion similar to article 1 on the outer ramus. Loss of article 2 with development of apical spines on article 1 of the outer ramus would resemble the condition of Weckeliids, whereas simple reduction in article 2 would resemble Hadziids. Nevertheless, the Weckeliid uropod 3 in several species becomes similar to Ceradocids by streamlining of the rami. Complete loss of inner lobes on the lower lip occurs occasionally in Hadziids, whereas in Weckeliids weak creases or slight bulges remain.

The dominant genera of other marine amphipods (Ceradocids, Melitids), bear a strongly developed male gnathopod 2 with very large and strongly subchelate hand and shortened wrists, somewhat similar to the Acanthogammarids. The second gnathopod of marine females is strongly distinct from that of males, being much smaller, with more elongate wrist, and relatively ordinary palm. Except for Protohadzia, Hadziids are characterized by having gnathopod 2 of both males and females in a condition intermediate between the marine male and female, in that gnathopod 2 is reduced in size, the palm is even, unsculptured or otherwise lacking specializations and the wrist is somewhat elongate. The wrist (article 5) is armed with medial pubescence and articles 4 and 6 often bear fuzz also, thereby resembling the Meltitid gnathopod 1 characteristic of the group.

If Hadziids have any affinities to Paraweckelia (which seems to be near the base for Weckeliids), then the relationship would have to be with an ancestor of Paraweckelia because that genus has already lost much of its full complement of medial maxillary setae. Gnathopod 2 of Hadziids usually has Hadziid setae, those bristles which are stiff and partly curved or curled apically; they often occur on the hand of gnathopod 2, usually also on the posterior margin of the hand.

Saliweckelia (2, Curacao and Bonaire, marine and anchialine) appears to be the basic Hadziid, differing from Paraweckelia in the loss of inner lobes on the lower lip, strongly setose maxillae and dispariramous uropod 3. It is the only Hadziid retaining lobation on coxa 4.

The next group of 4 genera lacks lobes on the wrists of the gnathopods and the setae on those wrists are therefore posteromarginal. Metahadzia (2, Portugal and Italy, hypogean) is the basic member of the group, with normal telson, magniramous uropod 3, gnathopod 1 lacking setal brush, male gnathopod 2 palm spinose and uropod 3 magniramous. Other characters include distinct palm on female gnathopod 2 and medial telsonic spines.

The next two genera differ from Metahadzia in the presence of a setal brush on male gnathopod 2, parviramous uropod 3, poor spination on palm of male gnathopod 2, the indistinction of the palm on female gnathopod 2, and the absence of medial telsonic spines. Protohadzia (1, Caribbean, marine, in Thalassia beds) bears a weakly pigmented eye lacking ommatidia and has a displaced basofacial spine on uropod 1. Dulzura (1, California, marine),

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* Here as elsewhere we do not want to confuse the reader by the wording; we are not implying that Psammoniphargus is the ancestor of anything nor that any group has its origins on Reunion; the crucial word is "visualize"; one may visualize the kind of morphology in this particular taxon.

has an almost neotenic gnathopod 2 in the male, lacks palmar spines but is furnished with dense setation on the hand; the wrist is scarcely elongate. This gnathopod in the female is small, the wrist much more elongate and has Hadziid setae along the posterior margin of the hand; the palm is indistinguishable. Dulzura is found in the heavily wave dashed intertidal of California and western Mexico, is blind and virtually without pigment as in other Hadziids. It bears the identical comb on the peduncle of uropod 2 characteristic of so many other Hadziids, a feature that is poorly recorded and should be looked for in all Hadziids and Weckeliids. Unlike Protohadzia, Dulzura lacks lateral spines on the telson.

Metaniphargus (9, Caribbean Islands, mostly hypogean) is the largest genus of the group and is recognized by the short telson. It otherwise has a variramous uropod 3, fully spinose telson, and more or less regular gnathopods like Metahadzia. The genus has spread in aquifers through the Antilles, island by island, and on some islands is subspeciated (Stock, 1977). We prefer to elevate these subspecies to full level for simplicity of presentation in the species list. The comb on uropod 2 is either present or absent.

The final two genera have modified gnathopod 2, the wrist having a posterior lamellar lobe on which the normally posterior setae are found facially or submarginally. Liagoceradocus (2, central Pacific, anchialine or atoll-lagoon), appears to be more plesiomorphic than Hadzia (3, Yugoslavia, hypogean) in that article 1 of the mandibular palp is normally short (or scarcely elongate) whereas in Hadzia it is usually as long as article 2. But in Liagoceradocus article 5 of gnathopod 1 is elongate and the telson has lateral spination. Liagoceradocus pusillus from Ifaluk lagoon remains to be clarified in several points, as it is not known to be distinct from its congenera found in anchialine lava ponds of Hawaii. These ponds, seeps, and wells are percolated seawater, occurring inland in recent lava flows; the salt water is diluted by fresh groundwater.

Metacrangonyx Group

Like Pseudoniphargus, Metacrangonyx is a very advanced genus but has affinities with Hadziids. The genus, with 4 diverse species, is confined to interstitial waters of northwestern Africa, Algeria and Morocco and on the island of Mallorca.

Metacrangonyx resembles Hadziids and Eriopisellids in the fully developed Melitid stage of gnathopod 1 and has the Hadziid gnathopod 2 with elongate apically curved setae on the posterior margin of the hand. The palmar spines are well developed and apically dentate as in Crangonyctids. The lower lip lacks inner lobes as in Hadziids. The maxillae are strongly setose medially but the palp of the mandible is very slender and only apically setose in the type-species but reduced to two or one articles in the other species. Uropod 3 is the most strongly reduced of any Hadziid. It is scarcely longer than a spine on uropods 1 or 2, the inner ramus is reduced to a minute vestige or is absent and the outer ramus is slightly longer to greatly shorter than the peduncle. The telson is also reduced, entire and very short. Article 3 of antenna 1 is elongate. In terms of severely reduced uropod 3, M. remyi is considered distinct generically from the other species (see Appendix VI) and was relegated to Pygocrangonyx by Karaman and Barnard (1979:151).

Melita Group

The Melitids appear to be one of the more primitive marine groups with dispariramous uropod 3. They may be the ancestors of several groups, such as Eriopisellids, Nuuanuids (Gammarellas), Ceradocopsids and possibly the typical Hadziids, less Weckeliids.

Uropod 3 is retained in the enlarged form, the gnathopods never become fully mittenform, although *Galapsiellus* approaches that condition, the inner lobes of the lower lip, usually fleshy, never are completely lost, though they are often severely reduced and female gnathopod 2 does not become fully Hadziid, though this condition is approached in *Psammoniphargus*.

Gnathopod 1 of Melitids holds fairly close to a morphotype conveniently described as "Melitid." The gnathopod is small, has an elongate wrist, the hand is almost rectangular and the palm is transverse and short. If the palm is oblique, the gnathopod is termed "Ceradocid." In a few Melitids gnathopod 1 becomes Ceradocid. For example, it is found in the type-species of *Eriopisa*, a taxon that is highly derived and far removed both geographically and evolutionarily from the ordinary *Psammogammarus* (= old concept of *Eriopisa*). The Melitid gnathopod 1 is carried outward into the Nuuanuids, Pseudoniphargids, Hadziids (sensu stricto) to some extent, and perhaps indirectly, to the Niphargids, and into *Paraweckelia*, a genus with aequiramous uropod 3 completely foreign to Melitids. All other Hadzioids have the Ceradocid gnathopod 1 or modifications thereof.

An important point is that the old genus *Eriopisa* is now divided into 3 genera, *Eriopisa* (1 species), *Psammogammarus* (6) and *Victoriopisa* (3). These are called "Eriopisids." *Psammogammarus* is the most primitive of the three.

If the magniramous or variramous uropod 3 is taken as the mark of a primitive Melitid, then *Psammogammarus longiramus* would represent the most primitive member. The type-species of that genus, *P. caeca*, with shorter inner ramus, has numerous specializations removing it from a direct ancestry to the marine *Melita* but *P. longiramus* might lie on the ancestry of the other members in the genus.

Psammogammarus longiramus is known only from a bitter well on Entedebir Island off Eritrea, while the more advanced *P. caeca* occurs in Yugoslavian phreatics. The only other magniramous Hadzioids are the unique type-species of *Pontoniphargus* (found in wells of Rumania near the Black Sea), in the Niphargidae and several species of *Hadzia*. Weckeliids are omitted from this approximation for the moment. Several Hadzioids, such as the Ceradocopsids and Nuuanuids approach magniramous conditions only secondarily through severe reduction of the outer ramus on uropod 3.

Psammogammarus (6) resembles the typical member of *Eriopisa* (1, bathyal boreal) in the elongate article 2 on the outer ramus of uropod 3 and the short anterior coxae, but, unlike *Eriopisa*, gnathopod 2 of the female often approaches the condition found in *Hadzia*. The resemblance is seen in the slightly elongate wrist and the presence on the hand of sparse groups of posterior setae which bend apically. The palm remains distinct and is lined with small trigger spines, whereas in *Hadzia* the palm and posterior margin of the hand merge together and the bent setae extend onto the palmar part. Gnathopod 1 is Ceradocid rather than Melitid. *Psammogammarus* retains fleshy inner lobes on the lower lip wheres these are lost in

Hadzia. Mandibular palp article 3 is linear and nonfalcate whereas in *Hadzia* article 3 is weakly falcate and the D and E setae are more strongly distinct from each other than in *Psammogammarus* or *Eriopisa*.

Psammogammarus is otherwise primarily a circumtropical genus of shallow seas that invades interstitial environments in the non-marine biomes. It is as widespread in the fully marine world as the Hadzioids. The known species have been found around the world in fully marine habitats. Except for *P. seurati*, from a well in south Tunisia, the species can be distinguished from *Hadzia* by the heavily elongate article 2 on the outer ramus of uropod 3. Some species of *Psammogammarus* are therefore so close to *Hadzia* that only by examination of the lower lip or female gnathopod 2 can a generic determination be made. The telsonic lobes remain separated basally.

Evolutionary trends within *Psammogammarus* include the reduction of coxae, the tendency toward vermiformization of the body, reduction of article 2 on the outer ramus of uropod 3, the inflation of the hand on gnathopod 1 as a departure from the Melitid form, basal fusion of the telsonic lobes and loss of medial setation on the maxillae. Female gnathopod 2 tends to have the Hadziid form, with elongate wrist and clumps of stiff, long and curved posterior setae on the hand.

The loss of medial setation on the maxillae has been a minor problem in confusion over the taxonomic differences between *Psammogammarus*, *Eriopisa* and *Eriopisella*. The latter genus forms the type of a group characterized by neotenic male gnathopod 2 and will be discussed in the following section.

Another important focal point is *P. chilkensis*, from Chilka Lake, a brackishwater lagoon in India. Like *Protohadzia schoenerae*, it bears the vestiges of eyes and, in addition, has the short posterior pereopods with expanded article 2 on pereopod 7 so atypical of Hadziids and Eriopisids. *Psammogammarus chilkensis* is apparently a very common nestling species in that lagoon and is apparently the only member known with eyes. The inner lobes on the lower lip appear to be poorly developed but the elongate article 2 on the outer ramus of uropod 3 and the well developed male gnathopods mark it as an Eriopisid.

Eriopisa, now restricted to one northern bathyal species, differs from *Psammogammarus* in the diversity of article 2 on pereopods 5-7 and the elongate article 2 on the mandibular palp. *Victoriopisa* (3, Indian Ocean, especially cool-temperate) differs from both genera in the fused base of the flagellum on antenna 2, the dilated article 4 of pereopod 7 and the loss of facial setae on maxilla 2.

Maleriopa (1) from the sublittoral of Mauritius, differs from *Psammogammarus*, *Victoriopisa* and *Eriopisa* in the loss of medial setae on the maxillae. It is plesiomorphic to *Paraniphargus*, the freshwater Andaman-Javan genus, because it retains article 2 on the outer ramus of uropod 3.

Melita is one step removed from typical Eriopisids in uropod 3; the second article on the outer ramus is small, vestigial or absent. Otherwise uropod 3 is fully parviramous and male gnathopod 2 is either very well developed or only weakly tending to be heterochronous. Six genera, *Melita*, *Dulichiella*, *Melitoides*, *Paraniphargus*, *Rotomelita* and *Nainaloa* constitute this grade of evolution.

Melita (61) is one of the most significant marine genera because of its circumtropical and temperate ubiquity and because it is often associated with brackish waters. It would be the ideal ancestral form in an ecological sense for a wide range of Gammarids thought to have entered non-marine habitats but, morphologically, it has many disadvantages. Except for its possible descendents associated in the above list, it may be a dead end in evolution unless one may demonstrate that a reduced article 2 on the outer ramus of uropod 3 can be greatly enlarged in descendents of *Melita*. A hypothetical ancestor could be envisioned to fit the need for a more universal antecedent.

More species of *Melita* remain to be described. There are several subgroups in the genus and these may be worthy of generic rank. For example, the rivermouth species in the IndoPacific, typified by *M. zeylanica*, have a special form of male gnathopod 2 characterized by an enlarged hand with uniform posterior margin, heavy facial setation and ornamentation on the medial surface and an overriding dactyl. The striking *M. appendiculata* (= *M. fresneli*) with male second gnathopods reminiscent of a fiddler crab is considered to form a distinctive genus, *Dulichiella*, with several species.

Tegano (1) is simply an anchialine genus, of the Solomon Islands and the Bismarck Archipelago, in which an ancestral *Melita* appears to have undergone reduction of the mandibular palp.

The *Melita* complex may be ancestral to *Psammoniphargus* with relatively normal marine gnathopod 2, and might be ancestral to *Galapsiellus*, *Netamelita*, and *Indoniphargus*, the latter 3 with increasingly neotenic or heterochronous gnathopod 2. The last two genera, however, appear to have more affinity to Eriopisellids because of the mitten-shaped male gnathopod 2 and will be discussed in that section. *Eriopisella* probably is not a descendent of *Melita* because of the enormous article 2, on the outer ramus of uropod 3, which ties it to *Eriopisa*. The ancestors of *Melita* may have had magniramous uropod 3 but, if true, they appear to be extinct or so rare as to be undiscovered. *Ceradocopsis* (= *Maeracunha*) is poor material for this assignment (see later section).

Although the two blind species of *Paraniphargus* live in freshwater springs in Java and in the south Andaman Islands (altitude 152-244 m), they scarcely differ from *Melita*. As pointed out by Schellenberg (1931b:497) they differ, together, only in the weak setation of the mandibular palp and maxillae, the loss of the anteroventral cusp on the head and the reduced accessory flagellum. The loss of article 2 on the outer ramus of uropod 3 is not a good generic character, as many species of *Melita* (but not most of the European species) have lost that article or have it so strongly reduced that it is hidden by adjacent spines.

Melitoides, the blind monotypic sublittoral arctic genus, differs from *Melita* in the reduced maxillary setation, the shortness of uropod 3 relative to the other uropods and the *Maera-quadrimana*-like palm of the second gnathopod.

