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AMPHIPACIFICA is an international journal of invertebrate systematics, aimed primarily at publication of monographic treatments that are too large or bulky (50 - 100 printed pages including plates) for acceptance by standard taxonomic journals. Initially, the contents will feature monographic studies on crustaceans of the faunistically rich and geologically ancient North American Pacific coastal marine region. The scope of this new journal extends, geographically to other broadly Pacific regions, and faunistically to other arthropods, mollusks, annelids, to other regional invertebrate taxa, both aquatic and terrestrial, including parasites, and to aspects of vertebrate animals that may involve systematics, ecology and behaviour.

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(1) **Subscriptions and Correspondence:** Dr. E. L. Bousfield, Managing Editor, c/o Natural History Division, Royal B. C. Museum, Victoria, B. C., Canada. V8V IX4.
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DEDICATION

The Journal AMPHIPACIFICA is dedicated to the promotion of systematic biology and to the conservation of Earth's natural resources.

Cover Design: Adapted from the title page of S. J. Holmes (1904). "Amphipod Crustaceans of the Expedition." Harriman Alaska Expedition, pages 233-244.

From our Readers . .

The second number of the new journal was mailed to subscribers in early June, and this issue in October. We acknowledge slippage in planned publication dates, and our efforts to remove mechanical errors from the text have not yet been entirely successful. However, the number of favourable comments being received from the general readership concerning the material and illustrations is encouraging. We are increasing the use of offers from colleagues for referee services in their fields of specialization, and plan to include their comprehensive review articles on topics of aquatic biological concern. Continuing modification of the editorial terms of reference, outlined below, have expanded the scope of our service to both contributors and readership. Collaboration with the library exchange program of the Royal British Columbia Museum, and the steadily increasing numbers of new subscribers, have broadened the total to nearly 200 committed subscriptions, as of this date.

Positive and helpful commentary has been received from Jan Stock (Amsterdam), Niel Bruce (Copenhagen), Nina Tzvetkova (Leningrad), Horoshi Morino (Japan), Phil Oshel (Chicago), Patsy McLaughlin (Anacortes), Ann Quayle (Nanaimo), and several other colleagues. An item in a recent issue of the Memorial University Alumnae "Gazette", by Carla Pomeroy, concerns a new species of phoxocephalid amphipod that has been named *Mandibulophoxus mayi*, Jarratt & Bousfield, 1994 (see also p. 66 of this issue). In Pomeroy's article, Dr. May, President and Vice-Chancellor of the University, comments "I've always wanted to spend my life on the beaches of British Columbia. I never made it, but now I'm there in name! In all seriousness, when the Latin version of your name is used as the species designate for an animal or plant, you're in quite good company, and we're running out of animals to name. Usually this is reserved for those directly involved in taxonomy". The editorial board of AMPHIPACIFICA encourages the use of patronyms by contributors of manuscripts in recognizing those who actively promote scientific investigation, and the conservation of the world's natural resources.

A few readers have been concerned, understandably, about the possibility of competition for submissions between AMPHIPACIFICA and other journals of systematic biology. To a very limited extent, such may be the case. However, AMPHIPACIFICA was designed initially to replace former Canadian outlets for systematic biology such as the "Publications in . . ." series (Canadian Museum of Nature, Ottawa), "Contributions" and "Technical Reports" (Royal British Columbia Museum), and to some extent the Canadian Journal of Zoology and the Journal of Fisheries and Aquatic Sciences (Ottawa). For many years, these journals had been publishing both long and short taxonomic papers, but recently these outlets have been discontinued and/or no longer accept long (>20 pp.) papers on taxonomy or systematic biology. AMPHIPACIFICA accepts mainly long papers on systematics (>30-40+ printed pp.) with em-

phasis mainly on aquatic invertebrates, mainly of the North Pacific region. Also, its page charges are modest, less than those of most other journals that do assess page charges, thereby hopefully stimulating publication by authors who may be without institutional backing or other major financial resources, and might otherwise be unable to publish good systematic work.

In this issue we present further systematic and biogeographical features of the North American Pacific fauna as revealed by the dexaminoidean amphipods. Generic and species diversity of this group in the North Pacific is relatively low, but remarkable in consisting mainly of very primitive and very advanced genera, with few phylogenetically intermediate representatives. In analyzing this fauna, in combination with that recorded elsewhere in the scattered literature, the authors have been able to recognize, within the superfamily, two clearly defined families, each with four morphologically and biogeographically distinctive subfamilies. The North Pacific is the probable centre of origin and evolution of this relatively ancient and primitive group which has since spread mainly into the Indo-Pacific region. The more advanced members are now re-penetrating the North Pacific as commensals on tunicates, sponges, and other sessile colonial invertebrates. A second major paper outlines morphological and behavioural evidence for the development of new phyletic classificatory concepts within the Amphipoda broadly. Amphipods may be grouped semi-phylogenetically and pragmatically into two main assemblages, the swimmers ("Natantia"), and the bottom crawlers ("Reptantia") based mainly on major differences in their reproductive morphology and life style. The authors recognize the subordinal distinctiveness and relatively primitive position of the small, hypogean, relict Ingolfiellidea viz-a-viz the Gammaridea. At the same time, they provide evidence that would derive the relatively advanced pelagic Hyperiidea from a common ancestor that is least far removed from the gammaridean superfamily Stegocephaloidea; the benthic, clinging Caprellidea had earlier been derived, by others, from podocerid members of superfamily Corophioidea. Possible submergence of both the Hyperiidea and the Caprellidea as infraordinal taxa within Suborder Gammaridea therefore merits further consideration.

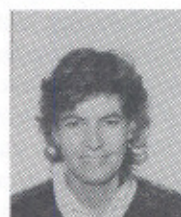
Our editorial policy has been modified to accept review articles concerning aquatic biology, environmental protection, and biological conservation. It has been broadened to accept short articles, where publication of the new taxa is urgent, and where inclusion of the paper can be accommodated within the total pagination of an issue at a required minimum of 140-150 pages. Accordingly, we have included here, on brief notice, a short paper by Kathleen Conlan on new isacid amphipods from off the coast of California (pp. 67-74).

We conclude this editorial by thanking the editors of "Deep Sea Research" and "The Canadian Field-Naturalist" for recent publicizing of AMPHIPACIFICA in those journals. A notice concerning the history and aims of the "Canadian Field-Naturalist" is provided in this issue (p. 75).

About Our Authors . . .



Jane Kendall, B.Sc., majored in biology, with minors in chemistry and mathematics, at Ottawa University. In 1988 she commenced a 3-year, part-time period of identification work on CMN collections of North Pacific amphipod crustaceans, with special attention to family groups within the Dexaminioidea and Lysianassoidea. She is currently a teacher of biology and mathematics at secondary schools of the Carleton Board of Education. She is married, with one child, and now resides in the picturesque town of Burritt's Rapids, Ontario, south of Ottawa, the nation's capital.

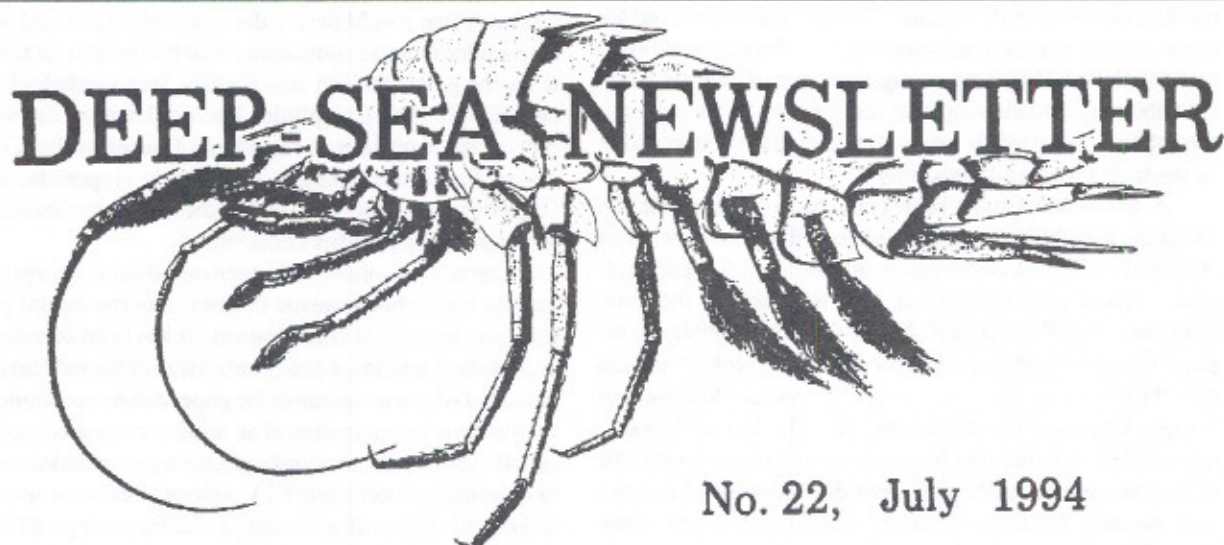


Kathleen E. Conlan, obtained an Honours B.Sc. in Biology at Queen's University, a Master's Degree in Marine Ecology at the University of Victoria, and a PhD in Systematics and Evolution at Carleton University, Ottawa. From 1979 to 1989, Dr. Conlan worked with Dr. E. L. Bousfield, at the Canadian Museum of Nature, on systematics of corophioidean amphipods. Since then she has expanded her research to ecology and behaviour. She has recently initiated studies in Antarctica, the High Arctic, and the deep sea, both on questions concerning amphipods, and more broadly on benthic community response to anthropogenic disturbances.



Chiang-tai Shih, PhD, is a Research Scientist (formerly Curator of Crustacea) at the Canadian Museum of Nature, Ottawa. Although broadly interested in aquatic biology, he specializes in the systematics of crustaceans, with emphasis on planktonic amphipods and copepods. His research in biogeography of planktonic crustaceans led to development of his theory of speciation in marine zooplankton that is termed planktopatric speciation.

Commentary on Dr. E. L. Bousfield was published in *Amphipacifica* I(1): 2, 1994.



ANNOUNCEMENT: 7th Deep Sea Biology Symposium

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Thursday, Sept. 29 - Tuesday, Oct. 4, 1994.

THE AMPHIPOD SUPERFAMILY DEXAMINOIDEA ON THE NORTH AMERICAN PACIFIC COAST; FAMILIES ATYLIDAE AND DEXAMINIDAE: SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

by E. L. Bousfield¹ and J. A. Kendall²

ABSTRACT

Based mainly on study material from North American Pacific coastal marine waters (from the Bering Sea region to northern California), this study treats the systematics and distributional ecology of regional family and subfamily members of the gammaridean amphipod superfamily Dexaminoidea. Cluster analysis of 22 component genera supports subdivision of this taxonomically difficult group into two principal families, the primitive, thin bodied Atylidae, and the more advanced, broad bodied Dexaminidae. Family Atylidae encompasses the subfamilies Atylinae Leach 1814 (revised status); Anatylnae Bulycheva 1955 (revised status), Lepechinellinae Schellenberg, 1926 (revised status); and **Nototropiinae**, new subfamily. Family Dexaminidae here encompasses subfamily Dexamininae Leach, 1814 (revised status); Prophiantinae (Nicholls, revised Barnard, 1970); **Dexaminoculinae**, new subfamily, and **Polycheriinae**, new subfamily.

Material from the study region contains representatives of both families and three component subfamilies. Within subfamily Atylinae are newly described and figured *Atylus georgianus*, new species and *A. borealis*, new species. Newly recorded from the study region and/or refigured are: *Atylus atlassovi* (Gurjanova, 1951), *A. bruggeni* (Gurjanova, 1938), *A. collingi* (Gurjanova, 1938), and *A. levidensus* Barnard, 1954, *A. tridens* (Alderman, 1936), and the type species *A. carinatus* J. C. Fabricius, 1783. Rediagnosed and refigured from the western Pacific region are *Atylus ekmani* Gurjanova, 1938 and *A. rylovi* Bulycheva, 1952. Based on analysis of the literature and records from the western Pacific, subfamily Anatylnae here encompasses *Anatylus pavlovskii* Bulycheva, 1955, and *Kamehatylus japonicus* (Nagata, 1961). Subfamily Nototropiinae contains the western Pacific *Nototropis* sp. (cf. *guttatus* Costa) and the abyssal species, *Atylus aberrantis* (Barnard, 1962), here transferred from subfamily Lepechinellinae in the monotypic new genus *Aberratylus*.

Within family Dexaminidae, subfamily Polycheriinae is moderately well represented in amphi-North Pacific waters. Newly described and figured are *Polycheria carinata*, new species, and *P. mixillae*, new species, and *Polycheria osborni* Calman, 1898 is redescribed. Subfamily Prophiantinae, is represented in Asiatic Pacific coastal waters by about a dozen described species, but in the North American study region, the sole species identified to date is *Guernea reduncans* (J. L. Barnard, 1958). Subfamily Dexamininae is well represented in the western North Pacific by species of *Paradexamine* but is absent from the eastern North Pacific.

Biogeographically, within family Atylidae, members of the primitive subfamily Atylinae are endemic to the North Pacific region. From there, members of the more advanced Nototropiinae and Anatylnae have apparently radiated into the Indo-Pacific and former tethyan warm-water regions. Members of subfamily Lepechinellinae, having a common ancestor with the Nototropiinae, have become abyssal. Nearly all members of the more advanced family Dexaminidae are warm-temperate and tropical but a few species of the most advanced subfamily, Polycheriinae, have penetrated into the cold temperate North Pacific, apparently from two different sources. The sole North American Pacific prophiantin species appears more closely related to counterparts in the North Atlantic region than to prophiantins of the western North Pacific.

Except for the abyssal Lepechinellinae, most dexaminoideans are littoral-sublittoral in depth range and all are exclusively marine. In life style, they mainly nestle on the bottom, in sea grass clumps, coral clusters, empty shells, or in pits excavated in the tests of colonial invertebrates, but the Prophiantinae apparently burrow in soft sediments. Species densities are seldom high and total biomass is low, presumably with little significance in regional food energy cycles. The group may be considered a specialized relict offshoot of early gammaroidean ancestral types, from which may have also evolved the closely related, but ecologically more successful, ampeliscoidean amphipods that are tube-dwelling and deposit-feeding in soft sediments, world-wide.

¹ Researcher Emeritus, Canadian Museum of Nature, Ottawa, Ontario K1P 6P4

² R. R #1, Burritt's Rapids, Ontario K0G 1B0

INTRODUCTION

The superfamily Dexaminioidea encompasses a group of benthic nestling amphipods that occur mainly on hard substrata in tropical and warm temperate regions of the world. The number of described species is relatively small (< 200), and populations are generally of low density. However, morphological diversity within the group is relatively high (cf. Gammaroidea with 5 times the number of species), possibly reflecting the wide variety of solid (and some sedimentary) substrata on which various subgroups of Dexaminioidea have been modified for existence.

The animals are characterized by variously carinated or dorsally processiferous bodies, fused usosome segments 2 & 3, a tendency to prehensility (subchelation) of pereopods 3-7, and a reproductive life style that involves mating freely in the water column. The gnathopods are weakly (or not) sexually dimorphic, but in the type genus *Dexamine* and close relatives, the anterior margin of the propod of gnathopod 1 (in the male) bears a characteristic notch or sharp excavation, of presumed (but unknown) reproductive function. Although basically free-living, with well developed pereopods, pleopods, and tail fan, the animals are typically slow-moving, even sedentary, in vegetative life style. Most species are deposit or trypton feeders, frequently employing specialized setae of the antennae and anterior pereopods to rake in organic food material, from a nearly fixed position on the bottom. Members of the specialized genus *Polycheria* are commensal on the tests of colonial tunicates and sponges where they live "upside down" in pits excavated in the surface of the host. However, unlike the closely related ampeliscoideans, of similar "upside-down" feeding style, dexaminioideans lack spinning glands in the anterior pereopods and are incapable of tube building.

The classification of the group within suborder Gammaridea has gone through an early period of stability, followed by a recent period of relative instability. Early workers (e.g. Sars, 1895; Stebbing, 1908) maintained the atylids and dexaminids as separate families, and recognized the close similarity of atylids to the basic "Gammaridae" amphipod type. Such stability was extended to the Lepechinellidae (Stebbing, 1908) and the Prophliantidae (Nicholls, 1939) by more recent major workers (e.g. Gurjanova, 1951; Barnard, 1969a). Soon afterwards, however, a developing trend to fusion of related higher taxa, led to submergence of all dexaminid groups within family Dexaminidae (e.g. Bellan-Santini, 1982) or to formal creation of a new superfamily group, Dexaminioidea, in which family levels of distinction could be maintained (e.g. Bousfield, 1979, 1982).

Dexaminioidean amphipods are among the few regional North Pacific gammaridean groups that have received significant taxonomic attention. Within the Dexaminidae proper, *Polycheria osborni* was described from California by Calman (1898). Within family Atylidae, the genus *Atylus* had been unknown from the Pacific coast of North America prior to Alderman's (1936) description of *A. tridens* from

California. That record was closely followed by Gurjanova's (1938) description of *A. collingi* from eastern Siberia and Bering sea regions, and by J. L. Barnard's (1956) description of *A. levidensis* from California. Based on CMN material collected along the Pacific coast of Canada, 1955 - 1959, Mills (1962) provided illustrated descriptions, keys, and distributional data on those three species from the coastal marine region of British Columbia. Further records from California were added by Barnard (1962, 1969b) and Cadien (1991). Barnard (1975), and Staude (1987) included dexaminids in keyed and illustrated popular regional works and Austin (1985) summarized records from the cold temperate northeast Pacific region. Within family Prophliantidae, *Guernea* (*Prinassus*) *reduncans* Barnard had been recorded widely along Californian coasts by Barnard (1958, 1969b, 1972) and Cadien (1991). The biology of *Polycheria osborni* was studied in detail by Skogsberg & Vansell (1928), and some members of the Lepechinellidae were recorded from the eastern Pacific abyss by Barnard (1967, 1972).

In the western North Pacific, the early work of Gurjanova (1938), and Stephensen (1944) was encompassed by Gurjanova (1951). Subsequently Bulycheva (1952, 1955) proposed further species of *Atylus*, *Polycheria* and *Anatylus*; and Birstein & Vinogradov (1955) recorded an abyssal lepechinellid. From Japanese waters Nagata (1961) described the aberrant *Atylus japonicus*. The more recent work of Gamo (1981) on *Lepechinella*, of Hirayama (1984a,b, 1984, 1986) on species of *Paradexamine*, *Polycheria*, *Guernea*, and *Atylus*, and Ishimaru (1987) on *Guernea*, and others, has been summarized most usefully in a catalogue of dexaminid amphipods of Japan by Ishimaru (1994).

Dexaminid systematics and distribution have been treated comprehensively and most usefully by Barnard & Karaman (1991). However, the lumping of diverse subgroups within one family, with recognition of only one additional subfamily and no superfamilies, and the use of too few, or phylogenetically non-significant, character states in diagnoses and keys, tends to create problems of inconsistency in taxonomic analysis and an unwieldiness of classification that may also apply elsewhere within gammaridean classification (e.g. within family Eusiridae). Our purpose here is to (1) develop new basic taxonomic information and analytical criteria from a study of the present North Pacific material; (2) incorporate this information with previous knowledge as a basis for numerical analysis of natural relationships between higher taxonomic categories, and (3) modify existing classifications in a manner that more consistently reflects distributional, ecological, and behavioural, as well as taxonomic and phylogenetic, differences between the subgroups.

The authors have recently examined extensive new material in the amphipod collection of the Canadian Museum of Nature (CMN), Ottawa, that supplements the earlier material of Mills (1961), and material from the Bering Sea region (Peter Slattery expeditions) and elsewhere. Station lists for CMN museum material, 1955 - 1980, are provided

by Mills (1962), Bousfield (1958, 1963, 1968), Bousfield and McAllister (1963), and Bousfield and Jarrett (1981).

This report provides an extensive review of the systematics, distributional ecology of the dexaminoid fauna from the North American Pacific coastal marine region and relates it phylogenetically and biogeographically to counterpart faunas of the western North Pacific and elsewhere in the world.

ACKNOWLEDGEMENTS

This study could not have been completed without the help of many biological research agencies and interested colleagues. The field surveys were carried out with the full support of the National Museum of Natural Sciences (now Canadian Museum of Nature) in Ottawa, and received vital technical assistance and ship-time from Canadian Pacific research centres and their staffs. These included the Pacific Biological Station, the Bamfield Marine Station, the Pacific Environmental Institute, the Royal British Columbia Museum, the University of Victoria, University of British Columbia, and the Institute of Ocean Sciences, Sidney, and, in the United States of America, the Friday Harbor Marine Laboratory and the College of Fisheries, University of Washington. We are particularly indebted to Dr. Peter Slattery, Moss Landing, CA., for provision of material from the Bering sea region. Full acknowledgement to individuals of those agencies, and to many others, are provided in the previously published station lists (above), to whom we again express our deepest appreciation. We are grateful for the splendid published work of our colleagues elsewhere on whose illustrations we have drawn freely in development of taxonomic and phyletic relationships. We thank especially Museum colleagues Ed Hendrycks and Judith C. Price for curatorial and cataloguing assistance. Preparation of the line illustrations was most capably assisted by Susan Laurie-Bourque, Hull, Québec. We are grateful to Dr. J. D. Thomas, USNM, for review of the text and kind permission to adapt illustrations from the pertinent research publications of the late J. L. Barnard. Work by the senior author, and by the artist, was also supported by operational grants from the Royal Ontario Museum, Toronto, and the Natural Sciences and Engineering Research Council, Ottawa.

SYSTEMATICS

DEXAMINOIDEA Leach (revised Bousfield)

Dexaminoida: Bousfield, 1979: 350.—Bousfield, 1982: 277.—Bousfield, 1983: 263.—Schram, 1986: 180.
Dexaminidae Barnard, 1970: 161.—Ishimaru, 1987: 1412.—Barnard & Karaman, 1991: 260.

Families: 1. Atylidae G. O. Sars, 1882: 26. Includes subfamilies Atylinae Sars (revised status); Lepechinellinae Schellenberg 1926 (revised status); Nototropiinae, new subfamily; and Anatylinae Bulycheva, 1955 (revised status).

2. Dexaminidae Leach, 1813/14: 432. Includes subfamilies Dexamininae Leach (revised status); Polycheriinae, new subfamily; Dexaminoculinae, new subfamily; and Prophliantinae Nicholls, 1939 (revised status, Barnard 1970).

Diagnosis (after Bousfield, 1982): Rostrum present, variable. Body (especially urosome) usually with mid-dorsal, and often dorso-lateral, carinations or teeth. Urosome segment 1 dorsally carinate. Urosome segments 2 & 3 coalesced, often dorsally carinate. Sexual dimorphism pronounced in eyes, antennae, uropod 3, and coxal gills, but weakly expressed in gnathopod 1. Eyes pigmented and multi-faceted, lacking in bathyal forms. Antennae variable; peduncles of flagella (male) armed with brush setae. Antenna 1, peduncular segment 2 usually longer than 1; segment 3 short; accessory flagellum minute or lacking. Antenna 2 trending to shortening (female); flagellum elongate, non-calceolate (male).

Mouthparts trending to modification. Upper lip entire. Lower lip, inner lobes variously developed. Mandibular molar triturative, but trending to reduction; left lacinia basically 5-dentate; palp various, weak or lacking. Maxilla 1, inner plate 0-8 setose, outer plate 7-11 spinose; palp often 1-segmented. Maxilla 2, inner plate the smaller, trending to loss of marginal setae. Maxilliped, outer plate large, inner plate and palp trending to reduction in size and loss of setae.

Coxal plates 1-4 medium to small, often notched or incised below; coxa 5 strong, often antero-lobate. Gnathopods small, weakly subchelate (palms convex), generally dissimilar in form. Gnathopod 1, propod may be distinctively sexually dimorphic.

Peraeopods 3 & 4 subequal, or peraeopod 4 smaller, trending to shortening of segment 5. Peraeopods 5-7 variable in form and size, bases unequally broad, trending to linearity; segment 5 variable; segment 6 and dactyl trending to subchelation.

Pleopods usually strong, especially in male. Uropods 1 & 2, rami unequal, lanceolate, apically spinose. Uropod 3 aequiramous; rami lanceolate, outer ramus 1-segmented, margins setose in male, often so in female.

Telson bilobate, lobes variously fused basally, apices spinose, notched or finely crenulated.

Coxal gills sac-like, on peraeopods 2-7(6), often pleated or phylloform, especially in male. Brood lamellae medium broad or strap-like, trending to linearity.

Reproductive Life Style: synchronous, mating freely in water column (presumed from morphology - nearly all members).

Taxonomic and Biogeographic Commentary: Cluster analysis of all 22 generic-level taxa within superfamily Dexaminoida recognized here (p. 56) supports the validity of the family and subfamily components listed above, and detailed in the following systematic accounts. The most primitive subfamily, Atylinae is endemic to the boreal-subarctic North Pacific; others are components of mainly Indo-Pacific faunas marginally present in this region.

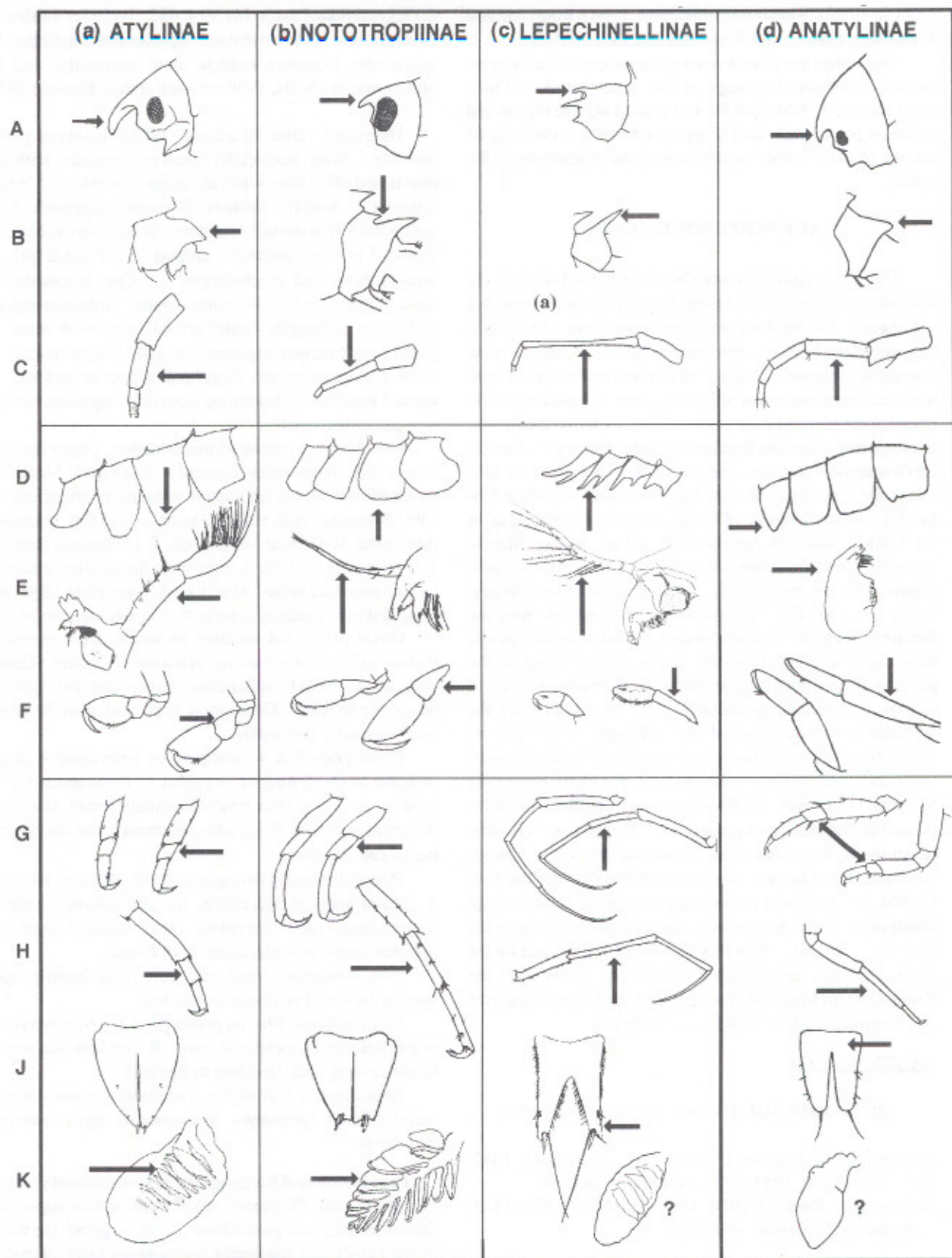


FIG. 1. ATYLIDAE: TYPICAL CHARACTER STATES

A - Rostrum; B - Urosome 1; C - Antenna 1; D - Coxa 1; E - Mandible; F - Gnathopod 1;
G - Peraeopods 3-4; H - Peraeopods 5-7; J - telson; K - coxal gills 2-5; (from text plates)

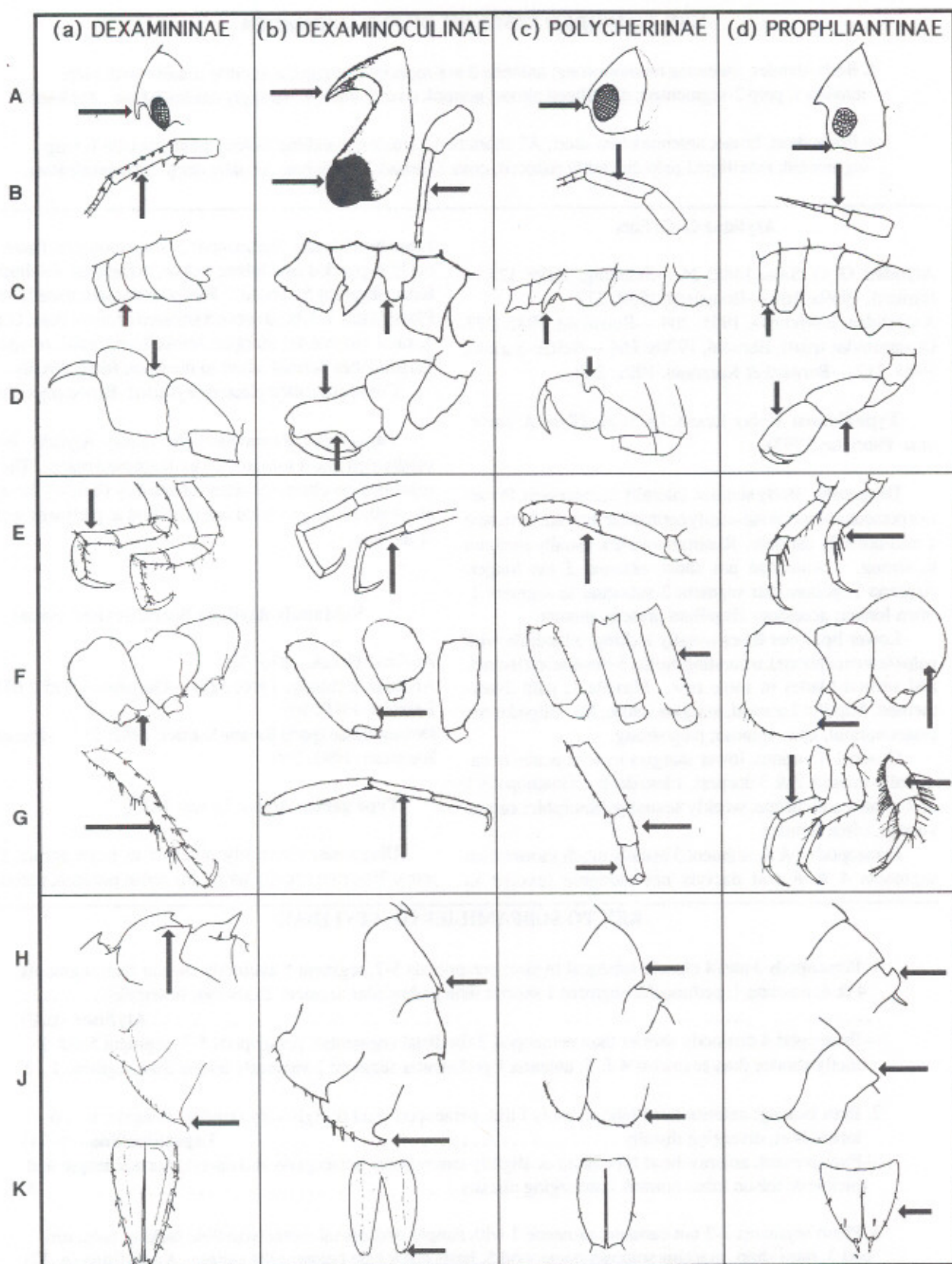


FIG. 2. DEXAMINIDAE: TYPICAL CHARACTER STATES

A - Rostrum; B - Antenna 1; C - Cõxa 1-4; D - Gnathopod 1 (male); E - peraeopods 3-4; F - peraeopods(5-7 bases)
G - peraeopods 5-7 (distal); H - abdomen dorsum; J - Pleon plates 2-3; K - telson (from text plates)

KEY TO WORLD FAMILIES OF DEXAMINOIDEA

1. Body slender; antennae medium-long; antenna 2 not reduced (female); mandible usually with palp; maxilla 1, palp 2-segmented; maxilliped almost normal; coxa 5 shallow, strongly antero-lobate. **Atylidae**.

—Body short, broad; antenna often short, A2 shortened (female); mandible lacking palp; maxilla 1, palp 1-segmented; maxilliped palp distinctly reduced; coxa 5, broad, aequilobate, usually deep. **Dexaminidae**.

Atylidae G. O. Sars

Atylidae: G. O. Sars, 1882: 26.—Stebbing, 1906: 327.—Barnard, 1969a: 161.—Bousfield, 1982: 277.

Anatylidae: Bulycheva, 1955: 204.—Bousfield, 1982: 277
Dexaminidae (part): Barnard, 1970a: 164.—Bellan-Santini, 1983: 212.—Barnard & Karaman, 1991: 260.

Type Genus: *Atylus* Leach, 1815: 21. (Type *A. carinatus* Fabricius 1793).

Diagnosis: Body slender, laterally compressed. Posterior peraeon and pleon variously carinate or smooth. Urosome 1 mid-dorsally carinate. Rostrum various, usually medium to strong. Antennae not short, antenna 2 the longer. Antenna 1, peduncular segment 2 subequal to segment 1, often longer; accessory flagellum present, minute.

Lower lip, inner lobes usually lacking. Mandible with palp (few exceptions), triturating molar, 5-dentate left lacinia, and several blades in spine row. Maxilla 1, palp 2-segmented. Maxilla 2 normal, margins setose. Maxilliped inner plates normal, apex spinose; palp strong.

Coxae 1-4 various, lower margins may be acute, occasionally incised, 2 & 3 deepest, 1 less deep. Gnathopods 1 & 2 weakly subchelate, weakly sexually dimorphic; carpus various, often slender.

Peraeopods 3 & 4, segment 5 usually much shorter than segments 4 & 6 and dactyls not elongate (except in

Lepechinellinae). Peraeopods 5-7 not elongate, bases variously expanded and lobate below, somewhat dissimilar in form; segment 5 various. Pleopods various, usually strong. Pleon plates 1-3, hind corners squared or acuminate. Uropod 3, rami lanceolate, margins setose (esp. male) or spinose. Telson lobes normal, short to medium, fused basally.

Coxal gills often pleated or plaited. Brood plates broad.

Taxonomic Remarks: The family Atylidae is here subdivided into 4 subfamilies as diagnosed below. They are separated on character states of the key (below) for which illustrations are provided in Fig. 1, and in pertinent sections of the text.

Subfamily Atylinae Boeck (revised status)

Atylinae Boeck, 1876: 320.

Atylidae Stebbing, 1906: 327.—Gurjanova, 1951: 678.—Barnard, 1969: 163.

Dexaminidae (part) Bellan-Santini, 1982: 212.—Barnard & Karaman, 1991: 260.

Type genus: *Atylus* Leach, 1815.

Diagnosis: Generally medium to large atylids (5-40 mm). Rostrum usually large. Posterior peraeon, pleon, and

KEY TO SUBFAMILIES OF ATYLIDAE

1. Peraeopods 3 and 4 closely subequal in size; peraeopods 5-7, segment 5 distinctly shorter than segments 4 & 6; antenna 1, peduncular segment 1 shorter than peduncular segment 2 (always, in female)

Atylinae (p. 8)

—Peraeopod 4 distinctly shorter than peraeopod 3 (in distal segments); peraeopods 5-7 segment 5 not distinctly shorter than segments 4 & 5; antenna 1 peduncular segment 2 variously longer than segment 1 . 2.

2. Eyes lacking; anterior head lobe strongly bifid; peraeopods and dactyls very slender, elongate; telson lobes short, diverging distally

Lepechinellinae (p. 31)

—Eyes present; anterior head lobe blunt or slightly emarginate; peraeopods and dactyls normal length and thickness; telson lobes normal, converging distally 3.

3. Pleon segments 1-3 not carinate; urosome 1 with simple mid-dorsal tooth; mandible lacking palp; uropod 3, rami short, margins spinose; peraeopod 5, basis not lobate below; gills simple. **Anatylinae** (p. 32)

—Pleon segment 1-3 usually carinate mid-dorsally; urosome 1 with tooth and notch; mandible with palp (weak); uropod 3, rami lanceolate, margins setose (esp. male); peraeopod 5, basis with lower hind lobe; gills phylliform **Nototropiinae** (p. 28)

urosoma usually dorsally carinate. Antennae large, setose.

Mouthparts basic. Mandibular molar, spine row, and palp well developed. Maxilla 1, inner plate separate, apically setose. Maxilla 2, plate margins setose. Maxilliped normal, plates and palp well developed.

Coxal plates 1-4 medium, lower margins often weakly incised or subacute anteriorly. Gnathopods medium, subsimilar, weakly sexually dimorphic.

Peraeopods 3 & 4 subsimilar in form and size; segment 5, distinctly shorter than segments 4 & 6. Peraeopods 5-7, bases broadened; segment 5 variously shorter than segments 4 & 6. Peraeopod 5, basis, hind lobe weak, not produced below. Peraeopod 7, basis very broad, posterior lobe present, acute or rounded below.

Pleopods strong. Uropod 3, rami strong, margins spinose and usually setose (both sexes). Telson lobes medium to large, with apical spine(s). Anterior coxal gills usually pleated, especially in males.

Taxonomic and Distributional Commentary: The subfamily Atylinae presently contains a single genus, *Atylus*, encompassing about a dozen species, almost all endemic to the boreal and subarctic North Pacific region. The range of morphological variation is sufficiently great that recognition of internal groupings (e.g. the *collingi* subgroup) may eventually justify subgeneric recognition.

The principal features of subfamily Atylinae are contrasted with those of other subfamilies of Atylidae in Figure 1. In summary: (referred to in following text, where pertinent).

Atylus Leach, 1815

Atylus Leach, 1815: 21.—Mills, 1961: 17 (key).—Barnard, 1956: 38.—J.L. Barnard, 1969a: 163.—J.L. Barnard, 1970a: 164.—Barnard & Karaman, 1991: 262 (part).

Nototropis Gurjanova, 1951: 680 + key. (part)

non *Anatylus* Bulycheva, 1955: 205.—Tzvetkova, 1967: 391.

non *Kamehatylus* Barnard, 1970b: 93.

Type Species: *Gammarus carinatus* J. C. Fabricius 1793, monotypy.

Species: *A. atlassovi* (Gurjanova, 1951); *A. borealis*, new species; *A. bruggeni* (Gurjanova, 1938); *A. collingi* (Gurjanova, 1938); *A. ekmani* (Gurjanova, 1938); *A. georgianus*, new species; *A. levidensus* (J.L. Barnard, 1956); *A. rylovi* Bulycheva, 1952; *A. tridens* (Alderman 1936); *A. villosus* Bate 1862. (*A. orientalis* Hirayama, 1886).

Diagnosis: Large atylids (10-30+ mm). Rostrum medium to large. Anterior head margin rounded, rarely bifid. Antennae moderately strongly sexually dimorphic. Ant-

enna 1, peduncular segment 2 not longer than 1; accessory flagellum minutely 1-segmented. Antenna 2, peduncular segments 4 & 5 strong, often setose.

Lower lip, inner lobes weak or lacking. Mandible: molar triturative; palp normal, 3-segmented. Maxilla 1, inner plate with 4-8 apical setae. Maxilla 2, inner plate with 1-8 proximal plumose marginal setae. Maxilliped, palp normal, 4-segmented.

Coxae 1-4 medium deep, smooth or subacute below; coxa 3 antero-distally deepest. Coxa 5, anterior lobe broadly or sharply rounded below. Gnathopods 1 & 2 ordinary, very weakly or not sexually dimorphic; propod & carpus medium, usually subsimilar in length.

Peraeopods 3-7 not elongate, dactyls relatively short. Peraeopods 3 & 4, segment 5 markedly shorter than 4 & 6. Peraeopod 5 distinctly smaller than peraeopods 6 & 7; basis with small postero-distal lobe. Peraeopod 7, basis broad, postero-distal lobe present, rounded or acute below. Peraeopods 5-7, segment 5 markedly shorter than segments 4 & 6.

Pleopods regular; pleon plates rounded below and behind. Uropod 2 short, rami unequal. Uropod 3 strong, rami lanceolate, margins setose in male, setose and/or spinose in female.