Rotomelita (2) belongs to a recently discovered generic complex with one genus in the Hawaiian Islands and one, *Nainaloa* (1), in the Bismarck Archipelago. These species have the Melitid uropod 3 and very poorly developed inner lobes on the lower lip but otherwise appear to have relationship with *Psammoniphargus* from Reunion. That genus approaches Hadziids, although it is retained in the Melitids. *Rotomelita* is characterized by loss of medial setation on the maxillae and by the strangely quadrate telson bearing broad sinuous apical margins. The genus is blind and occupies anchialine waters. Whether or not it has become interstitial is unknown. The mandibular palp of *Rotomelita* is very poorly setose but that of *Psammonipharqus* is vestigial and *Psammonipharqus* retains weak medial setation on maxilla 1, although the oblique row on maxilla 2 has been lost. The telson of *Psammonipharqus* is very short and broad but has not assumed the distinctive form of *Rotomelita*. Both genera can be derived easily from *Melita*. Gnathopod 2 of the male in both genera is tending towards heterochrony, with *Rotomelita* losing most of the palmar spines. The well developed coxae suggest they have certain more primitive features than does *Eriopisa* and, therefore, the mixture of primitive and derived characters in the two subgroups suggests they are on different evolutionary lines.

The development of strong pedicles on the gills of *Rotomelita* (*Psammonipharqus* is unstudied) like those of certain Hadziids, suggests that this feature is replicatory. Pediculate gills are found in diverse family groups (also in Crangonyctids). The same may be true of supernumerary dactylar setation seen rudimentarily in *Rotomelita* but so prevalent in Australian freshwater Amphipoda and several of the Holarctic freshwater groups.

Psammonipharqus, from a resurgence of freshwater on the beach of Reunion, poorly fits the Hadziid concept. Ruffo (1956b:94) notes the resemblance of the genus to *Weckelia* and *Hadzia* (as *Metanipharqus*). We now know that *Psammonipharqus* differs from the magniramous *Weckelia* by the parviramous uropod 3 (information on *Weckelia* from J.R. Holsinger, in litt.), but otherwise resemble each other in the vestigial palp of the mandible. *Weckelia* bears very weak inner lobe creases on the lower lip, a longer accessory flagellum and spiny epimera but *Psammonipharqus*, by its parviramous uropod 3 would appear to be more strongly related to *Hadzia* than to *Weckelia*. This character is also more conducive to the biogeographical discontiguity between *Weckelia* and *Psammonipharqus*, as *Hadzia* is potentially a marine or brackish occupant of the western Indian Ocean. There is a fairly strong sexual dimorphism in gnathopod 2 of *Psammonipharqus* but gnathopod 2, though distinctly subchelate, bears the typical Hadziid posterior setae. The gills of *Psammonipharqus* are unknown but the telsonic lobes are weakly joined at the base. The fully parviramous uropod 3 and weakly joined telsonic lobes prevent *Psammonipharqus* from being the perfect intergrade between Melitids and Hadziids but it obviously stands near such a connection.

In a sequence confined to Melitids, *Psammonipharqus* descends from *Paranipharqus*, the freshwater genus in the heart of the IndoPacific region.

Galapsiellus forms the ultimate but remote evolute in the Melitids. It is known for one species from anchialine and phreatic systems in the Galapagos Islands. Gnathopod 2 of both sexes is enfeebled, slender, with elongate wrist and distinct but oblique palm. Gnathopod 1 is of the Melitid form but gnathopod 2 does not fully approach the mitten-form gnathopod 2 of Eriopisellids. The maxillae are poorly setose medially and the anterior coxae are reduced as in *Psammogammarus*. Weak inner lobes are retained on the lower lip and the telson remains fully cleft. Article 2 on the outer ramus of uropod 3 is absent. *Galapsiellus* is especially noted for the elongate peduncle on uropod 3, which resembles the analogous condition in Maerella and Jerbarnia, but those taxa have magniramous and aequiramous third uropods. Galapsiellus could be derived from Psammogammarus or, remotely, Paraniphargus.

Anchialella (1), also an anchialine species from the Galapagos Islands, appears to form the transition between Psammogammarus (old Eriopisa) and Galapsiellus. Anchialella has not progressed as far as Galapsiellus because female gnathopod 2 is not fully enfeebled, the telsonic lobes are not turgid and the outer plate of maxilla 1 retains the normal odd number of 7 spines. But, Anchialella differs from Psammogammarus and Paraniphargus in the elongate peduncle of uropod 3 and the beginnings of enfeeblement on female gnathopod 2.

Continental Incursions from the Sea

The major ingressors to continents are the Niphargids, Pseudoniphargus, the Eriopisids and the Salentinellids, plus a few taxa outside the Gammaridans to be found in a later section. Of course, Amphipods probably came originally from the sea so that Crangonyctids and their Gammaroid descendents are also continental ingressors.

Eriopisella Group

The Eriopisellids comprise a group of 5 genera with Melitid affinities, especially to Eriopisids, in which male gnathopod 2 is severely reduced. The five genera are Eriopisella, Netamelita, Microniphargus, Indoniphargus and Giniphargus. The male first or second gnathopod is about as small as gnathopod 1, has a similar mitten-like structure but has article 5 produced into a fuzzy posterior lobe extending somewhat distalwards and guarding article 6. Microniphargus and Indoniphargus are exceptions in that gnathopod 1 and not gnathopod 2 is furnished with the lobe. In these cases, axial reversal in gnathopods appears to have occurred. In one species, Eriopisella madagascarensis, the lobe is obsolete on gnathopod 2 but article 5 is very elongate and the gnathopod retains the unusual appearance. Eriopisellids are also characterized by weak maxillary setation. All species, except Eriopisella sechellensis and Netamelita cortada, have defective eyes or are anoculate.

Eriopisella comprises 8 species with the main center of distribution confined to the Indian Ocean along the shores of Asia from Japan westward through India to Madagascar and South Africa. One species occurs in Normandy, France. Eriopisella sechellensis extends eastward to the Hawaiian Islands. There is a great deal of diversity in gnathopods in the genus. The absence of a lobe on article 5 of gnathopods 1-2 in Eriopisella madagascarensis suggests a generic differentiation of this species from Eriopisella and Indoniphargus. Other characters of Eriopisella also vary a great deal to the extent that several genera may have to be split away from Eriopisella. Undoubtedly, a great deal of exploration will be required to satisfy the impression that many more unknown species await discovery; the Indian Ocean, Southeast Asia, Indonesian Archipelago, northern Australia and East Africa are very poorly studied for Amphipoda. Although a few species of Eriopisella may occur close to shore near brackish water influences, most of the species are fully marine and some have been collected in waters as deep as 50 m.

The close resemblance to Eriopisa is marked by the elongate article 2 on uropod 3 in several of the species, but others, even E. sechellensis, have this article considerably shortened. Netamelita differs from Eriopisella mainly in the loss of that article. The monotypic Netamelita is found in southern California in depths of 20 m. The monotypic Microniphargus, found in a cave puddle near Liege, Belgium, differs from the other two genera in the axial reversal of gnathopods but also, like Nipharguses, has the telsonic lobes fused basally so that the telson is cleft only halfway. The condition of gnathopod 2 in the Melitid, Galapsiellus, in comparison to Eriopisellids, is somewhat primitive but almost all other charactristics of that genus are highly advanced so that it cannot be construed as a primitive stage in the development of Eriopisellids.

Indoniphargus indicus is found in eastern India in freshwater springs, wells, and mine pits. Unlike the other genera here placed, Indoniphargus lacks inner lobes on the lower lip and bears 3 supernumerary basofacial spines on uropod 1 (4 total). The pleosome and urosome are more spiny dorsally than in various Hadziids, Melitids, Eriopisids and Eriopisellids. Article 2 on the outer ramus of uropod 3 is absent (? or vestigial). The spininess of this genus, including articles 4-6 of pereopods 5-7, plus the relative uniformity of article 2 on pereopods 5-7 (on which pereopods 6-7 have a weakly produced posteroventral lobe), suggests the possibility that this genus might be related to the Accubogammarus group of Gammaroids. Otherwise, this genus would represent a case where spininess on the urosome can develop from marine ancestors. Apparently Indoniphargus lacks a coxal gill on pereopod 7 but as stated elsewhere this is not always a firm indication that a genus has a marine origin. The gills are pedunculate and the right and left palps of maxilla 1 are diverse as in many freshwater Gammaroids. Indoniphargus should be considered a possible Gondwanan import via the tectonic raft of India.

Giniphargus (1) from Australia represents the fifth genus of Eriopisellid. The gnathopods are mittenform but also very hammer-like, as in Niphargids. The body is strongly vermiform and article 2 on the outer ramus of uropod 3 is elongate, but the inner ramus is absent. Coxal gills are pediculate, apparently sternal gills are absent, and the gnathopods lack densely packed bifid spines, so that Giniphargus cannot be linked to Crangonyctoids. Presumably, it is a genus that has crawled from the sea into the hypogean environment of Australia. Neither gnathopod has a posterior lobe on article 5, and that article on gnathopod 2 is elongate. The pleopods are normal (to make reference to a similar morphotype, Paracrangonyx in New Zealand). Full medial maxillary setation is retained, article 3 of the mandibular palp is weakly falcate, and well differentiated D and E setae are retained, suggesting affinities with Eriopisids, rather than Eriopisella. Moderately developed inner lobes on the lower lip are retained.

Relationship between Eriopisellids and Niphargids

The close morphological affinities between Eriopisella (and Eriopisids) and Niphargus have been pointed out by Chevreux (1920), Ruffo (1953) and Gurjanova (1965). Gurjanova concludes that these genera probably fall onto 3 independent lines of evolution. Nevertheless, the convergence is striking. The question might be asked, "Is there any morphological evidence to support the evolutionary descent from Niphargus (Palearctic phreatic) to Eriopisella (Indian Ocean marine primarily) or, vice versa, could Niphargus or its allies be descendents of Eriopisella?" On the basis of the known species in both groups the answer to the second question is "yes". This answer is based on the absence of coxal gill 7 in Niphargids, which therefore could descend from Eriopisellids as well as from some hypothetical descendent of the (Chaetogammarus) group.

In the above paragraph the question of interrelationship is based just on the known Neogenic faunas. Both genera have progressed too far in their evolution to be ancestors of each other but the possibility remains that oculate ancestors of Niphargus might have been ancestors to Eriopisella through transformation of the gnathopods into the mittens of Eriopisella.

The gnathopods of Eriopisella nagatai, from India near the mouth of the Ganges, are a very striking replicate of the Niphargid gnathopodal morphology. Besides eyes and gills the two groups differ in the absence of a posterior lobe on article 5 of gnathopod 2 in Niphargus and its presence in Eriopisella. The Indian species has this lobe but its gnathopods are otherwise much closer to the broad handed hammer-like form found in Niphargus. Eriopisella nagatai otherwise makes a poor intermediate because of specializations in pereopods (expanded and lobate article 2 of pereopod 7) and other characters. Most Eriopisellids and Eriopisids also resemble Niphargids in the immensely enlarged article 2 on the outer ramus of uropod 3 but in a few species of each of the three groups, this article is severely reduced, as it is in E. nagatai.

Both pairs of gnathopods in the average species of Niphargus have very stout hands. This disguises the inherent Melitid form of gnathopod 1 seen in both pairs but which is well reflected in the aberrant Pseudoniphargus africanus, a subterranean species widely distributed around the Mediterranean basin. Gnathopod 2 of that monotypic genus is small and very Melitid in form, whereas gnathopod 2 is enlarged but the hand is not as broadened as in Niphargus and the attachment between the short wrist and longer hand has not become as "Eusirid" as it is in Niphargus. Imperfect eyes occur in Pseudoniphargus. The male has the normal Niphargid-Eriopisellid uropod 3 with immensely elongate article 2 but that article is lost in the female. The lobes of the telson in Pseudoniphargus are much more coalesced together than in the average species of Niphargus, more in resemblance of the American Crangonyctids. Pseudoniphargus, therefore, is not a good intermediate between any of the other genera but shows on some of its appendages the stages necessary to bridge the morphological gaps between Eriopisids and Niphargids. Pseudoniphargus has well developed inner lobes on the lower lip as in Eriopisella and Niphargus and the maxillae are poorly setose in all 3 genera. Pseudoniphargus is one of the few Palearctic freshwater Gammaroids with the Melitid gnathopod 1.

Several evolutionary sequences might be constructed. They require the formulation of hypothetical intermediate stages and ancestors. An ancestor to both Niphargus and Eriopisella would bear well developed eyes, Melitid gnathopod 1, the commencing enlargement of article 2 on the outer ramus of an otherwise parviramous uropod 3, the presence of coxal gills on pereonite 7, and a fully cleft telson. Gnathopod 2 would have its normal Gammarid enlargement in the male. This kind of amphipod is reflected to some extent in the Dikerogammarids.

The evolutionary steps toward *Niphargus* would then entail the enlargement of gnathopod 1 by widening of the hand, the assumption by gnathopod 2 of the morphology of gnathopod 1 and together both gnathopods would have a narrowing of the attachment point between articles 5 and 6. The Eriopisellid line would undergo a reversal in gnathopods. The sharp Melitid form of gnathopod 1 would be blunted, the palm become somewhat more oblique, article 4 enlarged and fuzzy and gnathopod 2 would assume the same form but article 5 would develop a fuzzy posterior lobe. Coxal gill 7 would be lost.

If Eriopisids were to be drawn into the sequence, then the ancestor would require heavy maxillary setation and the descendents would then develop a somewhat stronger male gnathopod 2 with increase in sexual dimorphism, only to have this regress later in several species. If this regression in gnathopod 2 and loss of maxillary setation occurred in Eriopisids, they could represent the ancestor of *Eriopisella*.

Because the ancestor with full maxillary setation and gill 7 is apparently extinct, one cannot know whether it was of marine or freshwater provenance, but a good supposition is that the ancestor occurred in Palearctic freshwater. This is based on the modern lack of gill 7 in marine Gammaridans, except in the Boreal Pacific Anisogammarids and the Arctic Gammarellids.

The absence of gill 7 in marine Gammarids of the Hadziid-Melitid-Ceradocid groups might suggest that the occurrence of sternal gills in freshwater amphipods of the southern hemisphere, in Australia, South Africa and the Falkland region, is a selective compensation for absence of gill 7 in the ancestors of those groups and that, therefore, those ancestors were originally of marine occurrence. The strength of this theory is much disturbed by the fact that Nearctic Crangonyctids, bearing gill 7, also have sternal gills. One might dismiss this by accepting the thesis that sternal gills have evolved twice. Actually the development of supernumerary gill structures in amphipods is far more widespread than immediately apparent. The South American Hyalellids in freshwaters, especially in Lake Titicaca, are presumably of marine origin and have accessory gills. A species of Eusirid in anchialine waters of Japanese southern volcanic islands has accessory gills but this taxon may actually be a Crangonyctoid. The Anisogammarids have accessory coxal gills. Many fully marine amphipods have elaborate gill structures (for example Lysianassidae). Whether or not gill 7 once lost can be reconstructed in an evolutionary line is a moot point but the development of other gill specializations is clearly of common occurrence in amphipods.

Bathyonyx Group

Bathonyx devismesi Vejdovsky, from Lough Mask, Irish Sea, is a strange but inadequately described amphipod. It has the appearance of a newly hatched Gammarid. The following attributes are unknown or imprecisely indicated: gills, lower lip, inner plate of maxilla 1, palmar spination, maxillipedal palp. The body is stout but the coxae are all short and contiguous, the gnathopods are almost mittenform, with gnathopod 1 slightly the dominant, the inner plate of maxilla 2 is medially setose, the mandible is normal, at least in terms of the presence of setose 3-articulate palp and triturative molar, uropod 3 is weakly variramous, with article 2 on the outer ramus well developed, the accessory flagellum is 2-articulate, the head is large and subcuboidal, the antennae are reduced but articles 2-3 of the peduncle are scarcely shorter than article 1, the telson is elongate, deeply cleft and has the dorsal setules shifted apically, pereopods 5-7 are thin, and the outer plate of maxilla 1 strangely bears only 4 spines. The genus also appears to stand close to Hadziids or to the Paraweckelian Melitids and is close to the Salentinellas.

The mittenform gnathopods are used here to place Bathyonyx near the Eriopisellids until more can be learned of this genus.

Salentinella Group

The Salentinella group is composed of 2 genera, and is closely similar to the Eriopisellid and Hadziid groups. Salentinella, however, may not be a Gammaridan, according to Dr. Bousfield (in litt.). The gnathopods are very close to being mittenform and gnathopod 2 apparently lacks close set spines on the palm but Salentinellids are marked by the apically shifted telsonic setules, and the absence of inner lobes on the lower lip. Salentinellids differ from Hadziids and Eriopisellids in the strongly reduced antennae, the loss of medial setation on the maxillae and the stronger ventral lobation on article 2 of pereopods 5-7 with the remaining articles being much shortened. There is a great similarity to Bathyonyx except for pereopods 5-7.

The loss of medial maxillary setation resembles that of Eriopisellids but the lobations on article 2 of pereopods 5-7 are not highly unusual because these occur frequently in Eriopisids, where a wide variety of morphotypes occurs.

Salentinella (10) is found in brackish and phreatic waters along the northern shores of the Mediterranean from Dalmatia westward.

Parasalentinella (1), a phreatic form from the French Pyrenees, has uropod 3 reduced to a single short ramus lacking article 2, the telson is shortened and entire, pereopod 5 lacks the pendant setae near the base of the dactyl on article 6, antenna 1 is crested and the epimera are almost rounded.

Pseudoniphargus Group

Pseudoniphargus (1), from anchialine salt pools in the western Mediterranean, belongs with the Niphargids but differs in the more normal Gammaroidean gnathopods at least to the extent that they are not both hammer-like. Gnathopod 1 is small and almost of Melitid form, with transverse palm, while gnathopod 2, though much enlarged, has the hand longer than broad and the palm oblique. Coxal gill 7 is absent and accessory gills are absent (Dr. Holsinger, conversation). The maxillae are poorly setose and uropod 3 has the typical Niphargus-form, with article 2 on the outer ramus greatly elongate, at least in the male; however, the female has article 2 absent. This is reminiscent of the situation in Allocrangonyx, where the male has serial segmentation of the outer ramus while the female does not. Pseudoniphargus also resembles Allocrangonyx in the presence of two kinds of setae on the outer plate of maxilla 2; the shapes of the plates are similar and the two groups also differ from the Crangonyctids in the poorly setose maxillae but Allocrangonyx has spiny palms on the gnathopods whereas Niphargids do not. Pseudoniphargus has these spines so greatly reduced that the hand resembles the comb-like hand of Niphargids more than the spiny hand of Crangonyctids; but in the end Pseudoniphargus resembles neither genus very closely because of such strong reduction in the hand.

Unlike other Niphargids the telson of Pseudoniphargus is almost entire.

Pseudoniphargus forms a reasonably good ancestral model to both Niphargids and Allocrangonyx but would appear to be apomorphic (more strongly descendent) than Crangonyctids which have well setose maxillae and coxal gill 7.

The generalized Pseudoniphargus form could also be ancestral to the Hadziids or to the Melitids (or to Psammogammarus) as the diverse gnathopodal type is already present, while gnathopod 1 is almost of Melitid form, but Pseudoniphargus could also be positioned far down the scale near Eriopisa and Eriopisella.

Pseudoniphargus differs from Eriopisids in the fully reduced maxillary setation (although the trend to this is present in Eriopisids) and from Eriopisella in the enlarged gnathopod 2. It differs from both genera in the fused telsonic lobes.

Niphargus Group

The Niphargids comprise 6 genera, Pontoniphargus, Niphargus, Niphargellus, Carinurella, Haploginglymus and Niphargopsis. Karamaniella is synonymous with Niphargus owing to intergradation of antennal character differences (Karaman, 1974f:23). Niphargids are characterized by weak maxillary setation, the presence of inner lobes on the lower lip, the hammer-like gnathopods 1-2 with very stout hands, subtransverse palms and the tendency to "Eusirid" articulation between the wrist and the hand. Coxal gill 7 is absent. Except for Pontoniphargus, uropod 3 is of the parviramous form but article 2 on the outer ramus is immensely elongate in most species. The dactyls of the pereopods often have supernumeray setation or spination. All species are blind and all occur in subterranean or incipiently subterranean habitats of Palearctica. There is a tendency in the group towards vermiformization of the body, shortness of coxae and partial fusion of the telsonic lobes with broadly spinose apices. Except in the satellite genus, Pseudoniphargus, the latter trend does not approach that seen in Crangonyctids.

Niphargids apparently are well adapted to the interstitial mode of inhabitation. They are apparently highly errant and this may be reflected in uropod 3, which often reaches half the length of the body. Its triarticulate flexibility suggests that it may be used as a posterior feeler, so that organisms can move rapidly backwards in tight spaces. Why such a third uropod in the marine genera Eriopisa and Eriopisella would have value is a mystery.

Niphargus (Maps 59-65, Tables 11, 12), with more than 130 species, is confined to Palearctica west of the Caspian Sea, north of the Mediterranean, south of the farthest main advance of glaciation and is absent or poorly represented in Iberia, southern Italy and Sardinia. Ruffo (1953c:34,fig. 5) believes that this distribution was effected by the interplay of Quarternary glaciation and Tertiary expansion of Pontian seas. He also notes (p. 33) that the number of species declines severely at the

TABLE 11.--Long Distance Distribution of Species in *Niphargus*, top 12 in rank.

Map	Species Number	Species	Distribution
61	72	*longicaudatus*	W. Pyrenees to Caucausus, to Greece, Carpathia, Belgium, mid-Italy
63	64	*kochianus*	Ireland to Bulgaria, to Carpathia, Germany, Pyrenees
60	120	*stygius*	W. Italy to Caucausus, to Carpathia
62	100	*puteanus*	W. Germany to Caucasus, to to Carpathia, Bulgaria, Turkey
62	12	*aquilex*	England to Rumania, to Denmark, France, E. Hungary
62	59	*illidzensis*	N.W. Yugoslavia to E. Turkey
61	45	*foreli*	Pyrenees to Rumania
63	111	*skopljensis*	Pyrenees to Rumania, to Macedonia
59	124	*tauri*	W. Italy to S. Turkey
60	44	*fontanus*	England to E. Austria, to Pyrenees
62	63	*jovanovici*	E. France to Macedonia, to E. Hungary
61	109A	*schellenbergi*	Pyrenees to E. Germany

boundaries of the distribution noted above. Niphargids would therefore appear to be expanding outward from this region, at least towards the south where they were not constrained by glaciation. It is possible, however, that Mediterranean drying, not mentioned by Ruffo, may have caused harm to the group. In contrast, the Pyrenees represent a formidable barrier to Niphargids and their northern limit rather neatly fits certain of the glaciation advances. The only species found deeply into Iberia was originally placed in its own genus, *Haploginglymus*, based on the absence of article 2 on the outer ramus of uropod 3; it remains held there temporarily.

Niphargus is blind and mainly subterranean though many species survive in the first few meters of springs and a few are found living openly in lakes, such as Ohrid, Prespe, and in the Black Sea and Caspian Sea. The main populations of these species may also live in subterranean waters. Numerous subspecies have been described, but much consolidation can be expected.

Niphargus is considered to be much younger than *Gammarus* or *Crangonyx* and to have a direct marine Mediterranean origin; it developed too late to penetrate Africa or America and has progressed only about halfway across Palearctica. The center of the genus now appears to be northwestern

TABLE 12.--Wide spread (bulk in contrast to long distance) Areal Distribution of Species in Niphargus, top 37 in rank (area or latitude).

Map	Species Number	Species	Distribution
61	72	longicaudatus	W. Pyrenees to Caucausus, to Greece, Carpathia, Belgium, mid Italy
62	12	aquilex	England to Rumania, to Denmark, France, E. Hungary
63	64	kochianus	Ireland to Bulgaria, to Carpathia, Germany, Pyrenees
62	100	puteanus	W. Germany to Caucausus, to Carpathia, Bulgaria, Turkey
60	44	fontanus	England to E. Austria, to Pyrenees
62	63	jovanovici	E. France to Macedonia, to E. Hungary
61	109a	schellenbergi	Pyrenees to E. Germany
61	45	foreli	Pyrenees to Rumania
60	120	stygius	W. Italy to Caucausus, to Carpathia
62	59	illidzensis	N.W. Yugoslavia to E. Turkey
60	129	valachicus	Sickle of Hungary-Czechoslovakia south to Greece, northeast to Ukraine
63	111	skopljensis	Pyrenees to Rumania, to Macedonia
59	124	tauri	W. Italy to S. Turkey
59	123	tatrensis	W. Germany to E. Czechoslovakia
60	86	pachypus	Limburg to Pyrenees
63	132	virei	Limburg to Riviera, to Baden
61	61	inopinatus	W. Germany to E. Czechoslovakia
60	57	hrabei	Austria to Ukraine, through Rumania
63	110	serbicus	Trieste to Rumania
59	103	rhenorhodanensis	Rhone Valley

TABLE 12, continued

60	42	*elegans*	N. Italy, W. Yugoslavia
60	67	*ladmiraulti*	France

others: 30 *ciliatus*, 26 *carpathicus*; 2 *ablaskiri*,
99 *pupetta*, 75 *maximus*, 11 *andropus*,
80 *molnari*, 68 *laisi*, 117*stefanelli*,
87 *pancici*, 47 *gallicus*, 77 *microcerberus*,
89 *pasquinii*, 24 *bureschi*, 49 *gineti*.

Yugoslavia, a country with 58 species. The next greatest occurrences are France with 20 and mainland Italy with 18 species. Many collections in Bulgaria remain unidentified (as denoted by crosses in Andreev, 1972, indeed some earlier records now appear to be returned to unidentified status in this depiction). Rumania remains only moderately explored (as shown by the sparsity of the records in Dancau, 1972).

Nipharqus, with 139 species (1979 Aug.) has more than 80 with constrained distributions, confined to one locality or a few square kilometers (species marked with single dot on our maps).

One presumes that the heavy concentration of species in Yugoslavia owes much to the karstic nature of the dolomitic alps, with its plethora of subterranean habitats. Karaman senior devoted his life to exploring this environment for amphipods and other taxa and his son followed in his footsteps for almost 2 decades but now tells me the alpha stage of exploration for new taxa is complete. The genus is so important to Europeans that several conferences on it since 1969 have been held, in Verona 1969, Schlitz 1975, Virginia (USA) 1978 and Lodz (1980, 1981) (see nearby BOX). Several hundred scientists today are dealing with problems in this genus, though not necessarily full time. The meetings have expanded to include *Gammarus* and groundwaters, and grow more numerous and greater in time and scope than when first conceived by Profs. Dancau and Ruffo.

The distributional charts of this genus, compiled herein from the literature of hundreds of localities and several maps (for example, Balazuc, 1954, 1957, Schellenberg, 1942, Pesce and Vigna-Taglianti, 1975, Hynes, 1955, Hynes, Macan and Williams, 1960, Ruffo and Vigna-Taglianti, 1968, Morand-Chevat 1972, Andreev, 1972, Dancau 1972b, Straskraba 1972b, Skalski, 1972, and others), reveal incomplete tasks in the taxonomy. Many of the so-called subspecies are probably not realistic as they show a scattering, intermingling and spotty overlap; they may be phenotypes, ecotypes, or clines. We must remember however, that the mechanics of underground stream capture and isolation are very complex and strange distributions may well occur. One could imagine two sympatric species existing in vertical isolation within distinct aquifers.

Long-distance distribution is depicted in Table 11 where the top 12 species are listed in rank according to the extremes of their distributions, the longest being *N. longicaudatus* from the W. Pyrenees to the Caucausus. This species probably also has the most extensive area of occupation, a subject formulated in Table 12. These rankings are approximations based on subjective estimates of plotted areas.

Thirteen taxonomic groups of *Niphargus* formulated during the First International Colloquium at Verona are cited by Straskraba (1972b). Very

International Amphipod Conferences

The International Colloquium on *Gammarus* and *Niphargus* originated as a meeting of specialists on *Niphargus* alone in Verona in 1969 under the leadership of Professors Dancau and Ruffo. The results were published in 1972 in Memorie del Museo Civico di Storia Naturale di Verona, (fuore ser.) 5. A second meeting of similar nature concerning *Gammarus* was held in Karlsruhe in 1971. As interests and participants overlapped a combined meeting known as the 2nd Colloquium on *Gammarus* and *Niphargus* was held in Lyon in 1973 and the results were published in several later issues of Crustaceana. The 3rd Colloquium was held in Schlitz in 1975 under leadership of Professors Husmann and Meijering and the results published in Supplement 4 of Crustaceana. The 4th Colloquium was held in Blacksburg, Virginia under leadership of Professors Holsinger and Buikema and results were issued in Supplement 6 of Crustaceana. The 5th Colloquium was held in abbreviated form in Lodz in September 1980, and again in 1981, under leadership of Professors Jazdzewski and Skalski.

little since that time has been elucidated from this formulation, evolutionary studies in the group not having gone forward with the speed one now expects in a group so widely studied. However, by the groupings of subspecies, the continuing changes in synonymies and taxonomic revisions, much is being said about evolutionary grouping but this information is not being assimilated and synthesized.

Pontoniphargus (1), from hypogean Rumania, has the most primitive condition of uropod 3. The appendage is almost magniramous in the male, with the inner ramus greatly more extended than in other Niphargids. This condition was also noted for *Niphargus skopljensis hebereri* by Schellenberg (1937b:7, fig. 3c), who termed the condition atavistic. The genus also has a weakly filtrative maxilla 2 similar to *Niphargus skopljensis* but not as strongly developed as in *Niphargopsis*.

Nipharqellus (2) differs from *Niphargus* in the reduction of setae and simplification of shape on article 3 of the mandibular palp. This genus occurs across middle Europe from western Poland to southern England.

Niphargopsis (2) is characterized by the immense development of spines and setae on the outer plate of maxilla 2, possibly as a filtering device. This kind of maxilla is also seen in *Zenkevitchia* and has recently been found by J.R. Holsinger (in litt.) in a new American subterranean genus and by Cole and Watkins (1977) in a species of subterranean *Hyalella* (Hyalellidae) from Arizona. *Niphargopsis* occurs in midsouthern Europe from approximately Vienna to Grenoble, again as a subterranean species.