Telson lobes not elongate, fused basally, not diverging distally. Coxal gills sac-like, weakly to moderately pleated. Brood plates medium broad, not slender.

Variables: Rostrum long (type), medium (*A. collingi*, *A. georgianus*); posterior peraeonites carinate (type), smooth (*A. borealis*, *A. rylovi*, *A. tridens*); pleon carinate (type), smooth (*A. borealis*, *A. rylovi*, *A. tridens*); gnathopod 2, propod & carpus short, stout (type), slender (*A. bruggeni*, *A. ekmani*, *A. villosus*); peraeopods 5-7, segment 5 only slightly shorter than segments 4 & 6 (*A. villosus*).

Taxonomic Commentary: Some species of the genus *Atylus*, as here defined, overlap in some character states, with some species of *Nototropis*, as defined below (p.28). However, the two genera are distinguished by the characters of the subfamily key (p. 8) and, in combination, by the larger rostrum, heavier mandibular palp, the weak (or lacking) hind lobe of the basis of peraeopod 5, heavier uropod 3, and the pleated, rather than phylloform (or dendritic) anterior coxal gills, especially in the male.

Distributional Commentary: Most species are confined to subarctic and boreal coastal marine waters of the North Pacific region, and are mainly benthic. *Atylus carinatus* is holarctic, but *A. villosus* has been recorded only from the southern oceans and may not be a natural member of the genus.

Members of the genus *Atylus* (sens. str.) are virtually non-overlapping distributionally with members of the genus *Nototropis*, as here defined.

KEY TO NORTH PACIFIC SPECIES OF ATYLUS*

(Character states illustrated mainly in Fig. 1, p. 6)

1. Peraeon segments 6 & 7 and pleon mid dorsally toothed or carinated; urosome segment 1 with single (or bifid) mid-dorsal tooth; coxa 4 various, not crescent shaped posteriorly 2.
—All segments of peraeon and pleon mid-dorsally smooth; urosome segment 1 with single mid-dorsal tooth and preceding notch; coxa 4 crescent-shaped postero-ventrally 8.
2. Rostrum large (1/2 head length); uropod 3 large, rami longer than twice peduncle, margins with spines and setae; telson lobes elongate, 1 1/2 - 2 X basal width 3.
—Rostrum medium, 1/4-1/3 head length; uropod 3 medium, rami shorter than twice peduncle, margins spinose; telson lobes short, length \approx width 7.
3. Gnathopod 2, propod and carpus stout, depth of each > 1/2 length; peraeopod 7, basis, posterior lobe large, acute below; fused urosome segments 2 & 3 with low mid-dorsal carination; mandible, palp stout, segment 3 setose 4.
—Gnathopod 2, propod and carpus slender, depth < 1/2 length; peraeopod 7, posterior lobe small, shallowly rounded below; fused urosome segments 2 & 3, dorsal process erect, projecting well above mid line 5.
4. Peraeopods 3 & 4 & peraeopod 6, segment 5 short, length < 1/2 segment 4; gnathopod 2, propod stout, length > carpus *A. atlassovi* (p. 11)
—Peraeopods 3 & 4, and peraeopod 6, segment 5 medium, length > 1/2 segment 4; gnathopod 2, propod small, length < carpus *A. carinatus* (p. 11)
5. Eyes large; fused urosome 2 & 3 with bifid mid-dorsal tooth; uropod 3, margins of rami with spines and setae; peraeopod 7, basal lobe subacute *A. bruggeni* (p. 14)
—Eyes small; fused urosome 2 & 3 with single mid-dorsal tooth; uropod 3 (female), ramal margins spinose; peraeopod 7, basal lobe rounded below 6.
6. Pleon segment 3 and urosome segment 1 with bifid mid-dorsal tooth; western Pacific, Sea of Japan *A. ekmani* (p. 16)
—Pleon segment 3 and urosome 1 with single mid-dorsal tooth; endemic to the North American Pacific coast *A. levidensus* (p. 16)
7. Coxa 4 acute below; fused urosome 2 & 3 with low mid-dorsal ridge; gnathopod 1, propod, postero-distal angle with 5-6 transverse row of stout spines *A. collingi* (p. 24)
—Coxa 4 rounded below; urosome segments 2 & 3, with erect mid-dorsal tooth; gnathopod 1, postero-dorsal. angle of propod with 3 transverse rows of spines *A. georgianus* (p. 26)
8. Peraeopod 6, segment 5 short (< 1/4 segment 4); telson large, length >> width 9.
—Peraeopod 6, segment medium (= 1/2 segment 4); telson short, basal width about equal to length *A. rylovi* (p. 18)
9. Antennae long, flagella with more than 20 segments; uropod 3 (female), apices of rami acute; telson elongate, length 1.5 X width *A. tridens* (p. 20)
—Antennae shorter, flagella with fewer than 20 segments; uropod 3 (female) apices of rami rounded; telson medium, length 1.3 X width *A. borealis* (p. 22)

* *Atylus orientalis* Hirayama not included

Atylus carinatus (Fabricius)
(Fig. 3)

Gammarus carinatus J. C. Fabricius, 1793: 515.
Atylus carinatus Sars, 1895: 471, pl. 166.—Stebbing, 1906: 328.—Shoemaker, 1920: 14E.—Shoemaker, 1955: 45.—Gurjanova, 1951: 679.—Dunbar, 1954: 762.—Barnard, 1975, fig. 61.—Barnard & Karaman, 1991: 262.

Material Examined: North-west Territories: Slidre fiord, Ellesmere I., Arctic Biol. Sta., FRB, Canada, July 25, 1962 - 1 male (22.0 mm) (slide mount); 1 female ov (28.0 mm) (slide mount). Many specimens in CMN Canadian arctic collections; none from immediate study region.

Diagnosis Female (25.0-30.0 mm): Body large, laterally compressed. Peraeon and pleon segments with mid-dorsal ridge, increasingly elevated as carinations on peraeon segments 5-7, pleon 1-3, and urosome segment 1. Fused urosome segments 1 and 2 with low mid-dorsal and paired dorso-lateral ridges. Head: rostrum large ($> 1/2$ head length); anterior head lobe blunt, slightly emarginate. Eye small. Antenna 1, peduncular segments 1 & 2 subequal in length, setose posteriorly; accessory flagellum small, 1-segmented. Antenna 2 slightly the longer, peduncular segments heavily setose posteriorly.

Lower lip lacking inner lobes. Mandible: molar large, strong; spine row with 5-7 blades; left lacinia 5-dentate; palp normal, strong. Maxilla 1, inner plate with 7 apical setae; palp large, 2-segmented. Maxilla 2, inner plate with 1-3 stout plumose inner marginal setae. Maxilliped normal, palp strong.

Coxal plates 1-4 medium deep; coxa 1 shortest, directed anteriorly; coxa 3, lower margin anteriorly subacute. Coxa 5, anterior lobe broadly rounded. Gnathopods 1 & 2, very weakly sexually dimorphic; carpus and propod relatively short, deep, subequal in length. Peraeopods 3 & 4, segment 5 shorter than segments 4 & 6, dactyls stout. Peraeopods 5-7 (especially bases) somewhat dissimilar in form and size; segment 5 slightly shorter than corresponding segments 4 & 6. Peraeopods 5 & 6, lower hind low very small, not produced. Peraeopod 7, basis broad, postero-distal lobe rounded.

Pleon plates 1-3 broad, hind corners squared. Uropod 1, rami lanceolate, subequal. Uropod 2, outer ramus markedly shorter than inner. Uropod 3, rami narrowly lanceolate, $> 3\times$ peduncle; margins setose in female and male.

Telson lobes deeply separated, not diverging, each with apical and subapical spines. Coxal gills large, sac-like, on peraeopods 2-7, anterior gills (male) weakly pleated basally.

Distributional Ecology: Holarctic, in North America south to the Saguenay fiord in the east, and northern Bering Sea (Kotzebue Sound) in the west (Shoemaker, 1955) mainly in shallow coastal waters (0-50 m), along mixed stony and silty shores. The species has been recorded from the stomach

contents of various arctic shallow-water fishes, and from eider ducks, and bearded and ringed seals (Dunbar, 1954).

Taxonomic Commentary: *Atylus carinatus* is a distinctive species of the genus that exhibits several plesiomorphic character states. These include the accessory flagellum, strongly carinated dorsum of the posterior thoracic and abdominal segments, and the strongly marginally setose rami of uropod 3 (both sexes). As the type of the genus *Atylus*, its combination of character states separate it at genus level from *Anatylus pavlovi* Bulychova, 1955, and from *Nototropis smitti* (Goes, 1866) with which *A. carinatus* overlaps distributionally in high arctic and subarctic waters.

Atylus atlassovi (Gurjanova)
(Fig. 4)

Nototropis atlassovi Gurjanova, 1951: 690, figs. 77A, B.
Atylus atlassovi Mills, 1961: 19 (key only).—Barnard & Karaman, 1991: 262.

Material Examined: Bering Sea region: Amchitka Island, Constantine Harbor, C. E. O'Clair coll., Oct. 5, 1969 - July 14, 1970: 4 lots with 15 specimens, including males, females, and immatures; female ov. (20 mm) (slide mount) fig'd. St. Matthew Island, Walrus Cove, P. Slattery coll., June 29, 1983 - 1 male (28.0 mm) (fig'd) CMN collections.

Diagnosis. Female (20.0 mm): Body large compressed. Peraeon segments each with shallowly indented mid-dorsal ridge, slightly elevated to weak carinations on segments 6 & 7. Mid-dorsal carination weak on pleon segments 1-3, strong on urosome 1, medium on fused urosome segments 2 & 3. Head: rostrum large ($> 1/2$ head length); anterior head lobe broad, shallowly imarginate. Eye medium, vertically ovate. Antenna 1, peduncular segment 2 not longer than 1, hind margin thickly short-setose; peduncle 3 short; accessory flagellum minute. Antenna 2, peduncular segments 4 & 5 stout, anterior and posterior margins setose.

Lower lip lacking inner lobes. Mandible: molar strong; spine row with 8-10 blades and accessory setae; left lacinia 5-dentate; palp stout, setose. Maxilla 1, inner plate with 10-12 apical setae; palp stout, 2-segmented. Maxilla 2, inner plate with several inner marginal plumose setae. Maxilliped stout, palp segment 2 short.

Coxal plates 1-4 relatively broad, lower margins nearly straight; coxa 1 about as deep as 2, weakly directed forward. Coxa 5, anterior lobe acute below. Gnathopods 1 & 2 stout, 2 larger, moderately sexually dimorphic; propods relatively large, deep; carpus deep, shorter than respective propod. Gnathopod 1, propod with single distal row of pectinate setae; posterodistal angle with 3 rows (4-5 in male) of stout clasping spines. Gnathopod 2, propod, postero-distal angle with 2 rows (3 in male) of stout spines.

Peraeopods 3 & 4 stout, margins spinose; segment 5 small, much shorter than segments 4 & 6; dactyls short. Peraeopods 5-7, not markedly dissimilar; segment 5 much

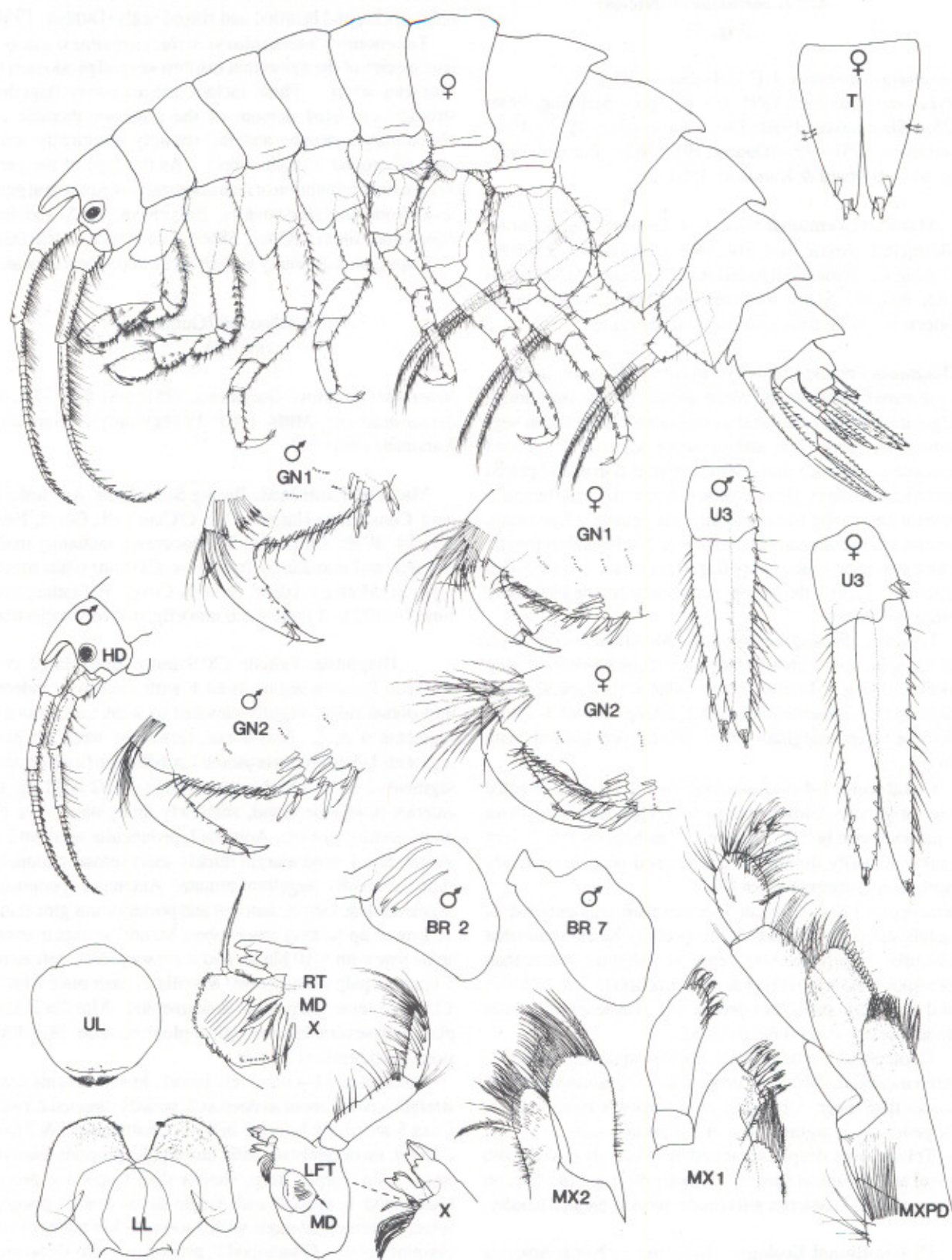


FIG. 3. *Atylus carinatus* (Fabr.). Female (28.0 mm), Male (22.0 mm) Slidre Fiord, Ellesmere I.

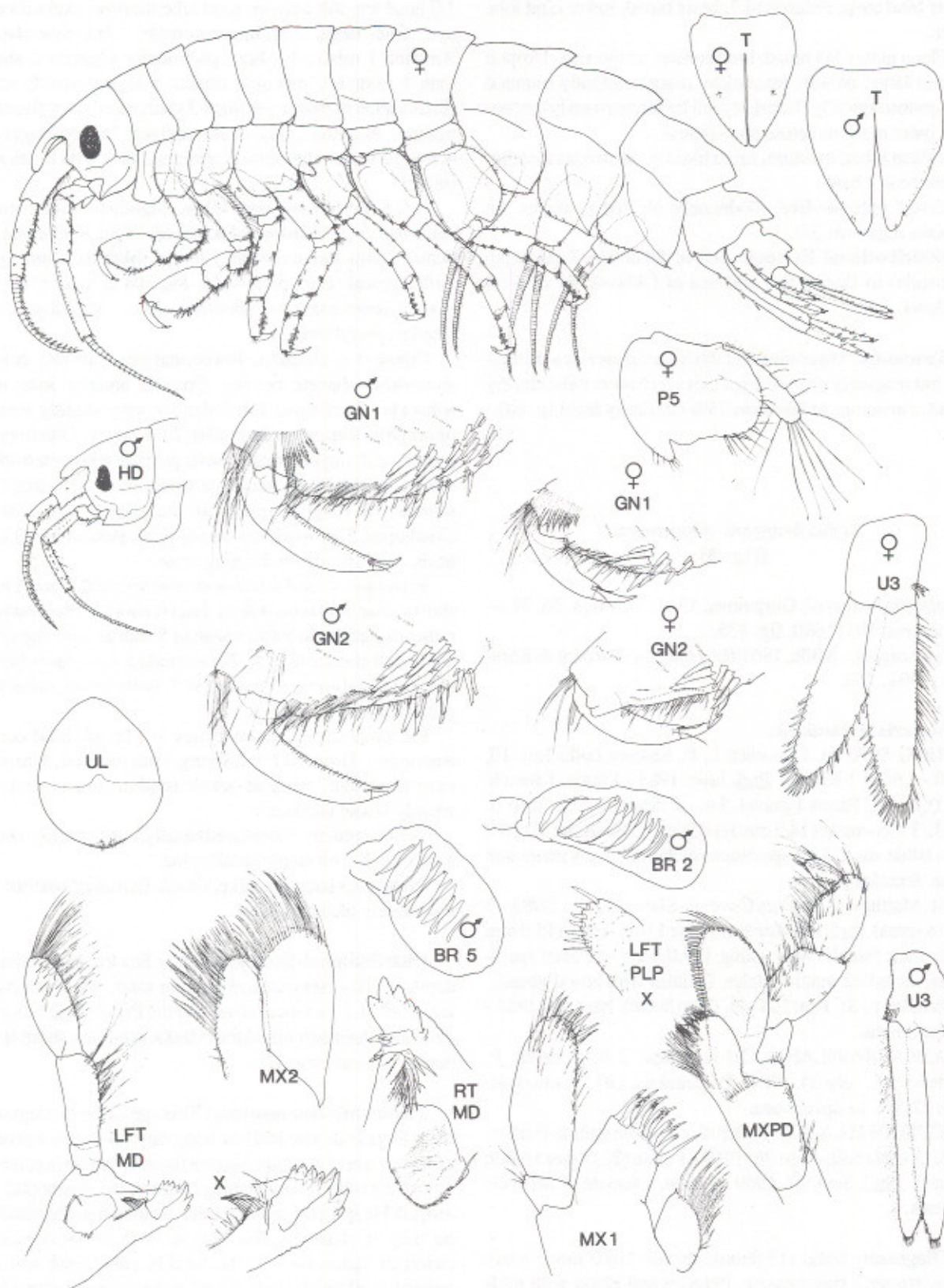


FIG. 4. *Atylus atlassovi* (Gurjanova). Female br. III (20.0 mm) Constantine Harbor, Amchitka I. Male (27.0 mm). St. Matthew I., Bering Sea.

shorter than segments 4 & 6; pereopod 5, basis with weak lower hind cusp. Pereopod 7, basis broad, lower hind lobe acute.

Pleon plates 1-3 broad, hind corners acuminate. Uropod 3, rami large, broadly lanceolate, margins bluntly rounded and spinose apically (female); rami larger, narrowly lanceolate, inner margins setose and spinose.

Telson lobes, medium, fused basally, narrowing distally, apices nearly bare.

Coxal gills sac-like, moderately pleated in males, on pereopod segments 2-7.

Distributional Ecology: Sea of Okhotsk (Kamchatka peninsula) to Bering Sea and Sea of Okhotsk, in subtidal shallows.

Taxonomic commentary: *Atylus atlassovi* is a distinctive but relatively primitive species. It clusters most closely with *A. carinatus*, at less than 75% similarity level (p. 60).

Atylus bruggeni (Gurjanova)
(Fig. 5).

Nototropis bruggeni Gurjanova, 1938: 325, figs. 36, 37.—Gurjanova, 1951: 680, fig. 475.

Atylus bruggeni Mills, 1961: (key only).—Barnard & Karaman, 1991: 263.

Material Examined:

BERING SEA: St. Lawrence I., P. Slattery coll., July 10, 1980 - 1 male 1 female. *Ibid.*, June, 1983 - 1 male, 1 female (br. I), 10 im. Panuk I., gravel, 5 m., P. Slattery coll., June 6, 1983, 3 lots - male (14.5 mm) (slide mt.); female br. II (16.0 mm) (slide mt.); 200+ specimens including many males and some females ov.

St. Matthew I., Walrus Cove, P. Slattery, June 27/83 - 3 lots (8 spms). *Ibid.*, Big Bite Bay, June 15/86 - male (15.0 mm) (slide mt.); female, with young (19.0 mm) +40 other specimens, including mature males, females with brood young.

Pribilof I., St. Paul I., D. B. Quayle coll. Nov. 21, 1965 - 11 specimens.

ALASKA MAINLAND: Off Icy Cape, 2 ft. in depth, P. Slattery coll., June 24, 1984 - 4 specimens. Off Wainwright, June 22/84 - 11 specimens.

ALEUTIAN ISLANDS: Amchitka I., Constantine Harbor, C. E. O'Clair coll. April 26, 1969 - 1 male (22.0 mm) (slide mount). *Ibid.*, Sept. 27, 1969 - 1 male, 1 female. CMN collections.

Diagnosis: Male (15.0mm), female (10.0 mm): Body large, strongly compressed. Peraeon and pleon with mid-dorsal ridge, elevated to medium strong carina on pereopod segments 6 & 7, and pleon segments 1-3. Urosome segments 1, and fused 2 & 3, each with bifid mid-dorsal carina,

posterior tooth much the stronger. Head: rostrum large (>> 1/2 head length); anterior head lobe shallow, excised below eye. Eyes large, oval, larger in male. Antennae slender. Antenna 1 relatively short, peduncular segment 2 shorter than 1 (female), subequal (male), margins weakly setose (brush setae in male); segment 3 short, accessory flagellum minute. Antenna 2, peduncular segment 5 much longer than 4, margins sparsely setose; segments 3 & 4 with brush setae (male).

Lower lip lacking inner lobes. Mandible: molar strong; spine row with 5 blades and accessory setae; left lacinia 4(5) dentate; palp slender, weakly setose. Maxilla 1, inner plate with 8 apical setae; palp stout. Maxilla 2, inner plate with several inner marginal pectinate setae. Maxilliped, palp slender, dactyl long.

Coxae 1-4 medium, lower margins various; coxa 3, anteriorly subacute below. Coxa 5, anterior lobe small subacute. Gnathopod 1 & 2 slender, very slightly sexually dimorphic, somewhat dissimilar, 2 the larger. Gnathopod 1, propod and carpus small, short; propod with antero-distal row of about 15-20 pectinate setae, and 3 clusters (2 in female) of longish spines at the postero-distal angle. Gnathopod 2, propod and carpus more slender and longer; basis, margins lined with long setae.

Pereopods 3 & 4 medium strong; segment 5 small, much shorter than segments 4 & 6; dactyls short. Pereopods 5-7 rather dissimilar in form; segment 5 shorter than segment 6 and much shorter than 4. Pereopods 5 & 6, bases lacking postero-distal lobes. Pereopod 7, basis broad, subacutely produced below.

Pleopods strong. Pleon plates 1-3 broad, hind corners acuminate. Uropods 1 & 2 strong, rami unequal. Uropod 3, rami lanceolate, margins setose (male), spinose and very weakly setose (female).

Telson ordinary, lobes fused basally, not diverging distally; apices each with single small spine.

Coxal gills large, sac-like, simple (female); anterior gills moderately pleated (male)

Distributional-Ecology: Bering Sea to Sea of Japan, in depths of 10 - 80 metres, mainly on sand. In North America, from St. Lawrence Island and the Pribilof Islands to the Aleutian chain and mainland Alaska, from the shore line to depths of more than 10 m.

Taxonomic commentary: This species is distinguished by its large body size and low body carinations, except on the urosome where it is bicusate on fused urosome segments 2-3. Among other distinguishing features, the gnathopods and uropod 3 (esp. in the male) are very setose, and the mandibular palp is slender. This species evinces plesiomorphic character states such as the weakly subchelate and long wristed gnathopods (both sexes) and strongly rostrate head. It also possesses apomorphic features such as the weakly 5-dentate mandibular left lacinia and weakly pleated coxal gills.

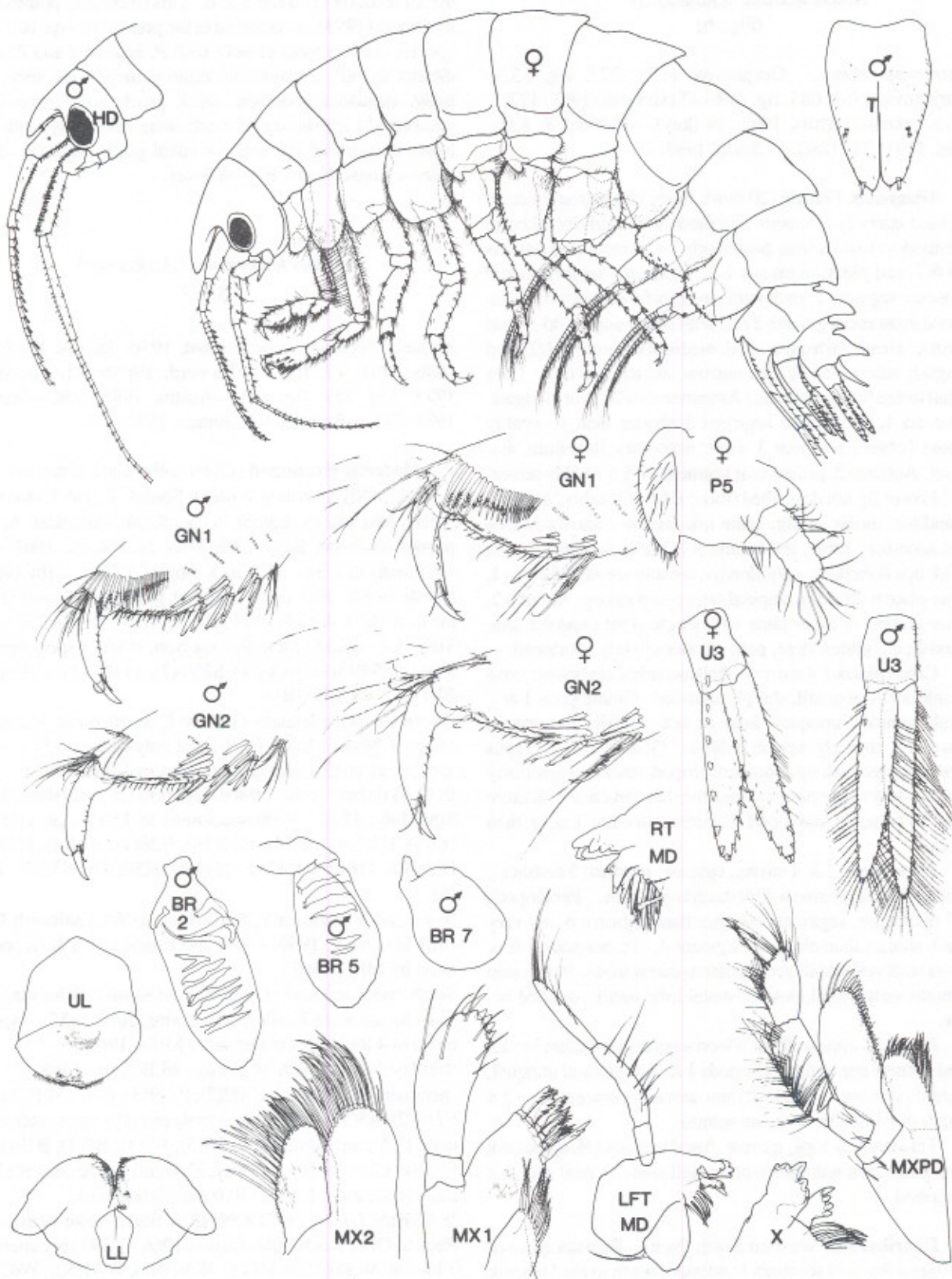


FIG. 5. *Atylus bruggeni* (Gurjanova). St. Matthew I., Bering Sea. Female ov (19.0 mm)
Male (15.0 mm).

Atylus ekmani (Gurjanova)

(Fig. 6)

Nototropis ekmani Gurjanova, 1938: 323, fig. 35.—Gurjanova, 1951: 685, fig. 473.—Tzvetkova, 1968: 172.

Atylus ekmani Mills, 1961: 19 (key).—Barnard & Karaman, 1991: 264 (list).—Okado, 1993: 7.

Diagnosis. Female (20 mm): Body large strongly compressed laterally. Peraeon and pleon with mid-dorsal ridge elevated to low carinae posteriorly on peraeonal segments (5) 6-7, and pleon segments 1-2. Pleosome segment 3 and urosome segment 1, each with strong bifid mid-dorsal tooth. Fused urosome segments 2 & 3 with single acute mid-dorsal carina. Head: rostrum arched, medium to large (~1/2 head length); anterior head lobe narrow, angles rounded. Eyes small to medium, subovate. Antennae slender, not elongate. Antenna 1, peduncular segment 2 shorter than 1, weakly setose behind; segment 3 short; accessory flagellum vestigial. Antenna 2, peduncular segments 4 & 5 weakly setose.

Lower lip not described (inner lobes probably lacking). Mandible: molar strong; spine row with 6-7 narrow blades and accessory setae; left lacinia 5 1/2 dentate; right lacinia bifid, tips flabellate; palp slender, weakly setose. Maxilla 1, inner plate with about 6 apical setae; palp strong. Maxilla 2, inner margin of inner plate with single stout plumose seta. Maxilliped, plates large, palp slender slightly shortened.

Coxal plates 1-4 narrow, shallow, subacute below; coxa 5, anterior lobe small, sharply rounded. Gnathopods 1 & 2 small, slender, unequal, little or not sexually dimorphic, bases not strongly setose behind. Gnathopod 1, carpus medium depth, as long as propod; propod, inner face anteriorly with 5-6 rows of pectinate setae, distal 2 rows each with more than 20 setae. Gnathopod 2, carpus slender, longer than propod.

Peraeopods 3 & 4 strong, spinose; segment 5 distinctly shorter than segments 4 & 6; dactyls medium. Peraeopods 5-7 dissimilar, segment 5 shorter than segment 6 and very much shorter than elongate segment 4. Peraeopods 5 & 6, bases with very small acute postero-distal lobes. Peraeopod 7 moderately broad, postero-distal lobe small, rounded below.

Pleopods undescribed. Pleon segments medium broad, hind corners mucronate. Uropods 1 & 2 stout, rami unequal, margins spinose. Uropod 3, rami subequal, lanceolate, ~2X length of peduncle, margins spinose.

Telson lobes long, narrow, fused in basal 1/4, apices not diverging, each with notch and small spine. Coxal gills not described.

Distribution: Western North Pacific: Russian coast of the Japan Sea and southern Hokkaido, north to the Okhotsk and western coast of the Bering Sea, at subtidal depths.

Taxonomic Commentary: Mills' key to species of *Atylus* includes *A. ekmani* erroneously in the group with 2

dorsal teeth on urosome 5 & 6. This oversight, pointed out by Okada (1993), is corrected in the present key (p. 10). The species clusters most closely with *P. bruggeni* and *P. levidensis* (p. 60). Features in common include the very thin body, carinated abdomen, weak gnathopods (propod of gnathopod 1 with heavy pectinate setae), unevenly scalloped lower margins of the anterior coxal plates, and the short, spinose uropod rami in both sexes.

Atylus levidensis J. L. Barnard

(Fig. 7)

Atylus levidensis J. L. Barnard, 1956: 38, pls. 13, 14.—Mills, 1961: 19, fig. 1.—Barnard, 1969b: 94.—Barnard, 1975: 340, 359, fig. 133.—Austin, 1985: 604.—Stauder, 1987: 382.—Barnard & Karaman, 1991: 264.

Material Examined (CMN collections, Ottawa):

S. E. ALASKA: Prince William Sound (Kayak I.) through outer coast (Sitka region), to southern Alexander Archipelago (Bronson Bay), ELB Stns, June-Aug., 1961 - 51 specimens in 8 lots, at: A3(1), A6(1), A22(11 - [including female br III (10.5 mm) (slide mt.), male (7.0 mm) (slide mt.)], A75(7), A80(5), A112(1), A151(5), A175 (20). ELB Stns., Lisianski Strait to Sitka region, 1980 - 8 specimens in 5 lots at: S4B3(1), S4B4(1), S8B1(2), S11B2(1), S19B1(3). BRITISH COLUMBIA:

Queen Charlotte Islands: Graham I., north, outer, and inner coasts + Masset Inlet, ELB Stns, July-Aug., 1957 - ~100 specimens in 13 lots (reported upon by Mills, 1961).

B. C. Mainland coast: Prince Rupert to Calvert Island, ELB Stns, July, 1964 - ~200 specimens in 15 lots, at: H1(19), H5(3), H7(50), H8(14), H12(16), H26(1), H33(1), H35(4), H39(50), H44(9), H47(6), H49(3), H50(10), H53(3), H65 (6).

North end Vancouver I., Cape Scott to Wickaninnish Bay, ELB Stns, July, 1959 - ~30 specimens in 6 lots (reported upon by Mills, 1961).

South end Vancouver I., outer coast south to Victoria, surf coast locations, in *Fkyllospadix* corals; July, 1955 - 7 specimens in 4 lots (reported upon by Mills, 1961).

Barkley Sound south to Sooke, ELB Stns, 1964-77 - 80 specimens in 17 lots, at: P702(2), P719(5), P710(5), P711(1), P714(2); B3(52) [including female ov (10.5 mm) (slide mt.), male (8.5 mm) (slide mt.)], B4(5), B5(3); B8(1), B19(18). Strait of Georgia, English Bay, ELB coll. - 1 female ov (12.0 mm) (slide mt.); 1 male (10.0 mm) (slide mt.).

WASHINGTON, OREGON: ELB Stns., Strait of Juan de Fuca to Otter Rock, July-August, 1966 - ~250 specimens in 7 lots, at: W30 (2), W34(13), W36 (62), W40(50), W42(6), W58(65), W60(48).

Coos Bay, Oregon, to Mendocino Co., CA, KE Conlan Stns, July, 1986 - ~50 specimens in 5 lots, including 1 female br. III (10.0 mm) (slide mt.); 1 male (7.0 mm) (slide mt.).

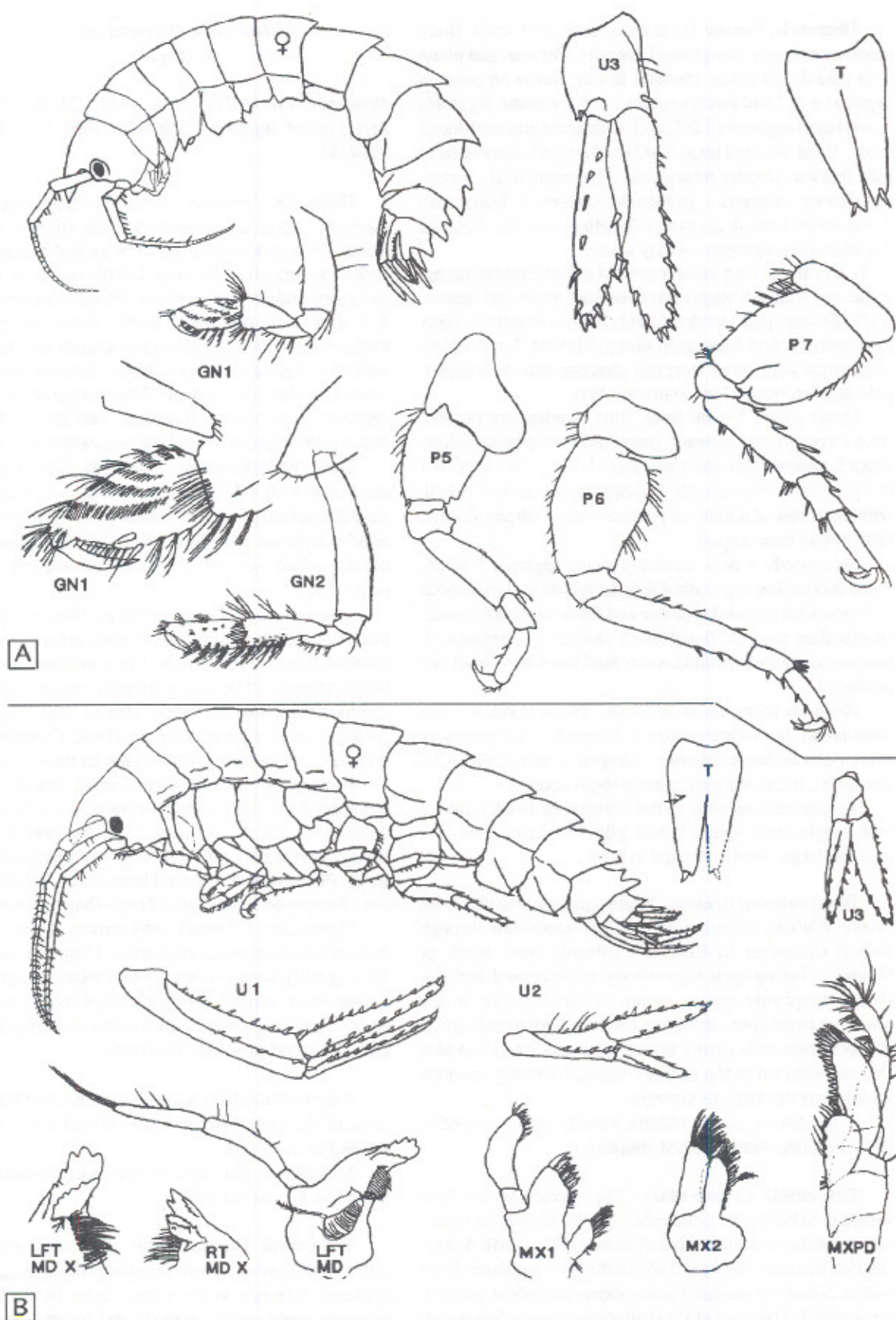


FIG. 6. *Atylus ekmani* Gurjanova A. Female (20.0 mm). Japan Sea. (modified from Gurjanova, 1951) B. Female (20.0 mm) (modified from Okada, 1993).

Diagnosis. Female (12.0 mm); male (7-8 mm): Body medium, strongly compressed laterally. Peraeon and pleon with mid-dorsal ridge, elevated to low carina on peraeon segment 6 & 7 and pleon segments 1-3. Urosome segments 1, and fused segments 2 & 3, each with acute elevated dorsal tooth. Head: rostrum large (~1/2 head length); anterior head lobe shallow, slightly emarginate. Eye small, oval. Antennae slender. Antenna 1, peduncular segment 2 shorter than 1, not setose behind; accessory flagellum minute. Antenna 2, peduncular segments weakly setose.

Lower lip lacking inner lobes. Mandible: molar strong; spine row with 4-5 blades and accessory setae; left lacinia 4 1/2 - dentate; palp slender, weakly setose. Maxilla 1, inner plate with 5 apical setae, palp strong. Maxilla 2, inner plate with single large inner marginal plumose seta. Maxilliped, palp slender, inner plate relatively short.

Coxal plates 1-4 medium, little overlapping basally; coxa 1 not directed forward; coxa 3 anteriorly acute below. Coxa 5, anterior lobe narrowly acute below. Gnathopods 1 & 2 not discernibly sexually dimorphic; propod short, small, with distal row of numerous pectinate setae; carpus slender, little longer than propod.

Peraeopods 3 & 4 relatively short; segment 5 small, much shorter than segments 4 & 6; dactyls short. Peraeopods 5-7 somewhat dissimilar in size and form; segment 5 small, shorter than segment 6 and much shorter than segment 4; bases moderately expanded, lower hind lobes very small, not produced.

Pleopods relatively short, weak. Pleon plates 1-3 medium broad, hind corners obtuse. Uropods 1 & 2 relatively short, outer ramus the shorter. Uropod 3, rami short (~2X peduncle), thick, margins spinose (both sexes).

Telson lobes narrow, slightly diverging distally, apices with single stout spine. Coxal gills on peraeopods 2-7, medium large, weakly pleated in male.

Distributional Ecology. North American Pacific: from Prince William Sound (S.E. Alaska) southward through British Columbia to Central California (rare south of Monterey) along open, high salinity, surf-exposed, bedrock shores, frequently among corals of *Phyllospadix*, in the lower intertidal zone. It was not taken in dredge hauls and is therefore ranked as a truly littoral zone species. It was also seldom collected in the summer-warm, relatively brackish shallows of the Strait of Georgia.

A. levidensus, and *A. tridens*, were the only two species of *Atylus* collected in modest abundance.

Taxonomic Commentary: The species shows little variation in body size or morphology throughout its range, but is endemic to cold-temperate waters of the North American Pacific coast. It clusters above the 75% similarity level with *A. ekmani* of western Pacific shores but only at the 65% level with *A. bruggeni* of the intervening Bering Sea region (Fig. 30, p. 60).

Atylus rylovi (Bulycheva)

(Fig. 8)

Nototropis rylovi Bulycheva, 1952: 221, fig. 21.

Atylus rylovi Barnard & Karaman, 1991: 264. Ishimaru, 1994: 42.

Diagnosis. Female ov. (11.0 mm): Body medium, compressed. Peraeon segments dorsally smooth. Pleon segments 1-3 with low mid-dorsal ridge that becomes a weak carina posteriorly. Urosome 1 with posterior mid-dorsal carination and pre-ceding notch. Fused urosome segments 2 & 3 with raised mid-dorsal tooth. Head: rostrum arched medium-large (@ 1/2 head length); anterior head lobe notched medially. Eyes medium, reniform. Antenna medium. Antenna 1, peduncular segment 2 not longer than 1 but ~3 X segment 3; accessory flagellum vestigial? Antenna 2, peduncular segments 4 & 5 strong, moderately setose.

Lower lip lacking inner lobes. Mandible: molar strong; spine row with 4-5 blades(?); lacinia not described; palp medium, apically setose. Maxilla 1 inner plate with 3 apical setae; palp broad. Maxilla 2, inner plate, inner marginal setae not described (several?). Maxilliped ordinary, plates and palp strong.

Coxal plates 1-4 medium large, hind margins setose, lower margins gently convex. Coxa 5, anterior lobe broadly rounded below. Gnathopods 1 & 2 medium slender, 2 the larger; margins of bases not strongly setose. Gnathopod 1, carpus not elongate, slightly shorter than propod; distal pectinate setae of propod not described. Gnathopod 2, propod and carpus longer and more slender than in gnathopod 1.

Peraeopods 3 & 4, segment 5 small, much shorter than segments 4 & 6; dactyls short. Peraeopods 5-7 not markedly differing in length; segment 5 shorter than 6 and much shorter than segment 4 (especially in peraeopod 6); dactyls short. Peraeopods 5 & 6, hind lobes small, not produced below. Peraeopod 7, hind lobe of basis sharply rounded below.

Pleon plates 1-3 broad, hind corners obtuse. Uropods 1 & 2 not clearly shown or described. Uropod 3, rami short (~2X length of peduncle), broadly lanceolate, margins spinose. Telson short (width 3/4 length), lobes short, fused basally, apices narrowing abruptly, each with 1-2 short spines. Coxal gills and brood plates not described.

Distributional Ecology: Peter-the-Great Bay, Russian coast of the Sea of Japan, in the littoral zone. Oviparous females in September.

Material of this species was not obtained at North American Pacific stations.

Taxonomic Commentary: Although originally assigned to the genus *Nototropis* (Bulycheva, *loc. cit.*), *rylovi* is clearly referable to the genus *Atylus* in the form of its antennae, peraeopods, uropods and telson. *Atylus rylovi* clusters with the *A. tridens* group, including *A. borealis*.

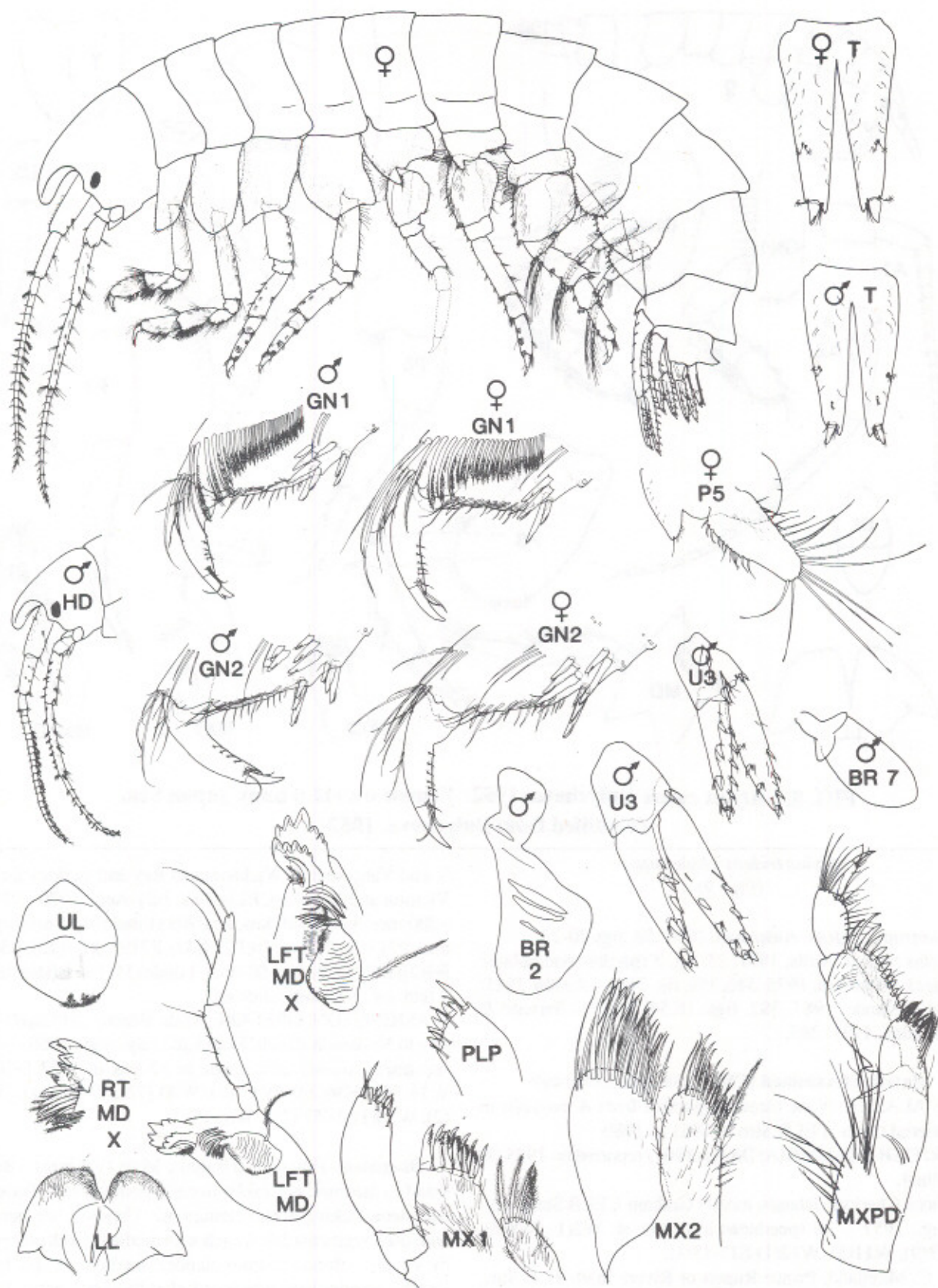


FIG. 7. *Atylus levidensus* Barnard. English Bay, B. C. Female ov (12.0 mm) Male (10.0 mm)

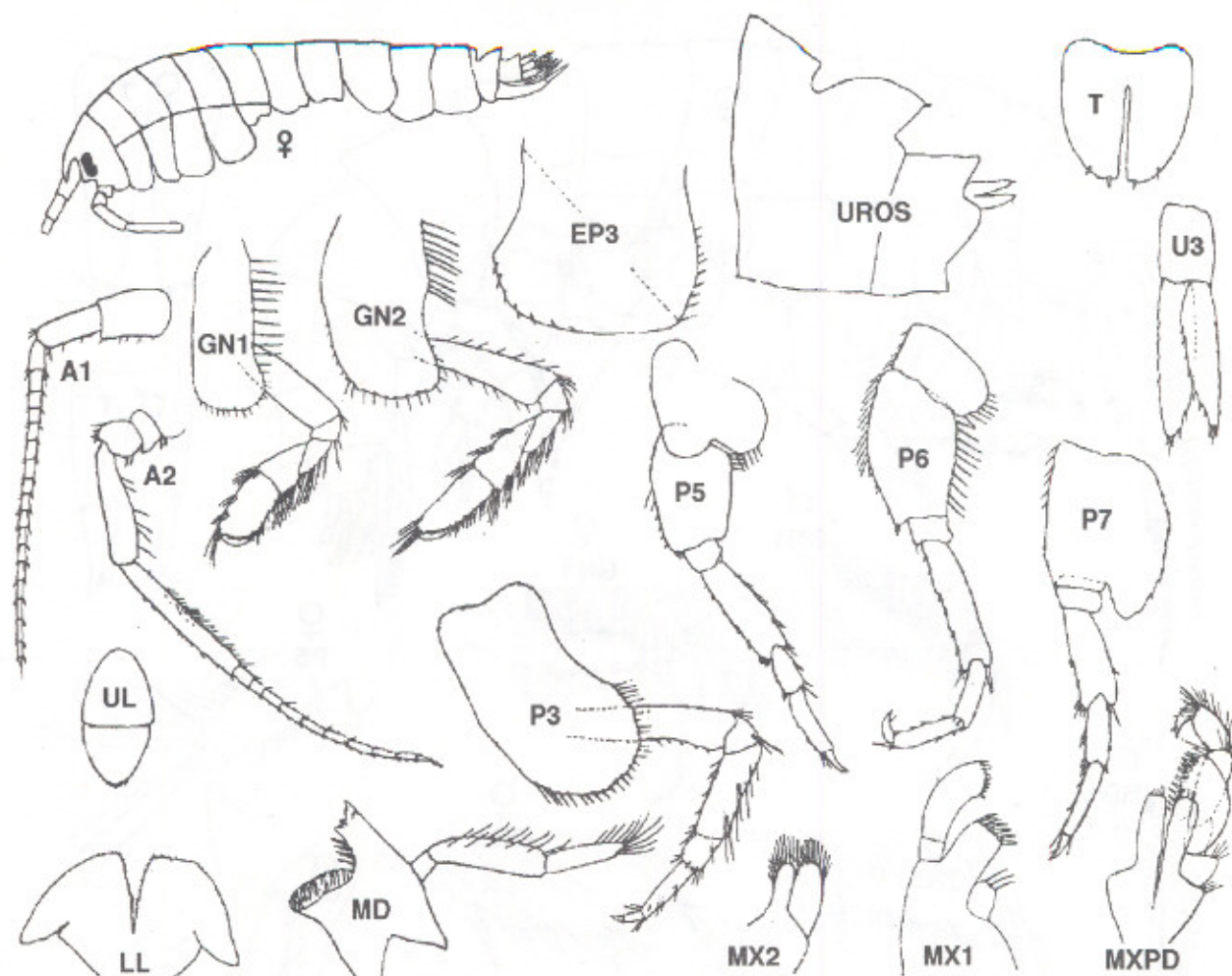


FIG. 8. *Atylus rylovi* Bulycheva, 1952. Female ov. (11.0 mm). Japan Sea.
(modified from Bulycheva, 1952)

Atylus tridens (Alderman)
(Fig. 9)

Nototropis tridens Alderman, 1936: 58, figs 20-25.

Atylus tridens Mills, 1961: 25, fig. 3 (partim- non-pelagic stage).—Barnard, 1975: 346, 359, fig. 216. —Austin, 1985: 604.—Staude, 1987: 382, figs. 18.54, 18.63.—Barnard & Karaman, 1991: 265.

Material Examined (CMN collections, Ottawa):

SE ALASKA: None clearly separable from *A. borealis* in material taken at ELB Stns in 1961 or 1980.

BRITISH COLUMBIA: [Mills (1961) reported on 1955-59 colls].

Queen Charlotte Islands, mostly Graham I, ELB Stns, July-Aug., 1957 - 20 specimens in 6 lots, at: W2(1), W8(3), W9(9), W11(5), W12(1) E17-18(1).

B. C. Mainland, Prince Rupert or Rivers Inlet, ELB Stns, July, 1964 - ~240 spms. in 11 lots, at: H1(3), H4(5), H7(15), H23(~80), H41(~85), H48(1), H49(2), H50(27), H52(2), H57(~30), H61(1).

S. end Vancouver I. Wickanninish Bay and Barkley Sd. to Victoria and Nanaimo, ELB Stns, July-Aug., 1970-1977 - ~200 specimens in 10 lots, at: P703 (1 male (11.5 mm) slide mt.), P713(1), P716(~50), P717(47), P719(2); B4(13), B5(2), B9(2); B5(31), B11a(~50 - incl. 1 male (11.0 mm)(slide mt.), 1 fem. ov (10.0 mm (slide mt)).

WASHINGTON, OREGON: Agate Beach, and Cape Flattery to Neskowin Beach, ELB Stns, July-Aug., 1966 - ~400 specimens, mostly immatures, in 17 lots at: W33 (~200), W34(54), W36(20), W39 (8), W40 (72), W42(11+), W46 (2), W50(1), W57 (24), W61 (5).

Diagnosis: Female (10.0 mm), Male (9.0 mm) : Body small to medium, not exceptionally compressed. Peraeon and pleon lacking dorsal carination. Urosome segment 1, and fused segments 2 & 3, each with medium tooth preceded by notch. Head: rostrum slender, medium (< 1/2 head length); anterior head lobe broad, slightly emarginate. Eyes very large, broad, subreniform (both sexes). Antennae long, medium strong. Antenna 1, peduncular segment 1 longer

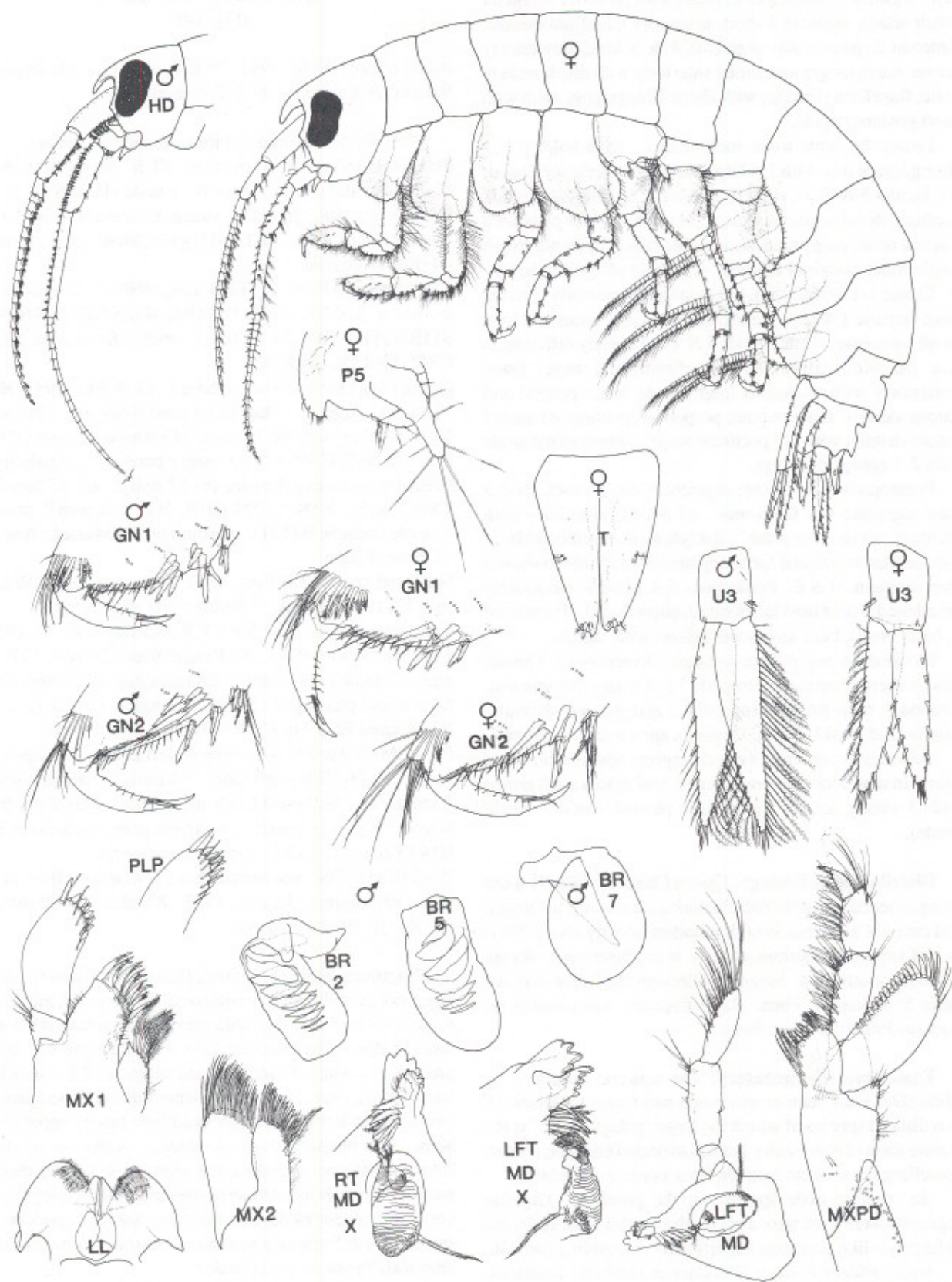


FIG. 9. *Atylus tridens* (Alderman) Wickanninish Bay, B. C. Fem. (10.0 mm) Male (11.0 mm).

than segment 2 (subequal in male, with posterior marginal brush setae); segment 3 short; accessory flagellum minute. Antenna 2, peduncular segments 4 & 5 long, moderately setose, much longer and armed anteriorly with brush setae in male; flagellum (female) with about 20 segments, each with short posterior spine.

Lower lip with weak inner lobes. Mandible: molar strong; spine row with 5-6 large blades and accessory setae; left lacinia 5-dentate, right lacinia bifid, tips flabellate; palp medium, distal segment setose. Maxilla 1, inner plate with 5 apical setae; palp broad, strong. Maxilla 2, inner plate with single inner marginal plumose seta. Maxilliped ordinary.

Coxae 1-4 broad, deep, lower margins variously convex; coxa 1 smallest, 4 largest and broadest. Coxa 5, anterior lobe small, subacute. Gnathopods 1 & 2 not grossly differing in size but moderately sexually dimorphic; bases lined posteriorly with numerous long simple setae; propod and carpus slender, not elongate; propod of gnathopod 1 armed antero-distally with 3-7 pectinate setae; postero-distal angle with 2-3 groups of spines.

Peraeopods 3 & 4 stout; segment 5 small, much shorter than segments 4 & 6 (in male, all armed posteriorly with plumose "swimming setae"); dactyls short. Peraeopods 5-7 dissimilar in size and form; segment 5 small, much shorter than segments 4 & 6. Peraeopods 5 & 6, basis moderately broadened, lower hind lobes small, unproduced. Peraeopod 7, basis broad, hind lobe acute below, with notch.

Pleopods strong, peduncles large. Pleon plates 1-3 broad, hind corners acuminate. Uropods 1 & 2 stout, rami unequal. Uropod 3, rami strongly lanceolate, margins setose (male) spinose and weakly setose (female), apex with 3 stout setae.

Telson ordinary; lobes not diverging, apices with small spine; in male, lobes more elongate and apices each armed with 3 strong setae. Coxal gills pleated, basally lobate (male).

Distributional Ecology: Queen Charlotte Islands south along outer coasts of British Columbia (few inner) to Oregon and central California, in high salinities (mostly above 29‰) in surf exposed situations, mainly in or above sand. Range extends south of *A. borealis*, although the latter was not taken S. of Juan de Fuca. Neither species was taken as far north as Prince William Sound.

Taxonomic Commentary: The material examined by Mills (1961) has been re-examined and found to consist of two distinct species of which the large "pelagic stage" is the mature form of *A. borealis*. It tends to occur in deeper, colder, upwelling areas, from Juan de Fuca north to SE Alaska.

In mature male specimens, the proximal flagellar segments were each armed posteriorly with what appeared to be calyx-like protozoa, superficially resembling calceoli.

Atylus tridens is more abundant at southerly locations, and in summer warm, brackish waters of the Strait of Georgia.

Atylus borealis, new species (Fig. 10)

Atylus tridens Mills, 1961: 29 & Table 2 (pelagic stage).—Barnard & Karaman, 1991: 265 (part)?

Material Examined (CMN collections, Ottawa):

SOUTHEASTERN ALASKA: ELB Stns, 1961: A16, MacArthur Bay, Kuiu I., June 6 - 1 male (17 mm), 9 imm.; A59, Dixon Hbr., greenling stomach contents, June 19 - 1 subadult male; A140, McLeod Harbor, Montague I., June 13 - 4 males 1 female, 1 im.

Chichagof I. to Kruzof I., ELB Stns, 1980: ~75 specimens in 8 lots at: S4B2(1), S4B3(1), S4B4(~40), S4B5(2), S4B6(1), S11B3(25), S18B1(2), S19B1(3 - incl. 1 female (br. III)). BRITISH COLUMBIA:

Queen Charlotte Islands, Graham I., ELB Stns, 1957: H14, Yakan Pt., Aug. 25 - Male (20.0 mm) Holotype, CMN Cat. No. NMCC1994-0384; 1 female (13.0 mm) Allotype, CMN Cat. No. NMCC 1994-0385; many paratypes, mostly juveniles, but including 4 males (to 17 mm), and 12 females, CMN Cat. No. NMCC1994-0386; H13 (Skonum R. mouth) - 1 male (subad); H11 (1/2 m. south of Old Masset), Aug. 27 - 1 male, 1 imm.

Mainland coast, ELB Stns, 1964: H10, Oval Bay, SW end, July 12, 1964 - 1 male, 5 females ov (slide mts.).

Vancouver Island, ELB Stn V4, Roller Bay, July 22, 1959 - 1 female, 3 imm; P703, McKenzie Beach, July 7, 1970 - 1 male 1 female (with young); Pachena Bay, P. Slaterry coll., from whale pits, April 15, 1982 - 6 males, 10 fem. (ov, Br. III), 8 imm; ELB Stn P708, July 17, 1970 - 1 male.

[Note: Mills listed to following material from B. C. (pelagic form): Sta F6 (Telegraph Cove, Victoria) - 2 pelagic males, 1 female ov (18.0 mm) (slide mt.); Sta. F8 (Garrison Bay, below) - 8 pelagic males (among eel grass, as below); Sta. H14 (Yakan Pt., QCI) - 5 males (as above)].

WASHINGTON: San Juan I., Stn F8, Garrison Bay, in eel grass, ELB colls., July 21, 1955 - 8 males (14-20 mm), 1 female (br. III) (slide mts.).

Diagnosis: Male (17.0 mm), Female (13.0 mm?): Body large, not exceptionally compressed. Peraeon lacking dorsal ridge or carination. Pleon with very low posterior mid-dorsal raised ridge. Urosome segment 1 with strong carination preceded by notch. Fused urosome segments 2 & 3 with low mid-dorsal carina. Head: rostrum medium, deflexed distally (< 1/2 head length); anterior head lobe broad, upper angle acute. Eye medium (large in male). Antennae medium strong. Antenna 1, peduncular segment 2 shorter than 1, weakly setose (brush-setose posteriorly in male); segment 3 very short; accessory flagellum minute. Antenna 2 peduncular segments 4 & 5 margins moderately setose (segments 3 & 4 anteriorly brush setose in male).

Lower lip, inner lobes lacking. Mandible: molar strong; spine row with 6 blades and accessory setae; left lacinia 5-dentate; right lacinia bifid-flabellate; palp medium, segment

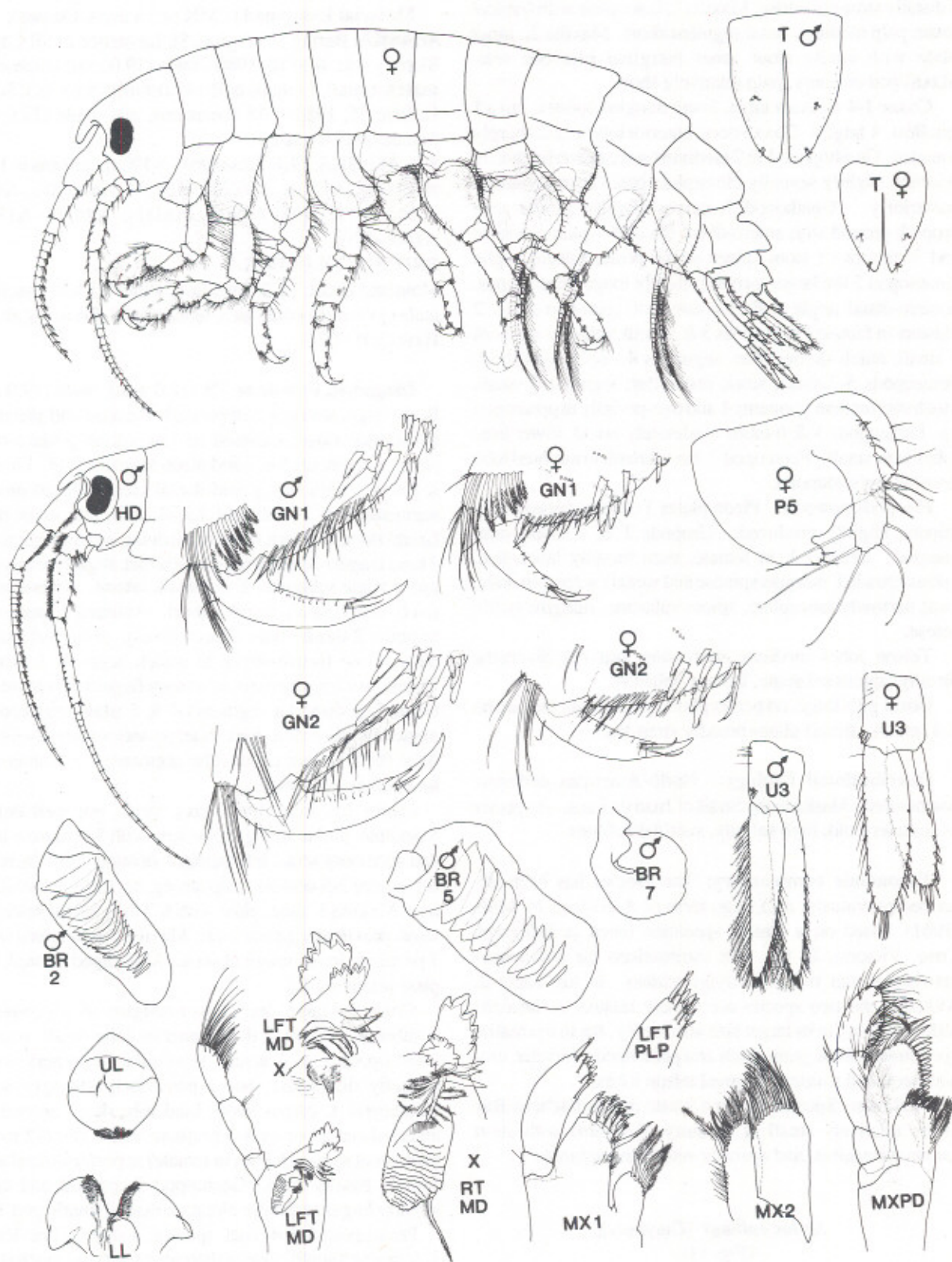


FIG. 10. *Atylus borealis*, new species. Yakan Pt. Q. C. I., B. C. Male (20.0 mm) Fem. (13.0 mm)

3 distally strongly setose. Maxilla 2, inner plate with 6 apical setae; palp medium, basal segment short. Maxilla 2, inner plate with single stout inner marginal plumose seta. Maxilliped ordinary, palp relatively short.

Coxae 1-4 medium large, lower margins convex; coxa 1 smallest, 4 largest. Coxa 5 deep, anterior lobe small, sharply rounded. Gnathopods 1 & 2 medium (more powerful than in *tridens*), slightly sexually dimorphic; bases strongly setose posteriorly. Gnathopod 1, carpus slightly shorter than propod; propod with antero-distal fan of 6-7 plumose setae and 3 clumps of stout spines at the postero-distal angle. Gnathopod 2 the larger; propod slightly longer than carpus, postero-distal angle with 3 clusters of spines in male, 2 clusters in female. Peraeopods 3 & 4 stout, spinose; segment 5 small, much shorter than segments 4 - 6; dactyls short. Peraeopods 5-7 short, stout, dissimilar; segment 5 small, much shorter than segments 4 and 6 (especially in peraeopod 6). Peraeopods 5 & 6 bases moderately broad, lower hind lobes very small. Peraeopod 7, basis broad, lower hind lobe deep, sharply rounded.

Pleopods powerful. Pleon plates 1-3, hind corners acuminate, slightly produced. Uropods 1 & 2 stout, rami unequal. Uropod 3, in female, rami broadly lanceolate, apices rounded, margins spinose and weakly setose; in male, rami narrowly lanceolate, apices subacute, margins richly setose.

Telson lobes medium, narrowing and not diverging distally, apices subacute, lacking spine(s).

Coxal gills large, on peraeopods 2-7, strongly pleated on 2-4 (male). Brood plates broadly strap-like.

Distributional Ecology: North-American endemic; southeastern Alaska to the Strait of Juan de Fuca. A species of summer-cold, high salinity, subtidal habitats.

Taxonomic commentary: The species has been described previously, as a large form of *A. tridens*, by Mills (1961), based on a female specimen taken at Telegraph Cove, Victoria, B. C. He summarized the differences between it and the true *Atylus tridens* in his Table 2. Although the two species are closely related, *A. borealis* differs not only in its larger size at maturity, but in its smaller eyes, more robust gnathopods and peraeopods, broader uropod rami, and shorter, unarmed telson lobes.

Variants: Specimens from whale pits in Pachena Bay were relatively small at maturity (6-9 mm) with short antennal flagellae, and sparsely setose and spinose.

Atylus collingi (Gurjanova)
(Fig. 11)

Nototropis collingi Gurjanova, 1938: 328, fig. 38.—Gurjanova, 1951: 638, fig. 476.
Atylus collingi Mills, 1961: 23. (part).—Austin, 1985: (part).—Barnard & Karaman, 1991: 263.

Material Examined (CMN collections, Ottawa):

ALASKA: Bering Sea region. St. Lawrence I., SE Cape, P. Slattery coll. July 10, 1980 - male (19.0 mm) (slide mt.), 1 male subadult, 1 female br II. (17.0 mm) (slide mts.); St. Paul I., June 25, 1983 - 18 specimens, incl. male (11.0 mm), female ov (9.0 mm).

S.E. ALASKA: ELB Stns, 1961 - ~190 specimens in 13 lots at: A8(1), A12(1), A30(32), A33(5), A43(~85), A48(1), AA63(1), A71(2), A80(6), A81(1), A84(1), A133(1), A140(~55).

BRITISH COLUMBIA:

Mainland Coast: ELB Stns, July, 1964: H13(11 - including male (11.0 mm) (slide mt.), female ov (8.5 mm) (slide mt.), H16(1), H17(21).

Diagnosis. Female br. III (17.0 mm), male (19.0 mm): Body large, strongly compressed. Peraeon and pleon with mid-dorsal ridge, elevated to low carina posteriorly on peraeon segments 6 & 7 and pleon segments 1-3. Urosome segment 1 with strong mid-dorsal crest. Fused urosome segments 1 & 2 with mid-dorsal crest, and weak dorso-lateral ridges. Head: rostrum medium, nearly straight (~ 1/3 head length); anterior head lobe broad, slightly emarginate, upper angle subacute. Eyes small, lateral. Antennae relatively short, stout; flagella short. Antenna 1, peduncular segment 2 shorter than 1 (both sexes), posteriorly moderately setose (brush-setose in male); segment 3 medium; flagellum 12-segmented; accessory flagellum minute. Antenna 2, peduncular segments 4 & 5 stout, surfaced with numerous clusters of short setae; posterior margin with short setae (both sexes); peduncular segments 4 & 5 stouter and more elongate in male.

Lower lip, inner lobes very weak, not well defined. Mandible: molar strong; spine row with 5-6 narrow blades and accessory setae; left lacinia 5-dentate, right lacinia bifid, apices 3-5 dentate; palp strong, segment 3 distally setose. Maxilla 1, inner plate with 6-7 long apical setae; palp stout, proximal segment short. Maxilla 2, inner plate with 6-7 pectinate inner marginal setae. Maxilliped normal, inner plate relatively tall.

Coxae 1-4 large, deep, lower margins of 1-3 convex, of 4 subacute. Coxa 5 deep, anterior lobe small, rounded. Gnathopods 1 & 2 stout, subsimilar (2 larger), weakly sexually dimorphic, bases posteriorly strongly setose. Gnathopod 1, carpus short, hind lobe deep; propod with antero-distal group of 4-5 pectinate setae, and 6-7 rows of short stout spines (5 rows in female) at postero-distal angle; dactyls basally thick. Gnathopod 2, propod and carpus slightly larger and more elongate than in gnathopod 1.

Peraeopods 3 & 4 stout, spinose, 4 slightly heavier than 3; segment 5 small, shorter than segment 6 and much shorter than 4; dactyls medium (> 1/2 length segment 6). Peraeopods 5 - 7 dissimilar; segment 5 small, shorter than segment 6 and much shorter than segment 4. Peraeopods 5 & 6, bases moderately broadened, hind lobes moderate, not produced. Peraeopod 7, basis, postero-distal lobe rounded below.

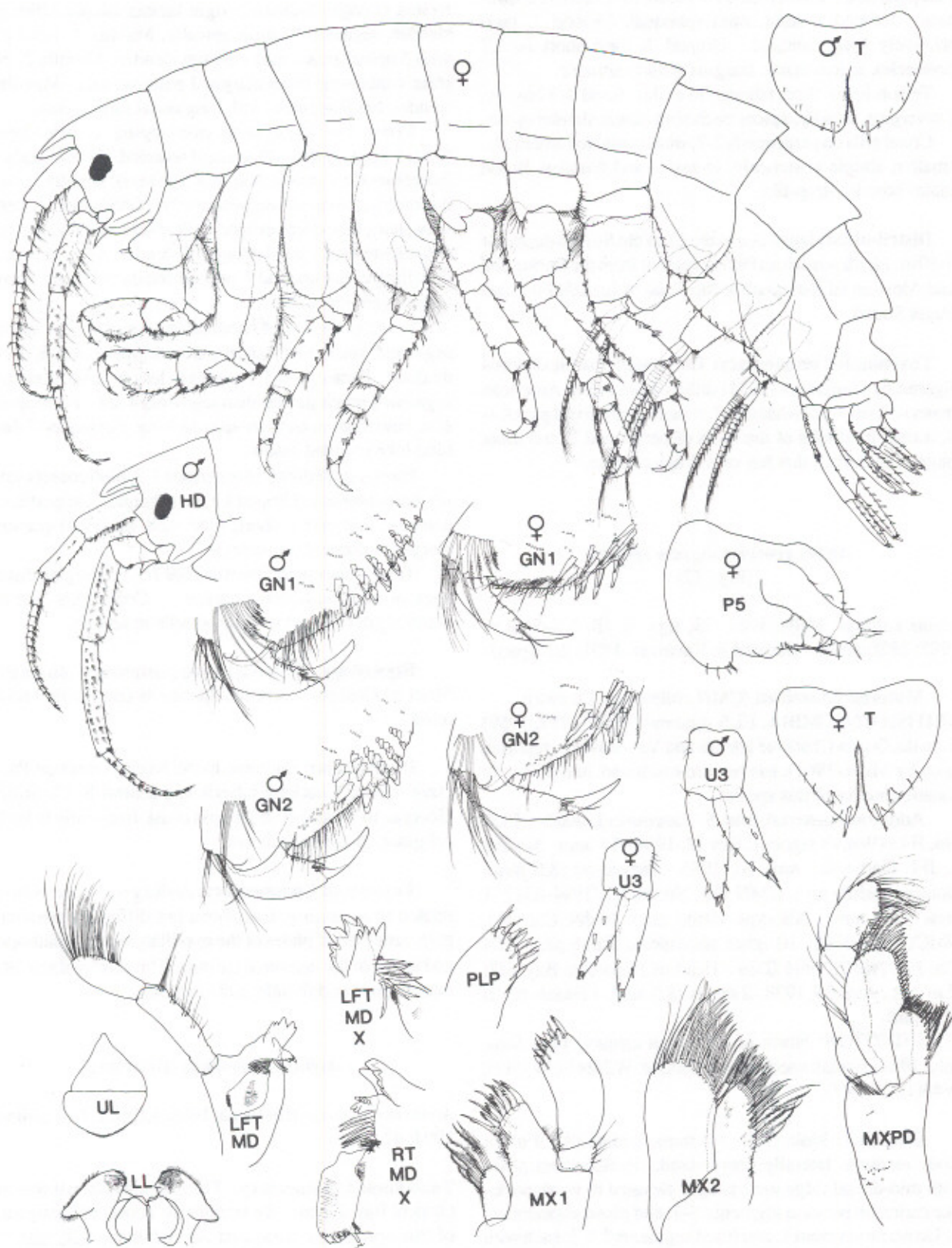


FIG. 11. *Atylus collingi* (Gurjanova) St. Lawrence I. Bering Sea.
Male (19.0 mm). Femalebr. III (17.0 mm).

Pleopods stout. Pleon plates 1-3 broad, hind corners acuminate. Uropod 1 stout, rami subequal. Uropod 2, rami relatively long, unequal. Uropod 3, rami short ($< 2X$ peduncle), apices acute, margins weakly spinose.

Telson lobes short (shorter in male), fused $1/3$ basally, converging distally, apices each with single slender spine.

Coxal gills on pereopods 2-7, weakly pleated anteriorly, smaller, simple posteriorly, in males and females. Brood plates broadly strap-like.

Distribution: Japan Sea to the Chukchi Sea, in depths of 3-10 m. North American Pacific region: from the Bering Sea and Aleutian Islands south to the Strait of Juan de Fuca and Puget Sound.

Taxonomic Commentary: The western Pacific material figured by Gurjanova (1951) differs from North American material in its somewhat smaller, more acute coxal plates 1-4, deeper hind lobe of the basis of pereopod 7, and inner plate of maxilla 2 that has only 3 apical setae.

Atylus georgianus, new species
(Fig. 12)

Atylus collingi Mills, 1961: 23, figs. 2, 4B A.—Stauder, 1987: 382(part?).—Barnard & Karaman, 1991: 263 (part).

Material Examined (CMN collections, Ottawa): BRITISH COLUMBIA: ELB material (1955, 1957, 1959) from the Queen Charlotte Islands and Vancouver I., reported upon by Mills (1961), has been re-examined, and proves to consist entirely of this species.

Additional material, from S. Vancouver I. includes: ELB Stn. H43 (Witty's lagoon), July 28, 1964 - 17 imm. Saturna I., JFL Hart coll., Aug. 26, 1955 - female ov (8.0 mm), Holotype (slide mt.), CMN Cat. No. NMCC1994-0387; 1 male (7.5 mm), Allotype (slide mt.), CMN Cat. No. NMCC1994-0388; 10 other specimens, Paratypes CMN Cat. No. NMCC1994-0389. Head of Departure Bay, JFL Hart coll., Aug. 25, 1938 - 2 males (8.0 mm), 1 female br. III (9.0 mm).

WASHINGTON: North of Columbia estuary, ELB Stns, July, 1966 - 6 small specimens in 4 lots at: W26b(1), W35(2), W40(1), W46(2).

Diagnosis: Male (7.5 - 8.0 mm); female (8 - 9 mm): Body medium, laterally compressed. Peraeon and pleon with mid-dorsal ridge increasingly elevated to weak posterior carina on pereopod segments 6-7, and pleon segments 1-3. Urosome segment 1, and fused segments 2 & 3, each with single elevated rounded tooth. Head: rostrum short, extending little beyond weakly acute anterior head lobe. Antennae medium, much as in *A. collingi*, but shorter and less setose.

Lower lip, inner lobes small. Mandible: molar medium; spine row with 6-7 slender blades and accessory setae; left

lacinia strongly 5-dentate; right lacinia simply bifid; palp slender, segment 3 setose apically. Maxilla 1, inner plate with 5 apical setae; palp medium slender. Maxilla 2, inner plate with single inner marginal plumose seta. Maxilliped slender, basal segment with long distal facial setae.

Coxae 1-4 large, deep, overlapping, rounded below. Coxa 5 deep, anterior lobe small rounded. Gnathopods 1 & 2 medium (less strong than in *A. collingi*); slightly sexually dimorphic; bases setose posteriorly. Gnathopod 1, carpus very short, lobe deep; propod with antero-distal group of 3-5 pectinate setae, and 4 groups of slender spines at postero-distal angle. Gnathopod 2, propod and dactyl larger, heavier than in gnathopod 1.

Pereopods 3 & 4 medium strong, margins spinose; segment 5 small, much shorter than segments 4 & 6, dactyls medium. Pereopods 5-7 medium, less spinose, dissimilar; segment 5 much shorter than segments 4 & 6. Pereopods 5 & 6, hind lobes of basis small or lacking. Pereopod 7, basis, hind lobe rounded below.

Pleopods medium. Pleon plates 1-3, hind corners squarish, not acuminate. Uropod 1, rami subequal. Uropod 2, rami unequal. Uropod 3 short, rami $\sim 2X$ length of peduncle, margins spinose (both sexes).

Telson lobes short, fused in basal $1/3$, converging distally, apex of each with slender spine. Coxal gills sac-like, anterior gills pleated in male, simple in female.

Etymology: The trivial name *georgianus* alludes to the Strait of Georgia where the species is commonly encountered.

Distribution: Endemic to the North American Pacific coast: Queen Charlotte Islands and central B. C., Strait of Georgia, to Washington-Oregon coast, frequently in beds of eel grass, in sandy shallows.

Taxonomic Commentary: *Atylus georgianus* is closely related to *A. collingi* Gurjanova but differs in mandibular palp, armature of plates of the maxillae, size of gnathopods, and shape of the uropodal carinae. The subequal size of the mature male and female is distinctive.

Atylus occidentalis Hirayama

Atylus occidentalis Hirayama, 1986: 4, figs. 1-4.—Ishimaru, 1994: 42.

Taxonomic Commentary. The original material was from Otsuchi Bay, Japan. We tentatively accept the designation of this species by Hirayama and Ishimaru (*loc. cit.*) as a member of the genus *Atylus* (*sens. str.*). Regrettably, however, we have seen no material of this species, and the literature is not available to us. The species is therefore not included to the regional key (p. 10) or analysis of species relationships (p. 58-59).