Carinurella (1), from Yugoslavia, is characterized by the absence of the inner ramus on uropod 3, as well as the absence of article 2 on the outer ramus and has urosomite 1 immensely dominant over the reduced urosomites 2-3 appended to it. Article 1 of the peduncle on antenna 1 is crested, as in *Karamaniella*, but the latter genus is said to intergrade too strongly to *Niphargus* to be maintained (G.S. Karaman, conversation).

Haploginglymus is an aberrant Niphargid because of the loss of article 2 on the outer ramus of uropod 3. The monotypic genus is known from a well in Portugal.

Other Freshwater Amphipods of the World

Several score of non-Gammaridan amphipods also live in freshwaters of the world and many more live in brackish waters. The most diverse of the freshwater penetrants are the Hyalellas, Chiltonias, Corophiums and Paramoeras but the most striking is Seborgia.

Only the gross outline of non-Gammarid nonmarine taxa is presented; time and space are allotted only to the genera with significant freshwater occupancy; doubtful and minor cases are ignored. Some collectors did not discriminate between fresh and salt waters in estuaries and several so-called freshwater species may live in salt waters penetrating upstream. The brackish Amphipoda deserve a book of their own so that, for the most part, only genera with truly freshwater species are discussed here.

Most of the non-Gammaridan freshwater species appear to have their origin from the sea; they mainly penetrate freshwaters by adjustment to lesser salinites in brackish waters near river mouths or brackish lagoons and then by evolutionary increments move into continental freshwaters. However, some of the Talitridae have moved into freshwater from a terrestrial existence. Those terrestrial taxa have a marine origin in the tropics, passing in an evolutionary cycle as beachhoppers onward to forest leafmold habitats. A few species apparently find open niches in freshwaters and become aquatic again.

The brackish water taxa are rapidly becoming widely distributed by man throughout the major world estuaries and, therefore, urgent exploration is required before the mixture prevents the discovery of the original homes of the species.

The greatest diversity of freshwater amphipods besides Gammaridans is found in the Hyalellidae, a family group of the superfamily Talitroidea, to which the beachhoppers are also assigned. Talitroideans are assumed to be phyletically remote from Gammaridans, though the only consistent gross difference appears to be the loss of the mandibular palp in all Taitroideans, a happenstance occurring rarely in Gammaridans (in Beaudettia, for example). In fact, Beaudettia so neatly bridges the gap between Gammaridans and Talitroideans that one might speculate about that evolutionary deployment in another study. Talitroideans usually also differ from Gammaridans in the shinier or opalescent cuticle and usually have very easily recognizable mouthparts in terms of shape and setation.

Talitroidea

The dominant freshwater talitroids are the South American Hyalellidae. The genus Hyalella is widespread throughout the Amazonian Basin (specimens in collections of USNM) and in Lake Titicaca, the famous alpine lake of Peru (Faxon, 1876). At least one species occurs in Patagonia. Freshwater talitroids are characterized by the loss of mandibular palp combined with loss of inner ramus on uropod 3. The species are very slick, shiny and non-setose, though often they may be spinose.

Hyalella is represented by about 31 species but many remain to be described. The genus has a semiterrestrial, beachhopper counterpart in Parhyallela, which is widespread in the IndoPacific region.

Talitroideans in New Zealand, Australia and South Africa are represented by the Chiltonias, now divided into Chiltonia and

Afrochiltonia. Formerly *Austrochiltonia* was used for the Australian representatives but Griffiths (1976) found *Austrochiltonia* and *Afrochiltonia* to be synonymous. The Chiltonias belong to the subfamily Chiltoniinae, a division of the Ceinidae, the latter differing from the Hyalellidae in the loss of ramus on uropod 3. This group has a strong aspect of relictness, because of the poorly speciated but generically diverse marine ancestry in New Zealand (perhaps barely surviving) and their widespread Gondwana distribution in freshwater. Again,* however, the South American connection is not only remote, it is nonexistent, thus indicating but not proving that Chiltonias and Hyalellas evolved separately after the disjunction of South America from Gondwanaland.

A few species of the terrestrial *Orchestia*, in the family Talitridae, have returned to aquatic environments; for example *Orchestia recens* occurs in a freshwater stream on New Zealand and *O. remyi* lives in a subterranean habitat on Corsica. The eyes of the latter species are reduced.

Parhyale hawaiensis, of the Hyalidae, is strongly oriented to brackish waters and may occur in purely freshwater, occasionally in the tropics.

Spelaeorchestia koloana, an endemic, is found in lava-tube caves of Kauai, Hawaii, along with two introduced epigean species, *Talitroides alluaudi* and *T. topitotum*. *Spelaeorchestia* is distinctly modified for cave existence, whereas the other two species are simply intruders from a subcosmopolitan pestiferous background.

An occasional species of the pandemic marine genus (antipolar) *Hyale*, such as *Hyale milloti* on the Comores Islands, penetrates freshwater. Various species living in grottos along seashores, such as in the Shimoni Grotto of Zanzibar, though with reduced eyes, are not truly of freshwater character (Chevreux, 1913).

The genus *Dogielinotus*, of brackish occurrence on the very cold margins of the north Pacific Basin, has two species reported from freshwater in cold northeastern Asia. A companion genus, *Haustorioides*, lacking a ramus on uropod 3, has 2 species in northeastern Asia, neither of which is apparently fully adapted to freshwater.

Corophioidea

Corophium commonly occupies brackish water and a few species penetrate purely fresh water. Only a few species of *Corophium*, such as *C. baconi*, are clearly marine, whereas the remainder are often associated with very shallow or diluted waters; they are often carried about by mankind, several species such as *C. acherusicum*, *C. insidiosum* and *C. uenoi* having been distributed widely into exotic estuaries (see Crawford, 1937a:616,617; J.L. Barnard, 1952c:28).

Corophium is an important genus in the PontoCaspian Basin, being represented by 14 species (See Appendix I). As a whole, the genus tolerates both brackish and freshwaters in the basin and is rapidly dispersing throughout European and west Asian freshwaters, mainly through the activities of mankind. Canals connecting PontoCaspian rivers with

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* The word "again" refers to the conclusion that South America drifted far away from Gondwanaland before its other parts dispersed.

other river systems provide access to northwestern Europe and deliberate transplantation, mainly by Russians, is undertaken to provide food for commercial fishes (Jazdzewski, 1970, 1980).

Corophioideans are characterized by fleshy telsons. *Corophium*, itself, is a very easily recognized genus looking like Limnoriid isopods, with a depressed urosome and somewhat cylindrical body. Like most Corophioideans, species of *Corophium* live in domiciles constructed from web spinning glands in pereopods 3-4. The tubes or nests are usually attached to particles of substrate, or to manmade structures such as pilings and ships. A few species can burrow (said to be true of *Corophium crassicorne* by Crawford, 1937a:607) and others may steal tubes from other organisms often in other phyla (such as polychaetes) (J.L. Barnard, 1958b:166).

Paracorophium (3) is very distantly related to *Corophium*; the two genera share the same kind of gnathopod 2 but their other attributes are so distinct that gnathopod 2 may be coincidental and not homologous. Gnathopod 2 has articles 4 and 5 overriding each other along a common face, often with super development of outer setal brushes. In *Paracorophium* article 5 forms a large freely extending elbow, not occurring in *Corophium*.

Whereas *Corophium* is cosmopolitan outside the poles, *Paracorophium* is of Gondwanaland provenance, having been found, so far, in New Zealand, Australia and Chile. The genus is both brackish and oligohaline.

Stenocorophium (1) is a tropical northern outlier of *Paracorophium*, being found in a freshwater stream on an island in the Palau group north of New Guinea (G.S. Karaman, 1979b). The genus, having an almost simple gnathopod 2, scarcely differs from *Paracorophium*.

Kamaka is a genus of 4 species occurring in cold northeastern Asia. The genus occurs in lakes (mainly Lake Biwa) and streams from Vietnam to Kamchatka. This genus looks somewhat like *Corophium* but has urosomites 1-2 amalgamated. *Corophium* has all urosomites free or fused but never the combination found in *Kamaka*.

Grandidierella is a circumtropical genus of more than 20 species oriented mainly to shorelines near freshwater or in brackish lagoons or various anchialine habitats. One species, *G. vietnamica*, has been reported in full freshwater but the other most strongly non-marine species are found mainly in places like Chilka Lake in India which is really a longshore lagoon. At least 3 species of the genus occur in Chilka Lake (*gilesi*, *macronyx* and *bonnieri*), while others occur in more restricted anchialine habitats such as the lava ponds on Hawaii (*koa* and *palama*).

Other corophioids reported from freshwater are clearly aberrant species, such as *Microphotis blachei*, which apparently occurs upstream in the Mekong River (Ruffo, 1952b).

Oedicerotids

Like the odd Corophioid occurring in freshwater one may mention the odd Oedicerotid, such as *Monoculodes limnophilus*, in rivers of China and Japan and *Metoediceropsis dadoensis* of a river in Viet Nam.

They are simply the exceptional species which have penetrated freshwater by making the necessary adaptations osmotically. Needless to say, these independently evolving taxa and their congruency in adaptations is of prime interest to evolutionists and these taxa should be studied intensively.

Eusirids-Calliopiids

This group of amphipods has close affinities to Gammaroids and is placed in the Gammaridans (section) but may have no monophyletic cohesiveness. We believe they represent a polyphyletic group of gradational apomorphs with ancestry in a variety of Crangonyctids and Gammaroids, Hadzioids and Bogidiellids.

Paramoera is the most diverse genus of this group with species beginning to move into fresh or brackish waters. So far all of these are in the northern hemisphere but it will be worth looking for the genus in southern streams near the sea. However, it would appear that in the southern hemisphere, at least in Australia and New Zealand, the freshwaters have been invaded by (1) analogous taxa, such as *Pseudomoera* and *Paramoerella*, (2) convergent taxa, such as *Paraleptamphopus*, an analogue of *Phreatogammarus*; and (3) highly apomorphic taxa, such as *Paracalliope*, worth placing in its own family.

Like other Eusirid-Calliopiids, *Paramoera* is characterized by the aequiramous uropod 3 lacking article 2 on the outer ramus, the rami being flattened and lanceolate, quite unlike the typical European *Gammarus* uropod 3. This could be called a marine uropod 3. It is present on several brackish and freshwater Gammaroids, such as *Gammaracanthus*, and *Acanthogammarus*.

Paramoera is a widely spread cool water littoral genus in both north and south boreal zones. More than 40 species have been described. At least 7 of these have penetrated inward from marine zones either to brackish-fresh waters on cold North Pacific shores (*carlottensis*, *columbiana*, *hayamensis* and *udehe*) or have been left behind as relicts in anchialine positions in Hawaii, where one must assume they lived in the open sea in earlier cool water eras. No species has yet been found in the southern hemisphere penetrating freshwater; other Eusirid-Calliopiids at present occupy this situation.

Three species of *Paramoera* in epigean Japan bearing sternal gills have recently been removed to a new genus *Sternomoera*. The marine uropod 3 of these species suggests an immediate origin independent of freshwater Crangonyctoids bearing sternal gills and therefore suggests that sternal gills have arisen at least twice in the Gammaridans.

Two other strange Japanese species formerly placed in *Paramoera* have been removed to *Relictomaera* recently. They are hypogean or cave dwelling and are characterized by the strange sinusoid shape of the anterior cephalic margin. Apparently they otherwise resemble *Paramoera* and lack sternal gills.

Paramoerella is another descendent of *Paramoera*, differing only in the partial loss of cephalic structures, such as rostrum and deepness of antennal sinus, reduction of eyes and loss of excavation on coxa 4. The unique species is found interstitially on sand beaches of South Africa.

In New Zealand, which one must consider to be the largest landmass most remotely disjunct from Pangaea, several non-Gammarid freshwater amphipods occur. Already discussed has been *Paracorophium*. The second is *Paraleptamphopus*, a genus appearing to have remote affinities with subantarctic Eusirids, such as *Oradarea* (in female gnathopod 2), and *Schraderia*, or Bogidiellids, such as *Spelaeogammarus* but which really has more in common with Phreatogammarus in terms of gnathopods and general facies. Male Paraleptamphopus could be said to be Phreatogammarus fragilis in which the telson has become entire, the accessory flagellum reduced, and the maxillipedal palp slightly modified (article 3 lobate, article 4 stubby and nail reduced). But the tympanic calceoli defy affinity with Crangonyctoids, which bear paddle-shaped calceoli.

A more diverse taxon is Paracalliope, originally discovered in New Zealand but subsequently found widely spread through Melanesia and southern Asia as far westward as India. The genus appears to have its roots in the southern and cool-water taxa that formed the ancestors to primitive Oedicerotids. This is marked by the puffy and inwardly turned pair of second gnathopods and the subflagellate pereopod 7. However, the distribution defies appraisal as there is difficulty in explaining how the genus has island hopped among New Zealand, New Caledonia, Philippines, and mainland Asia.

In southeastern Australia, generally in streams at altitudes of 1500 to 3000 feet (457-915 m), Pseudomoera is the Eusirid-Calliopiid representative genus. Two species occur there. The type-species, P. gabrieli, appears to be a close apomorphic replica of the second species, P. fontana, except that maxilla 1 has lost its medial setae. Pseudomoera fontana used to be placed in Paramoera but clearly differs in the geniculate wrists of the gnathopods. The difference on maxilla 1 between the two species is generally considered to be of generic significance but in this case the two species are otherwise so clearly of the same sibling pool that they will be kept in the same genus together.

The aequiramous uropod 3 removes this genus from the vicinity of freshwater Australian Crangonyctoids and the broadened, lobate wrists of the gnathopods make it a fairly unusual Eusirid-Calliopiid. The telson is deeply cleft and the brood plates very broad; points to remember about the genus are the dominant antenna 1 with 1-articulate accessory flagellum, small antenna 2, broad brood plates, long coxae, expanded and lobate article 2 of pereopods 5-7 and shortened outer rami of uropods 1-2.

These species must be studied very carefully because, like Gammarellus and Gammaracanthus they have many transitional characters between Corophioids and Gammaroids and they have biogeographic position of great importance (possibly being relicts of major evolutionary events).

Awacaris is a Japanese cave species with attributes resembling Laothoes, a boreal east Atlantic-Arctic marine genus; these may be coincidental but the relationship is worth exploring further; the two genera should be examined minutely for details that might shed light on their distinction (perhaps SEM exploration of setal types and cuticle would help).

Awacaris may simply be a convergence; the genus is comparable to Relictomoera but differs mainly in the reduced first maxillary palp, abnormal head and weaker gnathopod 1.

Sebids

One of the most amazing recent discoveries is that by Holsinger and Longley (1980) of the sebid amphipod in San Marcos Well, near San Antonio, Texas. Known as Seborgia relicta, the species is the second of Seborgia, a genus originally described from a lake on Rennell Island of the Bismarck

Archipelago (Bousfield, 1970). The family Sebidae contains only 2 genera, Seba and Seborgia. Seba has another species in the Mediterranean, species in the Australian region and several species in Antarctica. The entire family may consist of a series of relicts from a grander era on the way to extinction but preserved in odd habitats or a group having reached a low but stable existence, in an evolutionary or phyletic sense. The family contains species with poor to absent ocular powers, odd, almost chelate gnathopods with short lobed wrists, large coxae, derived mouthparts and Stenothoid uropod 3, i.e. inner ramus absent, outer ramus 1-2 articulate and subcylindrical.