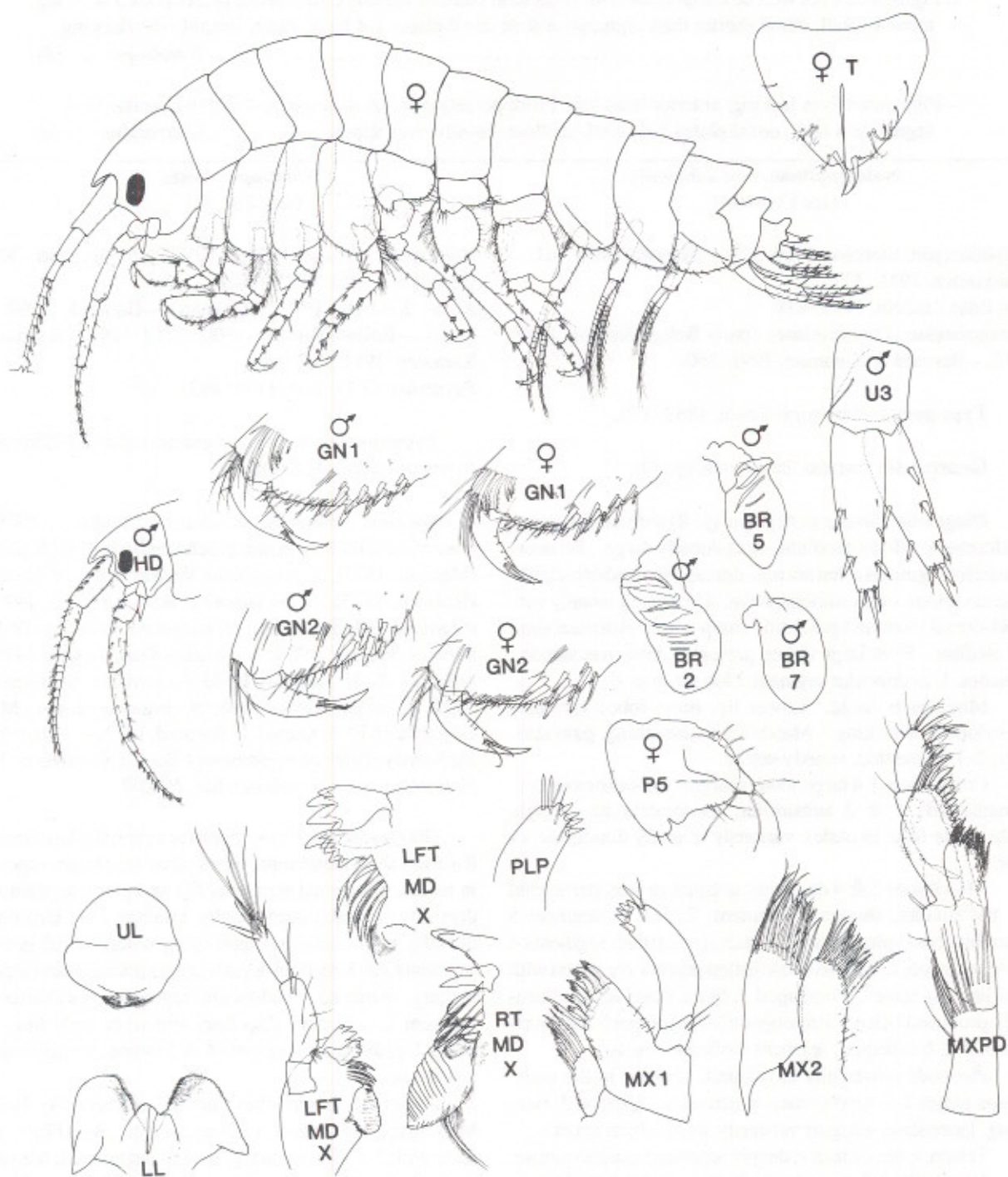


FIG. 12. *Atylus georgianus*, new species. Saturna I., B. C. Fem. ov. (8.0 mm) Male (7.5 mm)

KEY TO GENERA OF NOTOTROPIINAE

1. Pigmented eyes well developed; anterior head lobe blunt or slightly emarginate; peraeopods 3 & 4, segment 4 small, much shorter than segments 4 & 6; coxal plates 1-4 large, deep, strongly overlapping . . .

..... *Nototropis* (p. 28)

—Pigmented eyes lacking; anterior head lobe bifid; peraeopods 3 & 4, segment 4 slightly shorter than segments 4 & 6; coxal plates 1-4 small, shallow, basally overlapping only *Aberratylus* (p. 30)

Nototropiinae, new subfamily (see Fig. 1(b))

Atylidae (part) Stebbing, 1906: 329.—Barnard, 1969a: 161.—Gurjanova, 1951: 327.
Atylidae Lincoln, 1979: 438.
Dexaminidae (Dexamininae) (part) Bellan-Santini, 1982: 212.—Barnard & Karaman, 1991: 260.

Type genus: *Nototropis* Costa, 1853: 170.

Genera: *Aberratylus*, new genus (p. 30).

Diagnosis: Similar to Atylinae (p. 8) with the following differences: Body medium, occasionally large. Peraeon, posterior segments often not mid-dorsally toothed or carinate. Pleon various, often smooth above. Urosome 1 usually with mid-dorsal tooth and preceding sharp notch. Rostrum short to medium. Eyes large (when present). Antennae slender; antenna 1, peduncular segment 2 longer than 1.

Mouthparts basic. Lower lip, inner lobes variously developed, or lacking. Mandible, molar strong, palp slender, 2-3 segmented, weakly setose.

Coxal plates 1-4 large, lower margins smooth or rounded. Gnathopods 1 & 2 subsimilar, moderately to strongly subchelate (esp. in male), variously sexually dimorphic, or not.

Peraeopods 3 & 4 distinctly unequal in size, peraeopod 4 the smaller, shorter in segments 2, 5 & 6; segment 5 variable, but typically small, much shorter than segments 4 & 6; segments 2, 4, and 6 (male) often posteriorly armed with "swimming setae". Peraeopod 5, basis, posterior lobe usually produced below. Peraeopods 5-7, segment 5 not shortened, 5 & 6 subequal; segment 4 often elongate.

Pleopods powerfully developed, stronger in the male. Pleon plates 1-3, hind corners mucronate. Uropod 3, rami long, lanceolate, margins variously setose (both sexes).

Telson, lobes ordinary, deeply separated, apices spinose.

Coxal gills 2-5 strongly phylloform or dendritic (especially in male), simple on peraeopods 6 & 7. Brood plates medium to strap-like.

Taxonomic Commentary: The subfamily overlaps with subfamily Atylinae in a number of character states, but can be distinguished reliably by the combination of character states illustrated in Fig. 1(b) (p. 6).

Nototropis Costa (see Fig. 13)

Nototropis Costa, 1853: 170.—Stebbing, 1906: 329.—Gurjanova, 1951: 680 (most).
Atylus Lincoln, 1979: 438 (part).—Barnard, 1969: 163 (part).—Bellan-Santini, 1982: 212 (all).—Barnard & Karaman, 1991: 262 (part).
Paratylus G. O. Sars, 1895: 462.

Type species: *Nototropis guttatus* Costa 1953 (= *Nototropis spinulicauda* Costa).

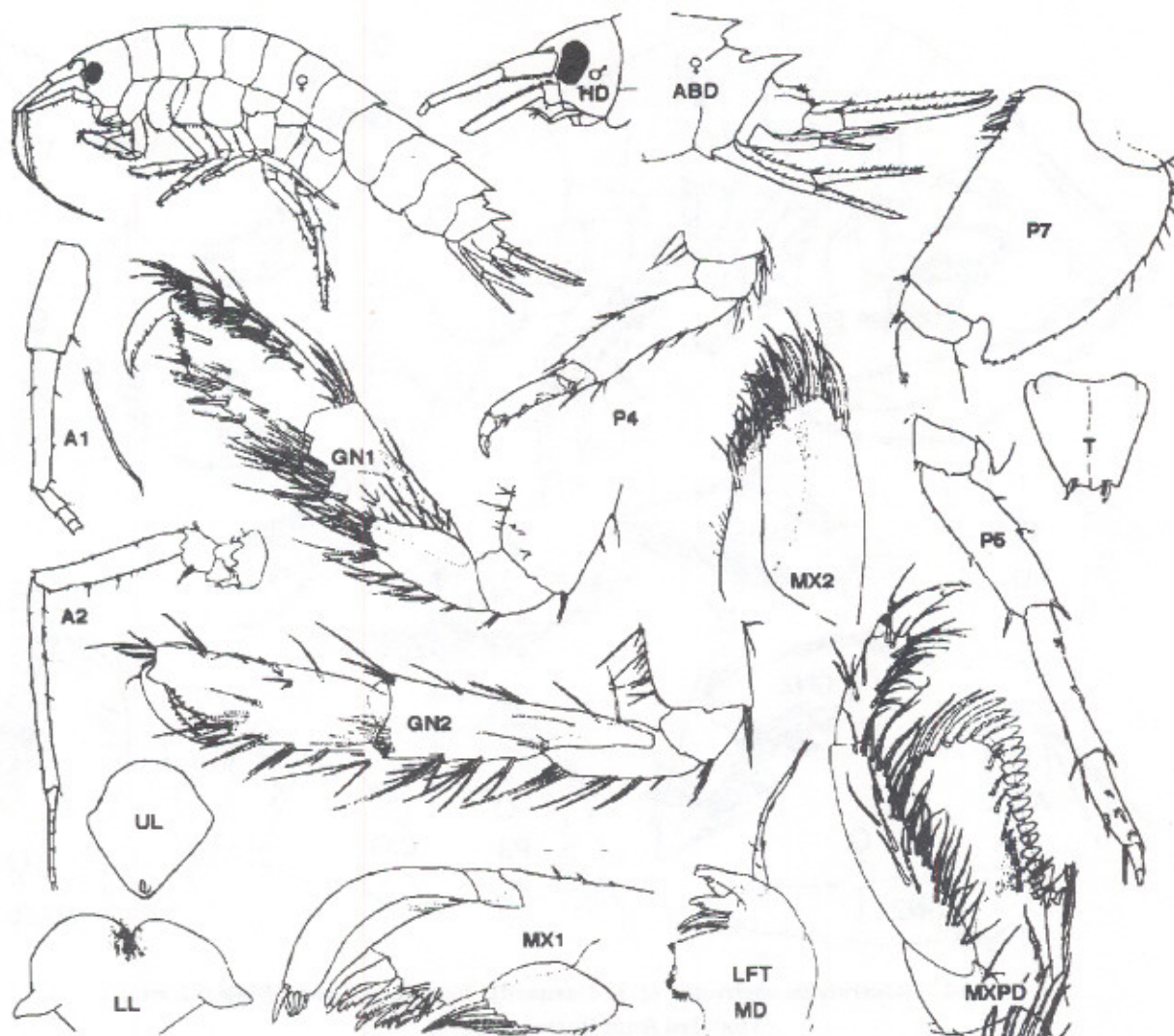
Species: *Nototropis brevitaris* Ledoyer, 1979; *N. comes* Giles, 1888; *N. dentatus* Schellenberg, 1931; *N. falcatus* (Metzger, 1871); *N. granulatus* Walker, 1904; *N. homochir* (Haswell, 1885); *N. massiliensis* Bellan-Santini, 1975; *N. megalops* (Moore, 1984); *N. melanops* Oldevig, 1959; *N. minikoi* Walker, 1905; *N. nordlandicus* Boeck, 1871; *N. reductus* K. H. Barnard, 1930; *N. serratus* Schellenberg, 1925; *N. smitti* Goes, 1866; *N. swammerdami* Milne-Edwards, 1830; *N. taupo* J. L. Barnard, 1972; *N. urocarinatus* McKinney, 1980; *N. vedlomensis* Bate & Westwood, 1863; *Nototropis* sp. (= *N. guttatus* Irie, 1965)?

Diagnosis: Small to medium (occasionally large) atyids. Rostrum short to medium. Eyes often very large, especially in males. Peraeonal segments 5-7 and pleon segments 1-3 dorsally smooth, occasionally mucronate. Urosome 1 dorsally with carina and preceding notch; fused urosome segments 2 & 3, median dorsal carina variously developed or lacking. Antenna 1, peduncular segment 2 not shorter than segment 1; accessory flagellum minute or scale-like. Antenna 2, peduncular segments 4 & 5 strong, weakly marginally setose.

Lower lip, inner lobes various, occasionally lacking. Mandible, palp slender, (2)3-segmented. Maxilla 1, inner plate with 3-8 apical setae; palp (1)2-segmented; Maxilla 2, inner plate with stout inner marginal plumose seta. Maxilliped, palp normal, slender.

Coxal plates 1-4 regular, medium, lower margins rounded or straight, not acute. Coxa 5 anterolobate, lobes rounded below. Gnathopods 1 & 2 variously sexually dimorphic; carpus and propod relatively short, subequal in length; propod of gnathopod 1 with antero-distal clusters of pectinate setae.

Peraeopod 4 distinctly smaller or shorter than peraeopod



**FIG. 13. *Nototropis guttatus* Costa, 1853. Female (9-11 mm)
Mediterranean Sea. (modified from Bellan-Santini, 1982)**

3; segment 5 (in both) usually much shorter than segments 4 & 6; in male, anterior and posterior margins of segments 4-6 and distal portion of segment 2 often lined with "swimming" setae. Pereopods 5-7 not strongly dissimilar in size and form; bases, hind lobes strong, often acute below; segment 5 large, usually longer than segments 4 and/or 6; dactyls medium.

Pleopods strong. Pleon side plates, hind corners acuminate, not produced. Uropod 1 rami subequal in length. Uropod 2, outer ramus the shorter. Uropod 3, rami strong, lanceolate, subequal, margins setose in male, spinulose and or setose in female. Telson regular, lobes medium, apices obliquely truncate.

Brood plates medium to broad, margins simple-setose. Anterior (pereopods 2-5) coxal gills strongly dendritic or phylliform, especially in the male.

Variables: Rostrum large (*N. smithi*); anterior peraeonal

segments dorsally carinate (*N. homochir*); gnathopod 2, propod and dactyl elongate (*N. taupo*, *N. smithi*); pereopod 7, basis, postero-distal lobe weak or lacking (*N. homochir*, *N. melanops*, *N. smithi*); urosome weakly or not carinate (*N. megalops*); telson lobes short (*N. smithi*). Further generic and/or subgeneric categories may yet be required to reflect the taxonomic significance of these variables.

Distributional Commentary: Component species of *Nototropis* are strongly tethyan in distribution, occurring mainly in tropical and warm temperate coastal waters of the Mediterranean-Caribbean Atlantic and Indian oceans, with a few morphologically aberrant outliers in arctic and austral regions. To date, one species, implausibly identified as the Mediterranean species *N. guttatus* Costa by Irie (1965) represents a questionable record of this genus and subfamily from Japanese waters. None was identified in present study material from the North American Pacific region.

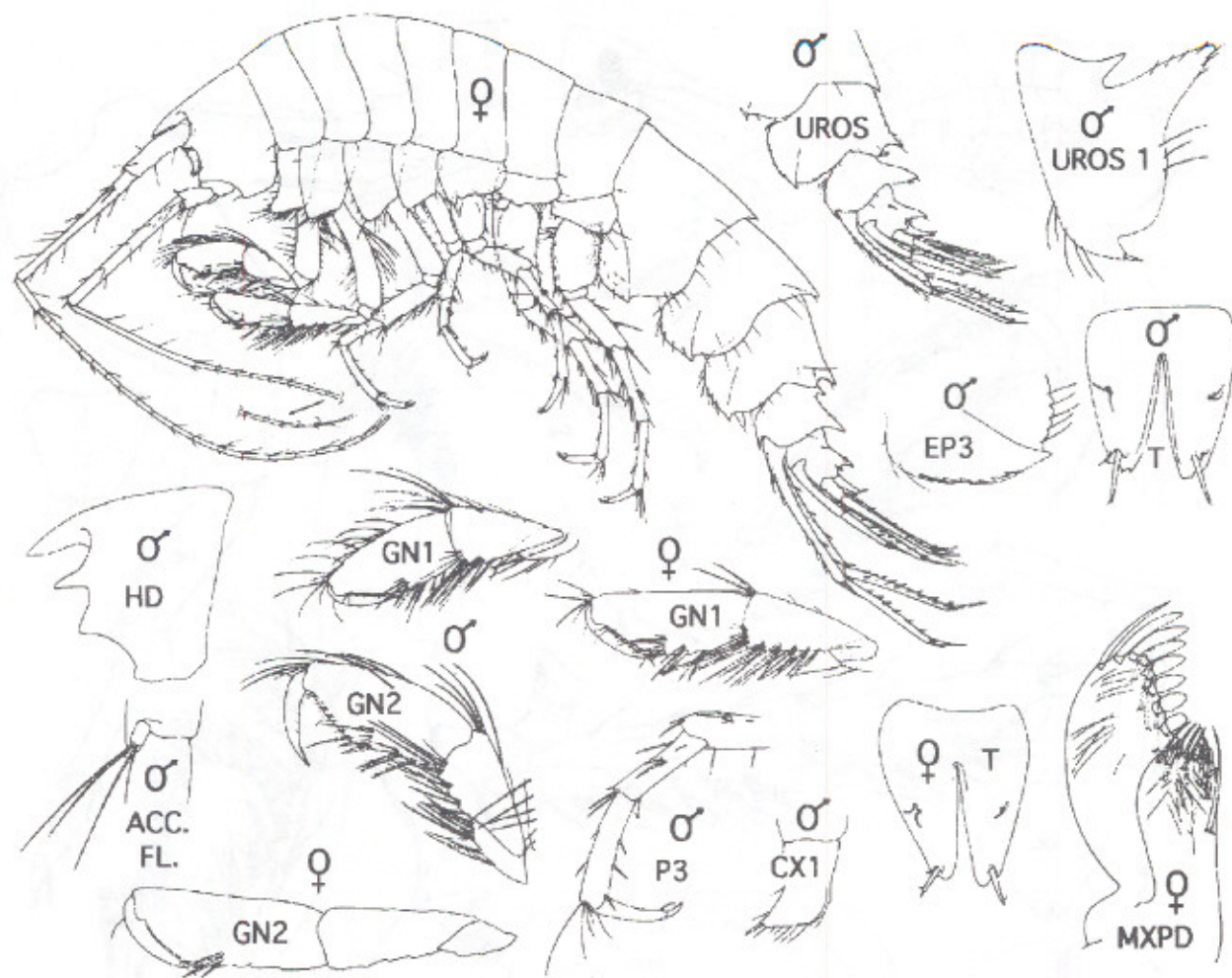


FIG. 14. *Aberratylus aberrantis* (J. L. Barnard). Female (4.8 mm) Male 6.1 mm)
(Modified from Barnard, 1973)

Aberratylus, new genus
(see Fig. 14)

Atylus J. L. Barnard, 1962: 69 (part.);

Lepechinella J. L. Barnard, 1973: 7 (part).—Barnard & Karaman, 1991: 261(part).

Type species: *Atylus aberrantis* J. L. Barnard, 1962: 69, figs. 66, 67.—Barnard, 1964: 40, fig. 32. (= *Lepechinella aberrantis* J. L. Barnard, 1973: 7, figs.).

Diagnosis: Rostrum medium. Peraeon segments 1-6 smooth dorsally. Peraeon segment 7 and pleon segments 1-3 posterodorsally mucronate. Urosome segment 1 mid-dorsally with two teeth and intermediate notch; fused urosome segment 2 & 3 with prominent carina. Anterior head lobe weakly bifid. Pigmented eyes lacking. Antenna 1, peduncular segment 2 slender, elongate; accessory flagellum 1-segmented. Antenna 2 peduncular segments slender, elongate, weakly setose.

Lower lip, inner lobes present. Mandible, palp weak, segment 3 short; axillal, palp broad, 2-segmented; inner

plate with 2 apical setae. Maxilla 2, inner plate with single inner marginal plumose seta. Maxilliped, palp and plates normal.

Coxal plates 1-4 small, basally contiguous or overlapping, lower margins entire, denticulate, not acute or processiferous. Coxa 5 anterolobate, anterior lobe various. Gnathopods 1 & 2 subsimilar (2 larger), very weakly sexually dimorphic; carpus and propod medium, palms very oblique.

Peraeopods 3 & 4 slender, but relatively short; segment 5 slightly shorter than segments 4 & 6; dactyls medium. Peraeopods 5-7 dissimilar in size; bases little broadened, lower hind lobes small, not acute; segments 4 & 5 subequal in length, both shorter than 6; dactyls medium (= segment 6).

Pleon plates 1-3 broad, hind corners mucronate. Uropods slender; uropod 1, rami subequal; uropod 2, outer ramus the shorter. Uropod 3, rami slender lanceolate, inner margins weakly setose.

Telson ordinary, lobes medium length, not diverging, apices with single spine.

Coxal gills not described (probably pleated). Brood plates not described.

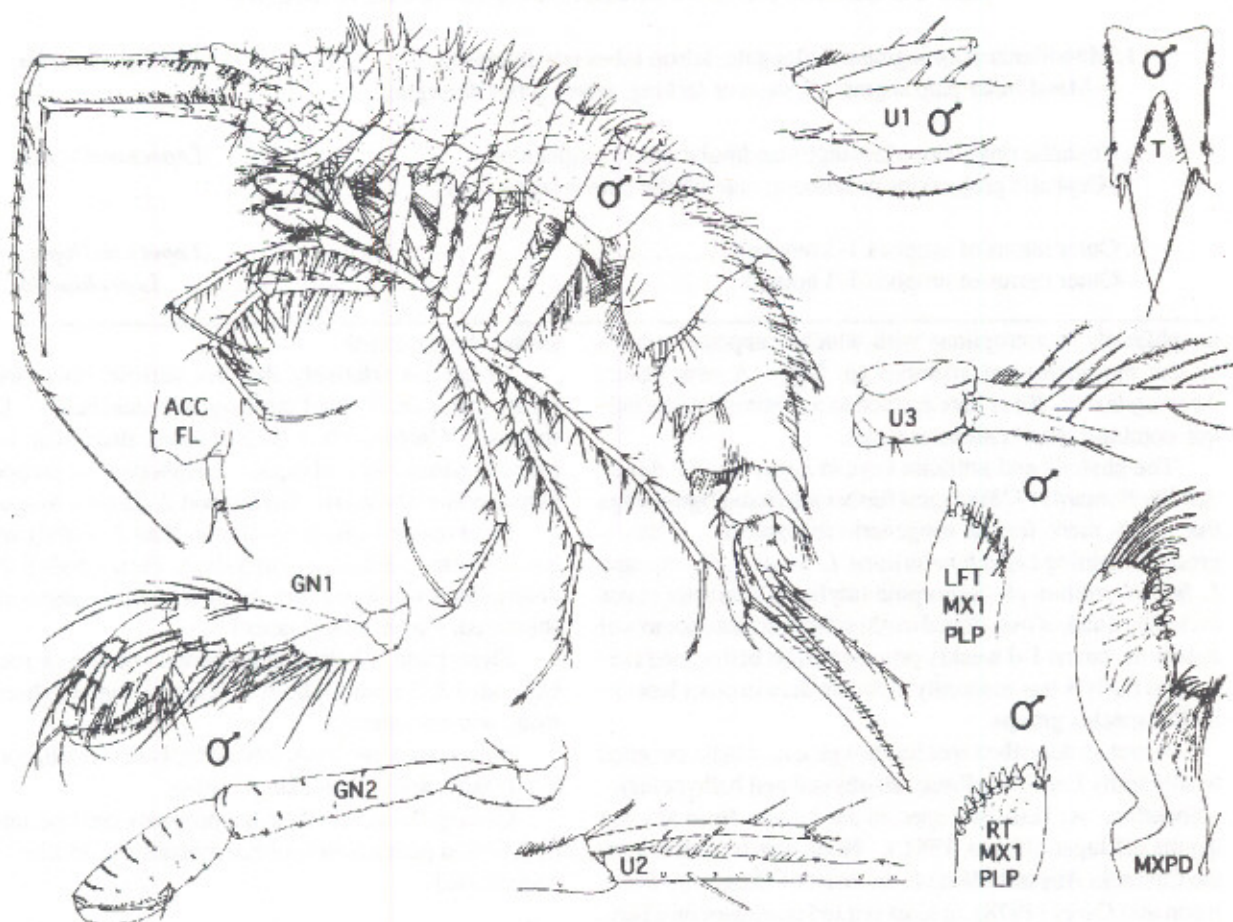


FIG. 15. *Lepechinella uchu* J. L. Barnard Male (7.6 mm) Female (8.5 mm)
(modified from Barnard, 1973)

Lepechinellinae Schellenberg (revised status)
(see Figs. 1(c); 15)

Lepechinellidae: Schellenberg, 1926: 344.—Gurjanova, 1951: 674.—Barnard, 1969: 286.—Bousfield, 1982: 278.
Dexaminidae (part): Barnard, 1973a: 5.—Bellan-Santini, 1982: 212.—Barnard & Karaman, 1991: 260.

Diagnosis: Peraeon (variously) and pleon segments mid-dorsally processiferous and/or densely covered with small setae and spines. Urosome 1 with single mid-dorsal process. Urosome 2 & 3 not carinate. Head, rostrum spike-like; antero-lateral head margin acutely bifid. Pigmented eyes lacking. Antennae long, slender (both sexes); antenna 1 the shorter; peduncular segment 2 long; accessory flagellum present, 1-segmented.

Lower lip, inner lobes well developed. Mandible, palp slender, reduced. Maxilla 1, palp 2-segmented, distal segment broadened. Maxilla 2, inner plate narrow. Maxilliped, outer plate large; inner plate arched disto-medially; palp 4-segmented.

Coxa plates 1-7 narrow, small, separated basally. Coxae 1-4 incised or acute, often bilobate below; coxa 1 distinctly

deepest; coxa 5 small, anterolobate. Gnathopods slender, weakly or not subchelate; carpus (especially in gnathopod 2) longer than propod.

Peraeopods 3-7 slender, elongate. Peraeopods 4 slightly shorter than 3, mainly in basis; segment 5 little (or not) shortened; dactyls elongate (often >segment 6). Peraeopods 5-7 subsimilar in form and size; bases sublinear.

Pleopods slender, elongate. Uropods 1 & 2 slender. Uropod 1, outer ramus enlarged. Uropod 2; outer ramus not shortened. Uropod 3, rami sublinear, rod-like, margins sparsely (or not) setose, apices spinose.

Telson lobes short to medium, fused basally by more than 1/3; apices usually diverging, distally narrowing. Coxal gills pleated.

Genera: *Lepechinella* (*Lepechinella*) Stebbing, 1908: 191; *Paralepechinella* Pirlot, 1933: 161; *Lepechinelloides* Thurston, 1980: 81; *Lepechinellopsis* Ledoyer, 1982: 365.

Taxonomic and Biogeographic Commentary: "*Lepechinella*" *aberrantis* J. L. Barnard, 1964, is basically an atylid that exhibits a very few "lepechinellid" character states (of head, peraeopods 3 & 4, and uropod 3). Accordingly, the species is here reassigned within family Atylidae

KEY TO GENERA AND SUBGENERA OF LEPECHINELLINAE

1. Mandibular palp segment 3 elongate, telson lobes not diverging. *Paralepechinella*
—Mandibular palp segment 3 short or lacking, telson lobes diverging 2.
2. Cephalic projections lacking; mandibular palp 1-segmented *Lepechinelloides*
—Cephalic projections prominent; mandibular palp 3-segmented 3.
3. Outer ramus of uropods 1-3 reduced *Lepechinellopsis*
—Outer ramus of uropods 1-3 normal *Lepechinella*

to subfamily Nototropiinae with which it appears to have closest morphological affinities (p. 28). A new genus, *Aberratylus* (p. 30) is here erected to accommodate its unique combination of character states.

The phyletic and artificial keys to *Lepechinella* developed by Barnard (1973) suggest further internal subgroupings that might merit formal subgeneric recognition. Thus, a group containing *Lepechinella auca*, *L. cachi*, *L. cetrata*, and *L. huaco* exhibits plesiomorphic (atylinid) character states including a lack of mid-dorsal teeth on three or more peraeonal segments, coxae 1-4 weakly processiferous below, and peraeopod dactyls less markedly elongate than in other lepechinellid species groups.

About 35 described species, in 4 genera, can be assigned to subfamily Lepechinellinae, all abyssal and bathypelagic-epibenthic. At least two species are known from abyssal depths off Japan (Gamo, 1981). None was recorded from the Cascadia Abyssal Plain off the coast of Oregon by Dickinson and Carey (1978), at least not in significant numbers, and none was found in CMN amphipod material from other North American Pacific deep-water sites.

Subfamily Anatylinae Bulycheva (Revised status) (Figs. 1(d); 16)

Anatylidae Bulycheva, 1955: 205.

Dexaminidae (Anatylinae) Barnard, 1969a: 202.

Dexaminidae (part) Barnard & Karaman, 1991: 260.

Type Genus: *Anatylus* Bulycheva 1955: monotypy.

Genera: *Kamehatylus* Barnard, 1970b: 93 (revised status).

Diagnosis: Small atylids (3-6 mm). Body thin. Peraeon segments 5-7 and pleon segments 1-3 variously carinate or smooth mid-dorsally. Rostrum weak. Anterior head lobe shallowly excavate. Pigmented eye small. Antennae 1 & 2 short; flagella short, 4-5 segmented. Antenna 1, peduncular segments 1 & 2 subequal; accessory flagellum vestigial. Antenna 2, peduncular segments weakly setose.

Lower lip, inner lobes very weak. Mandible: molar trending to reduction; left lacinia 4-dentate; palp lacking. Maxilla 1, inner plate with 2 apical setae; palp slender. Maxilla 2, inner plate slender. Maxilliped normal; palp

strong, 4-segmented.

Coxae 2-4 relatively shallow, narrow, lower margins gently excavate. Coxa 1 tapering, subacute below. Coxa 5 shallow. Gnathopods 1 & 2 slender, dissimilar in size; propod, palms very oblique. Gnathopod 1, propod and carpus relatively short. Gnathopod 2, carpus elongate.

Peraeopods 4 distinctly shorter than 3, mainly in basis and segments 5 & 6; segment 5 short. Peraeopods 5-7 bases dissimilar, lower lobes very small or lacking; segment 5 not shortened, longer than segment 6.

Pleon plate 1-3 deep, hind corners obtuse or rounded. Uropods 1 & 2, rami medium, unequal. Uropod 3 short, rami stout, margins spinose.

Telson medium short, lobes deeply separated, converging distally, apices with single spine.

Coxal gills undescribed, but probably sac-like, unmodified. Brood plates undescribed, probably strap-like. Male undescribed.

Taxonomic and Distributional Commentary: To date, the subfamily contains but 5 described species in two closely similar genera, of Indo-Pacific and western Pacific affinities, as detailed below. The present study restores the group to the subfamily status proposed initially by Barnard (1969a).

Anatylus Bulycheva

Anatylus Bulycheva, 1955: 205, original designation.—Barnard, 1969a: 202 (in Dexaminidae)

Atylus (part) Barnard & Karaman, 1991: 262.

Type Species: *Anatylus pavlovski* Bulycheva, 1955.

Diagnosis: Body medium, thin. Peraeon, segments 5-7 and pleon segments 1-3 carinate along dorsal margin (cf. *Atylus levidensis*). Rostrum medium strong. Anterior head lobe shallowly excavate. Pigmented eye small, round. Antennae 1 & 2 short; flagella 4-5 segmented. Antenna 1, peduncular segments 1 & 2 subequal; accessory flagellum vestigial. Antenna 2, peduncular segment 5 longest.

Lower lip, inner lobes present, moderate. Mandible: palp lacking; molar reduced, weakly triturative. Maxilla 1, inner plate fused to base of outer plate, with 2 apical setae; palp 2-segmented. Maxilla 2, inner plate small, lacking strong plumose inner marginal seta. Maxilliped normal, palp

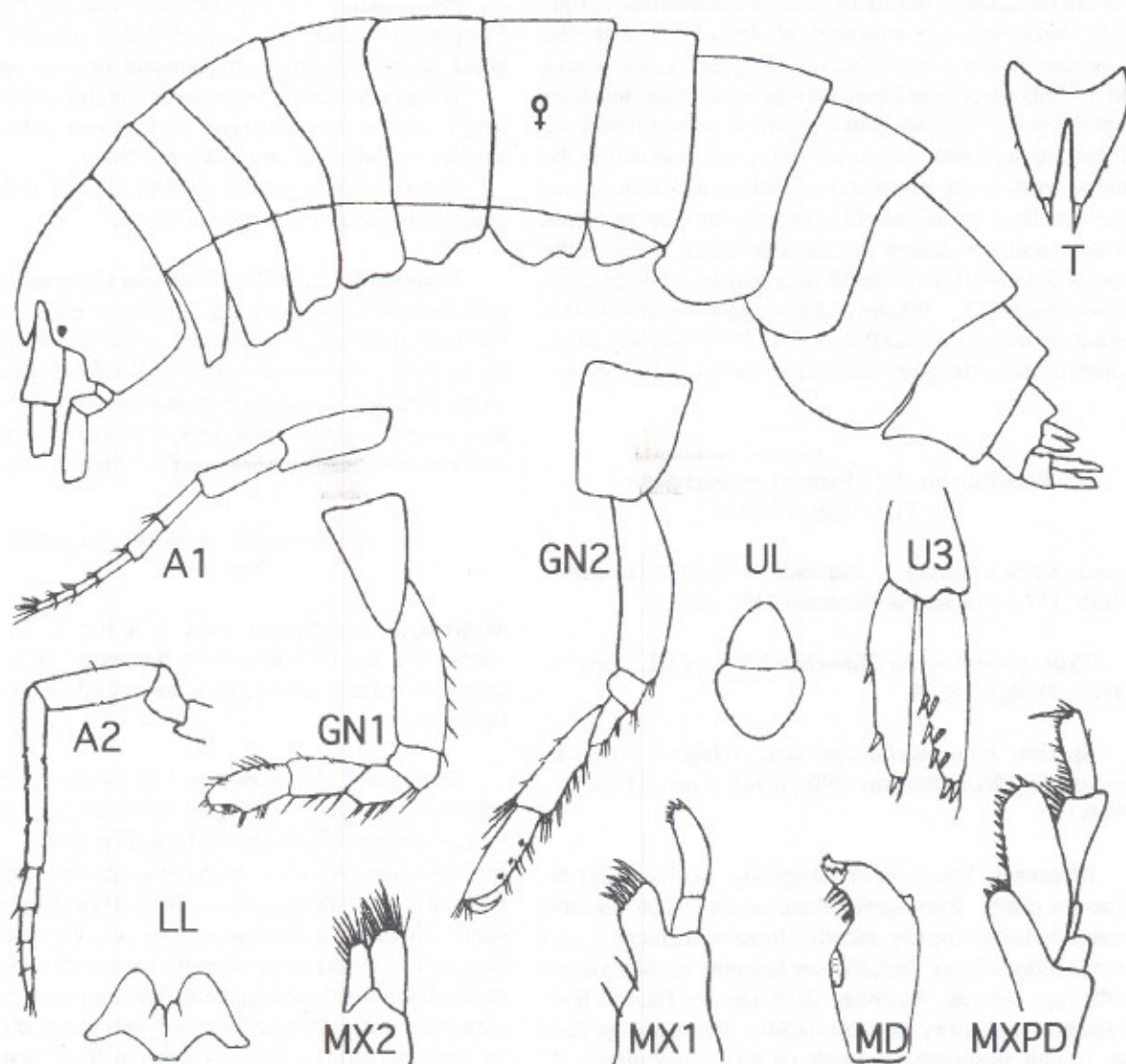


FIG. 16. *Anatylus pavlovskii* Bulycheva, 1955. Female (6-8 mm) Japan Sea (modified from Bulycheva, 1955)

strong, 4-segmented.

Coxae 2-4 relatively shallow, narrow, slightly emarginate below. Coxa 1 tapering, subacute below, almost as deep as coxa 2. Coxa 5 broadly antero-lobate. Gnathopods 1 & 2 slender, dissimilar in size (2 larger); carpus longer than propod, palms very oblique. Gnathopod 1, propod and dactyl relatively short. Gnathopod 2, propod and dactyl relatively long, slender.

Peraeopods 3 & 4, segment 5 shortened. Peraeopods 5-7 slightly dissimilar, segment 5 not described. Peraeopod 7, basis lacking distinct postero-distal process.

Pleopods not described, (not powerful?). Pleon plate 3 deep, rounded below. Uropods 1 & 2 not described.

Uropod 3 short, rami heavy, lanceolate, margins sparsely spinose (female). Telson medium short, lobes deeply separated, converging distally, apices each with single spine.

Coxal gills and brood plates undescribed.

Anatylus pavlovskii Bulycheva
(Fig. 16)

Anatylus pavlovskii Bulycheva, 1955: 206, fig. 6.—Bulycheva, 1957: 104.—Tzvetkova, 1967: 173.

Arylus pavlovskii Barnard & Karaman, 1991: 262, fig. 50A.

Diagnosis: With the characters of the genus

Distribution: The monotypic species *A. pavlovskii* is known only from the Russian portion of the Japan Sea (Peter-the-Great Bay), in medium depths (Bulycheva, 1955).

Taxonomic Commentary: As figured and described by Bulycheva (1955) and refigured by Barnard & Karaman (1991), this species bears a combination of character states

that are remarkably similar to those of *Kamehatylus*, originally diagnosed as a subgenus of *Atylus*, based on the Hawaiian species *K. nani* (below). Regrettably, Bulycheva did not fully describe or figure the diagnostic character states of pereopods 3-7. Until further material can be studied, the diagnostic subfamily character states are assumed to be similar to those of *Kematylus japonicus* which occurs at other localities in the Sea of Japan. The two genera appear closely similar in described character states, although the type of *Kamehatylus* is based on a species with all three urosomites fused. Whatever future studies reveal in this regard, the name *Anatylus* Bulycheva 1955 would be a senior synonym and is therefore retained here as a valid full genus.

Kamehatylus J. L. Barnard, revised status
(see Figs. 1(d); 17A,B)

Atylus (*Kamehatylus*) J. L. Barnard, 1970b: 93.—Ledoyer, 1979b: 157.—Barnard & Karaman, 1991: 262.

Typespecies: *Atylus* (*Kamehatylus*) *nani* J. L. Barnard, 1970b: 93, figs. 48, 49.

Species: *Kamehatylus japonicus* (Nagata, 1961); *K. processicer* (Siviprakasam, 1970); *K. tulearensis* (Ledoyer, 1984)?

Diagnosis: Small, morphologically modified atyids. Rostrum short. Eyes small. Peraeon and pleon dorsally weakly carinate or nearly smooth. Urosome segments 1, and fused 2-3 dorsally toothed; all three urosome segments fused in the type species. Antennae short, slender, flagella few-segmented; accessory flagellum lacking. Antenna 1, peduncle 1 with posterodistal tooth or process. Antenna 2, peduncular segments 4 & 5, margins nearly smooth.

Lower lip lacking inner lobes. Mandible: palp absent; molar process medium; spine row with 2-3 blades and accessory setae; left lacinia 4-dentate, right lacinia bifid-flabellate. Maxilla 1, inner plate with 2-3 apical setae; outer plate with 10 apical spines; palp slender, 2-segmented. Maxilla 2, inner plate, inner margin subapically with single large plumose seta. Maxilliped, palp slender, shortened.

Coxae 1-4 short, shallow, lower margins rounded or slightly incised. Coxa 1 subacute below. Coxa 5, anterior lobe small. Gnathopods 1 & 2 slender, dissimilar, probably little or not sexually dimorphic. Gnathopod 1, propod shorter than carpus, with antero-distal median facial clusters of pectinate setae. Gnathopod 2, carpus slender, longer than in gnathopod 1.

Peraeopod 4 distinctly smaller in size than pereopod 3; segment 5 (of both) small, much shorter than segments 4 & 6; dactyls short. Peraeopods 5-7 subsimilar in size, bases not broadly expanded, lower hind lobes small or lacking; segment 5 not shortened, longer than segment 6, but not markedly longer than segment 4; dactyls short.

Pleon plates 1-3 regular hind corners mucronate. Pleopods not described. Uropods 1 & 2 slender, rami unequal. Uropod 3 rami short, subequal, margins spinose.

Telson lobes deeply separated, diverging distally, apices singly spinose, outer margins bare. Coxal gills sac-like, simple. Brood plates strap-like, not broad.

Mature male (Ledoyer, 1979b): Eye slightly larger, antennal flagella longer, than in female.

Taxonomical and Distributional Commentary. The few described species of this genus are essentially Indo-Pacific in distribution, northwards in the Pacific to southern Japan, but not yet recorded from the North American Pacific coast. The species appear morphologically specialized for a cryptic life style on coral reefs, in association with large, sessile invertebrates such as sea lilies (Siviprakasam, 1970).

Kamehatylus japonicus (Nagata)
(Fig. 17A)

Atylus japonicus Nagata, 1961: 216, figs. 1, 2.—Nagata, 1965a: 202, fig. 19.—Barnard & Karaman, 1991: 263.
non Atylus (*Kamehatylus*) *japonicus*—Ledoyer, 1979b: 156 fig. 7(II).

Taxonomic Commentary: The species has been well described and figured by Nagata 1961-1965, *loc. cit.* whose figures are partly reproduced here (Fig. 17A). Nagata's species conforms closely with the subgeneric diagnosis of Barnard (1970b) that was based on the Hawaiian species, *K. nani*. However, in the Japanese species, the posterior pereon and pleon are more strongly carinated, urosome segment 1 is not fused with segments 2 & 3, and the gnathopods are more slender. Despite these and other minor differences, the authors consider Nagata's material from Japan congeneric with that of Barnard, and have broadened the generic diagnosis to accommodate both species.

Ledoyer (1979b, *loc. cit.*) described a very similar species from the Moluccas Islands, Indian Ocean, to which he had perceptively assigned the name *Atylus* (*Kamehatylus*) *japonicus* Nagata. Ledoyer's figures, reproduced here (Fig. 17B), do show remarkable similarities to those of Nagata, including the relatively small eye and excavate anterior head lobe, the postero-distal process of peduncular segment 1 of antenna 1, and the unfused urosome segment 1. However, on close inspection, his Moluccas material is seen to differ in a number of specific features such as its weaker body carination, shorter carpus of gnathopod 2, and more acute apices of the rami of uropod 3. Ledoyer's material is therefore regarded here as a species different from *A. japonicus* Nagata, and awaits formal designation as a possible new taxon.

Distributional Commentary. *Kamehatylus japonicus* has been recorded from Japanese waters mainly from Honshu and more southerly localities (see summary of pertinent literature by Ishimaru, 1994).

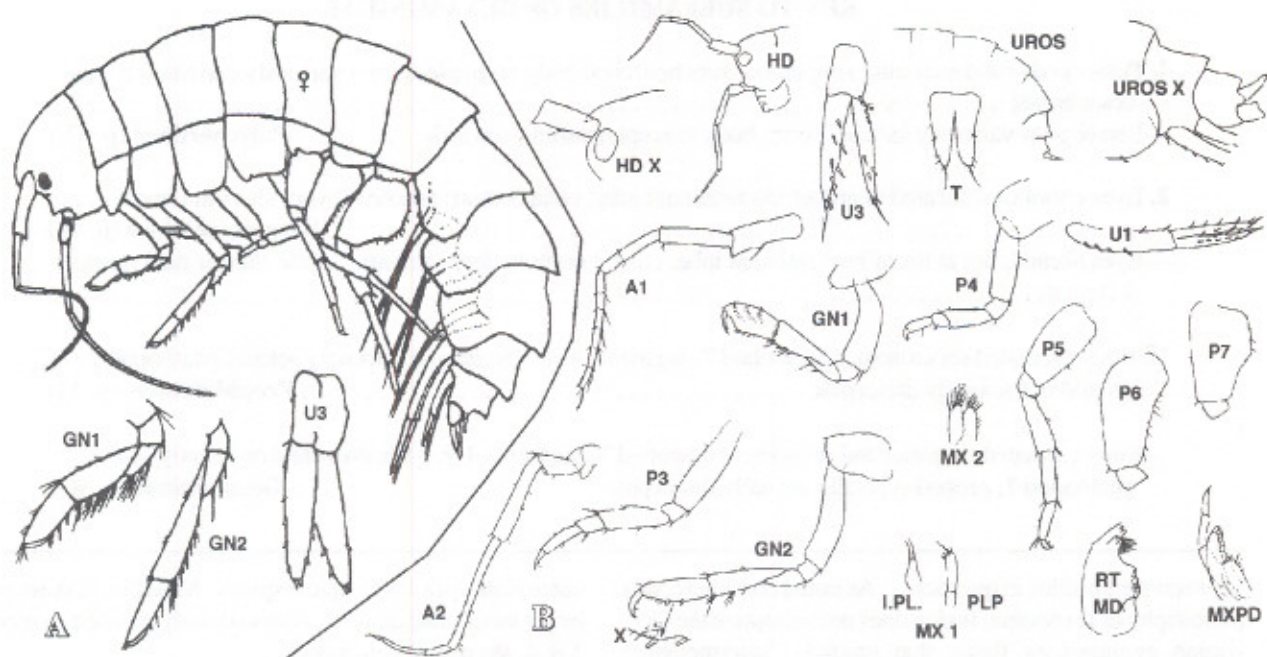


FIG. 17. *Kamehatylus japonicus*.

A. *K. japonicus* Nagata Female (3 - 5 mm) Seto Inland Sea (from Nagata, 1960)

B. *K. japonicus* Ledoyer Male (3.4 mm) Moluccas Ids. (from Ledoyer, 1979).

DEXAMINIDAE Leach

Dexaminidae Leach 1813/14: 432.—Stebbing, 1888: 573.
—Gurjanova, 1951: 788.—Lincoln, 1979: 448.—Bousfield,
1982: 212.

Dexaminidae (part) Barnard, 1969: 200.—Barnard 1970:
163.—Bellan-Santini, 1982: 277.—Barnard & Karaman,
1991: 260.

Subfamilies: Dexamininae Leach; Dexaminoculinae, new
subfamily; Polycheriinae, new subfamily; Prophliantinae
Nicholls.

Diagnosis: Body small, stout, compact, not compressed.
Sexual dimorphism expressed in eyes, antenna, uropod 3,
typically in gnathopod 1, pleopods, and telson. Peraeon seg-
ments 5-7 usually smooth above, occasionally with mid-
dorsal teeth and/or dorso-lateral mucronations. Pleosome
and urosome, less often posterior peraeon, armed dorsally
and occasionally dorso-laterally with teeth or spines. Ros-
trum short. Anterior head margin rounded or acute; may be
produced strongly as ocular lobe. Eyes medium to large.
Antennae short (female), Antenna 2 often reduced, not
longer than 1. Antenna 1, peduncular segment 2 various;
accessory flagellum minute or lacking.

Lower lip, inner lobes usually strong. Mandible, molar
usually strong, triturating; spine row weak; left lacinia often
4-dentate; palp lacking. Maxilla 1, palp 1-segmented (rarely
2); outer plate with 7-11 apical spines; inner plate with 0-2
apical setae. Maxilla 2, plates variously reduced, often

weakly setose. Maxilliped, inner plate reduced, with apical
setae only; outer plate large, broad; palp variously shortened,
dactyl reduced or lacking (3-segmented).

Coxae 1-4 deep, shortest anteriorly, little (or not) in-
dented below. Coxa 5, broad, often deep. Gnathopods, un-
equal, subchelate (rarely chelate); gnathopod 1 the smaller,
with short carpus, propod (male) strikingly notched or ex-
cavate anteriorly. Gnathopod 2, carpus usually longer than
propod.

Peraeopods 3 & 4 subequal, various, segments 5 & 6
trending to reduction in length, and subchelation. Peraeopods
5-7 subequal in length; bases typically unequally expanded,
trending to linearity; segment 5 normal, occasionally short-
ened, segment 6 & dactyl often shortened.

Pleopods short to medium. Pleon plates 1-3, hind corners
acuminate, often produced. Uropod 1, rami subequal, tips
spinose. Uropod 2 much shorter than 1, outer ramus the
shorter. Uropod 3, rami lanceolate (often broadly), margins
variously plumose-setose, especially in male.

Telson deeply bilobate, lobes not diverging, apices
subtruncate, variously armed.

Coxal gills on peraeopods 2-7 (6), variously pleated, not
phylliform.

Taxonomic Commentary: As noted previously, Barnard
(1970a, *loc. cit.*) combined a number of dexaminoidae
families (including Atylidae, Anatyliidae, Lepechinellidae,
Prophliantidae) within family Dexaminidae. His decision
was based on the presence of one or more species deemed
intermediate in form (often on single character states only)

KEY TO SUBFAMILIES OF DEXAMINIDAE

1. Peraeopods fundamentally simple, not subcheliform; body (esp. pleosome) variously carinated or processiferous; 2.
 —Peraeopods variously subcheliform; body (except urosome) smooth **Polycheriinae** (p. 37)
2. Eyes enormous, located at end of interantennal lobe; coxa 3 short; antenna 2 very short in female **Dexaminoculinae** (p. 49)
 —Eyes normal, not at tip of interantennal lobe; coxa 3 normal, deep; antenna 2 little shorter than antenna 1 (female) 3.
3. Body carinated on urosome; peraeopod 7, segments 4 & 5 broadened, strongly setose; gnathopod 1 propod not sexually dimorphic **Prophiantinae** (p. 51)
 —Body carinated on pleon and urosome; peraeopod 7, segments 4 & 5 not broadened or heavily setose; gnathopod 1, propod typically sexually dimorphic **Dexamininae** (p. 36)

between the families in question. As noted elsewhere, this philosophy of taxonomic fusion does not recognize the Darwinian evolutionary thesis that predicts "intermediate" morphotypes existing, at one time or other, between all extant and past organisms. Thus, we agree with Ishimaru (1993) that the presence of single taxa that appear to "bridge" otherwise morphologically discontinuous higher taxa does not, alone, constitute a valid basis for merging of the pertinent higher taxa. The Barnardian classification is therefore not followed here.

In this study, numerical taxonomic analysis (p. 56) strongly supports recognition of just two family-level dexaminoid subgroups, the Atylidae (p. 8) and the Dexaminidae (above). The analysis further supports recognition of four distinct subfamily groupings within family Dexaminidae, as listed and keyed above.

Subfamily Dexamininae (revised) (see Fig. 2(a))

Dexamininae (part): Barnard & Karaman 1991: 260.
 Dexamininae Ishimaru, 1987: 1412.

Type genus: *Dexamine* Leach, 1813/14.

Genera: *Dexamine* Leach, 1814: 432; *Dexaminella*, Schellenberg, 1928: 654; *Paradexamine*, Stebbing, 1899: 210; *Sebadexius* Ledoyer, 1984: 56; *Syndexamine* Chilton, 1914: 332.

Diagnosis: Body generally toothed or processiferous above, not strongly compressed. Rostrum medium. Eye normal. Antennae regular.

Mouthparts typical of family: Lower lip, inner lobes variously developed. Mandible, spine row weak. Maxilla 1,

outer plate with 10-11 apical spines. Maxilliped, outer plate large; inner plate distinct; palp variously reduced, segments 3 & 4 shortened or vestigial.

Coxae 1-4 regular, deep, 1 smallest. Coxa 5 medium. Gnathopods typically subchelate, occasionally chelate; carpus not elongate. Gnathopod 1, propod sexually dimorphic.

Peraeopods normal, not subcheliform nor elongate; segment 5 not unusually lengthened or shortened; dactyls medium; peraeopods 5-7 subequal in length, bases dissimilar in form, variously broadened; segment 5 normal.

Pleon segments dorsally and dorso-laterally carinate. Pleon plates 2-3, hind corners variously acuminate or produced.

Telson elongate, lobes deeply separated, not diverging. Brood plates sublinear.

Taxonomic and Biogeographic Commentary: As here defined, the subfamily Dexamininae encompasses five genera and about 60 species that occur mainly in southern oceans. *Paradexamine*, with more than 40 described species, is essentially Indo-Pacific, with outliers extending to the Mediterranean, South America, and Japan. The Japanese fauna comprises ~8 described species (Ishimaru, 1994), all confined to Kyushu and the southern archipelagos; none reaches northern Honshu, and no member of the genus reaches the Pacific coast of North America. *Sebadexius* is monotypic in New Caledonia. *Syndexamine* contains 6 species, in littoral waters of New Zealand and southern Australia. *Dexaminella*, containing 3 species, is confined to the northwestern Indian Ocean and Red Sea. However, *Dexamine*, with only 3 recognized species (Barnard & Karaman, 1991) is confined to the boreal and temperate North Atlantic region, extending southward along eastern shores to the Mediterranean and Senegal, and along western shores to the Middle Atlantic States and Chesapeake Bay. Members of this subfamily have yet to be recorded authentically from the North American Pacific region and are not treated further in this study.

KEY TO WORLD GENERA OF DEXAMININAE

1. Gnathopods cheliform; maxilliped palp various, usually small to vestigial *Sebadexius* Ledoyer.
- Gnathopods subcheliform, maxilliped palp 3-4 segmented 2.
2. Pleon segments distinctly carinate mid-dorsally and/or dorso-laterally, integument normal 3.
- Pleon segments indistinctly or not carinated; integument often thick, heavy 5.
3. Pleon segments 1-3 carinate laterally and dorsally *Paradexamine* Stebbing
- Pleon segments carinated dorsally only 4.
4. Maxilliped palp 3-segmented *Dexaminella* Schellenberg
- Maxilliped palp 4-segmented *Dexamine* Leach
5. Uropods 1 & 2, inner rami reduced; pereopod 6 massive *Delkaryle* J. L. Barnard
- Uropods 1 & 2 normal; pereopods 5-7 subequal, 6 not massive *Syndexamine* J. L. Barnard

POLYCHERIINAE, new subfamily (See Fig. 2(c))

Dexaminidae (part) Stebbing, 1906: 514.—Barnard, 1969: 200.—Lincoln, 1979: 448.—Bellan-Santini, 1982: 212.—Barnard & Karaman, 1991: 260.

Type Genus: *Polycheria* Haswell, 1879: 345.

Generic Content: *Tritaeta* Boeck, 1876: 317.

Diagnosis: Body smooth, carinate (weakly) only on urosome. Head: rostrum very weak or absent. Anterior head lobe variously rounded. Eyes pigmented, large. Antennae 1 & 2 medium, subequal, flagella usually setose. Antenna 2, peduncular segment 4 longer than 5. Accessory flagellum lacking.

Upper lip, epistome weakly produced anteriorly. Mandibular molar, left and right sides unequal. Maxilla 1, outer plate with 7-9 apical spines. Maxilliped palp 3-, or weakly 4-segmented. Coxa 1-7 shallow, variously bifid or acute below. Gnathopods slender, dissimilar in length; weakly subchelate.

Pereopods 3-7 delicately prehensile (subchelate, or pseudo-carpochelate); segment 4 elongate; segments 6 and/or 5 shortened. Pereopods 5-7 subsimilar, bases sublinear. segment 7 and dactyl often reversed.

Pleopods medium, peduncle and rami not powerful. Pleon plates 1-3, hind corners mucronate. Uropod 1, rami subequal. Uropod 2 short, rami unequal. Uropod 3, rami lanceolate, margins setose (male). Telson lobes elongate, deeply separated, marginally spinose.

Coxal gills weakly pleated, on pereopods 2-7. Brood plates sublinear, strap-like.

Species of both *Tritaeta* and *Polycheria* are commensal mainly on sponges and colonial tunicates (Vader, 1969), clinging upside down in small pits excavated in surface test of host, and feeding in the fashion of ampeliscoideans.

Taxonomic and Distributional Commentary: The subfamily presently contains two genera, *Polycheria* and *Tritaeta*, not very closely related (p. 57), characterized by a trend to prehensility (subchelation) of pereopods 3-7. The pereopods of *Tritaeta* are carpochele (fig. 28). About 20 species of *Polycheria* are known, most from tropical and warm temperate Indo-Pacific regions. Three species were previously described from temperate waters of the Asiatic Pacific coast (Bulycheva, 1952; Hirayama, 1984) and one from the Pacific coast of North America (Calman, 1898; Barnard, 1969b). *Tritaeta* contains only two species (many synonymies), both in the northeastern Atlantic and Mediterranean regions (Lincoln, 1979; Bellan-Santini, 1982).

The phyletic relationships of subfamily Polycheriinae are with the Dexamininae (p. 36; fig. 2(a)). Thus, males of the more primitive genus *Tritaeta* retain the distinctive dexaminid dorsally notched form of the propod of gnathopod 1.

Polycheria Haswell

Polycheria Haswell, 1879:345.—Stebbing, 1906:519.—Holman & Watling, 1983: 221.—Thurston, 1974: 18.—Barnard & Karaman, 1991: 271.

Type Species. *Polycheria tenuipes* Haswell 1879.

Species (North Pacific region). *Polycheria osborni* Calman 1898; *P. carinata*, new species (p. 42); *P. mixillae*, new species (p. 44); *P. amakusaensis* Hirayama, 1984a; *P. orientalis* Hirayama 1984a; *P. japonicus* Bulycheva, 1952.

KEY TO GENERA OF SUBFAMILY POLYCHERIINAE

1. Peraeopods 3-7 pseudo-carpochelate (carpus expanding and strongly spinose distally, propod lacking palm); antennal flagella smooth; gnathopod 1, propod markedly sexually dimorphic *Tritaeta*.

—Peraeopods 3-7 distinctly subchelate (propod with distal palm, carpus not expanding distally); antennal flagella strongly setose; gnathopod 1, propod not markedly sexually dimorphic . . . *Polycheria* (p. 37).

Diagnosis: Body stout, broadest at peraeon segments 4 & 5, mid-dorsally carinated on urosome segment 1; paired dorso-lateral ridges or small spines usually present on fused urosome segments 2 & 3. Head: rostrum very weak; anterior head lobe variously rounded; eyes large, sexually dimorphic. Antenna 1, flagella usually strongly setose.

Lower lip, inner lobes well developed. Mandible, left and right molars dissimilar in size. Maxilla 1, outer plate with 7-9 apical spines. Maxilla 2, apical setae weak. Maxilliped, palp 4-segmented.

Gnathopods very weakly subchelate. Gnathopod 1, propod not strikingly sexually dimorphic; palmar margin short to obsolescent.

Peraeopods 3-7 delicately subchelate; dactyl short, closing on short fixed finger; segment 5 short, not expanded or strongly spinose distally, variously shorter or longer than segment 6. Peraeopods 5-7, bases sublinear (may be slightly broadened in peraeopods 5 & 6).

Uropod 2, outer ramus usually the shorter. Uropod 3 (female), rami variously unequal.

Telson lobes variously fused basally, margins spinose.

Sexual dimorphism strongly expressed in eyes, antennae, pleopods, and uropod 3.

Taxonomic and Distributional Commentary: North American Pacific species differ from Asiatic Pacific species in several character states, mostly apomorphically (pp. 61-62 and key below). Both groups differ from the generally more primitive species of the southern hemisphere as exemplified by the *P. antarctica* complex of species (Holman & Watling, *loc. cit.*). Species of the North American study region are characterized by: maxilla 1, outer plate with 7 (vs. 9) apical spines; maxilliped palp short (vs. medium); coxa 1 acute (vs. rounded) below; gnathopod palmar margins distinct (vs. obsolete); peraeopods 3-7, segment 5 shorter (vs. longer) than segment 6; uropod 2, inner ramus (vs. outer ramus) the shorter; uropod 3 (female), rami subequal (vs. unequal); and telson lobes more strongly fused basally. These differences point to the need for an extensive revision of the genus, based on re-examination of species world-wide, that is beyond the scope of the present study.

Polycheria osborni Calman
(Figs. 18, 19, 20)

Polycheria osborni Calman, 1898: 268, pl. 32, fig. 2.—Skogsberg & Vansell, 1928: 268, figs. 1-26.—Barnard, 1975: 363, key + fig. 55.—Barnard, 1969a: 103.—Barnard,

1969b: 200, fig. 25g.—Staude, 1987: 382 + key.—Barnard, 1979b: 38.—Barnard & Karaman, 1991: 272 (list). *Polycheria antarctica* (Stebbing, 1875): Stebbing, 1906: 520 (part).—Alderman, 1936: 63.—Barnard, 1954a: 21.

Material Examined (CMN collections, Ottawa):

SE ALASKA: Stitka region, Slocum Pt., ELB Stn S4B4, under boulders, July 27, 1980 - 1 female ov (slide mt.).

BRITISH COLUMBIA:

Queen Charlotte Islands: none taken at outer coast sites.

North Central coast: Oval Bay, surf shore at LW, ELB Stn H10, July 12, 1964 - 1 female br. II (slide mt.), 2 other females.

S. end Vancouver I: Ucluelet, outer coast, J. Macoun coll., July, 1909. (identified initially as *P. tenuipes* Haswell) - 1 lot dried specimens.

Barkley Sd. region, ELB Stns, 1975-76:

Taylor I., Trevor Channel, ELB Stn. P5b c, on ascidians and sponges, LW, July 25, 1975 - 1 female br II (4.5 mm) (slide mt.); 1 female ov (5.2 mm) (slide mt.); 2 female ov. (4.5, 4.8 mm) (slide mts.); 1 male many specimens.

Kirby Pt., Diana I., ELB Stn. P17d, on sponges and ytunicates from rocky walls of surge channels, LW and subtidal, Aug. 6, 1975 - 1 female ov. (5.8 mm) (slide mt - fig'd specimen); 1 male (3.7 mm) (slide mt. - fig'd specimen), 2 subad. males (4.3, 4.5 mm); 1 subad. female (4.2 mm) (slide mt.); several other specimens.

Bordelais Islets, mouth of Trevor Ch., ELB Stn. P20c, from sponges and tunicates on rocky walls of surge channels, Aug. 9, 1975 - 1 female ov. (6.0 mm) (slide mt.) 2 subad. males (5.0 mm, 3.8 mm)

Edward King I., Taylor I., ELB Stn B28a, under boulders at LW, July 10, 1976 - 1 female ov. (5.0 mm) (slide mt.); 1 female br. II (5.3 mm) (slide mt.); several other specimens, mostly subad. females.

WASHINGTON-OREGON: No specimens were found in collections from apparently suitable habitats at localities along the outer coast (see Bousfield & Jarrett, 1981).

Diagnosis. Female ov. (5.8 mm): Urosome 1, mid-dorsal carina low, weakly toothed behind. Eye medium, covering anterior half of head, golden brown in colour in fresh material. Anterior head lobe broadly rounded. Antenna 1, segment 3 short; flagellum 20+ segmented, moderately setose. Antenna 2, flagellum 18-segmented.

Mandible, spine row with 2-3 short blades. Maxilla 1, inner plate with 1-2 apical setae; outer plate with 7 slender apical spines; palp short. Maxilla 2, plates small weakly

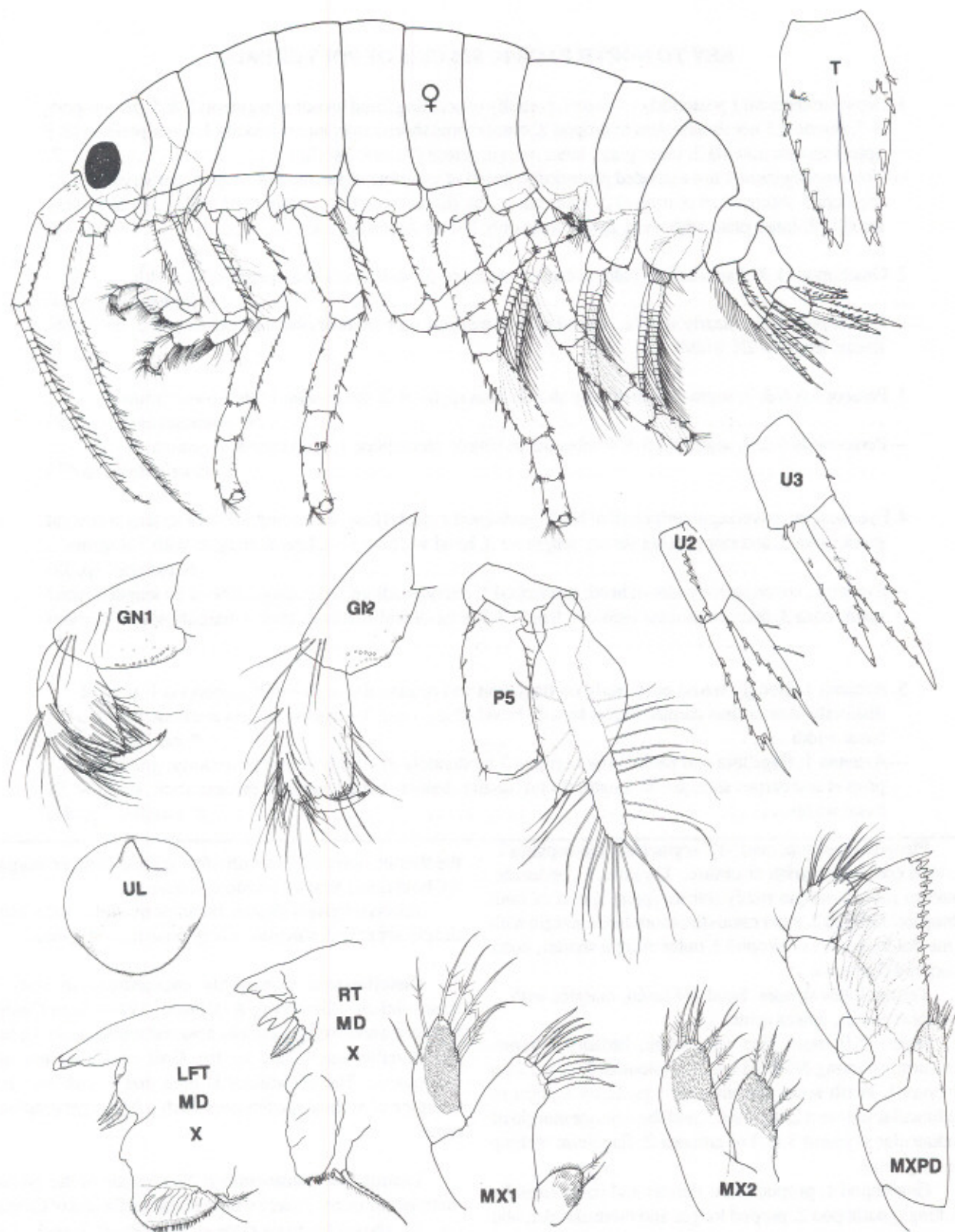


FIG. 18. *Polycheria osborni* Calman. Kirby Pt., Diana I., Barkley Sound. Female ov (5.8 mm).

plumose-setose. Maxilliped, outer plate with 12 inner marginal spines; palp shorter, dactyl thick.

Coxa I sharply acute anteriorly; coxa 3, anterior process elongate, length $> 3\times$ basal width. Gnathopod 1, carpus and propod subequal in length, carpus proximally deepest; dactyl slender, projecting $> 50\%$ of its length beyond short palm.

Gnathopod 2, propod more slender, shorter than carpus, palm short but distinct, slightly exceeded by closed dactyl.

Pereopods 5-7, segment 5 shorter than segment 6. Pereopods 3 & 4, basis slightly broader than distal segments. Pereopods 5-7, bases sublinear, not broadened; segment 6 shorter than in pereopods 3 & 4.

KEY TO NORTH PACIFIC SPECIES OF POLYCHERIA

1. Urosome segment 1 posteriorly extended, partially concealing fused urosome segments 2 & 3; peraeopods 3-7, segment 5 not shorter than 6; uropod 2, outer ramus shorter than inner; maxilla 1, outer plates with 9 apical spines; maxilla 2, inner plate, inner margin setose (Asiatic Pacific) 2.
 —Urosome segment 1 not extended posteriorly, based of urosome segments 2 & 3 open; peraeopods 3-7, segment 5 shorter than 6; uropod 2, inner ramus the shorter; maxilla 1, outer plate with 7 apical spines; maxilla 2, inner plate with weak apical setae only (North American Pacific). 4.
2. Gnathopods 1 & 2 subchelate, palm distinct; peraeopod 5, basis expanded, length < 2X width *P. japonicus* (p. 44)
 —Gnathopods 1 & 2 nearly simple, propod palmar margins very short or obsolete; peraeopod 5, basis sublinear, length > 2X width 3.
3. Peraeopods 6 & 7, segment 6 distinctly shorter than segment 5; pleon plate 1, hind corner rounded *P. amakusaensis* (p. 46)
 —Peraeopods 6 & 7, segments 5 & 6 subequal in length; pleon plate 1, hind corner acuminate *P. orientalis* (p. 47)
4. Eye medium, covering anterior half of head; gnathopod 1, dactyl long, extending > 50% of its length beyond palm; coxa 3, anterior process strong, length > 3 X basal width; telson, lateral margins with 7-8 spines *P. osborni* (p. 38)
 —Eye large, covering 3/4 width of head; gnathopod 1, dactyl medium, extending < 50% of its length beyond palm; coxa 3, anterior process medium, length 2-3 X basal width; telson, lateral margins with 5-6 spines 5.
5. Antenna 1 strongly setose posteriorly on flagellum and peduncular segment 2; gnathopod 1, propod distinctly shorter than carpus, dactyl basally broad, thick; coxa 3, anterior process medium, length > 2X basal width *P. carinata* (p. 42)
 —Antenna 1, flagellum and peduncular segment 2 moderately to weakly setose posteriorly; gnathopod 1; propod and carpus subequal in length, dactyl basally slender; coxa 3, anterior process short, length < 2X basal width *P. mixillae* (p. 44)

Pleopods medium, rami 12-segmented; pleon plates 1-3, hind corners squarish or obtuse. Uropods 1, peduncle, anterior (outer) margin richly setose, apical spines of rami elongate. Uropod 2, inner ramus the short, inner margin with 2 medial long spines. Uropod 3, outer margin shorter, outer margin 4-5 spinose.

Telson, lobes slender, basal 1/4 fused, margins with 7-8 short spines, apices acute.

Male. (5.0 mm): Eye very large, broadly reverse-renaliform, covering 5/6 head width. Antennae 2 longer than antenna 1, brush setae present on the posterior margin of peduncular segment 2, antenna 1, and the anterior margin of peduncular segment 3 & 4 of antenna 2; flagellum lacking feeding setae.

Gnathopod 1, propod more slender and palm virtually lacking; gnathopod 2, propod longer and more slender, and palm very much shorter, than in female.

Pleopods, peduncles strong, massive, nearly 2X longer than in female; split-tipped clothespin spines on 5-6 proximal segments of inner ramus. Urosome, mid-dorsal carina elevated, not mucronate behind; fused urosome segments 2 & 3 with mid-dorsal notch. Uropod 2, inner margin of peduncle with a few plumose setae; inner margin of inner ramus with 3 slender spines. Uropod 3, outer ramus slightly

the shorter, outer margin with a few spines, all other margins (of both rami) heavily plumose-setose.

Telson relatively shorter, broadest medially, lobes more deeply separated, margins less spinose than in female.

Distribution: Commonly encountered in tests of *Amaroucium* (Skogsberg & Vansell, 1928), from Central California north to British Columbia and southeastern Alaska; questionably southward to the Gulf of California and Galapagos. The probability is high that *P. osborni* is a complex of sibling species over such a broad geographical range.

Taxonomic Commentary: The female of the present material compares closely with the original figures of Calman (fig. 19, above) based on material from Puget Sound. Particularly diagnostic of the species is the small palm of gnathopod 1, greatly exceeded by the dactyl. The species *Polycheria antarctica* (Stebbing, 1888), described originally from sponges in the Antarctic and ANZAC regions, is not a true synonym of *P. osborni*, but is a distinctive species that exhibits generally more plesiomorphic characters states (p. 49, fig. 25).

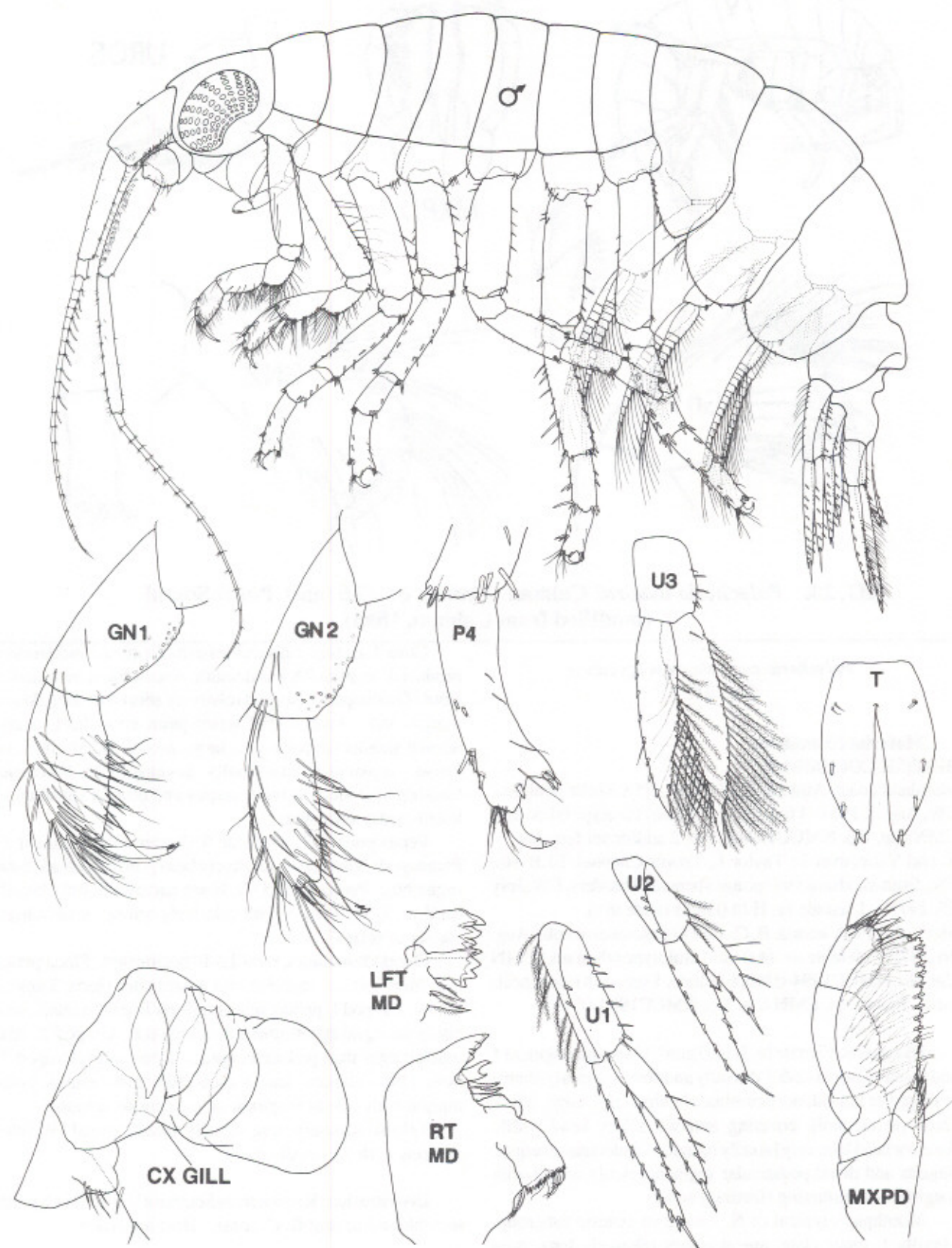


FIG. 19. *Polycheria osborni* Calman. Kirby Pt, Diana I, Barkley Sound. Male (3.7 mm)

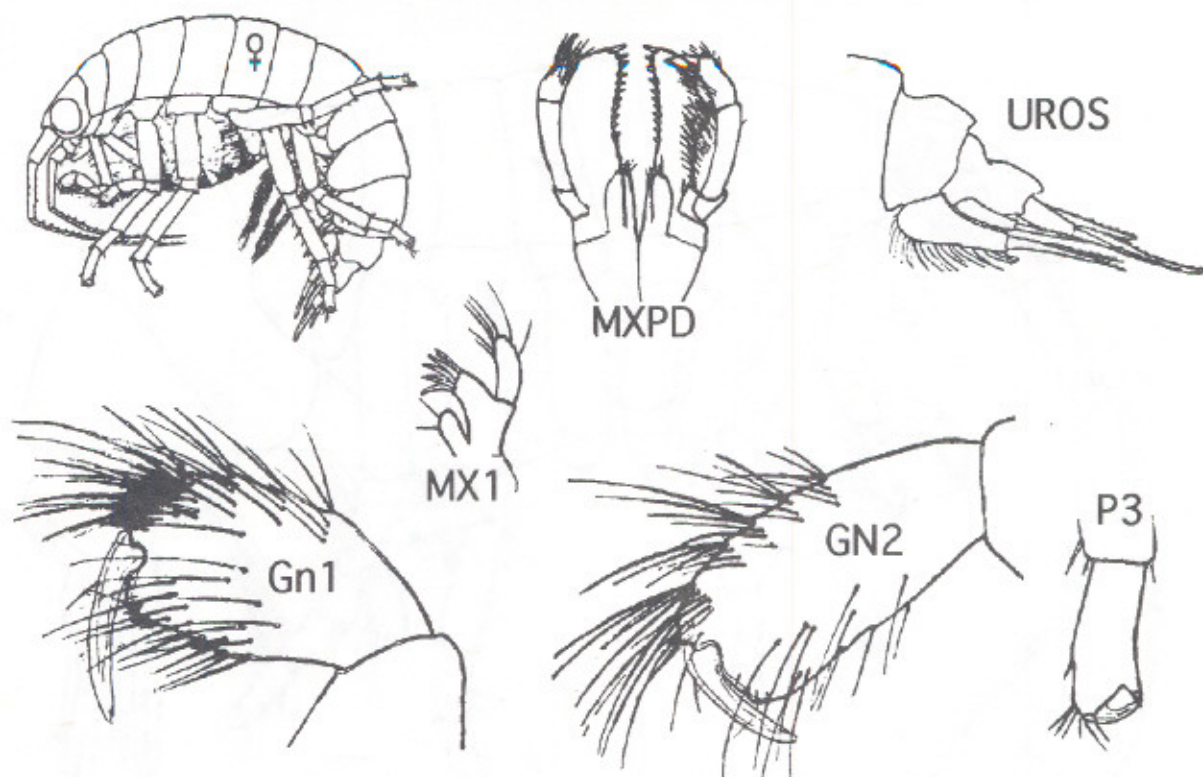


FIG. 20. *Polycheria osborni* Calman. Female ov. (7.0 mm) Puget Sound (modified from Calman, 1898)

Polycheria carinata, new species
(Fig. 21)

Material Examined:

BRITISH COLUMBIA:

Mainland coast: Athlone I., ELB Stn. H53, under boulders, LW, Aug. 7, 1964 - 1 female ov (5.8 mm) Paratype (slide mt.) CMN Cat. No. NMCC1994-0392; 2 additional females.

S. end Vancouver I.: Taylor I., Trevor Channel, ELB Stn. P5c, from ascidians and sponges beneath boulders, LW, July 25, 1975 - 1 female br. II (4.0 mm) (slide mt.).

McCaulay Pt., Victoria, B. C., GW O'Connell dive coll., Aug. 26, 1976 - 1 female ov. (4.0 mm) Holotype (slide mt.) CMN Cat. No. NMCC1994-0390; 6 female, 1 subadult male specimens, Paratypes, CMN Cat. No. NMCC1994-0391.

Diagnosis. Female br. II (4.0 mm). Urosome segment 1 and fused segments 2 & 3 dorsally and dorso-laterally sharply ridged or keeled, not acuminate behind. Eye large, red or black (in alcohol), covering anterior 3/4 of head width. Anterior head lobe very broadly rounded. Antennae subequal, flagella and distal peduncular segments richly armed with longish food-gathering (feeding) setae.

Mouthparts typical of N. American generic subgroup. Maxilla 1, outer plate, apical spines relatively long, palp short. Maxilla 2, outer plate, apex subtruncate, weakly setose. Maxilliped, palp very short, dactyl small; outer plate with 10 inner marginal spines.

Coxa 1 acutely produced anteriorly; coxa 3 moderately produced, length > 2X basal width; coxa 4 blunt, rounded in front. Gnathopod 1, propod relatively short and deep, lower margin with several stiff setae; palm very short, dactyl normal slender (in paratype), large, heavy, basally thick or broad, apparently abnormally developed in holotype. Gnathopod 2 more slender, carpus and propod subequal in length, palm very short.

Pereopods 3-7, segment 5 shorter than segment 6. Pereopods 3 & 4, basis relatively heavy, broader than distal segments. Pereopods 5 - 7, bases narrow, slightly broadened in 5; segment 6 with relatively strong antero-distal cluster of setae.

Pleopods medium, rami 12-14 segmented. Pleon plates 2-3, hind corners squarish, not acuminate; pleon 3 setose below. Uropod 1, peduncular anteriorly line with setae; rami closely subequal apical spines not elongate. Uropod 2, rami much longer than peduncle, apical spines short. Uropod 3, outer ramus slender, length about 80% inner ramus, outer margin with 2-3 short spines, other margins spinose.

Telson lobes narrowing distally, fused in basal 1/4, outer margins with 5-6 small spines.

Distribution: Known from Southern Vancouver I, north to Athlone I central B. C. coast. Host unknown.

Taxonomic Commentary: The species is closest to *P. mixillae* in most character states, but is distinguished mainly by features of the key (p. 40).