Caspicolidae

Caspicola is a monotypic genus of the Caspian Sea. Caspicola knipovitschi is a strange species with commensalistic or inquilinous properties, the mouthparts being modified somewhat in the piercing-sucking mode. As no Gammaroid ancestry can be of immediate contiguity one must suggest a Sebid ancestry for this peculiar genus.

Lysianassidae

Onisimus (= Pseudalibrotus) is the well known Lysianassid genus of arctic shallows and the Caspian Sea. The genus clearly has affinity for diluted nearshore waters but probably plays the same ecologic role of Orchomene, which swarms in antarctic shallows. The genus probably penetrated the Caspian Sea through an arctic seaway.

Summary

Several new ideas about interrelationships of Amphipoda are promulgated. (1) The marine Corophiida are considered to be more primitive than the Gammarida, based on the hypothesis that the telson of Gammarida is very specialized. (2) The large Holarctic, mainly freshwater, genus Gammarus, is considered to be more specialized than many of its relatives in Lake Baikal and perhaps a few in the Caspian Sea. (3) The Crangonyctid group of the Gammarida comprises genera found in Australia, South Africa, and Holarctica, which are identified at first sight by the presence of sternal gills and on second sight in derived forms lacking sternal gills by simple morphological congruences at specific level. (4) The Crangonyctids are considered to be more archaic than other Gammaridans; everywhere but in Nearctica, they are of relict status, meaning that they have undergone a decline in diversity and importance. In North America this group flourishes and is expanding its geographic and diversity indices. In Eurasia it is being overwhelmed by Gammarids and Niphargins. In the southern hemisphere it is being overwhelmed by tectonic events: Australia and South Africa have moved northward out of the favored Amphipod climate and South America apparently moved away from the rest of Pangaea before Crangonyctids arrived (or Crangonyctids were extinguished by modern Hyalellids and derived Bogidiellids). In a few places (Madagascar, for example) Crangonyctids by loss of sternal gills live in disguise as Gammarid-appearing.

These proposals lead to the conclusion that amphipods were in existence before Pangaea fragmented and because Gammaridans are considered to be more advanced than Corophiidans, one may safely propound that Amphipods existed in the late Paleozoic. This now extends their history backward from the upper Eocene.

Some of the consequences and elaboration of these ideas are:

1. In Australia and South Africa, the freshwater Crangonyctids have no close relatives in the ocean yet discovered (exploration in the sea is now very good there). If sternobranchiate Crangonyctids ever had intercontinental connections by sea those connections are now totally extinct. But we believe they never existed and the intercontinental connections between freshwater amphipods of south and north occurred when these continents all formed one landmass. Amphipods already were well advanced by that time so one might conclude Amphipods, by their present definition, existed in the late Paleozoic.

2. The freshwater amphipods of Australia and South Africa are largely of relict moribund character, whereas their sibling counterparts in North America are a burgeoning group undergoing postglacial revival and outward expansion; and new morphological advancement is occurring through the loss of sternal gills and pygidization.

3. Sternal gills require strong focus by physiologists. In lines of evolutionary deployment based on nonbranchial characters, sternal gills (also osmotic organs) disappear in apomorphic taxa. They appear to be marginally adaptive, easily lost "at the drop of a gene." Their reappearance in grandly apomorphic Hyalellids in South America suggests they are an organ of a group suddenly emerging from the sea but are later compensated for by physiological adjustments (which evolved rapidly).

4. The best candidate for Gammaridan ancestral proximity is the small genus _Phreatogammarus_ in New Zealand. That genus has the magniramous, almost aequiramous uropod 3, the somehat fleshy (albeit cleft) telson, the sternal gills and the remote, relict-like geographic position one might accord to an ancestral form. Clearly, of course, it has diverged strongly from the true ancestor, because _Phreatogammarus_ has lost coxal gill 7; and two of its species have lost sternal gills.

5. The species of _Gammarus_, today occurring in the Palearctic seas, are evolving outward from a freshwater ancestry and are not relicts of a movement from sea to freshwater. This fully fits their constrained distribution, poor marine diversity, low bathymetric range, poor adjustment to salt, and sensitivity to incursions of introduced species from exotic places. The conclusion is amplified to include most or all marine Gammaridans in cold northern climes which have affinities with freshwater Gammaridans. The marine forms originated from them and are not the ancestors of freshwater Gammaridans. In other words, marine _Anisogammarus_ and _Gammaroporeia_ are derived from freshwater ancestors, which themselves descended from Crangonyctoids bearing sternal gills.

6. Taxa other than Onisimus (= Pseudalibrotus) and Corophium in the Caspian Sea are not of marine origin but of freshwater origin, coming mainly from such well adapted ancestors resembling the modern Echinogammarus. This is one reason why so many of them move rapidly up rivers, then across man made canals and now infest most of northeastern Europe and much of western Asia. This is why many of them are so easily transplanted into manmade lakes for the purpose of feeding commercial fishes. They are inherently freshwater taxa and are extremely remote from their marine ancestors. This idea overturns the previously held belief that PontoCaspian Amphipoda are of Tethyan origin.

7. The old idea that Niphargids, the greatly diverse hypogean group in Europe, have a direct marine origin is reinforced by their position in the scheme of evolutionary flow of morphology presented herein. How they have so readily overcome their osmotic problems is of extraordinary concern. Niphargus and Gammarus therefore do not have an immediate common ancestor, only some ancestor in the sea long lost by extinction. Niphargus is clearly younger than Gammarus, as Niphargus did not reach Nearctica. There is no good case for any supposition that Niphargus might have become extinct in Nearctica.

8. The Gammaridan paradox is the strange situation that this group of 1350 species (specifically meaning the old family Gammaridae and not including the full suborder Gammaridea) is most diverse in warm seas and in cold freshwater. In other words, freshwater Gammaridans abhor tropical zones and marine Gammaridans abhor frigid zones. For this reason, the writers are not wholly taken by general theories that all animals of Lake Baikal have a direct marine origin (such as the seal, dinoflagellates) but that the amphipods of Baikal came from an old freshwater ancestry in existence before Baikal. Only a few Baikalian-like taxa occur in cold northern seas (Gammaracanthus, Gammaroporeia and Mesogammarus) and these may be taxa returned to the sea from Baikal.

The old Bergian proposal that Baikalian taxa are of freshwater origin is, therefore, revived but attached only to the main body of amphipods and extended backwards from Pliocene times invoked by Berg to an ultimate Paleozoic fauna.

Appendix I

Lists of PontoCaspian Taxa

List of PontoCaspian Genera, each with code number for distribution of each species, in alphabetical and numerical order.

Akerogammarus, 332, 332, 332; *Amathillina*, 332, 332, 332, 332, 335; *Andrussovia*, foss., foss.; *Axelboeckia*, 332; *Baku*, 332; *Behningiella*, 332; *Cardiophilus*, 332, 334; *Cephalogammarus*, 332; *Compactogammarus*, 336; *Derzhavinella*, 332; *Dikerogammarus*, 084, 332, 332, 336, 337, 337, 337; *Echinogammarus*, 332, 335, 335, 337, 337, 337; *Euxinia*, 335, 335, 335; *Gmelina*, 332, 337; *Gmelinopsis*, 332, 336; *Iphigenella*, 335; *Jugogammarus*, 087; *Kuzmelina*, 335; *Lanceogammarus*, 336; *Niphargogammarus*, 332, 332, 332, 337; *Niphargoides*, 332, 332, 335; *Obesogammarus*, 084, 142, 332, 335, 335, 337; *Pandorites*, 336; *Paraniphargoides*, 332, 332, 337; *Pontogammarus*, 066, 332, 332, 335, 336, 337; *Pontoporeia*, 332; *Praegmelina*, foss., foss; *Shablogammarus*, 337; *Sowinskya*, 332; *Stenogammarus*, 332, 335, 335, 336, 336, 338; *Turcogammarus*, 068, 088, 331; *Uroniphargoides*, 337; *Yogmelina*, 332, 332, 334, 336, 337; *Zernovia*, 338.

Lists of Species

PontoSarmatian Species in:

Black Sea:

Amathillina cristata, Cardiophilus marisnigrae, Compactogammarus compactus, Dikerogammarus fluviatilus, D. haemobaphes, D. villosus, Echinogammarus behningi, E. major (formerly recorded as E. ischnus), E. placidus, E. warpachowskyi, Euxinia maeoticus, E. sarsi, E. weidemanni, Gmelina aestuarica, Gmelinopsis tuberculata, Iphigenella acanthopoda, Kuzmelina kusnezowi, Lanceogammarus andrussowi, Niphargogammarus intermedius, Niphargoides corpulentus, Obesogammarus crassus, O. obesus, O. olvianus, Pandorites podoceroides, Paraniphargoides motasi, Pontogammarus aestuarius, P. borceae, P. robustoides, Shablogammarus chablensis, Stenogammarus carausui, S. compressus, S. macrurus, S. similis, [S. sp., = macrurus of Carausu 1943, not counted], Uroniphargoides spinicaudatus, Yogmelina cocalita, Y. ovata, Y. pusilla. Data based on Greze (1977) but with new taxa in Karaman and Barnard (1979) and conservatively dropping Akerogammarus subnudus and Pontogammarus abbreviatus and P. aralensis (Aral Sea only?); also with opinions of Miloslawskaja and Pauli (1931), Carausu (1943) and Carausu, et alia (1955) about Cardiophilus marisnigrae.

Azov Sea:

Amathillina cristata, Cardiophilus marisnigrae, Dikerogammarus bispinosus, D. haemobaphes, D. villosus, Echinogammarus behningi, E. major, E. placidus, E. warpachowskyi, Euxinia maeoticus, E. sarsi, E. weidemanni, [Gammarus aequicauda, considered as non PontoSarmatian], Iphigenella acanthopoda, Kuzmelina kusnezowi, Niphargoides corpulentus, Obesogammarus crassus, O. obesus, O. olvianus, Pandorites podoceroides, Pontogammarus robustoides, Stenogammarus macrurus, S. similis, Yogmelina ovata. Data based on Miloslawskaja and Pauli (1931) and Birstein and Romanova (1968).

Aral Sea:

Dikerogammarus aralychensis, Turcogammarus aralensis.

Caspian Sea: originally endemic in italics;

Akerogammarus contiguus, *A. knipowitschi*, *A. subnudus*, *Amathillina affinis*, A. cristata, *A. maximovitschi*, *A. pusilla*, *A. spinosa*, *Axelboeckia spinosa*, *Baku paradoxus*, *Behningiella brachypus*, Cardiophilus baeri, *Cephalogammarus macrocephalus*, Compactogammarus compactus, *Derzhavinella macrochelata*, *Dikerogammarus caspius*, D. haemobaphes, *D. oskari*, Echinogammarus behningi, E. ischnus, E. pauxillus (=hyrcanus), E. warpachowskyi, Euxinia maeoticus, E. sarsi, E. weidemanni, [Gammaracanthus loricatus caspius not counted], *Gmelina costata*, *Gmelinopsis aurita*, G. tuberculata, Iphigenella acanthopoda, Kuzmelina kusnezowi, Lanceogammarus andrussowi, *Niphargogammarus aequimanus*, *N. borodini*, *N. quadrimanus*, *Niphargoides boltovskoi*, *N. caspius*, N. corpulentus, Obesogammarus crassus, O. obesus, *O. platycheir*, Pandorites podoceroides, *Paraniphargoides derzhavini*, *P. grimmi*, *Pontogammarus abbreviatus*, P. aestuarius, *P. ?palmatus*, P. robustoides, P. setosus, *Pontoporeia* sp., *Sowinskya macrocera*, Stenogammarus carausui, S. compressus, *S. deminutus*, *S. dzjubani* (=Wolgagammarus), S. macrurus, S. similis, *Yogmelina brachyura*, *Y. laeviuscula*, *Y. pusilla*, *Zernovia volgensis*. Based on Birstein and Romanova (1968) and Karaman and Barnard (1979) and conservative approach.

Outside PontoCaspian Basin of today, though several species in attendant rivers but restricted far upstream:

Dikerogammarus balatonicus, Jugogammarus kusceri, Obesogammarus boeoticus, O. mediodanubialis, Pontogammarus setosus, Turcogammarus spandli, T.turcarum.

Non PontoSarmatian species in

Black Sea:

Ampelisca diadema, Ampithoe gammaroides, A. ramondi, Apherusa bispinosa, Atylus guttatus, Bathyporeia guilliamsoniana, Biancolina cuninculus, Cheirocratus sundevalli, Chelura terebrans, Colomastix pusilla, Corophium acherusicum, C. bonelli, C. chelicorne, C. crassicorne, C. curvispinum, C. maeoticum, C. mucronatum, C. nobile, C. orientalis, C. robustum, C. runcicorne, C. sowinskyi, C. volutator, Cymadusa crassicornis, Dexamine spinosa, Ericthonius difformis, E. hunteri, Gammarellus carinatus, Gammarus aequicauda, G. crinicornis, G. duebeni, G. insensibilis, G. marinus, G. olivii, G. subtypicus, [G. zaddachi, probably misidentified], Harpinia dellavallei, Hyale dollfusi, H. nilssoni, H. ?perieri, H. ?prevosti, H. pontica, Jassa dentex, J. ocia, J. pusilla, Leptocheirus pilosus, Megaluropus agilis, Megamphopus cornutus, Melita palmata, Microdeutopus anomalus, M. damnoniensis, M. gryllotalpa, M. stationis, M. versiculatus, Microprotopus longimanus, M. minutus, Monculodes gibbosus, Nannonyx goesii reductus (subspecies), Orchestia bottae, O. gammarella, O. mediterranea, O. montagui, Orchomene humilis, Perioculodes longimanus, Photis longicaudatus, Pythia carinata, Siphonoecetes dellavallei, S. tyicus, Stenothoe marina, S. monoculoides, Synchelidium maculatum, Talitrus saltator, Talorchestia brito, T. deshayesi, Tritaeta gibbosa. Sources: Greze (1977), Carausu et alia (1955), Miloslawskaja and Pauli (1931).

Azov Sea:

Ampelisca diadema, Dexamine spinosa, Ericthonius difformis, Gammarus locusta, G. marinus, Jassa ocia, Melita palmata, Microdeutopus gryllotalpa, Microprotopus longimanus, M. minutus, Orchestia bottae. Sources, Birstein and Romanova (1968), Miloslawskaja and Pauli (1931); species of Corophium not listed.

Caspian Sea:

Caspicola knipowitschi, Corophium chelicorne, C. curvispinum, C. monodon, C. mucronatum, C. nobile, C. robustum, C. spinulosum, C. volutator, Pontoporeia affinis microphthalma (subspecies), Pseudalibrotus (=Onisimus) cassius, P. platyceras.