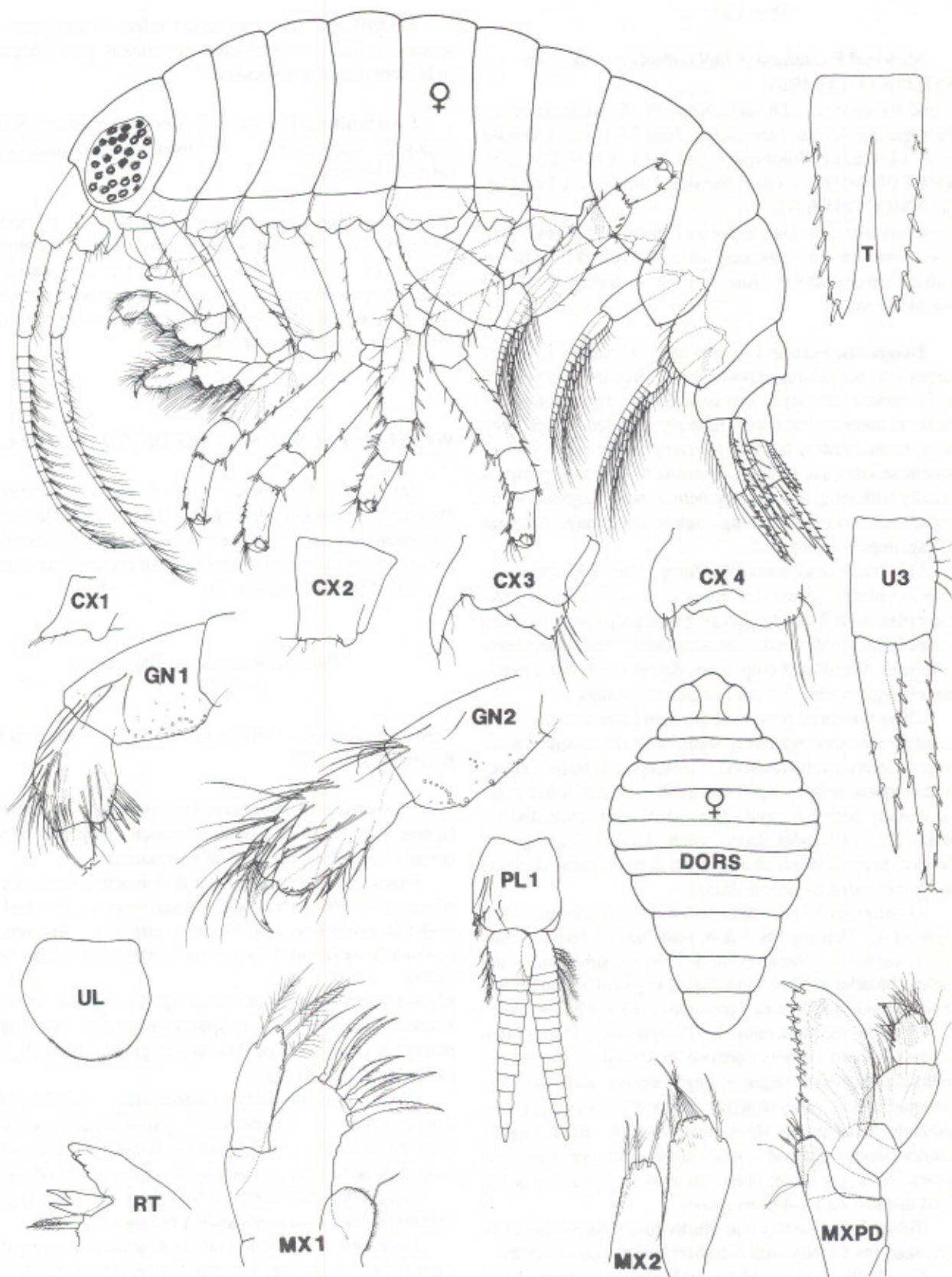


FIG. 21. *Polycheria carinata*, new species. McCaulay Point, B. C. Female Br. II (4.0 mm).

Polycheria mixillae, new species
(Fig. 22)

Material Examined (CMN collections, Ottawa):
BRITISH COLUMBIA:

S. end Vancouver I.: Diana I., Kirby Pt., R. Anderson coll., from sponge (*Mixilla incrustans*), June 25, 1976 - 1 female br II (4.0 mm) Holotype (slide mt.), CMN Cat. No. NMCC1994-0393; 9 other females, Paratypes, CMN Cat. No. NMCC1994-0395.

Bordelais Islets, entrance to Trevor Channel, ELB Stn. P20c, LW, in sponges and tunicates (undet.) collected from rocky walls of surge channels, Aug. 9, 1975 - 1 female br. II (4.0 mm)(slide mt.).

Diagnosis. Female ov. (5.0 mm). Urosome 1, dorsal carina low, not produced posteriorly. Urosome segments 2 & 3, carinae or ridges inconspicuous. Head relatively shallow, anterior head lobe strongly rounded. Eyes very large, ovate, weakly faceted, covering anterior 3/4 of head. Antennae subequal, slender. Antenna 1, segment 2 postero-distally with longish setae; segment 3 short, flagellum ~16-segmented, moderately strongly setose, setae long. Antenna 2, flagellum 3-segmented.

Lower lip broad, inner lobes large. Mandible, spine row with 2-3 blades. Maxilla 1, inner plate with 1 apical seta; outer plate with 7 slender apical spines; palp short. Maxilla 2, inner plate small, weakly setose apically; outer plate, apex subacute. Maxilliped palp short, dactyl stout; outer plate, inner margin with 7-8 weak masticatory spines.

Coxa 1, anterior process short, with 2 apical setae. Coxa 3, anterior process relatively short, with single apical seta; coxa 4, anterior lobe rounded. Gnathopod 1, basis lacking hind marginal setae; propod shorter than carpus, lower margin distally with 5-6 stout setae; palm short, exceeded by nearly 50% of slender dactyl when closed. Gnathopod 2 slender, propod much shorter than carpus, palm distinct, barely exceeded by simple dactyl.

Peraeopods 5-7, segment 5 shorter (or not longer) than segment 6. Peraeopods 3 & 4, basis heavy, broader than distal segments. Peraeopods 5-7, bases sublinear, very slightly broader in peraeopods 5 & 6; segment 5 shorter than in peraeopods 3 & 4; coxa 7 produced posteriorly, subacute.

Pleopods medium, rami ~13-15 segmented. Pleon plates 1-3 broad, hind corners squarish or obtuse. Uropod 1, peduncle, anterior margin strongly setose; rami slender, subequal, apical spines elongate. Uropod 2, rami longer than peduncle, inner ramus short, inner margin with 2 longish slender spines. Uropod 3, inner ramus with inner marginal spines and a few setae; outer ramus shorter, outer margin lined distally with 3-4 short spines.

Telson lobes basally one-fourth fused, narrowing distally, margins distally with 4-6 short spines, apices acute.

Coxal gills large, sac-like, weakly pleated, on peraeopods 2-5, smaller on peraeopods 6 & 7. Brood plates sublinear.

Mature male undescribed.

Etymology: The root name refers to the genus of sponges, *Mixilla*, with which the amphipod species appears to be commensally associated.

Distribution: Known only from the Barkley Sound region of Vancouver I. Commensal on *Demospongia* (*Mixilla incrustans*)

Taxonomic Commentary: The species is closely related to *P. carinata* within the North American taxonomic complex of species. *P. mixillae* is distinguished from it by characters provided in the key (p. 40), by the somewhat less strongly reduced palp of the maxilliped, and by the more setose inner ramus of uropod 3.

WESTERN PACIFIC SPECIES OF *POLYCHERIA*.

The principal character states of the three species of *Polycheria*, previously described and figured from the western Pacific region, are here summarized for inclusion in analysis of relationships of the North American Pacific fauna (see also Table III, and Fig. 31).

Polycheria japonica Bulychева
(Fig. 23)

Polycheria japonica Bulychева, 1952: 233.—Barnard & Karaman, 1991: 272.

Taxonomic commentary: The original description and figures were based on a male specimen, but pertinent non sexual character states are here summarized:

Fused urosome segments 2 & 3 bearing small dorsal spines and paired lateral ridges, antero-laterally masked by posterior projection of urosome segment 1. Antenna 1, peduncular segment 3 longer than adjacent flagellar segments.

Mandible, left and right molars unequally reduced. Maxilla 1, outer plate with 9 apical spines; palp large. Maxilla 2, inner plate strongly setose. Maxilliped, palp medium, slightly exceeding tall outer plate.

Coxae 1 & 2 anteriorly rounded below. Coxa 3 lacking anterior process. Gnathopod 1, propod relatively short, deep; palm large, not exceeded by dactyl. Gnathopod 2, propod slender, subequal in length to carpus, palm distinct.

Peraeopods 3-7, segment 5 larger (not smaller) than segment 6; bases stout, somewhat broadened.

Pleon plates 2-3, hind corners acuminate. Uropod 2, outer ramus the shorter. Uropod 3, outer ramus the shorter, outer margin spinose. Telson lobes narrowing distally, fused in basal one-sixth, margins weakly spinose.

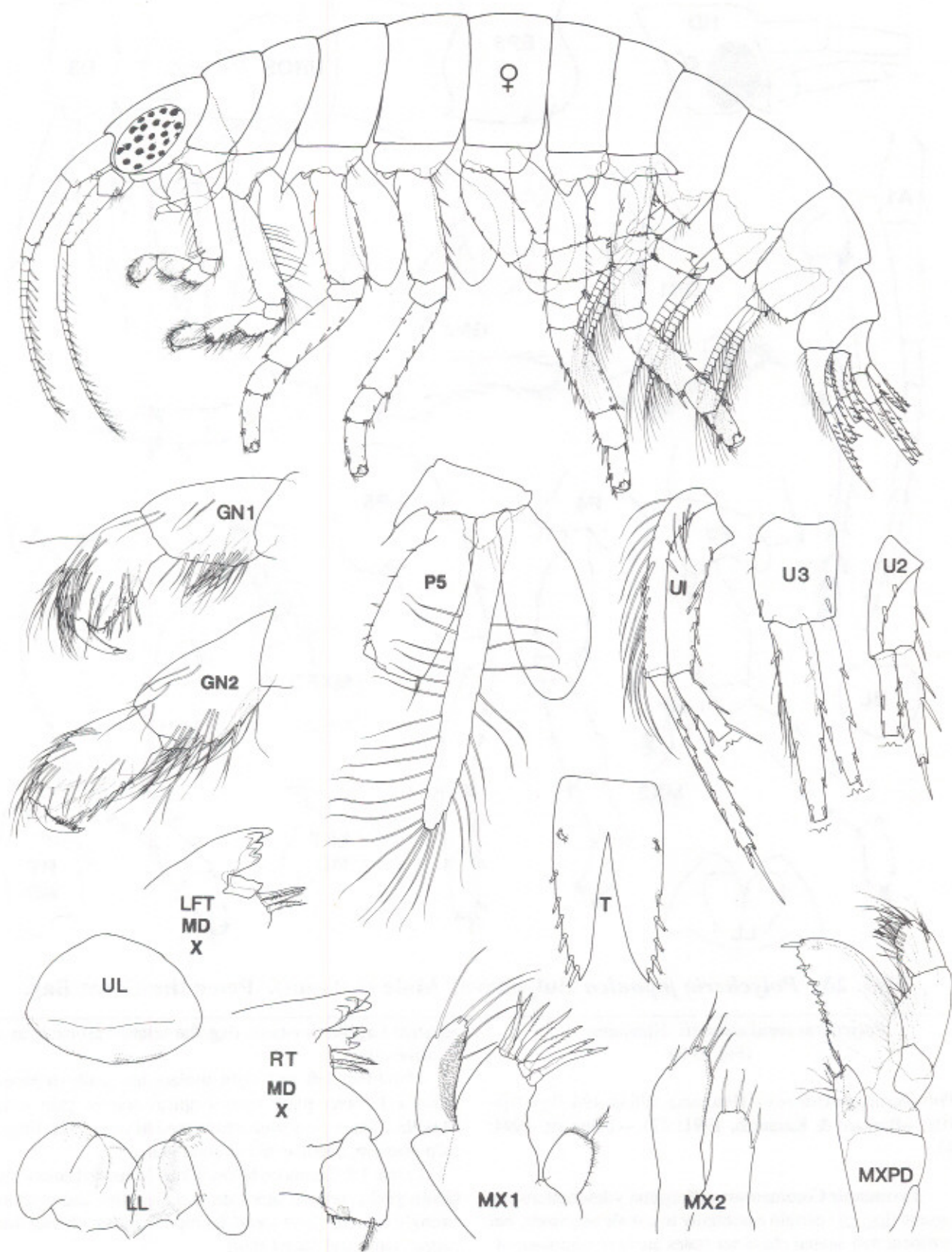


FIG. 22. *Polycheria mixillae*, new species. Diana I., Barkley Sound. Female ov (5.0 mm)

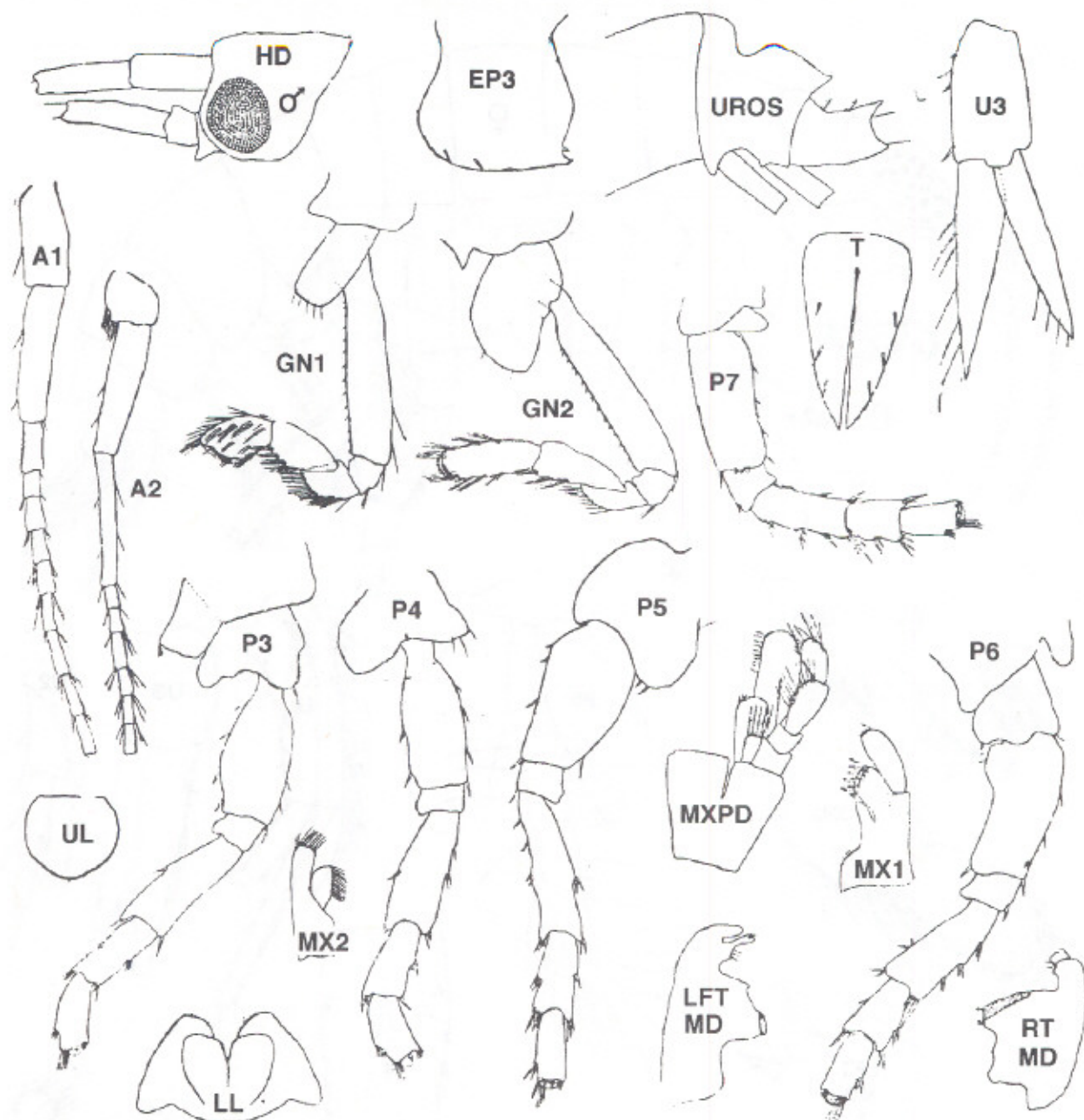


FIG. 23. *Polycheria japonica* Bulycheva. Male (5.0 mm). Peter-the-Great Bay.

Polycheria amakusaensis Hirayama
(Fig. 24B)

Polycheria amakusaensis Hirayama, 1984a: 194, figs. 106-108.—Barnard & Karaman, 1991: 271.—Ishimaru, 1994: 43.

Taxonomic Commentary: Hirayama's descriptions and figures (*loc. cit.*) pertain essentially to a male specimen, but pertinent non-sexual character states are here summarized:

Fused urosome segments 1 & 2 with paired lateral ridges, basally masked by posterior projection of urosome segment 1. Antenna 1, peduncular segment 3 longer than

adjacent flagellar segment; flagellar setation probably as in *P. orientalis*.

Mandible, left and right molars unequally reduced. Maxilla 1, outer plate with 9 apical spines; palp long. Maxilla 2, inner plate with strong medial setae. Maxilliped palp medium, about as tall as outer plate.

Coxae 1 & 2 rounded below. Coxa 3 rounded anteriorly. Gnathopod 1, propod subovate, lacking palm; dactyl short, strongly curved. Gnathopod 2, propod slender, shorter than carpus, palm and dactyl short.

Pereopods 3-7, segment 5 larger (not smaller) than segment 6; bases little broader than distal segments except in pereopod 5.

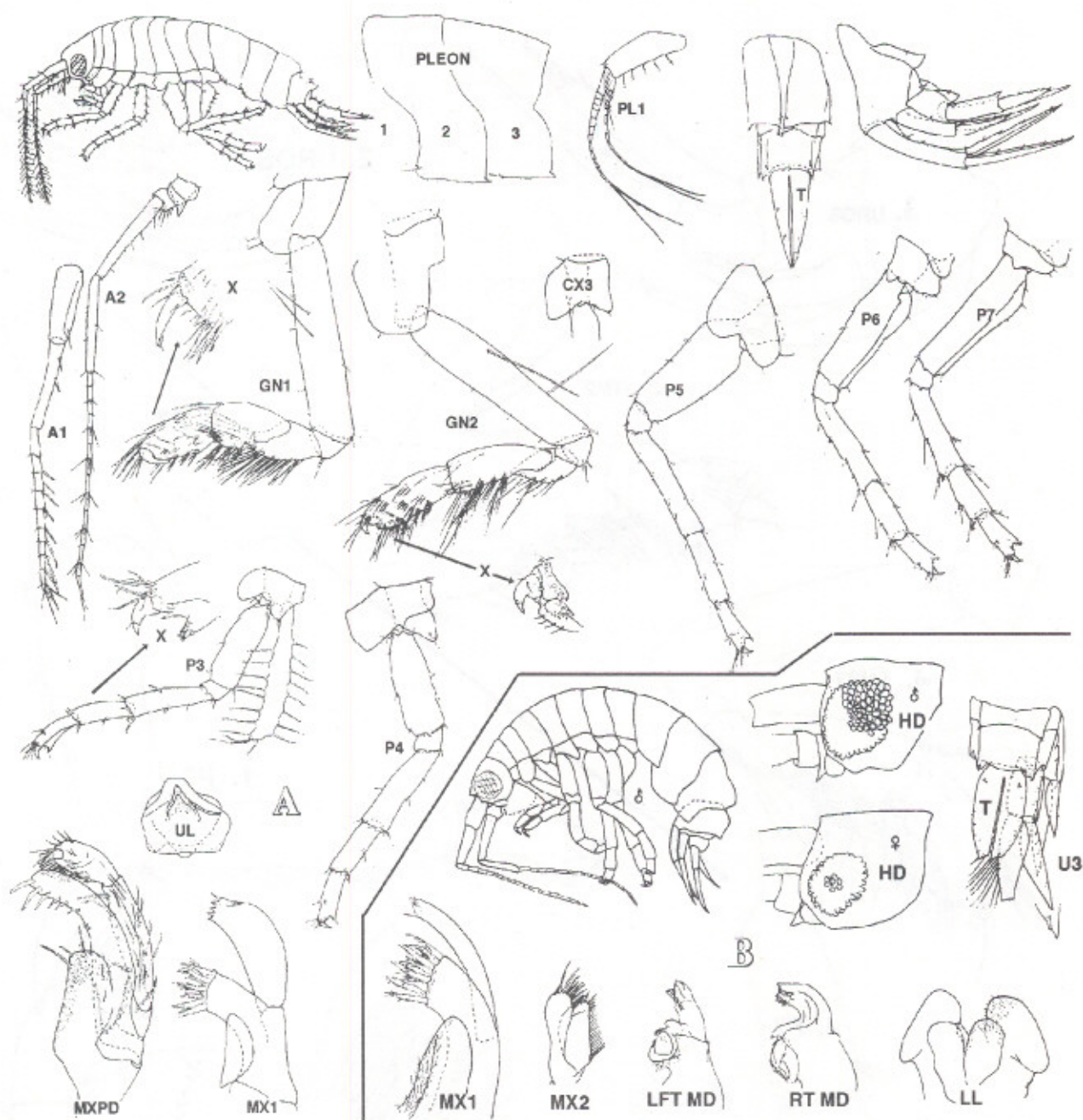


FIG. 24. *Polycheria* species. West Kyushu, Japan. (after Hirayama, 1984).

A. *P. orientalis* Female (4.5 mm). B. *P. amakusaensis* Male (4.5 mm).

Pleon plates 2-3, hind corners acuminate. Uropod 1, rami subequal. Uropod 2, outer ramus the shorter. Uropod 3, outer ramus slightly the shorter, outer margin weakly spinose. Telson lobes of female not described (probably as in *P. orientalis*).

Polycheria orientalis Hirayama (revised status)
(Fig. 24A)

Polycheria atollis orientalis Hirayama 1984a: 187, figs. 101, 103-105.—Barnard & Karaman, 1991: 272.—Ishimaru, 1994: 43.

Taxonomic Commentary: The pertinent taxonomic character states of Hirayama's description and figures, based on a female specimen, are summarized here:

Fused urosome segments 1 & 2 (one illustration shows an inter-segmental line!) with small spines and paired lateral ridges, based partly masked by posterior projection of urosome 1. Antenna 1, peduncular segment 3 longer than adjacent flagellar segment; flagellum richly armed with feeding setae.

Mandible, left and right molars not shown, probably as in *P. amakusaensis*. Maxilla 1, outer plate with 9 apical spines; palp large. Maxilla 2, inner plate marginally setose.

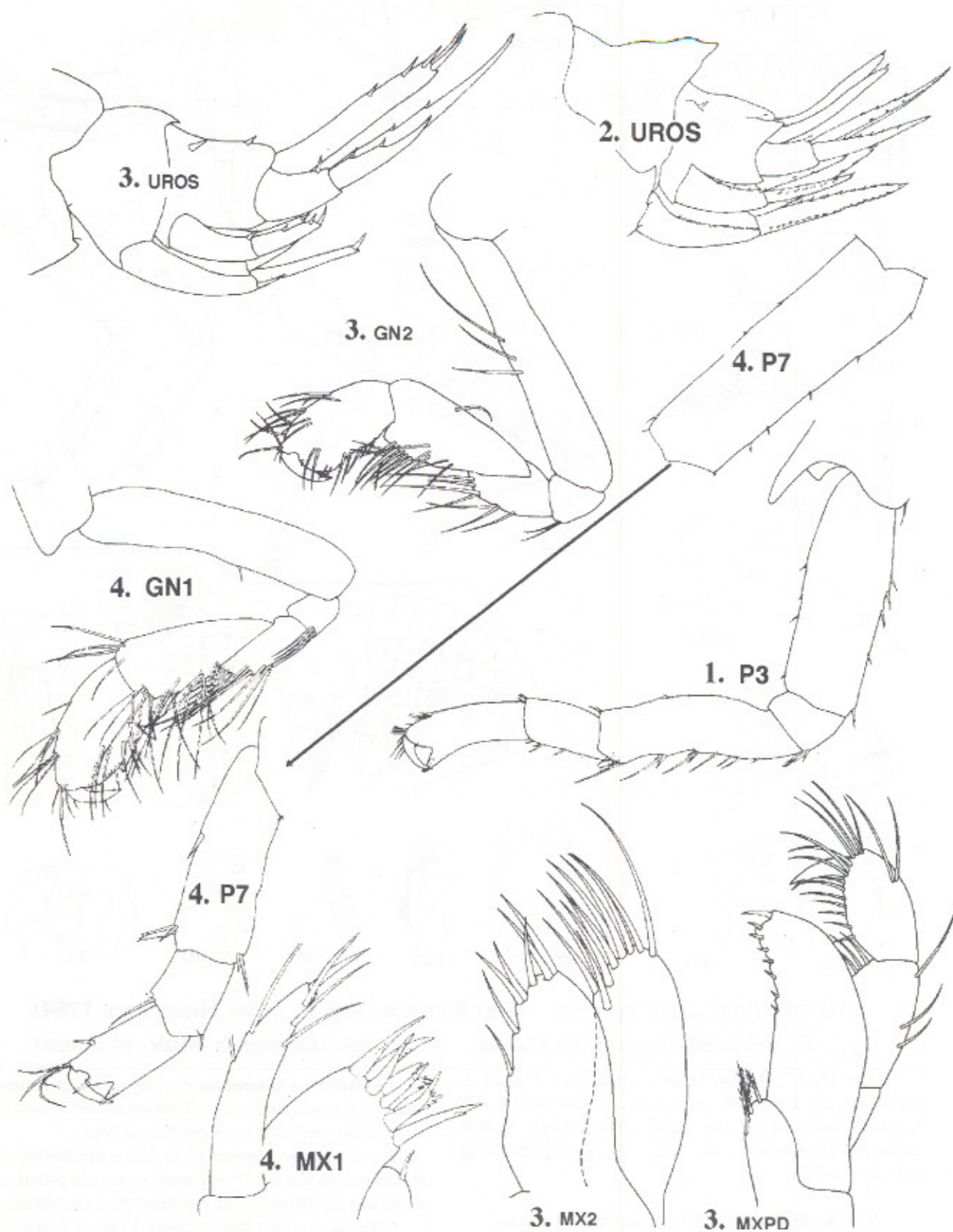


FIG. 25. *Polycheria antarctica* species complex 1. *acanthopoda* Thurston. 2. *dentata* Schell. 3. *gracilipes* Schell. 4. *nudus* Holman & Watling. (modified from Holman & Watling, 1983)

Maxilliped, palp slightly exceeding tall outer plate.

Coxae 1, 2, & 3 rounded antero-ventrally. Gnathopod 1, propod and carpus subequal; palm short, barely exceeded by dactyl. Gnathopod 2, propod shorter than carpus; palm small; dactyl very small, hook-like.

Peraeopods 3-7, segment 5 little shortened, distinctly longer than segment 6; bases sublinear but broader than in *P. amakusaensis*.

Pleon plate 2-3, hind corners acuminate. Uropod 1, rami subequal. Uropod 2, outer ramus the shorter. Uropod 3, outer ramus the shorter, outer margin weakly spinose. Telson lobes long, narrowing distally, fused in basal one-eighth, margins weakly spinose.

EXTRALIMITAL SPECIES

Polycheria antarctica (Stebbing) (Fig. 25.)

Dexamine antarctica Stebbing 1875: 184.

Tritaeta antarctica Stebbing 1888: 451

Polycheria antarctica Stebbing, 1906: 520, figs. 90, 91.—Schellenberg, 1931: 214.—Thurston, 1974: 18.—Holman & Watling, 1983: 221, figs. 6-9 (including forms *acanthopoda* Thurston; *dentata* Schellenberg; *gracilipes* Schellenberg; *nudus* (Holman & Watling).—Barnard & Karaman, 1991: 271.

Taxonomic Commentary: Pertinent taxonomic character states from an assemblage of "formae" of *P. antarctica* (cf. Holman and Watling, 1983), restored as distinct species of the *antarctica* complex by Barnard & Karaman (*loc. cit.*), provide broader perspective to the analysis of North Pacific species relationships (p. 61, fig. 31).

Fused urosome segments 2 & 3 dorsally with 4 spines, and paired lateral ridges. Urosome 1 with low dorsal carina, not produced postero-laterally to conceal base of urosome 2. Antenna 1, peduncular segment 3 slightly longer than adjacent flagellar segment; antennal flagella setose.

Mandibular molars probably unequally reduced (cf. illustration of Stebbing, 1906). Maxilla 1, outer plate with 9 apical spines; palp medium, slightly shorter than outer plate. Maxilla 2, inner plate with sparse inner marginal setae. Maxilliped, palp little reduced, exceeding tall outer plate.

Coxae 1 & 2 rounded below. Coxa 3 with strong antero-ventral process. Gnathopod 1, propod slender shorter than carpus; palm medium, little exceeded by dactyl. Gnathopod 2, propod shorter than carpus, palm relatively large, not exceeded by dactyl.

Peraeopod 3-7, segment 5 reduced, shorter than 6; bases sublinear, little broader than distal segments.

Pleon plate 2 & 3, hind corners weakly acuminate. Uropod 1, inner ramus distinctly the shorter. Uropod 2, rami subequal. Uropod 3, outer ramus much the shorter, outer margin nearly bare. Telson, lobes elongate, separated nearly to base, margins distally bare or weakly spinose, apices each with spine.

DEXAMINOCULINAE, new subfamily (see Fig. 2(b);26)

Incertae sedis. Barnard, 1969a: 480, fig. 173a.

Dexaminidae (part) Ledoyer, 1979: 65.—Lowry, 1981: 190. Prophiantinae Barnard & Karaman, 1991: 273 (key) (part).

Type genus: *Dexaminoculus* Lowry 1981: 191. (*Sphaerophthalmus* Spandl, 1923).

Diagnosis: An Indo-Pacific monotypic group, of unusual morphology, about which little is known except for the studies of Lowry (*loc. cit.*).

Body smooth or weakly toothed on peraeon. Pleon segments and urosome 1, each with mid-dorsal carination and postero-lateral marginal teeth or cusps. Urosome segments 1 & 2 ridged mid-dorsally and mid-laterally. Rostrum medium, slender. Eye large, on produced lateral cephalic lobe. Antenna 1 elongate (both sexes), accessory flagellum vestigial. Antenna 2 very short, flagellum vestigial (female); elongate, with peduncular brush setae (male).

Mouthparts nearly regularly dexaminid. Mandibular molar triturative, blades few. Maxilla 1, outer plate with 11 apical spines. Maxilla 2, plates not slenderized. Maxilliped, inner plate small; palp 3-segmented (female).

Coxae 1-4 medium, unequal, 3 smallest (allowing for respiratory current exit?), lower margins crenulate and/or setose. Coxa 5 large, anterolobate. Gnathopods dissimilar in size and form, distinctly subchelate. Gnathopod 1, propod sexually dimorphic, somewhat as in the typical dexaminid, but with the dorsal notch reduced to a shallow depression, and the palm deeply excavate, rather than convex. Peraeopods 3-7 slender, regular (not subchelate); peraeopod 5 slightly the longest. Peraeopods 5-7, bases dissimilar, variously broadened and lobate below; segment 5 not shortened; dactyls slender.

Pleon plates large; pleon plates 2 & 3, postero-lateral margin toothed, hind corners acuminate, hooked. Pleopods not described. Uropods 1 & 2 large, regular; uropod 2 short. Uropod 3, rami large, broadly lanceolate. Telson large, elongate, lobes not diverging apically.

Coxal gills and brood plates not described.

Species: *Dexaminoculus acutipes* Ledoyer, 1979 (Madagascar); *D. cavimanus* Ledoyer, 1982 (Madagascar); and *D. groebbeni* (Spandl, 1923) (Lowry, 1981) (Madagascar to Australia).

Taxonomic and Biogeographic Commentary: The genus *Dexaminoculus* was first described as *Sphaerophthalmus* by Spandl (1923) and placed in taxonomic category *incerta sedis* by Barnard (1969a). Two further species were described, both from Madagascar, by Ledoyer (1979, 1982). The genus is narrowly Indo-Pacific, not yet known from Japan and the North Pacific region, but might be anticipated at the northern limit of coralline substrata.

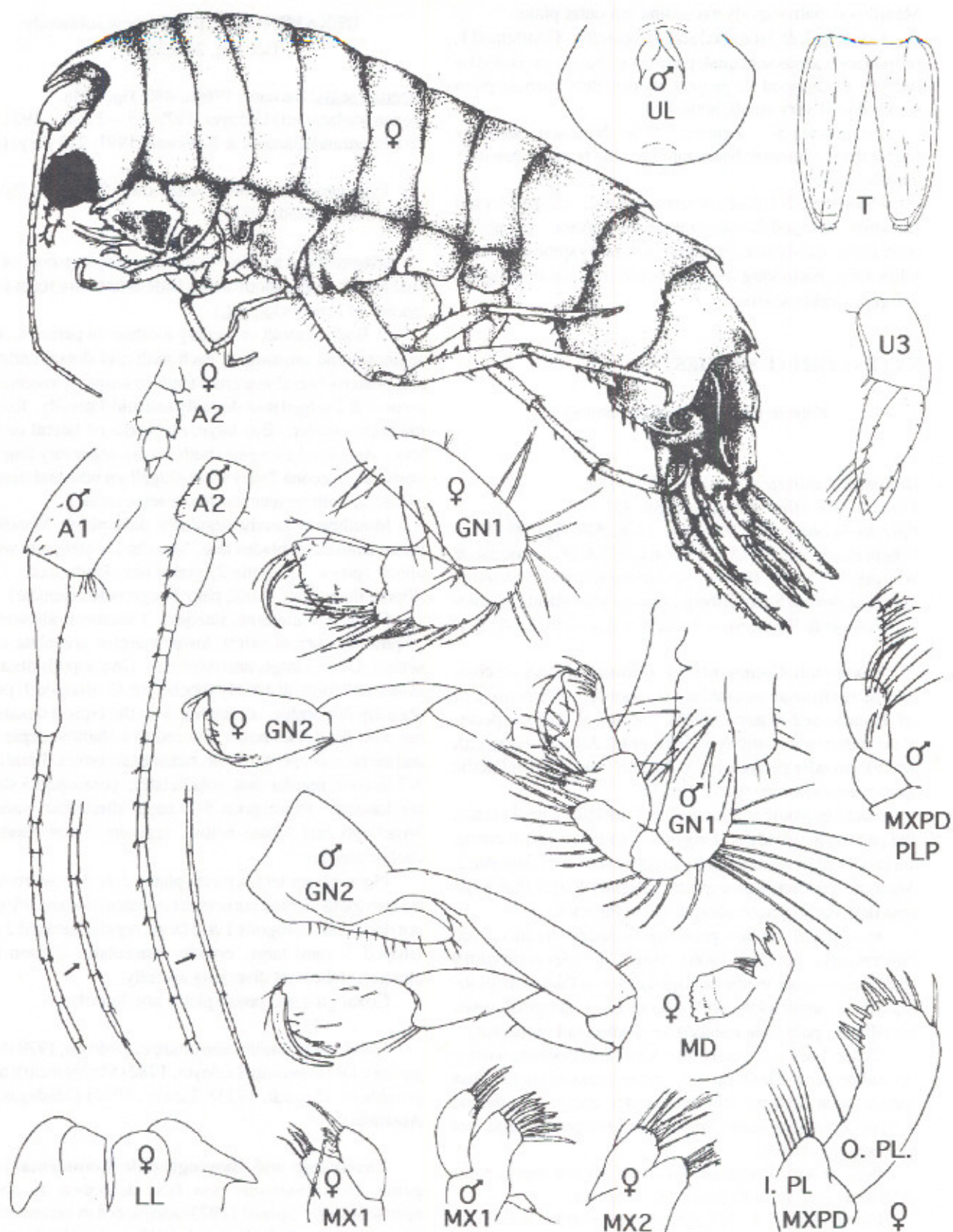


FIG. 26. *Dexaminoculus grobbeni* (Spandl). Female (3.6 mm) Male (3.9 mm)
Great Barrier Reef. (after Lowry, 1981).

The genus was renamed and fully redescribed by Lowry (*loc. cit.*), based on more complete material from the Great Barrier Reef of Australia (Fig. 26). He likened it most closely to the genus *Dexaminella* Schellenberg (1928). On questionable grounds, Barnard & Karaman (1991) placed the genus within their realigned subfamily Prophliantinae. However, as Lowry (*loc. cit.*) and Ishimaru (1987) concluded, the balance of character states of *Dexaminoculus* are closer to the true dexaminiins, *Dexamine*, *Paradexamine* and especially *Dexaminella* (Figs. 2(c); 29). Particularly significant is the form of the coxal plates, pleon carination, and the sexually dimorphic gnathopod 1, as well as mouthpart morphology. However, the extreme location of the eye is non dexaminiin, and the lack of subchelae on the peraeopods is non polycheriin. The authors therefore propose the new subfamily Dexaminoculinae to facilitate recognition of its distinctive, major, taxonomic differences.

Prophliantinae Nicholls (see Fig. 2(d))

Prophliantidae: Nicholls, 1939: 312.—Barnard, 1969a: 432.—Bousfield, 1982: 278.—Ishimaru, 1994: 43.
Dexaminidae (part): Barnard, 1970a: 163.—Bellan-Santini, 1982: 212.
Dexaminidae (Prophliantinae) Barnard, 1970: 161.—Ishimaru, 1987: 1413.—Barnard & Karaman, 1991: 273.

Type genus: *Prophlias* Nicholls, 1939: 312.

Genera: *Guernea* Chevreux, 1887: 302 (= *Prinassus*, = *Dexamonica*); *Haustoriopsis* Schellenberg, 1938: 12.

Diagnosis: Body small, short, broad, surface often with rugose integument. Peraeon with low mid-dorsal carina (part or all), but no dorsal processes. Urosome segment 1 may be fused with fused segments 2 & 3. Rostrum very short. Anterior head lobe mainly rounded. Eyes pigmented, medium. Antenna 1 (female) short, peduncular segment 2 shorter than 1. Accessory flagellum minute or lacking. Antenna 2 (female) short; in male, peduncle short, segment 4 broad, flagellum elongate.

Mouthparts modified. Lower lip, inner lobes distinct. Mandible; molar variously reduced or modified; spine row lacking. Maxilla 1, palp 1(2) segmented; outer plate with 7-9 apical spines. Maxilla 2, plates modified, reduced. Maxilliped, outer plate large, inner plate small, palp shortened.

Coxae 1-4 slender, deep; coxa 1 shortest. Coxa 5 very large. Gnathopods slender, weakly subchelate; carpus usually longer than propod; palmar margins small, distinct. Gnathopod 1, propod not sexually dimorphic.

Peraeopods 3 & 4 simple, not subchelate, segment 5 not strongly shortened. Peraeopods 5-7 short, generally dissimi-

lar in form but little in size (peraeopod 7 shortest); bases variously broadened, unlike; segment 5 little shortened, often broadened; dactyls simple, short to medium.

Pleopods small; peduncle broadened, rami short. Uropods 1 & 2 short; rami usually unequal in length. Uropod 3 short, margins spinose (weakly setose in male).

Telson lobes medium, separated nearly to base, not diverging, apices truncate, spinose.

Coxal gills simple, not strongly pleated or lobate, on peraeopods 2-6 only. Brood plates small, linear, with apical setae.

Taxonomic Commentary: The authors concur with the decision of Barnard (1970a), followed by Hirayama (1984, 1986), to transfer *Guernea* from family Dexaminidae to the Prophliantinae. Cluster analysis (p. 56, Fig. 29) further confirms its relatively close morphological similarity to *Prophlias* and *Haustoriopsis*. *Guernea* is a complex of diverse species groupings, some of which have been given formal generic and/or subgeneric status (*Prinassus* in the N. Pacific region and *Guernea* elsewhere). However, the authors also agree with the decision of Bellan-Santini (1983) and Ishimaru (1987) to resubmerge the names *Prinassus* and *Dexamonica* in the synonymy of *Guernea* Chevreux, 1887.

Barnard and Karaman (1991, *loc. cit.*) reduced the Prophliantidae to subfamily status within the Dexaminidae. This decision is supported by the present analysis (p. 56). As noted by Ishimaru (1987), those two authors also relegated the genus *Dexaminoculus* to the Prophliantinae on dubious grounds, and as noted here, without suitable concordance with their own subfamily diagnoses. The coral-dwelling *Dexaminoculus* is here considered distinctive at subfamily level (above). In balance, its phyletic affinities are closest to the primitive, nestling Dexamininae, and rather remote from the fossorially specialized and apomorphic Prophliantinae.

Guernea Chevreux

Guernea Chevreux, 1887b: 302.—Stebbing, 1906: 521 (part).—Barnard, 1970a: 11, figs.—Hirayama, 1985: 395.—Bellan-Santini, 1982: 225.—Ishimaru, 1987: 1395.—Ishimaru, 1994: 43.

Guernea (*Guernea*) J. L. Barnard, 1970a: 169.—Hirayama, 1985: 1.—Hirayama, 1986: 488.—Barnard & Karaman, 1991: 274.

Prinassus Hansen, 1888: 82.

Guernea (*Prinassus*) J. L. Barnard 1970a: 169.—Hirayama, 1985: 8.—Hirayama, 1986a: 493.—Barnard & Karaman, 1991: 275.

Dexamonica J. L. Barnard, 1958: 130, pls. 26-27.—Barnard, 1969a: 203.

Type Species: *Helleria coalita* Norman, 1868.

Species: About 24 described species and subspecies world-wide (Barnard & Karaman, 1991, updated). The following 11 species are recorded from the North Pacific region: *G. ezoensis* Ishimaru, 1987; *G. longidactyla* Hirayama, 1986a; *G. mackiei* Hirayama, 1986a; *G. magnaphilostoma* Hirayama, 1985; *G. minor* Ishimaru 1987; *G. nullispina* Hirayama, 1885; *G. quadrispinosa* Stephensen, 1944; *G. rectocephalus* Hirayama, 1985; *G. reduncans* J. L. Barnard, 1958; *G. sombati* Hirayama, 1986a; *G. terelamina* Hirayama, 1985; *G. tomiokaensis* Hirayama, 1985.

Diagnosis: Posterior peraeon and all pleon segments weakly carinated and/or posteriorly mucronate. Urosomite 1 separate, with mid-dorsal keel or hump (both sexes). Urosomites 2 & 3 coalesced, variously with small dorsal spines. Rostrum very short; anterior head lobe sharply rounded. Eyes medium, rounded, weakly faceted. Antennae (female) short. Antenna 1, flagellum 4-8 segmented; accessory flagellum minute or lacking.

Lower lip large, outer lobes with prominent shoulder cones. Mandibular molar variously triturative, often complexly divided; left lacinia 4(5) dentate. Maxilla 1, palp 1(2)-segmented, outer plate with 7-9 apical spines, inner plate 0(1)-setose. Maxilla 2, inner plate small, 2-5 setose. Maxilliped, inner plate very short, apex with 2-5 long setae; outer plate large, palp 4-segmented, dactyl short.

Coxae 1-4 medium, narrow, strongly overlapping, rounded below. Coxa 5 very large, deep, postero-lobate. Gnathopods 1 slightly smaller than 2, basis with distinct proximal "buccal bend"; carpus relatively short and deep, little longer than propod; palm distinct.

Peraeopods 3 & 4, segment 5 shorter than 4 & 6, posterior margin spinose; dactyls medium. Peraeopods 5-6 subsimilar in form and length; segment 5 not shortened, dactyls various, usually reversed. Peraeopod 7, basis very broad; segments 4 & 5 broadened (not greatly, and/or asymmetrically, as in *Haustoriopsis*), margins strongly setose; dactyl short.

Pleon plates 1-3, hind corners rounded, or squared. Uropods 1 & 2, outer ramus the longer (usually), apices with long apical spine. Uropod 3, rami short, subequal, inner margins spinose (setose in male). Telson lobes medium, not diverging, outer margin and apex variously armed with setae and/or spines.

Distribution: Mainly tropical and warm-temperate (Indo-Pacific and tethyan) coastal shallows; fossorial in fine sediments. Of the 24 species and subspecies described to date world-wide, 12 (one-half) have been recorded from the North Pacific region, but only one of these from the North American Pacific coast.

Taxonomic Commentary: In balance of character states, *Guerneia* appears more closely related to the type genus *Prophlias* than to the more highly specialized genus *Haustoriopsis*. It differs from *Prophlias*, however, in its stronger

gnathopods, unexpanded segment 4 of peraeopod 5, and its dorsally carinated, unfused urosome segment 1.

Guerneia reduncans (J. L. Barnard)

(Fig. 27)

Dexamonica reduncans J. L. Barnard, 1958: 130, pls. 26, 27.—Staude, 1987: 382.

Guerneia (*Prinassus*) *reduncans* Barnard, 1970a: 173, figs. 1-3—Barnard & Karaman, 1991: 275.

Guerneia reduncans Austin, 1985: 604.

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands, ELB Stns, 1957: H4a mouth of Yakoun Bay, July 19 - 1 female with juveniles; W11, Head of Gudal Bay, Graham I., July 28 - 1 imm.

Vancouver I., ELB Stn. B27, Dodger Channel, SW end Diana I., July 8, 1976 - 1 male, 1 female ov. Off McCauley, Pt., Victoria, B. C., G. W. O'Connell Stns., Aug. 28, 1976: W10B - 1 male; W156B - 1 male, 3 females (ov) (fig'd. specimens). Off Victoria, C. Low coll., Aug., 1981 - 3 males, 5 females, 10 imm.

Diagnosis: Female ov. (2.4 mm); male (2.5 mm). Peraeon segments 6 & 7, and pleon segment 1-3 with low mid-dorsal ridge, slightly acute behind. Urosomite 2 with recurved mid-dorsal carina. Fused urosomites 2 & 3 somewhat humped mid-dorsally, with 2-4 small spines. Eye medium, subovate, about 25-faceted. Antenna 1, flagellum 5-segmented; peduncular segments 1-3 (male), anterior margins minutely crenulated; segment 1 deep, posterior margin distally with clusters of longish brush setae. Antenna 2, flagellum 3-segmented; flagellum (male) elongate (20+ segments), peduncular segments 4 & 5 enlarged, anterior margin of 4 with clusters of short brush setae.

Mandible, grinding surface of molar modified but entire, distal plumose seta short; left lacinia 4-dentate. Maxilla 1, outer plate with 7 apical spines; palp 1-segmented, apex with 2 setae. Maxilla 2, inner plate narrow, with 5 marginal setae. Maxilliped, inner plate with 3 long apical setae; palp segment 3 and short dactyl exceeding tall outer plate.

Coxae 1-4, lower margins finely crenulate and weakly setose. Coxa 5, anterior lobe small rounded, hind lobe very large, deeply rounded. Gnathopod 1, carpus and propod relatively short, deep, subequal in length; propod widening distally to convex palm, with 3-4 postero-distal spines. Gnathopod 2 slightly larger than gnathopod 1; carpus and propod slightly more slender and elongate; palm of propod with 3 postero-distal spines.

Peraeopods 3 & 4, segment 5 distinctly shorter than 4 & 5, hind margin with 3 stout spines increasing distally; dactyls medium. Peraeopods 5 & 6, segments 5, 6, and dactyls reversed; basis of peraeopod 5, hind lobe not strongly produced below; segment 4 normally broadened. Peraeopod 6,

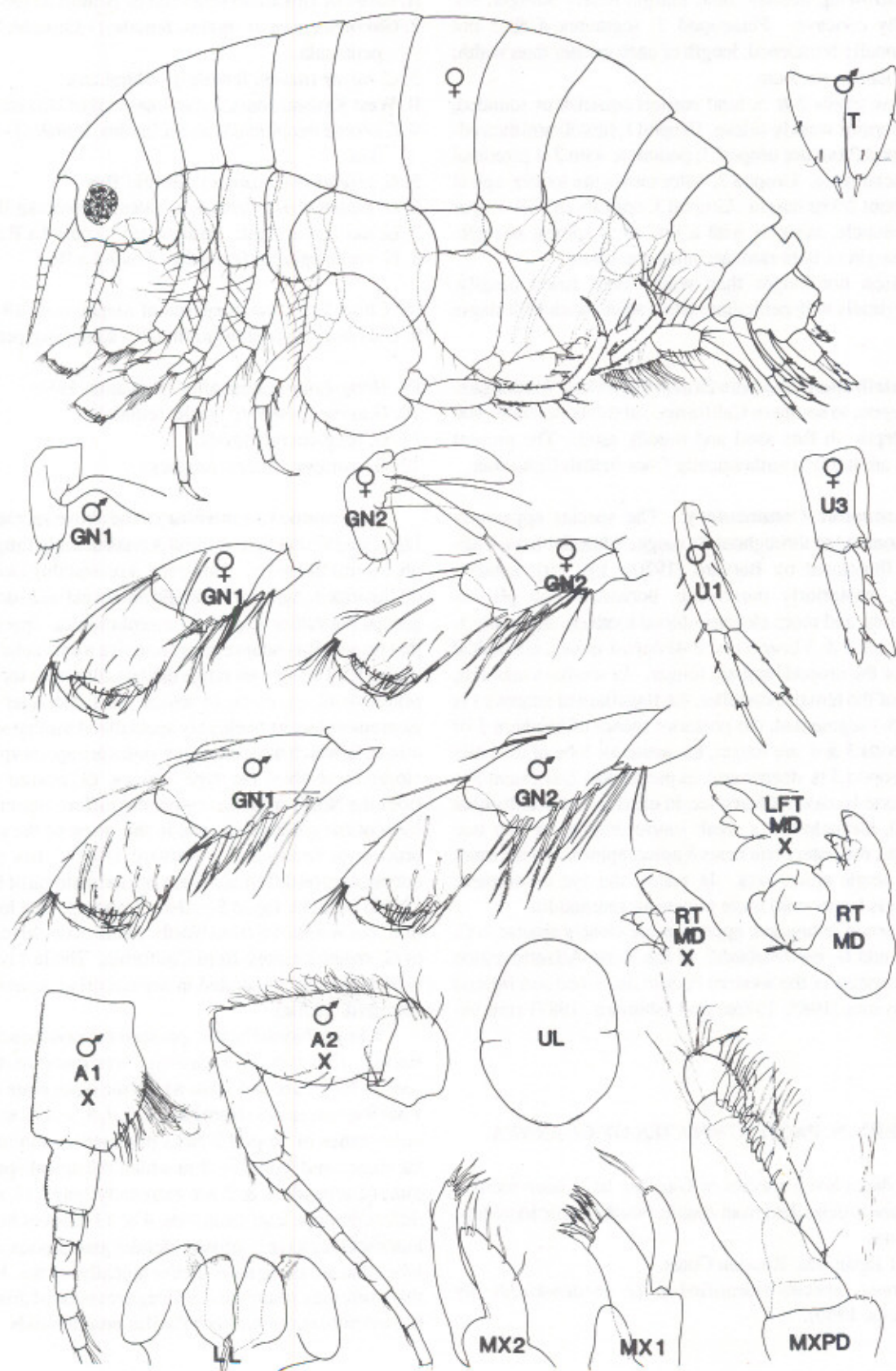


FIG. 27. *Guernea reduncans* (Barnard). Off Clover Pt., B. C. Fem. (2.3 mm) Male (2.0 mm)

basis narrowing distally, hind margin nearly straight, not markedly concave. Peraeopod 7, segments 4 & 5 not exceptionally broadened, length of each greater than width; dactyl slender, medium.

Pleon plates 2 & 3, hind corners squarish or rounded, lower margins weakly setose. Uropod 1, tips of rami exceeding uropod 2 but not uropod 3; peduncle with 3-4 proximal outer facial setae. Uropod 2, outer ramus the longer, apical spine about 2/3 its length. Uropod 3, rami about 50% longer than peduncle, margins with a few stout spines; in male, inner margin or both rami are plumose-setose.

Telson not longer than wide, lobes fused basally, submarginally with penicillate setae, apices each with single spine.

Distribution: Southern British Columbia, Washington and Oregon, to southern California, subtidally to about 100 m. in depth, in fine sand and muddy sand. The present records are the first authentically from British Columbia.

Taxonomic Commentary: The species apparently varies somewhat throughout its range. Material from California, illustrated by Barnard (1970a, *loc. cit.*), exhibits distinct, posteriorly mucronate, peraeonal and pleonal carinations, and more elevated dorsal tooth on urosomite 1. Urosomites 2 & 3 bear 6 (vs. 2-4) dorsal spines, and apical spines of the uropod rami are longer. In southern material, the eye of the female is smaller, the flagellum of antenna 1 is 6- (vs. 5-) segmented, the posterior spines of segment 5 of peraeopods 3 & 4 are longer, the posterior lobe of the basis of peraeopod 5 is deeper and, in peraeopod 7, segment 5 is shorter and broader. Moreover, in maxilla 1 of Californian material, the palp has a weak suture dividing it into two segments, the outer plate bears 8 apical spines, and the inner plate a single apical seta. In males, the eye of northern material is larger with more numerous ommatidia.

Guernea reduncans appears more closely similar to *G. coalita* and *G. nordenskioldi* of the North Atlantic region than to species of the western Pacific described and figured by Hirayama (1985, 1986a) and Ishimaru (1987) (see below).

WESTERN N. PACIFIC SPECIES OF GUERNEA

To date eleven species of *Guernea* have been recorded and/or newly described from Asiatic North Pacific localities, as follows:

I. Sea of Japan Sea, Russian Coast.

1. *Guernea* species (identified as *G. nordenskioldi* by Bulicheva, 1955).

II. Coast of Hokkaido (material of Ishimaru, 1987).

2. *Guernea ezoensis* (males, females) - Otsuchi, Notsuke peninsula.

3. *G. minor* (males, females) - Shirahama.

II. West Kyushu coast, Japan (material of Hirayama, 1985):

4. *Guernea magnaphilostoma* (males, females) - Ariake Sea.

5. *G. terelamina* (female) - Shijiki Bay.

6. *G. tomiokaensis* (females, males) - Tomioka Bay.

7. *G. nullispina* (male, immatures) - Tomioka Bay.

8. *G. rectocephala* (females) - Tomioka Bay.

III. China Sea Coast (material of Stephensen, 1944).

9. *Guernea quadrispinosa* (male) - Liao-tung peninsula.

IV. Hong Kong (material of Hirayama, 1986).

10. *Guernea sombati* (male, female).

11. *G. longidactyla* (male).

12. *G. mackiei* (males, females).

Taxonomic Commentary: The above species from the Japan and China Seas exhibit a considerable range of morphological diversity. However, a reasonably close perusal of illustrated character states did not reveal well-defined subgroups but rather a series of morphological specializations that presumably adapt each species for a particular niche and life style. The species range phylogenetically from the relatively primitive *G. ezoensis*, in which most character states are plesiomorphic, to the highly specialized minute species, *G. minor*, in which most character states are apomorphic. None closely resembles the type species, *G. coalita* (Norman) from the North Atlantic region, but differs especially in the form of the gnathopods, and in the shape of the mid-dorsal process of urosome 1. Barnard (1970a) has previously commented on differences between the material of Bulicheva (1955) from the Japan Sea (No. 1, above), and his material of *G. nordenskioldi* from North Atlantic coastal regions, and of *G. reduncans* from California. The last two species were both fully illustrated in his extensive generic revision (Barnard, 1970a).

A key to North Pacific species is beyond the scope of this study. However, *G. reduncans* was found to differ from species Nos. 2, 6, and 10 in which the outer plate of maxilla 1 has 9 apical spines; from Nos. 3, 5, 7, 8, and 12 in which the outer ramus of uropod 3 lacks plumose swimming setae in the male; and from No. 9 in which the apical spines of the rami of uropods 1 & 2 are extremely long. *G. reduncans* differs perhaps least from Nos. 4 & 11 (above) but both the latter species have relatively slender gnathopods, and telson lobes that are marginally and/or apically setose. Hopefully, this study may stimulate a thorough revision of this challenging assemblage of western Pacific prophiantids.

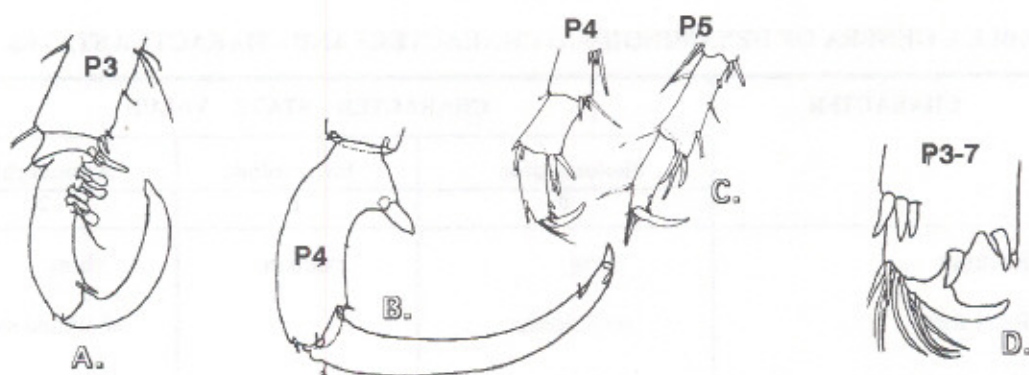


FIG. 28. Prehensile Peraeopods in Dexaminoidea
(modified partly from Vader, 1983)

A. *Nototropis falcatus* B. *Delkarlye enamalla* C. *Tritaeta gibbosa* D. *Polycheria obtusa*

Discussion and Conclusions.

This study treats the systematics and distributional ecology of some 12 species of dexaminoidean amphipod crustaceans occurring in North American Pacific coastal marine waters, from the Bering Sea to Northern California. This fauna is small and relatively minor in contrast to several large and diverse regional gammaroidean superfamilies previously treated (e.g. Gammaroidea (Bousfield, 1979); Ampeliscoidea (Dickinson, 1982, 1983); Corophioidea (Conlan, 1983); Phoxocephaloidea (Jarrett & Bousfield, 1994), and others of this series now in preparation (e.g. Talitroidea, Eusiroidea, Hadziroidea (Bousfield Staude, 1994). Moreover, regional dexaminoideans include only about 7% of the ~200 species described to date, world-wide. However, this small fauna is remarkable in containing: (1) a large component of the single most primitive subgroup, the subfamily Atylinae; (2) significant representation from the most advanced subfamily, the Polycheriinae; (3) only one species from the other six phylogenetically intermediate subfamily groups. Thus, in combination with counterpart dexaminoidean groups from the Asiatic North Pacific coastal marine region, this modest North American assemblage makes up in taxonomic and phyletic quality what it lacks in species numbers, and thereby provides a basis for review and reclassification of the entire world fauna not previously realized.

Natural relationships among species and generic groups are here tested more critically by means of a modification of the phenetic UPGMA (cluster analysis) system of Sneath and Sokal (1973). The modified but relatively unsophisticated system employs an overall criterion of phyletic similarity termed the Plesio-Apomorphic (P.-A.) Index in which low numbers signify phylogenetically primitive, and high numbers advanced, taxonomic groups. The system has been utilized effectively in similar studies by Conlan (1983), Staude (1986) and Jarrett and Bousfield (1994). Within the superfamily Dexaminoidea, analysis of generic similarities is based on 21 characters and corresponding 42 character states given in Table I (p. 57). The lepechinellids are here represented pragmatically by one genus, *Lepechinella*, mainly

because it contains more than 90% of the species, and the three other described genera do not show differences (from it) in the character states utilized in this analysis.

The resulting phenogram (Fig. 29) "clusters out" two main subgroupings at less than 50% similarity, viz. a primitive, thin-bodied, atylid family group (with P. A. indices of 9-24) on the left, and a relatively advanced, broad-bodied, dexaminid family group (with P.-A. indices of 15-29) on the right. The atylids are especially primitive in retaining a number of presumed ancestral features (e.g. Bousfield, 1983) such as basic body carination, peraeopods, pleopods, mouthparts, and pleated gill structure, whereas the dexaminoideans tend more strongly to reduction or loss of body carination, mouthpart armature, and modification of the peraeopods towards "prehensility" on the one hand (Fig. 28, above) or fossorial life style on the other (Fig. 2 (d), p. 7).

Within the Atylidae, four subgroups "cluster out" with paired character state similarities between 60 and 75%, that are here recognized at subfamily level. These include the very primitive large-bodied Atylinae (P.-A. Index of 9) on the one hand, and the advanced, small-bodied Anatylinae (P.-A. Index of 22-24) on the other. The other two groups, Nototropiinae and Lepechinellinae, intermediate in body size and phyletic positioning (P. A. indices of 16-19), trend to a more free-living, epibenthic and pelagic life style, with strong deep-water and abyssal components. The biogeographical significance of these phyletic relationships is noted below (p. 60).

Within family Dexaminidae, containing nearly twice the number of genera, four subfamily groupings are similarly recognized. These "cluster out" at slightly higher levels of character state similarity (60-77%). These subfamily groupings include the relatively primitive Dexamininae containing six relatively similar genera (P. A. indices of 15-24) on the left, and the advanced, highly specialized and commensal pair of genera comprising the Polycheriinae (P. A. indices of 27-29) on the right. The two phylogenetically intermediate subgroups (P. A. Indices of 19-21) encompass two subfamilies of widely differing morphologies and life styles, viz. the monotypic, coral-dwelling Dexaminoculinae, on the

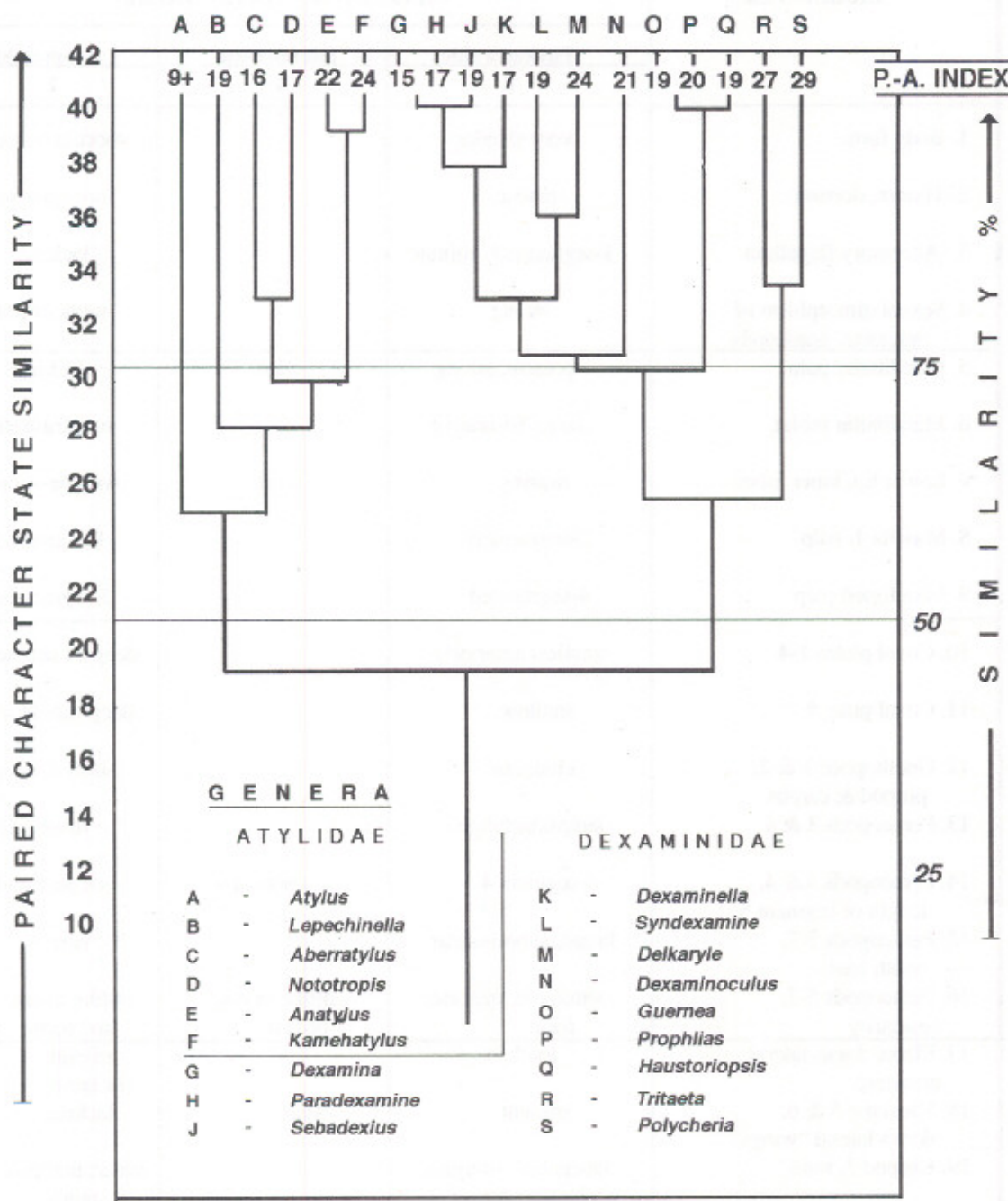
TABLE 1. GENERA OF DEXAMINOIDEA: CHARACTERS AND CHARACTER STATES

CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic	Intermediate	Apomorphic
	0	1	2
1. Rostrum	long	medium	short
2. Body form	very slender		short and stout
3. Thorax, dorsum	spinose		not spinose
4. Accessory flagellum	1-segmented	minute	lacking
5. Sexual dimorphism of antennae, gnathopods	strong		weak or none
6. Mandibular palp	present, strong	weak	lacking
7. Mandibular molar	large, tritulative		non-tritulative
8. Lower lip, inner lobes	lacking	weak	well developed
9. Maxilla 1, palp	2-segmented		1-segmented
10. Maxilliped palp	4-segmented		3-segmented
11. Coxal plates 1-4	smallest anteriorly		deepest anteriorly
12. Coxal plate 5	shallow		deep (about = 4)
13. Gnathopods 1 & 2, propod & carpus	elongate		short & deep
14. Peraeopods 3 & 4	simplidactylate.		subchelate
15. Peraeopods 3 & 4, length of segment 5	> segment 4	< segment 4	<< segment 4
16. Peraeopods 5-7, width basis	broad, suborbicular		narrow
17. Peraeopods 5-7, similarity	similar in size and form	unlike in size or form	unlike in size and form
18. Pleon, dorso-lateral armature	toothed		smooth (or nearly so)
19. Urosome 5 & 6, dorso-lateral "wings"	present	weak	lacking
20. Uropod 3, rami	lanceolate; margins plumose-setose		linear; margins spinose
21. Telson lobes	separate, converging		basally fused

one hand, and a complex of three small bodied, fossorial genera within the Prophliantinae on the other. The Dexaminoculinae and Polycheriinae are linked naturally to the Dexamininae by greater overall character state similarity of the peraeopods and most other body appendages, including similar sexual dimorphism of the propod of gnathopod 1, apparently unique to this family within all gammaridean

amphipod superfamilies (Fig. 2, p. 7). Close comparison of individual character states suggests that the Prophliantinae differ from the Dexamininae somewhat more strongly than semi-phyletic numerical taxonomic methodology actually reveals. This methodology may be arguably more susceptible to homoplasious or convergent similarities than cladistic analytical methodology. A broader cladistic analysis, not

FIG. 29. DEXAMINOIDEA: PHENOGRAM OF GENERA.



attempted in this regional study, may show greater phyletic significance to the differences, especially in gnathopod structure, and perhaps justify restoration of the Prophliantins to family level of recognition.

Within the monotypic genus *Atylus* (subfamily Atylinae), an amphi-North Pacific near-total assemblage of 10 species may be phenetically analyzed, based on 20 characters and character states outlined in Table II. The resulting phenogram (Fig. 30, p. 60) encompasses two not very closely similar subgroups, a primitive large bodied *carinatus-levidens* assemblage (P. A. Indices of 10-21) on the left, and a more

advanced, generally smaller bodied *collingi-tridens* assemblage (P. A. indices of 20-33) on the right. The most primitive members of the *carinatus* subgroup, *A. carinatus* and *atlassovi*, appear not far removed in basic morphology from large regionally occurring gammaroid amphipods (e.g. various Anisogammaridae, and the *Gammarus setosus-wilkitzkii* complex within family Gammaridae; see Bousfield, 1979). Within the *A. levidens* subcomplex, including *A. ekmani* and *A. bruggeni*, some reduction of mouthparts (e.g. mandibular palp) and specialization of body appendages (e.g. pectinate setation of gnathopod

TABLE II. SPECIES OF *ATYLUS*: CHARACTERS AND CHARACTER STATES.

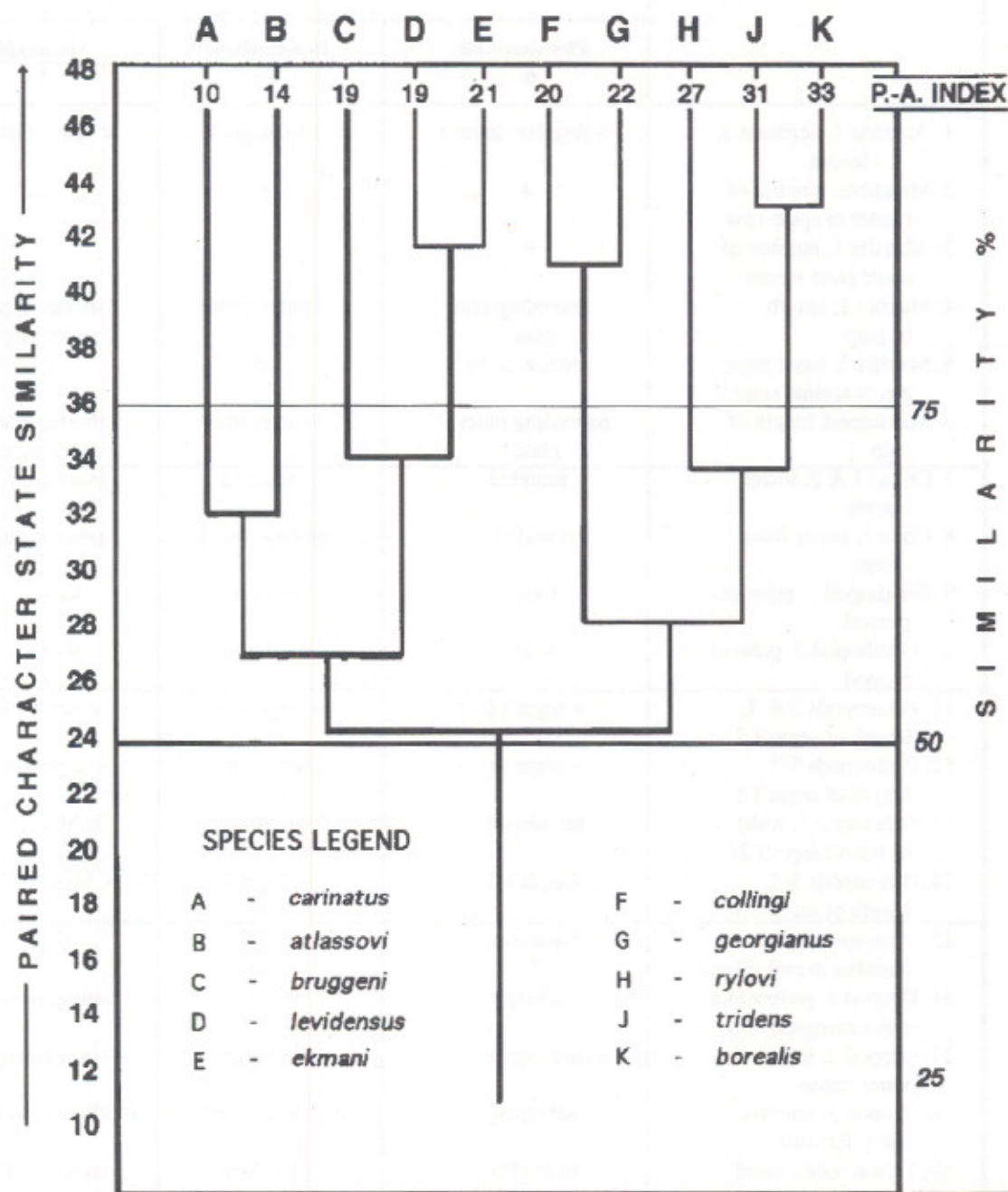
CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic	Intermediate	Apomorphic
	0	1	2
1. Body form	very slender		short and stout
2. Thorax, dorsum	spinose		not spinose
3. Accessory flagellum	1-segmented, minute		lacking
4. Sexual dimorphism of antennae, gnathopods	strong		weak or none
5. Mandibular palp	present, strong	weak	lacking
6. Mandibular molar	large, triturative		non-tritulative
7. Lower lip, inner lobes	lacking	weak	well developed
8. Maxilla 1, palp	2-segmented		1-segmented
9. Maxilliped palp	4-segmented		3-segmented
10. Coxal plates 1-4	smallest anteriorly		deepest anteriorly
11. Coxal plate 5	shallow.		deep (about = 4),
12. Gnathopods 1 & 2, propod & carpus	elongate		short & deep
13. Peraeopods 3 & 4	simplidactylate.		subchelate
14. Peraeopods 3 & 4, length of segment 5	> segment 4	< segment 4	<< segment 4
15. Peraeopods 5-7, width basis	broad, suborbicular		narrow
16. Peraeopods 5-7, similarity	similar in size and form	unlike in size or form	unlike in size and form
17. Pleon, dorso-lateral armature	toothed		smooth (or nearly so)
18. Urosome 5 & 6, dorso-lateral "wings"	present	weak	lacking
19. Uropod 3, rami	lanceolate; margins plumose-setose		linear; margins spinose
20. Telson lobes	separate, converging or straight.		basally fused, spreading

propods) is evident (Fig. 7). Within the *collingi* group, the more advanced *tridens* subgroup exhibits weakest body carination, and most strongly modified peraeopods in which character states trend, probably convergently, with comparable features of the Nototropiinae (Fig. 1(b)).

The North Pacific species of the highly specialized genus *Polycheria* (dexaminiid subfamily Polycheriinae) may

also be analyzed numerically on the basis of 20 characters and corresponding character states outlined in Table III (p. 61). Character states of the *P. antarctica* complex of species of southern oceans is included here for broader perspective on morphological relationships within the genus. The resulting phenogram (Fig. 31, p. 62) "clusters out" two major subgroups, a primitive *japonica* subgrouping of three west-

FIG. 30. PHENOGRAM OF SPECIES OF *ATYLUS*



ern Pacific species (P. A. indices of 8-19) on the left, and a highly advanced *osborni* subgroup (P. A. Indices of 26-28) on the left. The *osborni* subgroup exhibits significantly greater reduction of mouthparts and specialization of coxal plates, pereopods, and uropods, differences perhaps related to differing life styles in association with differing host organisms.

Although the combined North Pacific and *Polycheria antarctica* assemblages, *in toto*, represent only about one-third of the world-wide fauna, some tentative inferences may be drawn. The North American and Asiatic subgroups differ

very significantly from each other, clustering at less than 50% similarity, and perhaps meriting separate generic (certainly subgeneric) recognition of the North American assemblage. Such would seem further justified by the fact that the *antarctica* subgroup, closer to the generic type *P. tenuipes* Haswell from southern oceans, clusters much more closely with the Asiatic than with the North American Pacific *osborni* group. Hopefully, this limited study will point the way to a more broadly based solution to phyletic relationships and formal classification within subfamily Polycheriinae.

TABLE III. SPECIES OF *POLYCHERIA*: CHARACTERS AND CHARACTER STATES

CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic	Intermediate	Apomorphic
	0	1	2
1. Antenna 1, segment 3 length	> flagellar segm't	= flag. segm't	< flag. segm't
2. Mandible: number of blades in spine row	4	3	1-2
3. Maxilla 1, number of outer plate spines	9		7
4. Maxilla 1, length of palp	exceeding outer plate	= outer plate	shorter than outer plate
5. Maxilla 2, inner plate, No. marginal setae	many (>10)	3-5	0-2
6. Maxilliped, length of palp	exceeding outer plate	= outer plate	shorter than outer plate
7. Coxae 1 & 2, lower margin	rounded	squared	front acute
8. Coxa 3, lower front corner	rounded	process small	process large
9. Gnathopod 1, palm of propod	long	medium	short
10. Gnathopod 2, palm of propod	long	medium	short
11. Peraeopods 3 & 4, length of segm't 5	> segm't 6	= segm't 6	< segm't 6
12. Peraeopods 5-7 length of segm't 5	> segm't 6	= segm't 6	< segm't 6
13. Peraeopod 7, width of basis (segm't 2)	broadened	sl. broad	sublinear
14. Peraeopods 5-7, length of segm't 5	> segm't 6	= segm't 6	< segm't 6
15. Urosomite 2 & 3 Number dorsal spines	numerous	4	0-2
16. Uropod 1, peduncular outer marginal setae	lacking	few	strong row
17. Uropod 2, length of inner ramus	> outer ramus	= outer ramus	< outer ramus
18. Uropod 3, length of rami (female)	subequal	slightly unequal	markedly unequal
19. Telson lobes, basal fusion	little (1/6)	intermediate	much (1/3-1/4)
20. Telson lobes, number of lateral spines	many 7-8	intermed.(4-6)	few (0-3)

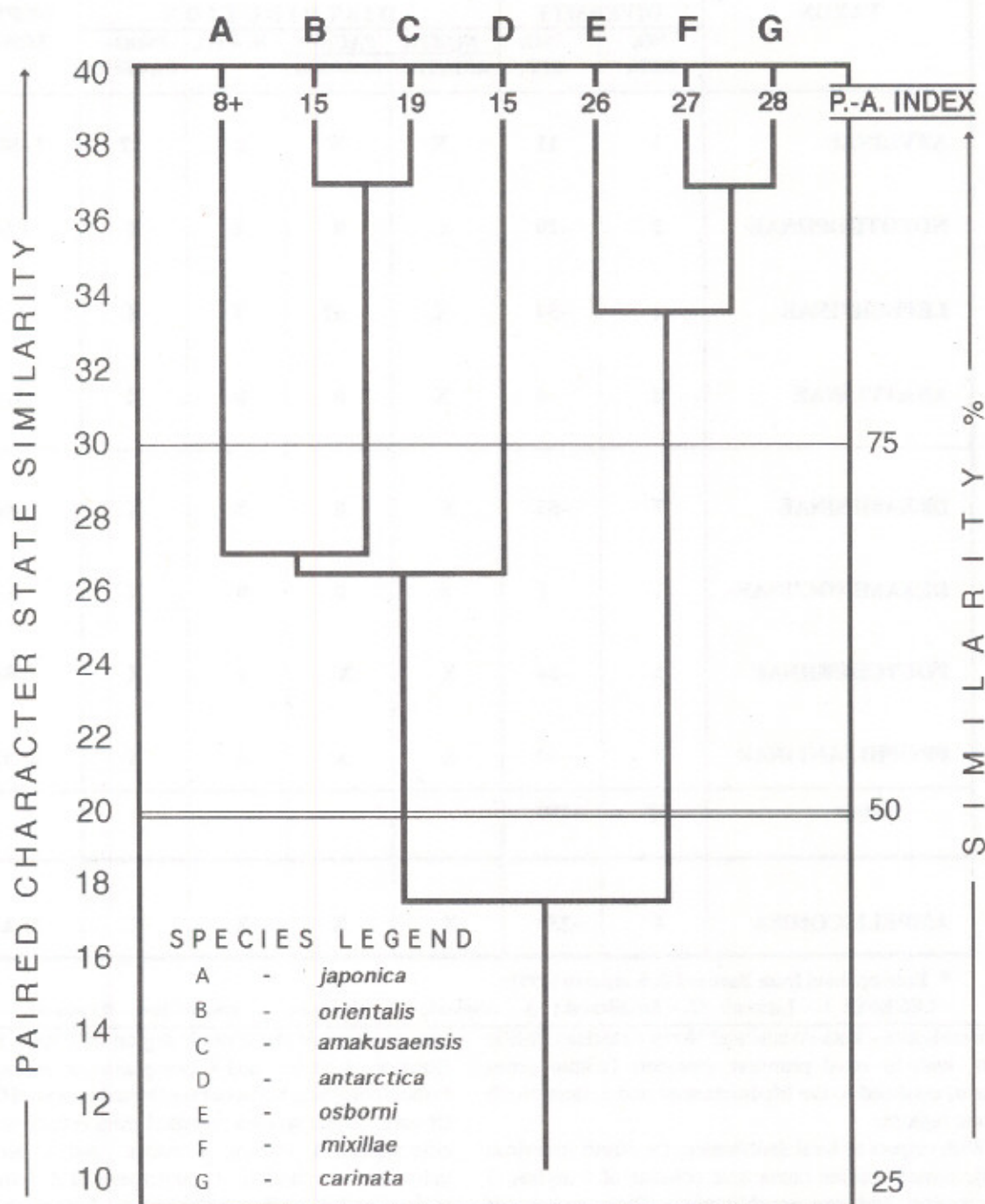
Biogeographic Considerations

The limited occurrence of Dexaminoid amphipods in the North Pacific region allows for few broad conclusions concerning regional biogeography of the group. However, the regional and world-wide distributional record of component families and subfamilies, including the more diverse western North Pacific dexaminoid fauna, is more helpful

(see Table IV, p. 62). Less than 200 world species are encompassed by 22 genera and 8 subfamilies (columns 1, 2). The low species/genus ratio provides a relatively high index of morphological diversity within the superfamily and, by inference, a relatively long or ancient evolutionary history of the group as a whole.

Within family Atylidae, 3 subfamilies are mainly littoral and sublittoral (column 7), whereas the Lepechinellinae

FIG. 31. PHENOGRAM OF SPECIES OF *POLYCHERIA*



(containing nearly half the known atylid species) is abyssal, mainly in Indo-Pacific and Atlantic regions. The 11 species of subfamily Atylinae (*Atylus*) are endemic to the North Pacific region, with a single outlier in the Atlantic and one possibly in the Antarctic. By contrast, the 20 species of Nototropiinae are mainly Indo-Pacific and Atlantic, with a few outliers reaching the western Pacific. The little known subfamily Anatylinae is also mainly Indo-Pacific, with 2 species reaching the Sea of Japan but none attain the North American Pacific coast.

Within the more diverse and species-rich family Dexaminidae, all four subfamilies are primarily Indo-Pacific, and the few described species within subfamily Dexaminoculinae are endemic there. A few members of the primitive subfamily Dexamininae penetrate into temperate waters of the North Atlantic and southern Japan (Kyushu). Subfamily Prophiantinae is also Indo-Pacific and southern, but with stronger representation in the North Atlantic and western Pacific regions. By contrast, the phylogenetically most advanced subfamily, Polycheriinae, penetrates fairly strongly

TABLE IV. GEOGRAPHICAL DISTRIBUTION OF DEXAMINOIDEA*

TAXON	DIVERSITY		DISTRIBUTION				DEPTH ZONE*
	NO. GEN.	NO. SPP.	NORTH ASIATIC	PACIFIC N. AMER.	N. ATL.	INDO-PACIFIC	
ATYLINAE	1	11	X	X	x	x?	L-SL
NOTOTROPIINAE	2	~20	x	0	X	X	L(A)
LEPECH'INAE	4	~34	X	x?	X	X	A
ANATYLINAE	2	4	X	0	0	X	L
DEXAMININAE	7	~55	X	0	X	X	L-SL
DEXAMINOC'INAE	1	1	0	0	0	X	L
POLYCHERIINAE	2	~24	X	X	x	X	L-SL
PROPHLIANTINAE	3	~40	X	x	X	X	L-SL
Totals	22	~190					
AMPELISCOIDEA	4	~230	X	X	X	X	L-A

* Data updated from Barnard & Karaman (1991).

*LEGEND: L - Littoral; SL - Sublittoral; A - Abyssal. X - common; x - species few; 0 - absent.

northwards along both Asiatic and North American Pacific coasts, with its most primitive members (within genus *Tritaeeta*) confined to the Mediterranean and eastern North Atlantic regions.