Appendix II

Baikal Taxal Indices

Baikal Index to Genera and (Subgenera)

[Taxa in Brackets Invalid]

Abyssogammarus Sowinsky
Acanthogammarus Stebbing
Asprogammarus Bazikalova, unavailable, to *Echiuropus*
[*Axelboeckia* Stebbing] (confined outside Baikal), Baikalian species, transferred to *Boeckaxelia*
Baikalogammarus Stebbing
(*Bathygammarus*) Bazikalova, valid subgenus of *Poekilogammarus*
Boeckaxelia Schellenberg
(*Brachyuropus*) Sowinsky, valid subgenus of *Acanthogammarus*
Brandtia Bate
[*Bronislavia* Rakowsky, = *Pallasea*]
Carinogammarus Stebbing
Carinurus Sowinsky
Ceratogammarus Sowinsky
Cheirogammarus Sowinsky
Coniurus Sowinsky
[*Constantia* Dybowsky, = *Macrohectopus*]
Corophiomorphus Bazikalova, formerly subgenus of *Eulimnogammarus*
Crypturopus Sowinsky
[*Ctenacanthus* Garjajeff = *Garjajewia*]
Dorogammarus Bazikalova
[*Dybowskia* Garjajeff, = *Pallasea*]
Echiuropus Sowinsky
[*Echinogammarus* Stebbing], all Baikalian species now reassigned mainly to *Eulimnogammarus*
Eucarinogammarus Sowinsky
Eulimnogammarus Bazikalova
Eurybiogammarus Bazikalova, formerly subgenus of *Eulimnogammarus*
Fluviogammarus Dorogostaivsky [*Fluviogammarus* S.Karaman and G.S. Karaman, junior homonym, those species lying outside Baikal]
(*Gammarisca*) Bazikalova, valid subgenus of *Micruropus*
Gammarosphaera Bazikalova
[*Gammarus* Linne], all Baikalian species now reassigned
Garjajewia Sowinsky
Gmelinoides Bazikalova
(*Gymnogammarus*) Sowinsky, valid subgenus of *Poekilogammarus*
Hakonboeckia Stebbing
Heterogammarus Stebbing
[*Homalogammarus* Bazikalova = *Pentagonurus* in *Pallasea*]
Homocerisca Bazikalova
Hyalellopsis Stebbing
Koshovia Bazikalova
Leptostenus Bazikalova
Lobogammarus Bazikalova

Macrohectopus Stebbing
Macropereiopus Sowinsky
(*Microgammarus*) Sowinsky, valid subgenus of *Micruropus*
Micruropus Stebbing
Odontogammarus Stebbing
Ommatogammarus Stebbing
[*Oniscus* J.C. Fabricius, Baikalian species all reassigned]
(*Onychogammarus*) Sowinsky, valid subgenus of *Poekilogammarus*
Pachyschesis Bazikalova
Pallasea Bate
Paragarjajewia Bazikalova
Parapallasea Stebbing
(*Pentagonurus*) Sowinsky, valid subgenus of *Pallasea*
Philolimnogammarus Bazikalova, formerly subgenus of *Eulimnogammarus*
Plesiogammarus Stebbing
[*Pleuracanthus* Garjajeff = *Pallasea*]
Poekilogammarus Stebbing
Polyacanthisca Bazikalova
(*Polyacanthus*) Garjajeff = *Acanthogammarus*
(*Propachygammarus*) Bazikalova, valid subgenus of *Pallasea*
(*Rostrogammarus*) Bazikalova, valid subgenus of *Poekilogammarus*
(*Setogammarus*) Bazikalova, valid subgenus of *Micruropus*
Smaragdogammarus Bazikalova, unavailable, to *Echiuropus*
Spinacanthus Dorogostaivsky

Baikal Index to Species

abyssalis Dybowsky, *Parapallasea borealis*
abyssalis Sowinsky, *Corophiomorphus*
abyssorum Dybowsky, subspecies of *Eurybiogammarus ussolzewi*
acera Dybowsky, subspecies of *Brandtia lata*
acerus Bazikalova, *Ceratogammarus*
affinis Sowinsky, *Eurybiogammarus*
aheneoides Bazikalova, *Eurybiogammarus*
aheneus Dybowsky, *Eurybiogammarus*
albinus Dybowsky, *Ommatogammarus*
albula Dybowsky, *Macropereiopus albulus*
albus Garjajeff, *Acanthogammarus*
alexandri Dybowsky, *Macrohectopus branickii*
amblyops Bazikalova, subspecies of *Poekilogammarus rostratus*
amethystinus Dybowsky, subspecies of *Ommatogammarus carneolus*
angarensis Bazikalova, *Fluviogammarus*
angarensis Dorogostaivsky, subspecies of *Eulimnogammarus lividus*
angarensis Dorogostaivsky, *Micruropus talitroides*
angarensis Dorogostaivsky, *Pallasea dybowskii*
araneolus Dybowsky, *Poekilogammarus*
arenicola Dorogostaivsky, subspecies of *Pallasea grubei*
armatus Dybowsky, *Spinacanthus*
asetus Bazikalova, subspecies of *Eurybiogammarus aheneus*
asper Dybowsky, *Pallasea dybowskii*
atrichus Bazikalova, subspecies of *Eurybiogammarus ibex*
aureus Dorogostaivsky, subspecies of *Eurybiogammarus fuscus*

baikalensis Sowinsky [subspecies of Boeckia spinosa Sars], no later reference
baikali Stebbing, Pallasea
balkirii Garjajeff (lapsus), Carinurus belkini
bathyphilus Bazikalova, Echiuropus (as Asprogammarus)
bazikalovae G.S. Karaman, Pachyschesis
bazikalowi G.S. Karaman, Carinurus
belkini Garjajeff, Carinurus
bergi Bazikalova, Pachyschesis
bicarinatus Bazikalova, Carinurus
bicornis Dorogostaivsky, Pallasea
bifasciatus Dybowsky, Heterogammarus
bifrons G.S. Karaman, Carinurus
bogucani Bazikalova, Micruropus
borealis Sowinsky, Crypturopus inflatus
borealis Sowinsky, Echinogammarus [not later allocated], ?Eulimnogammarus
borowskii Dybowsky, Parapallasea
brachycoxalis Bazikaloa, Eurybiogammarus
brachyurus Bazikalova, subspecies of Echiuropus rhodophthalmus (as Asprogammarus)
brachyurus Dorogostaivsky, Fluviogammarus
branchialis Dybowsky, Pachyschesis
brandti Dybowsky, Pallasea
branickii Dybowsky, Macrohectopus
brevicauda Bazikalova, Micruropus
brevicaudatus Sowinsky, subspecies of Echiuropus macronychus
brevipes Dorogostaivsky, subspecies of Odontogammarus calcaratus
brevirostris Bazikalova, subspecies of Poekilogammarus rostratus
brevis Bazikalova, subspecies of Plesiogammarus gerstaeckeri
brevispinus Dorogostaivsky, Acanthogammarus
burkani Bazikalova, Eulimnogammarus
byrkini Sowinsky, Eurybiogammarus
cabanisi Dybowsky, Garjajewia
calcaratus Dybowsky, Odontogammarus
calceolaris Bazikalova, Micruropus
calceolata Bazikalova, Polyacanthisca
calceolatus Sowinsky, Corophiomorphus
cancelloides Gerstfeldt, Pallasea
cancellus Pallas, Pallasea
canus Dybowsky, subspecies of Eulimnogammarus viridis
capellus Dybowsky, Heterogammarus
capreolus Dybowsky, Eurybiogammarus
carinata Sowinsky, Hyalellopsis
carinulata Dorogostaivsky, subspecies of Palicarinus puzyllii
carneolus Dybowsky, Ommatogammarus
carpenteri Dybowsky, Boeckaxelia
castaneus Dorogostaivsky, Dorogammarus
caudata Bazikalova, Homocerisca
chargoensis Sowinsky, Pseudomicruropus
chloris Dybowsky, synonym of Eurybiogammarus capreolus
ciliodorsalis Sowinsky, Micruropus

cinnamomeus Dybowsky, *Carinogammarus*
clavata Dorogostaisky, *Hyalellopsis stebbingi*
comatus Dorogostaivsky, subspecies of *Philolimnogammarus cyaneus*
cornutus Sowinsky, *Ceratogammarus*
costata Sowinsky, *Hyalellopsis*
crassicornis Sowinsky, *Corophiomorphus*
crassimanus Sowinsky, *Poekilogammarus*
crassipes Sowinsky, subspecies of *Micruropus littoralis*
crassus Sowinsky, *Pachyschesis*
cristatus Dorogostaivsky, *Micruropus*
cruentus Dorogostaivsky, *Eulimnogammarus*
curtus Bazikalova, variety of *Acanthogammarus flavus*
curvimanus Sowinsky, *Poekilogammarus*
curvirostris Bazikalova, *Poekilogammarus*
cyanellus Bazikalova, *Philolimnogammarus*
cyaneus Dybowsky, *Philolimnogammarus*
cyanoides Sowinsky, *Eulimnogammarus*
czerskii Dybowsky, *Eulimnogammarus*
czyrniaskii Dybowsky, *Hyalellopsis*
dagarskii Sowinsky, subspecies of *Macropereiopus wagneri*
dawydowi Sowinsky, *Pallasea*
demianowiczi Dorogostaivsky, subspecies of *Odontogammarus margaritaceus*
depressirostris Sowinsky, *Hyalellopsis*
dershawini Sowinsky, subspecies of *Garjajewia cabanisi*
dicerus Dybowsky, subspecies of *Brandtia lata*
dichrous Dybowsky, *Parapallasa borowskii*
dilatatus Dybowsky, *Crypturopus pachytus*
dogieli Bazikalova, *Garjajewia*
dryshenkoi Garjajeff, *Pallasea*
dybowskii Bazikalova, *Micruropus*
dybowskii Sowinsky, *Ceratogammarus*
dybowskii Sowinsky, *Pentagonurus*
dybowskii Stebbing, *Pallasea*
echinatus Bazikalova, subspecies of *Abyssogammarus sarmatus*
elegans Dorogostaivsky, subspecies of *Boeckaxelia carpenteri*
ephippiatus Dybowsky, *Poekilogammarus araneolus*
epimeralis Sowinsky, *Eurybiogammarus*
eugeniae Sowinsky, *Hyalellopsis*
eurypus Bazikalova, subspecies of *Micruropus talitroides*
extima Dorogostaivsky, subspecies of *Brandtia lata*
exiguus Bazikalova, *Philolimnogammarus*
fasciata Stebbing, *Gmelinoides*
fasciatoides Gurjanova, *Gmelinoides*
fixseni Dybowsky, *Micruropus*
flaviceps Dorogostaivsky, subspecies of *Pallasea brandti*
flavus Dybowsky, *Ommatogammarus*
flavus Garjajeff, *Acanthogammarus*
flori Dybowsky, *Macropereiopus*
fuscus Dybowsky, *Eurybiogammarus*
garjajewi Bazikalova, *Micruropus*
gerstaeckeri Dybowsky, *Plesiogammarus*
gerstfeldti Dybowsky, subspecies of *Pallasea cancellus*

glaber Dybowsky, *Micruropus*
glabra Bazikalova, subspecies of *Hyalellopsis tixtonae*
godlewskii Dybowsky, *Acanthogammarus*
gracilicornis Bazikalova, *Corophiomorphus*
gracilis Sowinsky, *Abyssogammarus*
grandimanus Bazikalova, *Eulimnogammarus*
grandimanus Bazikalova, *Macropereiopus*
grewingki Dybowsky, *Acanthogammarus*
grisea Dorogostaivsky, *Hyalellopsis*
grubii Dybowsky, *Pallasea grubei*
gulekani Bazikalova, *Echiuropus* (as *Asprogammarus* and *Smaragdogammarus*)
gurjanowae Bazikalova, *Micruropus*
hamata Sowinsky, *Hyalellopsis*
heterochirus Bazikalova, *Eulimnogammarus*
hyacinthinus Dybowsky, *Eurybiogammarus*
ibex Dybowsky, *Eurybiogammarus*
ibexiformis Sowinsky, *Eurybiogammarus capreolus*
ignotus Dybowsky, *Heterogammarus*
immundus Bazikalova, *Philolimnogammarus*
improvisus Dorogostaivsky, subspecies of *Odontogammarus calcaratus*
incertus Sowinsky, *Heterogammarus*
inconspicuus Bazikalova, *Philolimnogammarus*
inermis Sowinsky, subspecies of *Pallasea baikali*
inflatus Dybowsky, *Crypturopus*
inflatus Sowinsky, *Cheirogammarus*
insularis Bazikalova, *Gammarosphaera*
insularis Dorogostaivsky, *Spinacanthus*
intermedia Dorogostaivsky, subspecies of *Brandtia lata*
intermedius Bazikalova, *Fluviogammarus*
intermedius Bazikalova, *Echiuropus smaragdinus*
intermedius Sowinsky, *Corophiomorphus kietlinskii*
irinae Bazikalova, *Hyalellopsis*
ivanowi Bazikalova, *Micruropus*
jedorensis Bazikalova, *Poekilogammarus*
kessleri Dybowsky, *Pallasea*
kietlinskii Dybowsky, *Corophiomorphus*
klukii Dybowsky, *Micruropus*
korotneffi Garjajeff, *Acanthogammarus*
korotnewi Sowinsky, *Odontogammarus*
koshowi Bazikalova, *Micruropus*
kusnezowi Sowinsky, *Eurybiogammarus*
laevis Sowinsky, *Corophiomorphus*
laeviusculus Sowinsky, *Micruropus*
lagowskii Dybowsky, *Parapallasea*
lamellispinus Bazikalova, *Pallasea*
larviformis Dorogostaivsky, *Fluviogammarus*
lata Dybowsky, *Brandtia latissima* Gerstfeldt (senior synonym)
latior Dybowsky, subspecies of *Brandtia latissima*
latipes Bazikalova, *Hyalellopsis*
latissima Gerstfeldt, *Brandtia* (senior to *lata* Dybowsky)
latus Bazikalova, *Lobogammarus*

lepidiformis Bazikalova, *Pseudomicruropus*
lepidus Bazikalova, *Pseudomicruropus*
leptocerus Dybowsky, *Leptostenus*
leucophthalmus Sowinsky, *Macropereiopus*
levis Bazikalova, *Echiuropus* (as *Asprogammarus*)
littoralis Dybowsky, *Micruropus*
lividus Dybowsky, *Eulimnogammarus*
longicornis Dybowsky, synonym of *Eurybiogammarus polyarthrus*
longicornis Bazikalova, subspecies of *Eurybiogammarus fuscus*
longicornis Sowinsky, *Plesiogammarus*
longipes Bazikalova, *Poekilogammarus*
longirostris Bazikalova, subspecies of *Poekilogammarus rostratus*
lovenii Dybowsky, *Pallasea baikali*
lydiae Bazikalova, *Poekilogammarus*
maacki Gerstfeldt, *Eulimnogammarus*
macrocephala Bazikalova, *Hyalellopsis*
macrochirus Bazikalova, *Micruropus*
macroconus Bazikalova, *Micruropus*
macronychus Sowinsky, *Echiuropus*
macrophthalmus Bazikalova, *Corophiomorphus*
macropsis Bazikalova, *Echiuropus* (as *Asprogammarus*)
macrurus Sowinsky, *Poekilogammarus*
maculosus Dorogostaivsky, subspecies of *Acanthogammarus victorii*
magnus Bazikalova, subspecies of *Pseudomicruropus rotundulatus*
margaritaceus Dybowsky, *Odontogammarus*
margaritae Bazikalova, *Spinacanthus*
marituji Bazikalova, *Philolimnogammarus*
maximus Garjajeff, *Acanthogammarus*
megonychoides Bazikalova, *Poekilogammarus*
megonychus Sowinsky, *Poekilogammarus*
meissneri Bazikalova, *Pallasea*
meissneri Bazikalova, *Hakonboeckia*
melanochlorus Dorogostaivsky, *Philolimnogammarus*
melanophthalmus Dorogostaivsky, subspecies of *Ommatogammarus carneolus*
meyeri Garjajeff, *Pallasea*
microphthalmus Dybowsky, subspecies of *Echiuropus rhodophthalmus*
microphthalmus Sowinsky, *Eurybiogammarus violaceus*
microphthalmus Sowinsky, *Carinurus*
minimus Bazikalova, *Philolimnogammarus* (as *Eulimnogammarus*)
minor Bazikalova, subspecies of *Abyssogammarus gracilis*
minutus Sowinsky, *Micruropus*
mirabilis Bazikalova, *Koshovia*
mirus Bazikalova, *Macropereiopus*
morawitzi Dybowsky, *Echiuropus*
mozi Bazikalova, *Micruropus*
muricatus Pallas, *Pallasea cancellus*
murini Bazikalova, subspecies of *Micruropus glaber*
muriniformis Bazikalova, *Eurybiogammarus*
murinus Dybowsky, *Eurybiogammarus*
nana Bazikalova, *Hyalellopsis*
nassonowi Dorogostaivsky, *Acanthogammarus*
nematocerus Dybowsky, *Gammarus leptocerus*

nigra Garjajeff, *Parapallasea*
nigromaculata Dorogostaivsky, subspecies of *Pallasea baikali*
ninae Bazikalova, subspecies of *Garjajewia cabanisi*
obscurus Dorogostaivsky, *Carinurus*
obsoletus Bazikalova, *Philolimnogammarus*
oligacanthus Bazikalova, subspecies of *Eulimnogammarus verrucosus*
olivaceus Dybowsky, subspecies of *Philolimnogammarus viridis*
ongureni Garjajeff, subspecies of *Spinacanthus armatus*
orchestes Dybowsky, *Poekilogammarus*
pachycerus Bazikalova, *Corophiomorphus*
pachytus Dybowsky, *Crypturopus*
pallidus Dorogostaivsky, subspecies of *Eucarinogammarus wagi*
palmatus Sowinsky, *Coniurus*
paradoxa Sowinsky, *Hyalellopsis taczankowskii*
parasiticus Dybowsky, *Spinacanthus*
parvexi Dybowsky, *Eurybiogammarus*
parvexiformis Bazikalova, *Eurybiogammarus*
parvulus Bazikalova, subspecies of *Micruropus ciliodorsalis*
parvus Bazikalova, *Macropereiopus*
perla Dybowsky, *Homocerisca*
perloides Bazikalova, *Homocerisca*
perplexus Bazikalova, *Echiuropus* (as *Asprogammarus*)
petersi Dybowsky, *Paragarjajewia*
pictoides Sowinsky, *Poekilogammarus*
pictus Dybowsky, *Poekilogammarus*
platycarinus Sowinsky, *Carinurus*
platycerus Dybowsky, *Micruropus platycerus*
polyarthrus Dybowsky, *Eurybiogammarus*
polyspina Dorogostaivsky, subspecies of *Brandtia lata*
possolskii Sowinsky, *Micruropus*
potanini Dorogostaivsky, *Boeckaxelia*
profundalis Bazikalova, subspecies of *Axelboeckia carpenteri*
proximus Sowinsky, *Eurybiogammarus*
puella Dybowsky, *Micruropus*
puer Bazikalova, *Echiuropus* (as *Asprogammarus*)
pulchelliformis Bazikalova, *Echiuropus* (as *Asprogammarus*)
pulchellus Dybowsky, *Echiuropus*
pulcherrimus Dorogostaivsky, subspecies of *Odontogammarus calcaratus*
pullus Dybowsky, *Baikalogammarus*
puzyllii Dybowsky, *Palicarinus*
quadrispinosa Sars of Sowinsky, no later allocation
quinquefasciatus Dybowsky, *Poekilogammarus araneolus*
rachmanowii Sowinsky, *Eurybiogammarus*
radoschkowskii Dybowsky, *Coniurus*
radziszewskii Rakovsky, *Pallasea*
rectirostris Bazikalova, *Poekilogammarus*
reicherti Dybowsky, *Acanthogammarus*
reissneri Dybowsky, *Carinurus*
rhodophthalmus Dybowsky, *Echiuropus*
rodionowi Dorogostaivsky, subspecies of *Acanthogammarus flavus*
roseus Garjajeff, *Garjajewia cabanisi*
rostratus Sowinsky, *Poekilogammarus*

rotundulatus Bazikalova, *Pseudomicruropus*
rubra Garjajeff, *Boeckaxelia*
rugosus Dybowsky, *Crypturopus*
saphirinus Dybowsky, *Eurybiogammarus*
sarmatus Dybowsky, *Abyssogammarus*
sarsi Sowinsky, *Garjajewia*
schamanensis Dybowsky, *Eurybiogammarus*
scirtes Dybowsky, *Heterogammarus sophianosi*
seidlitzi Dybowsky, *Echiuropus*
selengensis Bazikalova, subspecies of *Hyalellopsis latipes*
semenkewitschi Sowinsky, *Poekilogammarus*
semenowi Bazikalova, *Micruropus*
sempercarinatus Bazikalova, subspecies of *Echiuropus*
  macronychus (as *Asprogammarus*)
setosa Sowinsky, *Hyalellopsis*
setosus Bazikalova, subspecies of *Micruropus koshowi*
setosus Dybowsky, subspecies of *Eurybiogammarus aheneus*
similis Sowinsky, *Eurybiogammarus*
simplex Sowinsky, *Micruropus*
simpliciformis Bazikalova, *Philolimnogammarus* (as *Eulimnogammarus*)
smaragdinus Dybowsky, *Echiuropus*
solskii Dybowsky, *Carinurus*
sophiae Dybowsky, *Corophiomorphus*
sophianosi Dybowsky, *Heterogammarus*
sowinskii Bazikalova, subspecies of *Acanthogammarus flavus*
sowinskii Bazikalova, subspecies of *Heterogammarus capellus*
spinosa Sars, [*Boeckia* var. *baikalensis* of Sowinsky],
  no later allocation
stanislavi Dybowsky, *Corophiomorphus*
stebbingi Sowinsky, *Hyalellopsis*
stenophthalmus Dybowsky, *Eurybiogammarus*
strauchi Dybowsky, *Hakonboekia*
strenuus Bazikalova,subspecies of *Echiuropus rhodophthalmus*
  (as *Asprogammarus*)
strenuus Sowinsky, *Corophiomorphus sophiae*
subbrevispinus Bazikalova, *Acanthogammarus*
sublittoralis Sowinsky, *Micruropus*
sukaczewi Sowinsky, *Poekilogammarus*
swartschewskii Sowinsky, *Abyssogammarus*
taczankowskii Dybowsky, *Hyalellopsis*
talitroides Dybowsky, *Micruropus*
talitrus Dybowsky, *Poekilogammarus*
tenera Sowinsky, subspecies of *Pallasea brandti*
tenuicauda Bazikalova, *Homocerisca*
tenuipes Bazikalova, *Crypturopus*
tenuipes Sowinsky, *Corophiomorphus*
tenuis Bazikalova, *Eurybiogammarus*
testaceus Dybowsky, *Philolimnogammarus*
tixtonae Sowinsky, *Hyalellopsis*
toxophthalmus Dybowsky, *Eurybiogammarus*
tuberculatus Dybowsky, *Crypturopus*
unguisetosus Sowinsky, subspecies of *Poekilogammarus semenkewitschi*

ushkani Bazikalova, *Micruropus*
ussolzewi Dybowsky, *Eurybiogammarus*
variabilis Dorogostaivsky, *Hyalellopsis*
verrucosus Gerstfeldt, *Eulimnogammarus*
victorii Dybowsky, *Acanthogammarus*
violaceus Dybowsky, *Eurybiogammarus*
virescens Dybowsky, *Eurybiogammarus violaceus*
virgatus Dorogostaivsky, *Eurybiogammarus*
viridiformis Sowinsky, *Eulimnogammarus*
viridis Dybowsky, *Philolimnogammarus*
viridis Garjajeff, *Pallasea*
viridulus Bazikalova, *Philolimnogammarus*
vittatus Dybowsky, *Philolimnogammarus*
vortex Dybowsky, *Micruropus*
vorticellus Bazikalova, *Micruropus*
wadimi Sowinsky, *Coniurus*
wasgi Dybowsky, *Eucarinogammarus*
wagneri Sowinsky, *Macropereiopus*
wahli Dybowsky, *Micruropus*
werestschagini Bazikalova, *Carinurus*
wosnessenskii Dorogostaivsky, subspecies of *Parapallasea borowskii*
zablotzkii Sowinsky, synonym of *Carinogammarus rhodophthalmus*
zebra Dybowsky (homonym), *Gmelinoides fasciatus*
zienkowiczi Dybowsky, *Plesiogammarus*

Appendix III

The Geographic Reporting System

We devised a coded geographic system that reports distributions of taxa by 3 digit numbers similar to a library Dewey decimal system. The similarity lies in the ability to decipher inherent geographic information from the numbers assigned, knowing that groups of numbers have certain similarities. Numbers ending in zeros (or fives) refer to large geographic areas, while numbers ending in other digits refer to small areas. For example, numbers in the 300's refer to warm-temperate zones in the northern hemisphere, the number 330 referring to a large area (warm eastern Atlantic Ocean) with 340 referring to the Mediterranean Sea in general, 344 to the Moroccan subdivision of the Mediterranean, 350 to the eastern Atlantic in general, 353 the Biscayan province (or subdivision) and 357 specifically to the islands of Madeira. Numbers are explained in the following list and in Maps 69-92.

Certain numbers are accompanied by letters explained in the list to follow. These refer to ecological positions of species not otherwise clarifiable by the numbers, for example F indicating freshwater and K indicating cobble-brackish or beach interstitial.

The system and reporting desiderata were designed with several protocols but the reader need not continue further in this discussion to use the system. The following words are only for persons interested in the design of the system or those who may detect seeming incongruencies.

The first protocol is that we report on the distribution of a species in as particularized fashion as possible. A widely distributed boreal marine species may be reported with a general number indicating that it is of boreal occurrence but a second species known only from one boreal locality is reported by a subdivisional number denoting the narrow distribution of the species. Despite our knowing that a species as yet reported only from an open coastal marine locality will probably be found much more widely distributed, we confined the reporting to reality and did not attempt to predict distributions.

The world is divided into as many small zones as are practicable and useful but fewer than 800 so as to allow for 200+ general zones (usually marked by 0 or 5 as the last digit). Many of the zones are classic biogeographic provinces such as those shown for the coasts of California and Mexico but others are quite arbitrary and based more or less on what we know about the literature of amphipods, the way biologists report distributions in old literature, and what kinds of problems we presently face in computerizing biogeographic data. The marine boundaries and geographic program are probably useful for most marine biologists because we follow conventional boundaries wherever known but the terrestrial divisions are only useful for amphipod biogeography. Every terrestrial group more or less produces a distinctive biogeographic zonation. We have adopted for Europe that system reported in Fauna Limnologicae but for Asia we used parts of the botanical system of Udvardy (1975) modified by our knowledge that amphipods live both in epigean and hypogean waters and are therefore controlled not only by plant zones but by aquifers and hence distribution of rock types. Many parts of several continents lack freshwater amphipods and remain unnumbered. A few numbers are held in reserve to use when future changes become necessary.

The Udvardy scheme is modified in the Paleotropical zone to follow more closely the implied recommendation of Mani (1974, chapters 1, 20) who cites Smith (1931-43) as the main source. We have altered this scheme to tighten up several places where we think amphipods would be affected more by topography than would reptiles, especially our Yunnan Province which incorporates mountainous tropical-subtropical east Asia from Bhutan eastward. We also are aware of Alcock (1910), Annandale (1911) and Prashad (1942) in these calculations.

Coastal biogeographic zones range between 0 and 200 m only even though they are depicted as much wider on the maps. Any depth greater than 200 m is then assigned to the adjacent deep-sea quadrant.

Many island groups have numbers of their own which are fitted into the marine system but are not replicated in the terrestrial or freshwater system. For example, the number 573 refers to "Samoa marine 0-200 m" but there is no special number for a freshwater amphipod in Samoa and such distribution is reported as 573F. On the other hand large islands such as Hokkaido may be reported in the marine scheme as 394 but in the freshwater scheme as 026. The distinction between the two tells the reader that the amphipod is either marine or freshwater and "F" is not required. Many freshwater species confined to upper parts of estuaries or in coastal streams are reported in the marine system by using various letters appended to marine numbers so as to make very particular reference to small scale distributions that otherwise would be diluted by the use of freshwater numbers covering such large areas. For example, a Chinese freshwater amphipod limited to a few coastal streams might be reported as 397F to denote its very particular distribution rather than as 031 which would indicate a widespread east Asian dispersal.

The final presentation as constructed for amphipods uses only 744 of a possible 1000 numbers, of which 161 are group numbers and 583 are particulate biogeographic zones. Many numbers are left blank in approprite places, such as terrestrial Africa and South America, where expansion and further division of the areas may become necessary in amphipods as exploration progresses. The terrestrial world is divided into 139 zones of which 102 are in Holarctica and the marine world is divided into 444 zones. The terrestrial world has 59 group numbers and the marine world has 102.

Future Usage of Zones with Computers

To test various biogeographic models made by others against amphipod distributions would require dividing our geographic blots into subsegments that replicate various classic models. For example one might wish to subdivide Asia into fragments based on the Smith-Mani-Barnard system overlain by the Udvardy-Barnard system in the main Paleotropics. The segments of the Smith-Mani-Barnard system are then subdivided into the portions forced by the Udvardy-Barnard overlap. These portions can be labeled as decimal subdivisions, for example 964.2 could be the southern portion of 964 divided off by the Attur River. When one wants to assemble in a computer the segments for an Udvardy-Barnard zone one would need to call for items from Smith plus Udvardy-Barnard. Of course, one may store data in a computer by latitude and longitude and make any kind of correlation very quickly after one inserts a program hierarchy for any zoogeographic system. However, a lot of work is necessary to (1) calculate all latitudes and longitudes; (2) write a program for each biogeographic system. It is much faster to input the data by approximating the zone blot from our charts than laboriously locating a fix. One can spend hours trying to find just one locality so that only in a labor-intensive country can this kind of activity be undertaken. Memory tapes for locality data are said to be available (for example from the Central Intelligence Agency of the USA) but we understand these tapes have not been cleansed of erroneous and replicate names. We already know that the gazeteers supplied to us from various governmental agencies of the USA (Army, Air Force, CIA) also have not been cleansed nor clarified; for example, we rarely can pinpoint a locality in Rumania because, for every name, there are several localities.

Key

Geographic Numbers

000-199 Northern hemisphere freshwater; terrestrial; continental or insular

200-299 Arctic-boreal marine

300-399 North warm-temperate marine

400-499 Tropical Atlantic marine

500-599 Tropical Pacific marine

600-699 IndoPacific marine (mostly Indian Ocean)

700-799 South warm-temperate marine

800-899 Antarctic-antiboreal marine

900-999 Southern hemisphere freshwater; terrestrial; continental or insular

Individual numbers are elaborated below.

Letters and Symbols

A, abyssal, 2000+ m depth in the sea; B, bathyal, 200-2000 m in the sea; C, cave(s); D, continental salt water; brine; E, estuarine or lagoon or brackish; F, fresh water; G, epigean; H, hypogean, phreatic, stygian, subterranean; I, inquilinous, commensalistic, parasitic (general and presumed); J, wells; K, cobble-brackish seashore or beach interstitial; L, lakes; M, sublittoral; N, neritic or epipelagic (often combined with A or B or M); O, not used; P, not used; Q, anchialine; R, in rivers or riparian; S, springs, sources; T, transferred by humans; U, high altitude; V, in cold water only; W, widespread, meaning extended outward from cited category; X, brackish, more restricted than category E; Y, interstitial divorced from seashores; Z, sea grotto.

Numbers enclosed in brackets are group categories not necessarily shown on maps.

+ : added to marine number indicating species both sublittoral and deeper, otherwise all marine numbers denoting sublittoral and littoral only.

001 [Holarctic]
002 [west Palearctica]
003
004
005 [Europe and west Asia]
006 [Asia Minor and Balkans]
007
008
009
010 [north Asia]
011 Kolyma
012
013 Kamchatka
014 Yana
015 [Central Asia]
016 [Japan and cold east Asia together]
017 Lake Biwa, Japan
018
019 Siberia
020 [east Asia]
021 Altai (Udvardy 35)
022 Mongol (Udvardy 30)
023 Sakhalin (Udvardy 7)
024 Manchu (Udvardy 14)
025 [Japan in general]
026 Hokkaido
027 Honshu
028 Shikoku
029 Kyushu; 029g Goto Islands; 029t Tshushima Islands
030 [China in general]
031 Honan (Udvardy 15 oriental forest)
032 Takla-Makan-Gobi (Udvardy 22)
033 Tibet (Udvardy 23)
034 Himalayas (Udvardy 38)
035 [Afghanistan in general, embracing Udvardy 20,24,36,37; including our 33,34,36,43,45]
036 Pamir-Tien Shan
037
038 [Middle East]
039 Pontian Steppe (old Karakum) (=Kazakh) (Udvardy 29, Limnofauna 25)
040 [west Asia]
041 Irtysh
042 Turanian (=Bukhara=Buchara, plus Karatau Mtns.) (Udvardy 21)

043	
044	Ural
045	Kerman (Udvardy 24)
046	Kurdistan
047	Tigris
048	Arab
049	Levant
050	[Lakes of Asia]
051	[Lake] Kossogol
052	Lake Teletzkoye
053	[Lake] Ubsa Nor
054	[Lake] Koko Nor
055	Lake Baikal
056	Lake Dalai
057	[Lake] Lop Nor
058	[Lake] Issykul
059	Lake Balkash
060	[Europe in general]
061	Kazakh
062	Taiga
063	Boreonemorial (Limnofauna 16, Udvardy 10)
064	
065	[Volga overlap area, parts of our 039, 041]
066	Caucausus (Limnofauna 24)
067	Turkey (Udvardy 19)
068	Anatolia
069	[Caucausus to Afghanistan regional, 036, 042 and 066]
070	[PontoCaspian basin in general]
071	Pontic
072	
073	
074	Tundra (Limnofauna 219)
075	[Scandinavia in general]
076	Scandanavia (Limnofauna 22)
077	Fjordane (Limnofauna 20)
078	Baltic (Limnofauna 15)
079	Lowlands (Limnofauna 14)
080	[Boreal Europe or Northern Europe, 063, 078, 079, 082)
081	[eastern Europe in general, 071, 083, 084]
082	Zentral (Limnofauna 9) (Mittelgebirge)
083	Carpathia (Limnofauna 10)
084	Hungarian (Limnofauna 11)
085	[Central Europe, 082, 083, 084, 096]
086	
087	Dinaric (Limnofauna 5)
088	Hellenic (Limnofauna 6)
089	Balkanic (east) (Limnofauna 7)
090	[Balkanian in general]
091	Cyprus
092	[Balkans and Italy together]
093	Crete
094	

095 [east Mediterranean coasts]
096 Alpine (Limnofauna 4)
097
098 Italy
099 [Southern Europe]
100 [West Mediterranean coasts]
101 Corsica
102 Sardinia
103
104 Sicily
105 [North Mediterranean coasts]
106 Malta
107 [West Europe, 79, 108, 109]
108 France
109 Loire
110 [Southern Europe]
111 [Southwestern Europe, 108, 112, 114]
112 Pyrenee (Limnofauna 2)
113 [Portugal, political area in particular]
114 Iberia (Limnofauna 1)
115 [Balearic in general]
116 Minorca
117 Majorca
118 Ibiza (plus Formentera)
119
120 [Lusitanian in general, = islands of eastern Atlantic]
121 Iceland (Limnofauna 19)
122
123
124 British Isles (Limnofauna 18)
125 [Britain in general]
126 Ireland
127
128
129 CircumMediterranean
130 [North Africa in general]
131 Libya
132
133 [North Africa and southern Europe together]
134
135 Morocco
136 Lake Balaton
137
138 Lake Skadar (Scutari)
139 Lake Ohrid
140 [Lakes of Europe]
141 [Alpine lakes]
142 Lake Iliki (Greece, Thebes)
143
144
145 Lake Egridir
146 Lake Tuz

147 Lake Van
148 Lake Urmia
149 [Northwest glacial lakes of Europe]
150 [Nearctica, including all of Mexico]
151 [Nearctic glacial lakes]
152 Canada (east)
153 Manitoba
154 Alberta
155 Columbia
156
157
158 Alaska
159
160 [United States of America in general]
161
162 Adirondack
163
164 Appalachia (south)
165 [Great Lakes in general]
166
167
168
169 Piedmont
170 [Audubonian, 164, 169, 174, SE of 176, SW of 162]
171
172 Gulf
173
174 Bactrurus region
175
176
177
178
179
180
181
182 Rockies
183
184 Edwards Aquifer (and San Marcos well)
185 Edwards Plateau
186 Cascades
187
188 Oregon
189
190 [Mexico in general]
191 Sonoran (including Sinaloa and Baja California)
192
193 Guerrerean
194
195 Chihuahuan
196 Tamaulipan
197
198 Yucatan

199
200 [Arctic-Boreal marine]
201 [Polar Basin, north of 85° N at all depths]
202 Greenland quadrant 75-85° N, 40° E-20° W, 200+ m
203 Baffin quadrant, 75-85° N, 20-80° W, 200+ m
204 Canadian quadrant, 75-85° N, 80-140° W, 200+ m
205 Fletchers quadrant, 75-85° N, 140° W-westward to 160° E, 200+ m
206 Siberian quadrant, north Asia coast to 85° N, 160-100°E, 200+ m
207 Russian (Nansen) quadrant, 75-85° N, 100-40° E, 200+ m
208 Mohns quadrant, polar circle to 75°N, 0-30° W, 200+ m
209 Thomson quadrant, polar circle to 60° N, 0-45° W, 200+ m
210 [Pan Boreal]
211 Scoresby quadrant, polar circle or 60° N to 65°N, 45-65° W, 200 m
212 Davis quadrant, 65-85° N, 50-80° W, 200+ m
213 Beaufort quadant, 65-75° N, 120-160° W, 200+ m
214 Chukchi quadrant, 65-75° N, 160° W-160° E, 200+ m
215 [West Atlantic and East Pacific boreal together]
216 [Cold North Atlantic and Arctic]
217 Kara quadrant, 65-75° N, 90-40° E, 200+ m
218 Scandia quadrant, 60-75° N, 40° E-0°, 200+ m
219 Northsea quadrant, 0° eastward, 60° N southward, 200+ m
220 [Arctic Basin in general]
221 Ireland (Celtic) quadrant, 45-60° N, 0-15° W, 200+ m
222 Reykjanes quadrant, 45-60° N, 15-30° W, 200+ m
223 Canyon (Gibbs) quadrant, 45-60° N, 30-45° W, 200+ m
224 Newfoundland quadrant, 45-60° N, 45-60° W, 200+ m
225 Juneau (Tufts) quadrant, 45-60° N, 120-150° W, 200+ m
226 Kodiak quadrant, 45-60° N, 150-165° W, 200+ m
227 Bering quadrant, 60° N to polar circle, 160-180° W, 200+ m
228 Unalaska quadrant, 45-60° N, 165° W-180°, 200+ m
229 Dateline quadrant, 45-60° N, 180°-165° E, 200+ m
230 [Boreal Pacific]
231 Petropavlovsk quadrant, 45-60° N, 165° E west to Kuriles, 200+ m
232 Alexandrovsk quadrant, 43-60° N, about 155° to 135° E but inside Kurile chain only, 200+ m
233 [Boreal Inland Seas and Glacial Relicts]
234 Bothnia
235 Baltic (Gulf of Finland)
236 Kattegat
237 Skagerrak
238 Norway
239 Britain
240 [Boreal east Atlantic]
241 [Britain in general]
242 Channel (English), including Jersey and St. Malo, Guernsey, Plymouth, Isle of Wight, Portsmouth, Dover, Calais, Lands End, Scilly Isles, Finisterre, Ushant Island
243 Shetland
244 Faeroe
245 Iceland

246	Hekla
247	Jan (Mayen)
248	Bear
249	Rockall
250	[Amphiboreal Atlantic, west and east]
251	Greenland
252	
253	Thule (West Greenland)
254	Cod (Cape May inclusive to Cape Elizabeth inclusive)
255	Breton
256	Gaspe
257	Labrador
258	Ungava
259	Hudson
260	[Boreal Western Atlantic]
261	Franklin
262	Foxe
263	McClintock
264	McClure
265	Sverdrup
266	Banks
267	Barrow
268	Oregon
269	Puget
270	[Boreal Eastern Pacific]
271	Vancouver
272	Sitka
273	Aleutian
274	Alaska
275	Saint Lawrence
276	Saint Matthew
277	Pribilof (Saint Paul)
278	Anadryski
279	Kamchatka
280	[Boreal Western Pacific]
281	Commander (Bering Island)
282	Shelikov
283	Okhotsk
284	Sakhalin
285	Tatar
286	Kurile
287	Siberia
288	Wrangel
289	Novosibirsky
290	[Bering Sea in general]
291	Lyahkovsky
292	Taimyr
293	Revolution
294	Franz Joseph
295	Spitzbergen
296	Guba
297	Novaya Zemlya

298 Murmansk
299 White
300 [Warm Temperate Marine]
301 Peloponneseus quadrant, Eastern Mediterranean to 15° E, 200+ m
302 Tropez quadrant, Western Mediterranean from 15° E westward, 200+ m
303 Portugal quadrant, 30-45° N, 15° W eastward to Gibraltar, 200+ m
304 Lusitania (Oceanographer, Blake) quadrant, 30-45° N, 15-30° W, 200+ m
305 Midocean (Oceanographer, Atlantis) quadrant, 30-45° N, 30-45° W, 200+ m
306 Grandbanks quadrant, 30-45° N, 45-60° W, 200+ m
307 Hudson (Blake) quadrant, 30-43° N, 60-75° W, 200+ m
308 Sohm
309 Viscaino quadrant, 15-30° N, 120° W eastward to coast, 200+ m
310 California quadrant, 30-45° N, 135° W eastward to coast, 200+ m
311 Clarion quadrant, 15-30° N, 120-135° W, 200+ m
312 Albatross (Tufts) quadrant, 30-45° N, 135-150° W, 200+ m
313 Aztec quadrant, 15-30° N, 135-150° W, 200+ m
314 Murray quadrant, 30-45° N, 150-165° W, 200+ m
315 Pele quadrant, 15-30° N, 150-165° W, 200+ m
316 Seascarp (Chinook) quadrant, 30-45° N, 165-180° W, 200+ m
317 Laysan (Musicians) quadrant, 15-30° N, 165-180° W, 200+ m
318 Pacific (Shatsky, Emperor) quadrant, 30-45° N, 180-165° E, 200+ m
319 Seamount quadrant, 15-30° N, 180-165° E, 200+ m
320 Mellish (Shatsky) quadrant, 30-45° N, 165-150° E, 200+ m
321 Necker quadrant, 15-30° N, 165-150° E, 200+ m
322 Emperor quadrant, 30-45° N, 150-135° E, to Japan coast, 200+ m
323 Volcano quadrant, 15-30° N, 150-135° E, 200+ m
324 Minami quadrant, 30-45° N, 135-120° E but N and W only to Japan or continent, 200+ m
325 Formosa quadrant, 15-30° N, 135-120° E, 200+ m
326 China quadrant, 15-30° N, 120-105° E but only N and W to China coast, 200+ m
327
328
329
330 [Warm Eastern Atlantic]
331 Aral sea
332 Caspian Sea
333 Azov Sea
334 Black Sea
335 [Caspian, Black, Azov Seas and their rivers together]
336 [Caspian and Black Seas together]
337 [Rivers or Limans of Black and Azov Seas together: Don, Danube, Donets, Dniester Rivers]
338 [Rivers or Limans of Caspian Sea; Volga, Ural, Emba Rivers]
339 [Mediterranean and Black Seas together]
340 [Mediterranean Sea in general]
341 Aegean
342 Cyprus
343 Libyan; 343s, Suez Canal
344 Morocco

344 Morocco
345 Adriatic
346 Greece
347 Sardinia
348 Riviera
349 Balearic
350 [Eastern Atlantic]
351 Gibraltar
352 [Warm Eastern Atlantic and Mediterranean and salty Black Seas]
353 Biscay
354 [AmphiAtlantic, warm temperate to Arctic, plus Mediterranean]
355 [Eastern Atlantic Warm Temperate to Boreal]
356 [Species Escaped from One River System to Another].
357 Madeira
358 [Lusitanian, Azores, Madeira, Canary to west Iberia together]
359 Azores
360 [Northwestern Atlantic]
361 [Western Atlantic Warm Temperate to Boreal]
362 [Western Atlantic Warm Temperate to Tropical]
363 Chesapeake
364 [Gulf of Maine southward to South Florida]
365 Carolina
366
367 Bermuda
368 [Northeastern Pacific Boreal]
369 [Eastern Pacific Warm Temperate to Tropical]
370 [Northeastern Pacific Warm Temperate]
371 Mendocino
372 Monterey
373 San Diego
374 Canalino
375 Guadelupe
376 Magdalena
377 Cortez
378 Revillagigedo
379 [Eastern Pacific Warm Temperate to Boreal]
380 [Middle Pacific]
381 Hawaii
382 Midway
383 Johnston
384 Wake
385 Marcus
386 Bonin
387 Parece Vela
388
389 [Japan Sea and Okhotsk Sea together]
390 [Northwest Pacific, Warm-Temperate and Boreal]
391 Japan Sea
392 [Western Pacific Warm Temperate and Tropical]
393 [Warm east Asia and warm northeast Pacific]
394 Hokkaido
395 Japan and Seto Inland Sea