With respect to local distribution, the North American Pacific coastal marine fauna here consists of 8 atylins, 3 polycheriins, and one prophliantin. Three species of lepechinellins occur at abyssal depths off the eastern Pacific continental slope, from Central America north to Baja and southern California but, to date, none has been recorded from off Oregon or points northward (Barnard, 1973; Barnard & Karaman, 1991). As noted previously in this text, of the 8 regional species of *Atylus*, three species within the more primitive *carinatus-levidensus* subgroup (i.e., *A. carinatus*, *A. atlassovi*, and *A. bruggeni*) do not extend south of the Bering Sea, and only *A. levidensus* reaches California. Within the advanced *collingi-tridens* subgroup, all four

species occur in the central region of British Columbia. However, *A. tridens* and *A. georgianus* do not extend north to the Bering Sea, but occur southward to central California. Of seven atylin species recorded from coastal western Pacific waters, *A. ekmani*, *A. rylovi*, and *A. occidentalis* (advanced morphological counterparts of *A. levidensus*, *A. tridens*, and *A. collingi*) also extend furthest southwards. The more southerly occurrence, in North American Pacific waters, of phylogenetically advanced members of major taxonomic units has been noted previously within subfamilies of the Phoxocephaloidea, especially subfamily Metharpiniinae (Jarrett and Bousfield, 1994) and subfamily Pleustinae within the Leucothoidea (Bousfield & Hendrycks, 1984). The evolutionary significance of this phenomenon is yet inconclusive, but possibly reflects the overall depressant effect of low temperatures on rates of evolution, all other factors being equal (Ekman, 1953).

The distribution of ampeliscoidean amphipods, considered to be close but more highly advanced and specialized phyletic counterparts of dexaminoideans, stands in marked contrast (Table IV). Through modifications of pereopods 3-7, ampeliscoideans are able to construct and live (in the "upside down" fashion of polycherins) within protective vertical tubes of their own construction. They thereby exploit, in vast numbers, the rich tryptonic and deposit food resources on and above sedimentary substrata. Ampeliscoideans occur abundantly along all marine coastlines, including the arctic and antarctic, but relatively few have penetrated the deep sea (Table IV, columns 3-6). However, relative to the dexaminoideans, the larger number of described species (column 2) is encompassed by only 4 genera and one subfamily (column 1), three-fourths in the essentially littoral-sublittoral genus *Ampelisca*. This high species/genus ratio implies a relatively low index of morphological diversity and a relatively recent evolutionary history. This difference would suggest that the Dexaminoidea is, palaeohistorically, an older superfamily group than the Ampeliscoidea. The most primitive members (e.g. of *Atylus*) now exist in phyletically relict or semi-relict fashion, still occupying marine "nestling" niches that gammaroideans and other more eurytopic and more successful ecological counterparts have apparently not yet penetrated.

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LEGEND FOR FIGURES

A1 - antenna 1; A2 - antenna 2; ABD - abdomen; ACC FL - accessory flagellum; BR - branchia (coaxal gill); CX - coxa; EP - epimera (pleon plate); GN - gnathopod; HD - head; JV - juvenile; LL - lower lip; LFT - left; MD - mandible; MX - maxilla; MXP - maxilliped; PL - pleopod; PLP - palp; RT - right; T - telson; UL - upper lip; U - uropod; UROS - urosome; X - enlarged; O - male; O - female.

NEW SPECIES OF THE AMPHIPOD CRUSTACEAN GENERA *PHOTIS* AND *GAMMAROPSIS* (COROPHIOIDEA: ISAEIDAE) FROM CALIFORNIA.

by Kathleen E. Conlan¹

ABSTRACT

Three new species of the amphipod superfamily Corophioidea have been found at depths of 92 to 2005 meters off the Pacific coast of California. *Photis* (*Photis*) *typhlops*, new species, *Photis* (*Photis*) *linearmanus*, new species, and *Gammaropsis* (*Podoceropsis*) *ocellata*, new species, are here described and illustrated, and their morphological relationships with other regional species are discussed.

INTRODUCTION

Three new species of Corophioidea have been found in benthic collections from offshore waters of the coast of California. These are *Photis* (*Photis*) *typhlops*, new species, an eyeless form recorded from depths of 812 to 2005 meters, *Photis* (*Photis*) *linearmanus*, new species, an eyed taxon from a single collection at a depth of 92 meters, and *Gammaropsis* (*Podoceropsis*) *ocellata*, new species, an unusual podoceropsid having faceted but unpigmented eyes, taken at a depth of 590 meters.

The most recent review of regional species of these genera is Conlan (1983). Lists and numbers of regional genera and species can also be found in overview treatments by Austin (1985), Cadien (1991), and Bousfield and Staude (1994). The new species are here described and compared with their local relatives. The present study raises the number of North Pacific species of *Photis* (*Photis*) to 32, and of *Gammaropsis* (*Podoceropsis*) to 9.

The corophioidean genera *Photis* and *Gammaropsis* are here assigned to family Isaeidae. Families Isaeidae and Aoridae had been merged within family Corophiidae by Barnard and Karaman (1991). However, continued recognition of the Isaeidae as a distinct corophioidean family is in keeping with the recent work of Myers (1988), and with North Pacific regional comprehensive listings of Ishimaru (1994) and Bousfield and Staude (1994).

ACKNOWLEDGEMENTS

This work was conducted as part of a contract with Science Applications International Corporation for production of a guide to the Corophioidea in the Taxonomic Atlas of the Macroinvertebrate Fauna of the Santa Maria Basin and the Western Santa Barbara Channel. Jim Thomas, Hans Kuck, Joel Martin, Paul Scott, Terry Gosliner, and Judith Price provided specimens and data. C.-t. Shih and E. L. Bousfield reviewed the manuscript. Susan Laurie-Bourque illustrated the three new species fully treated here.

METHODS

The amphipod specimens were part of a large collection of Corophioidea that was examined for preparation of a taxonomic atlas to the benthic invertebrates of the Santa Maria Basin and the western Santa Barbara Channel. Right appendages and mouthparts were illustrated from slide mounts in polyvinyl lactophenol. Body length was measured from the tip of the rostrum to the base of the telson. Material was deposited at the Canadian Museum of Nature (CMN), the California Academy of Sciences (CAS), the Smithsonian Institution, U.S. Museum of Natural History (USNM), the Los Angeles County Museum of Natural History (NHMLAC), and the Santa Barbara Museum of Natural History (SBMNH).

¹ Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, Ontario, Canada K1P 6P4.

SYSTEMATICS

Photis (Photis) typhlops, new species (Fig. 1)

Material examined. TYPE MATERIAL: Holotype: adult male (USNM, catalogue no. 266403), U.S.A.: California: off San Francisco (37° 22.31'N, 123° 19.24'W), station 3-18, 26.829, 9-91, EPA site 102, 1990 m, 15 Sept. 1991, J. A. Blake, collector. Allotype, adult female (USNM, catalogue no. 266404), same location. Paratypes, about 300 individuals (USNM, catalogue no. 266405 (adult males), 266406 (adult females), 266407 (unsexable juveniles)); 6 males, 8 females, 30 juveniles (CAS, catalogue no. CASIZ 085729); 6 males, 8 females, 30 juveniles (NHMLAC, catalogue no. LACM 91-190.1); 6 males, 8 females, 30 juveniles (CMN, catalogue no. NMCC1993-0001), all same location.

OTHER MATERIAL (excluded from the type series): 1 juvenile from U.S.A.: California: off Pt. Buchon (35° 15.72'N, 121° 04.68'W), 396 m, California Phase II Monitoring Program, Minerals Management Service, Pacific OCS Office, Santa Maria Basin Project, station 020-BSS-01-TX; 2 juveniles from same area, off Pt. San Luis (35° 05.07'N, 121° 00.75'W), 390 m, station 025-BSR-01-TX; 5 juveniles from same location as preceding, 390 m, station 025-BSR-02-TX; 2 juveniles from same location as preceding, 390 m, station 025-BSR-03-TX; 2 adult females, 4 juveniles from same area, off Purisima Pt. (34° 37.80'N, 121° 01.66'W), 591 m, 6 Jan. 1984, station 050-BSS-01-TX; 1 adult female, 7 juveniles from same area, off Pt. Arguello (34° 33.66'N, 120° 56.31'W), 590 m, station 055-BSS-01-TX (all of above SBMNH); 1 juvenile from Eel River Basin (41° 56.33'N, 124° 38.00'W), 552 m, dissolved oxygen 1.03 ml/l, bottom water temp. 5.86°C, silt-clay sediment, % organic carbon 1.473, 22 Nov. 1987, station SB-4 (NHMLAC); 1 juvenile from same area as preceding (41° 39.77'N, 124° 29.33'W), 524/549 m, dissolved oxygen 1.6 ml/l, bottom water temp. 5.92°C, sand-silt-clay sediment, % organic carbon 0.859/0.782, 22 Nov. 1987, station SB-12 (NHMLAC); 1 juvenile from same area as preceding (40° 57.00'N, 124° 23.42'W), 188 m, dissolved oxygen 4.35 ml/l, bottom water temp. 8.67°C, silt-clay sediment, % organic carbon 0.924, 19 Nov. 1987, station SB-14 (NHMLAC); 1 juvenile from same area as preceding (40° 57.20'N, 124° 33.20'W), 555 m, dissolved oxygen 2.51 ml/l, bottom water temp. 6.56°C, silt-clay sediment, % organic carbon not recorded, 18 Nov. 1987, station SB-16 (NHMLAC) (all Eel River Basin samples collected by MEC Analytical Systems Inc., Carlsbad, California).

Diagnosis. Eye lacking. Antennae half length of the body, with long setae. Coxae 1-5, ventral margins with 0-4 long setae. Gnathopod 1, carpus longer than propodus, propodus slender, palm convex or shallowly excavate.

Gnathopod 2 of male, basis with row of stridulation ridges angled across lateral face; palm of propodus transverse, with tooth and long spine at palmar defining corner and two small teeth in palm.

Description. Adult male (3.2 mm) Holotype: Head lobe triangular. Eye lacking. Antennae 1 and 2 about equal in length. Antenna 1 weakly setose, article 3 longer than article 1; accessory flagellum microscopic button. Antenna 2 moderately setose, flagellum not pediform, longer than article 5, distally spinose.

Upper lip, epistome triangular. Mandible with 3-4 raker spines; molar flake present; palp strong, article 3 hardly wider distally than proximally, both articles 2 and 3 with numerous setae, article 2 longer than article 3. Maxilla 1, inner plate without setae; palp narrower than outer plate. Maxilla 2, inner plate about same width as outer, with facial setae. Maxilliped, inner plate not reaching end of article 4; outer plate not reaching end of article 5; unguis (article 8) about equal in length to article 7.

Peraeopods 1-5, ventral margins of coxae with 0-2 long setae each. Gnathopod 1, coxa more anterodistally produced than coxa 2; basis inserted mid-proximally on inner face, not densely setose; carpus about equal in length to propodus, anterior margin distally setose; propodus, palm shallowly excavate, defined by single spine; dactyl longer than palm of propodus, posterior (inner) margin with few short setae and cusps. Gnathopod 2, basis, lateral face with row of stridulation ridges; carpus shorter than propodus; propodus, width 1.5 times width of propodus of gnathopod 1, palm transverse, with 2 excavations and tooth and spine at defining corner, setae at dactyl hinge less than half length of propodus; dactyl overlapping palm by length of unguis, without tooth, with spine and setal cluster proximal of unguis.

Peraeopod 3, coxa with row of stridulation ridges on ventral margin. Peraeopod 4, coxa, posterior margin not excavate. Peraeopods 3 and 4, basis not expanded, merus wider than carpus and produced anteriorly over less than 1/4 of carpus; dactyl shorter than propodus. Peraeopod 5, coxa similar in depth to coxa 4; basis broad, not posteriorly excavate; merus not posteriorly excavate; merus and carpus not spinose; propodus with only single long spine at anterodistal corner; dactyl with 2 pronounced cusps at junction of unguis. Peraeopods 6 and 7, coxae smaller than coxa 5; otherwise articles similar in shape to peraeopod 5, although bases narrower and dactyl not cusped.

Pleon plates 1-3 not posterodistally notched. Pleon and urosome without dorsally erect setae or cusps. Uropod 1, peduncle without lateral ecdysial spine proximally or tooth-like process extending ventrally below rami; rami tipped by 1-2 short spines. Uropod 3, peduncle not spinose; outer ramus nearly as long as peduncle and tipped by 1-2 long setae, inner ramus about 1/4 length of outer, tipped by single short spine. Telson apices marked by single long seta and small knob.

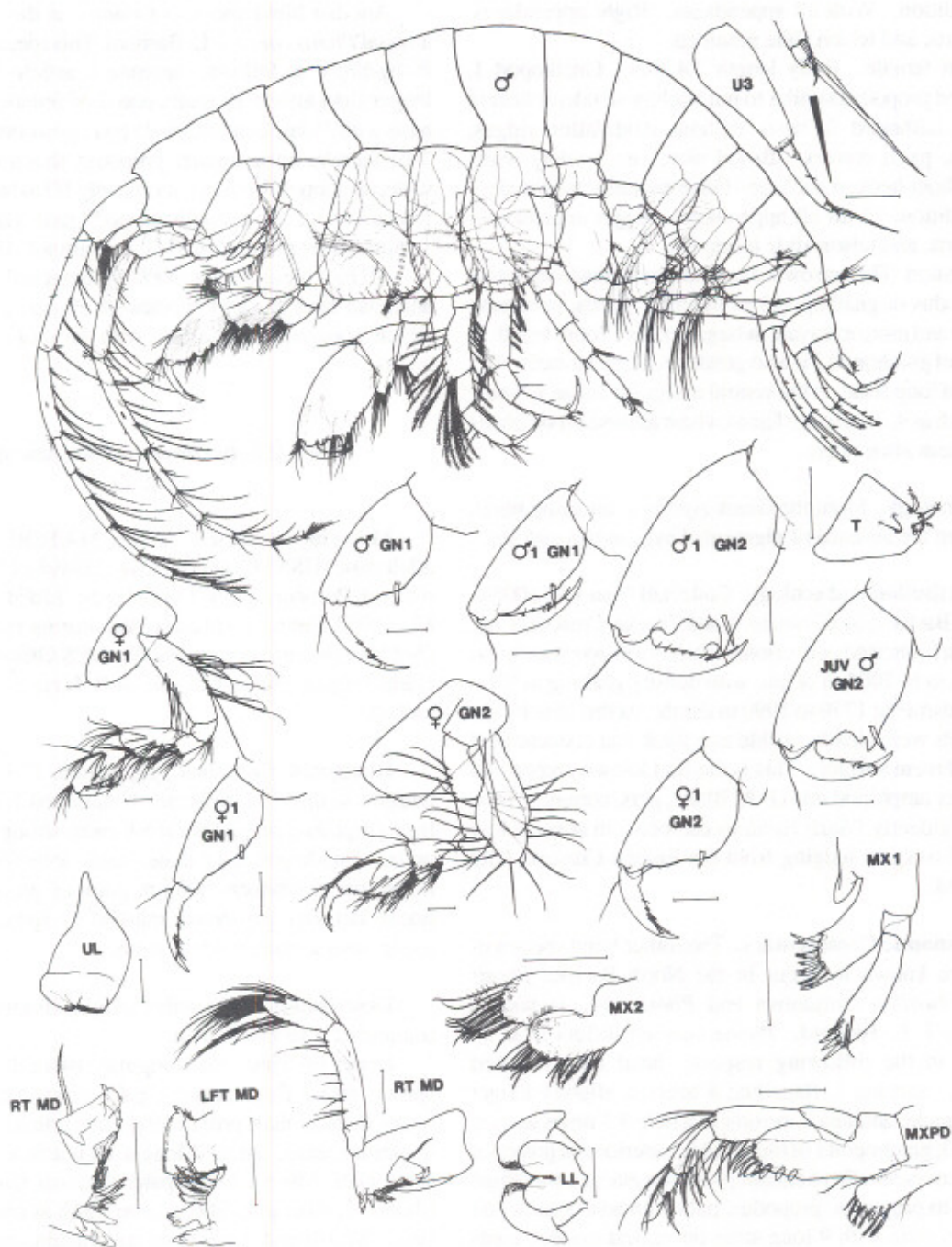


FIG. 1. *Photis typhlops*, new species. Adult male, (3.2 mm) HOLOTYPE: whole body, distal articles of gnathopods 1 and 2 (setae omitted), mouthparts, uropod 3, and telson. Adult male 1 (3.4 mm) PARATYPE: distal articles of gnathopods 1 and 2 (setae omitted). Juvenile male (2.9 mm): distal article of gnathopod 2 (setae omitted). Adult female br. III. (3.4 mm) ALLOTYPE: gnathopods 1 and 2. Adult female 1 br. III. (3.3 mm) PARATYPE: gnathopods 1 and 2, magnifications (setae omitted). Lateral views: whole body, maxilla 1, uropod 3, and telson; other views medial. Scale 0.1 mm.

Condition. With all appendages. Right appendages, mouthparts, and telson slide mounted.

Adult female. Body length 3.4 mm. Gnathopod 1, carpus and propodus similar to but slightly slenderer than in male. Gnathopod 2, basis without stridulation ridges; propodus, palm convex. Brood plates moderately wide, setae without hook at each tip. Other features as in male.

Condition. With all appendages. Right appendages, mouthparts, and telson slide mounted.

Variation. The narrowness and amount of indentation of the propodus of gnathopod 1 of the male varies, becoming narrower and more excavate in larger males. Tooth length in the palm of gnathopod 2 is also greater in larger animals. The number of long setae on the ventral margin of coxae 1-5 may be as much as 4. Immature females bear asetose brood plates or lack them altogether.

Etymology. From the Greek *typhlops*, meaning blind, alluding to the absence of pigmented eyes in this species.

Distribution and ecology. Collected from 188-2005 m off Santa Barbara, San Francisco, and Eureka-Crescent City. In the San Francisco collections, *Photis typhlops* was found from 812 m to 2005 m depth, with density peaking at 9500 individuals/m² at 1770 to 1990 m depth. At this density the amphipods were clearly visible as a thick mat concentrated at the sediment surface. This is the first known record of a deep water amphipod mat (J. A. Blake, pers. comm., 7 Dec. 1992). Evidently *Photis typhlops* can occur in areas of low dissolved oxygen, judging from the Eureka-Crescent City collections.

Taxonomic Commentary. Two other blind species of *Photis* are known to occur in the North Pacific: *Photis (Photis) kurilica* Gurjanova and *Photis (Cedrophotis) malinalco* J. L. Barnard. *Photis kurilica* differs from *P. typhlops* in the following respects: head lobe rounded ventrally; antenna 1, flagellum 8 articles, slightly longer than peduncle; antenna 2, peduncle article 4 3 times as long as article 3; gnathopod 1 of male, basis, anterior and posterior margins covered with abundant plumose setae, carpus equal in length to propodus, propodus, palm concave; gnathopod 2 of male, coxa with 9 long setae on ventral margin, basis with abundant short, stout setae anteriorly and long, slender setae posteriorly, propodus, palm concave, without tooth; gnathopod 2 of female, propodus, palm shallowly concave; uropod 1 with 8-11 lateral spines on peduncle and rami; uropod 2 with 2-12 lateral spines on peduncle and rami. *Photis kurilica* has only been recorded from the east coast of Russia (Gurjanova, 1955).

Photis malinalco, from the Cedros Trench, Baja California, has a much longer inner ramus on the third uropod (half the length of the outer - a defining character of the subgenus), more slender propodus of gnathopods 1 and 2, broader coxa 1, and less spinose uropods 1 and 2 (J. L. Barnard, 1967).

Another blind species of *Photis* is the South Atlantic abyssal *Photis coeca* J. L. Barnard. This species differs from *P. typhlops* as follows: antenna 1, article 3 only slightly longer than article 1; gnathopod 1 of female, coxa square, basis with 3 long setae anteriorly and 1 posteriorly; gnathopod 2 of female, coxa square, propodus much narrower than wide; peraeopod 3, coxa covering only 1/3 of basis; peraeopod 5, basis, width 3/4 of length; uropod 1 rami, outer ramus with 1 spine, inner ramus with 0 (J. L. Barnard, 1962).

All four blind species of *Photis* possess distinctly longer antennae than in eyed species of *Photis*, a characteristic which apparently correlates with lack of visual sensory organs.

Photis (Photis) linearmanus, new species
(Fig. 2)

Material examined. TYPE MATERIAL: Holotype: adult male (USNM, catalogue no. 239498), U.S.A.: California: off Purisima Point (34°43.0'N, 120°47.4'W), 92 m, May 1987, California Phase II Monitoring Program, Minerals Management Service, Pacific OCS Office, Santa Maria Basin Project, cruise 1-3, station R-4, replicate 1, Battelle, collector.

Diagnosis. Eyes small, pigmented. Coxae 1-5, ventral margins with 2-11 long setae. Gnathopod 1, carpus shorter than propodus; propodus broad; palm strongly excavate in male. Gnathopod 2 of male, basis with few stridulation ridges on anterodistal margin; palm of propodus oblique, linear, defining corner not marked by spine or change of angle, with 2 small teeth in palm.

Description. Adult male (3.4 mm) Holotype: Head lobe triangular. Eye black, oval.

Upper lip, epistome triangular. Mandible with 3 raker spines; molar flake present; palp strong, article 3 hardly wider distally than proximally, both articles 2 and 3 with numerous setae, article 2 longer than article 3. Maxilla 1, inner plate without setae; palp narrower than outer plate. Maxilla 2, inner plate about same width as outer, with facial setae. Maxilliped, inner plate not reaching end of article 4; outer plate not reaching end of article 5; unguis (article 8) about equal in length to article 7.

Peraeopods 1-4, ventral margin of coxa 2 with 11 long setae; coxae 1, 3, and 4 with 2-5 setae. Gnathopod 1, coxa different in shape from coxa 2, narrowed distally; basis inserted midway on inner face, not densely setose; carpus shorter than propodus, anterior margin setose only at anterior junction with propodus; propodus, palm concave, defined by single small spine; dactyl only as long as palm of propodus, posterior (inner) margin with few short setae and cusps. Gnathopod 2, basis, anterodistal margin with few stridulation ridges; carpus shorter than propodus; propodus, width

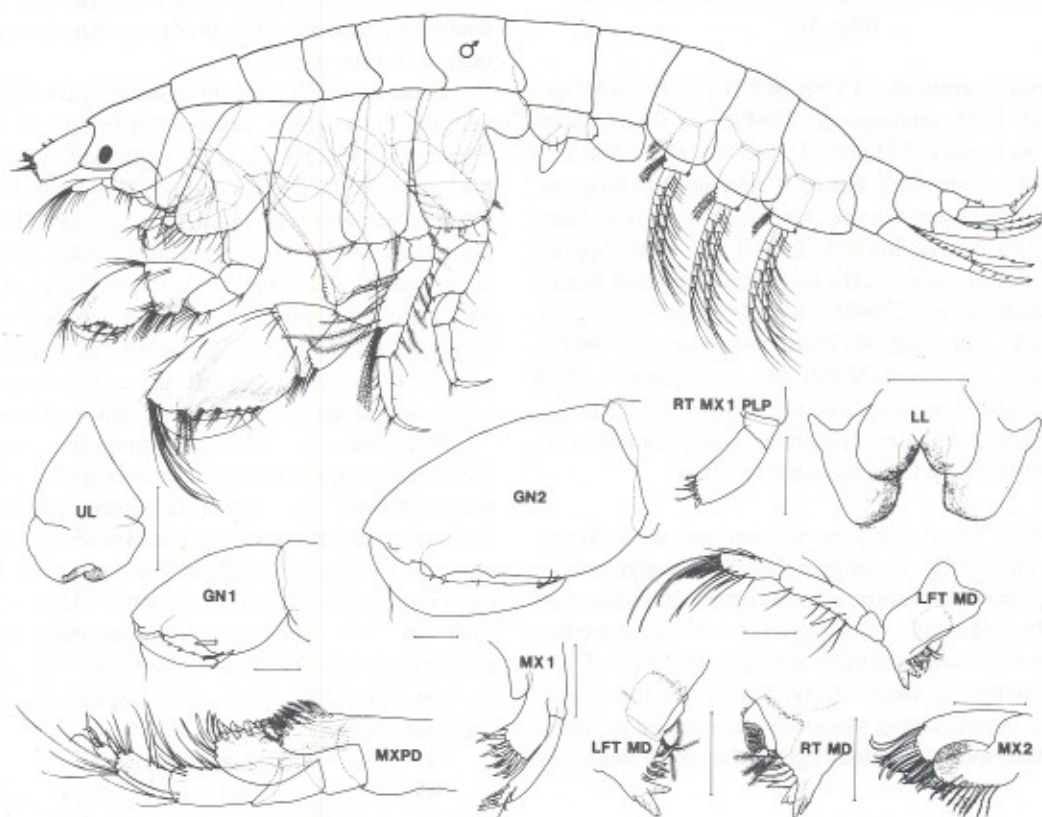


FIG. 2. *Photis linearmanus*, new species. Adult male (3.4 mm) HOLOTYPE. Lateral views: whole body, mandibles, and maxilla 1; other views medial. Scale 0.1 mm.

1.7 times width of propodus of gnathopod 1, palm oblique, with shelf at dactyl and shallow protuberance midway, setae at dactyl hinge nearly as long as propodus; dactyl scarcely overlapping palm, inner margin evenly curved, with spine and setal cluster proximal of unguis.

Peraeopod 3, coxa with row of stridulation ridges on ventral margin. Peraeopod 4, coxa, posterior margin not excavate. Peraeopods 3 and 4, basis not expanded; merus wider than carpus and produced anteriorly over about 1/4 of carpus; dactyl shorter than propodus. Peraeopod 5, coxa similar in depth to coxa 4. Peraeopods 6 and 7, coxae smaller than coxa 5; other articles of peraeopods 5-7 lacking.

Pleon plates 1-3 not posterodistally notched. Pleon and urosome without dorsally erect setae or cusps. Uropod 1, peduncle without lateral ecdysial spine proximally or tooth-like process extending ventrally below rami; rami tipped by 1 short spine. Uropod 3, peduncle with single spine ventrally at origin of rami; outer ramus 2/3 length of peduncle and tipped by 1 long seta; inner ramus about 1/4 length of outer ramus, tipped by single short spine. Telson apices marked by

single long seta and small knob.

Condition. Without antennae, right peraeopods 4-7, and left peraeopods 5-7.

Adult female. Unknown.

Etymology. From the Latin, *linearis*, meaning linear, and *manus*, meaning hand, referring to the oblique, nearly linear palm of the propod of gnathopod 2 of the mature male.

Distribution. Known only from this single collection in Santa Maria Basin, at 92 m in depth.

Taxonomic Commentary. This is the only species on the northeastern Pacific coast whose adult male has an oblique palm on the propodus of the second gnathopod. The relative sparsity of setae on the ventral margins of the coxae, the cluster of long setae at the origin of the dactyl on the male's gnathopod 2, and the concave palm of the male's gnathopod 1 are also distinctive, although not unique among regional species.

Gammaropsis (Podoceros) ocellata, new species

(Fig. 3)

Material examined. TYPE MATERIAL: Holotype: adult male (USNM, catalogue no. 239495), U.S.A.: California: off Pt. Arguello (34°33.66'N, 120°56.31'W), 590 m, 5 January 1984, California Phase II Monitoring Program, Minerals Management Service, Pacific OCS Office, Santa Maria Basin Project, station 055, BSS-01-TX, MBC Applied Environmental Sciences, collector. Allotype, adult female (USNM, catalogue no. 239496), same location. Paratypes: 1 adult female, 3 juveniles (USNM, catalogue no. 239497); 2 adult females, 2 juveniles (NHMLAC, catalogue no. LACM 84-285.1); 2 adult females, 2 juveniles (SBMNH, catalogue no. 35646); 2 adult females, 2 juveniles (CMN, catalogue no. NMCC1993-003), all from the same location.

Diagnosis. Eyes weakly faceted, unpigmented. Antennae, setae maximally as long as last peduncular article. Uropod 1, peduncular ventral spinous process less than half length of shortest ramus. Gnathopod 2 of male, propodus, palm nearly transverse, centrally notched, and defined by 1 spine and change in angle; dactyl not longer than palm. Peraeopod 5 of male, basis shallowly excavate on posterior margin. Gnathopod 2 of female, propodus, palm shallowly excavate.

Description. Adult male (3.8 mm) Holotype: Head lobe triangular, but not anteriorly acute. Eye oval, with about 12 unpigmented facets. Antennae 1 and 2 equal in length. Antenna 1 moderately setose with long setae posteriorly, article 3 longer than article 1; accessory flagellum microscopic button. Antenna 2 moderately setose, with long setae also, flagellum not pediform, longer than article 5, distally spinose.

Upper lip, epistome acutely produced. Mandible with 5 raker spines; molar flake present; palp strong, article 3 hardly wider distally than proximally, both articles 2 and 3 with numerous setae, article 2 longer than article 3. Maxilla 1, inner plate with single long seta; palp somewhat narrower than outer plate. Maxilla 2, inner plate nearly as wide as outer, with row of facial setae. Maxilliped, inner plate nearly reaching end of article 4; outer plate not reaching end of article 5; unguis (article 8) as long as article 7.

Peraeopods 1-4, coxae, ventral margins with minute setae only. Gnathopod 1, coxa similar in shape to and not shallower than coxa 2; basis inserted mid-distally on inner face, not setose anterodistally; carpus longer than propodus, with anterodistal cluster of setae; propodus nearly simple, palm indistinct, defined by single long spine; dactyl much longer than palm of propodus, posterior (inner) margin with several short setae and cusps. Gnathopod 2, basis without stridulation ridges; carpus shorter than propodus; propodus, width 2.5 times width of propodus of gnathopod 1, palm nearly transverse, with protuberance near origin of dactyl

followed by oval incision, spine at palmar corner, setae at dactyl hinge about 1/2 length of propodus; dactyl not toothed, only as long as palm.

Peraeopod 3, coxa without stridulation ridges on ventral margin. Peraeopod 4, coxa, posterior margin not excavate. Peraeopods 3 and 4 basis not expanded, merus wider than but hardly produced over carpus; dactyl not elongate, much shorter than propodus. Peraeopod 5, coxa as deep as coxa 4; basis moderately broad, shallowly posteriorly excavate in adult male; merus shallowly concave posteriorly; carpus with cluster of spines at posterior junction of propodus; propodus with few spines along anterior margin; dactyl not cusped. Peraeopod 7, coxa not expanded. Peraeopods 6 and 7 similar in shape to peraeopod 5, although bases narrower.

Pleon plates 1-3 with few minute setae posterodistally but without cusps or ridges. Urosome segments 1 and 2 with pair of dorsally erect setae but without cusps. Uropod 1, peduncle without lateral ecdysial spines, but with spinous process extending ventrally below rami about 1/3 length of outer ramus; rami tipped by 2-3 spines. Uropod 3, peduncle spinose dorsally at origin of rami; outer ramus nearly as long as peduncle and tipped by 1-2 long setae, inner ramus as long as outer, tipped by 1 spine. Telson apices marked by nipple and setal cluster.

Condition. Without peraeopods 5-7.

Adult female ov. (4.4 mm) Allotype: Gnathopod 2, propodus, palm shallowly excavate. Brood plates moderately wide, setae with hook at each tip. Other features as in male.

Condition. Without right peraeopods 4, 5, and 7, and left peraeopods 6 and 7.

Etymology. From the Latin *ocellata*, referring to the relatively small unpigmented eyes of this species.

Distribution. Known only from this single location in the Santa Maria Basin, at 590 m in depth.

Taxonomic Commentary. The faceted but unpigmented eye distinguishes *Gammaropsis ocellata* from other members of the subgenus on the North American Pacific coast. Another deepwater species, *Gammaropsis (Podoceros) kermadeci* Stebbing, also lacks pigmented eyes, but differs considerably from *G. ocellata* in having a much broader propodus of gnathopods 1 and 2, a more enlarged and transverse palm on the propodus of the male gnathopod 2, and a longer carpus relative to the merus on peraeopods 3 and 4. The body is also dorsally setose, which is not the case in *G. ocellata*. *Gammaropsis ocellata* most closely resembles *G. (P.) barnardi* Kudryashov and Tzvetkova, which has been described from southern and western Sakhalin, Russia (50°N, 145°W) and Vancouver Island, British Columbia (48°48'N, 125°12.5'W) (Kudryashov and Tzvetkova, 1975; Conlan, 1983). *Gammaropsis ocellata* differs from *G. barnardi* in having an unpigmented eye, more transverse

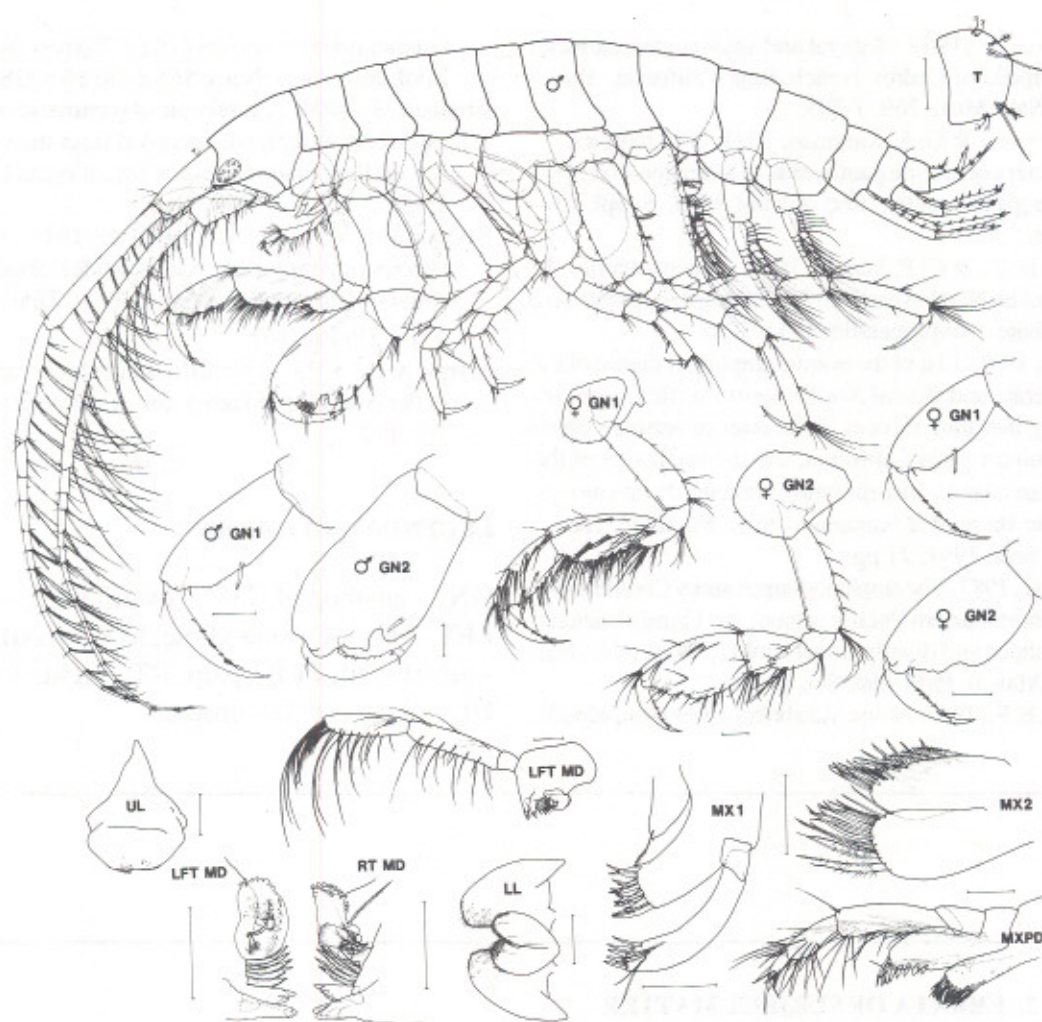


FIG. 3. *Gammaropsis ocellata*, new species. Adult male (3.8 mm) HOLOTYPE: whole body, distal articles of gnathopods 1 and 2 (setae omitted), mouthparts, and telson; Adult female (4.4 mm) ALLOTYPE: gnathopods 1 and 2. Lateral views: whole body, mandibles, and maxilla 1; other views medial. Scale 0.1 mm.

palm of gnathopod 2 in the male, more concave palm of gnathopod 2 in the female, and less excavate pereopod 5 basis in the male.

DISCUSSION

Photis typhlops and *G. ocellata* demonstrate the tendency of deepwater or cavernicolous amphipods to lose eye pigmentation and/or facets and lengthen their antennae. Since no phyletic treatment has been developed for either genus, it cannot be determined whether these species bear other apomorphic features. *Photis typhlops* and *P. linearmanus* belong to the poorly setose group of photids which lack a dense fringe of setae on the ventral margin of the coxae. Males of both species are stridulators and the second gnathopods are moderately sexually dimorphic. Stridulation is the norm for photids, and is presumably of value for communicating mating intent, particularly in the close commu-

nity contact that was found for *Photis typhlops*. *Gammaropsis ocellata* shows the same sort of sexual traits as other members of the subgenus. The subgenus is very conservative in its range of sexual dimorphism. *Gammaropsis ocellata* shows less exaggerated alteration of the second gnathopod and fifth pereopod than in some other species, suggesting that the specimen described here may not have reached fully mature size. However the loss of eye pigmentation is significant, and unique in the genus.

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LEGEND FOR FIGURES

GN - gnathopod; JV - juvenile; LL - lower lip; LFT - left; MD - mandible; MX - maxilla; MXPD - maxilliped; PLP - palp; RT - right; T - telson; UL - upper lip; U - uropod.

Vol I, No. 2. ERRATA OF SUBJECT MATTER

Editorial.

p. 1. The correct address for Roy J. Kropp is: Battelle Ocean Sciences, Duxbury, MA 02332 USA.

Paper No. 1: Pleustinae

p. 42 *et sequ.* Apologies are extended to readers who may have encountered difficulties in connecting labels with figures.

Paper No. 2: Phoxocephalidae.

p. 83. The tribute to Dr. Arthur May should read: "The species *Mandibulophoxus mayi* Jarrett & Bousfield, 1994, is named in honour of Dr. Arthur W. May, President and Vice-Chancellor of Memorial University, St. John's,

Newfoundland, and former President, Natural Sciences and Engineering Research Council of Canada".

p. 77 *et sequ.* Apologies are extended for the heavy overprinting of the plates, esp. figs. 8, 17, 28, 29.

p. 102, *et sequ.* Berkeley Sd. - corrected to Barkley Sd.

p. 120, Fig. 27. Reversed curved line on peraeon segment 2 should be removed.

p. 125. Add to the bottom of the page:
"*H. videns* is similar to *H. conlanae* and *H. ellisi*".

p. 147. All references following Austin, W. C., and before Barnard, K. H., are attributable to Barnard, J. L.

The Canadian Field-Naturalist

A continuation of 115 years of publication on northern North American biodiversity — 1880-1994.

The Canadian Field-Naturalist is the official publication of The Ottawa Field-Naturalists' Club and features both articles and notes on original research and observations on the natural history of northern North America (including distribution, faunal analyses, taxonomy, ecology, and behaviour). Issues include news and comment (Club annual meetings and awards, tributes and review papers) and book review and new title sections. Since 1984, it has presented edited Status Reports for individual species designated by the Convention on Species of Endangered Wildlife in Canada (COSEWIC). It is entirely supported through club membership and subscriptions, page and reprint charges. The Ottawa Field-Naturalists' Club has 1041 members and *The Canadian Field-Naturalist* an additional 248 individual and 573 institutional subscribers, for a distribution of 1862 copies.

The Ottawa Field-Naturalists' Club was formed in 1879 by scientists from embryonic federal departments including the Geological Survey and the Dominion Experimental Farm and leading amateurs; this type of mix remains its strength to this day. The Club quickly emphasized publication, and for seven years beginning in 1880, it annually issued the *Transactions of the Ottawa Field-Naturalists' Club*. With volume 3 in 1887, the *Transactions* became a subtitle of Volume 1 of *The Ottawa Naturalist*, a monthly publication. With Volume 3 of *The Ottawa Naturalist* in 1889 the emphasis changed from local members reports to national ones, and in 1919 the journal was renamed *The Canadian Field-Naturalist* (starting with Volume 33 which was Volume 35 of the *Transactions* but this subtitle was subsequently dropped). The issues per year were gradually reduced from 12 to 9 to 6 and eventually to 4, the latter beginning with Volume 67 in 1953. However, the annual number of pages increased, in 1988 (volume 102) reaching a record of 798 with a the largest single issue of 216 pages in 102(2). Since 1967, the Club has separately published a local (Ottawa area) natural history journal, *Trail & Landscape*, now also issued 4 times a year.

Submissions to *The Canadian Field-Naturalist* and predecessors have long been peer reviewed, first through a "Publishing Committee", later "Sub-editors", and then "Assistant Editors" until the designation "Associate Editors" was adopted in 1885 and maintained ever since. Currently, most submissions also go to at least one (and often more) additional reviewer(s). Associate Editors are listed in every issue and since 1982 additional reviewers been acknowledged annually in the Editor's Report. A formal publication policy was published in *The Canadian Field-Naturalist* 97(2): 231-234. "Advice to Contributors" is published in one or more issues annually. The current subscription rate is \$23 for individuals and \$38 for institutions. Postage outside Canada is \$5.00 additional. Subscriptions should be sent to The Canadian Field-Naturalist, Box 35069 Westgate P.O., Ottawa, Ontario, Canada K1Z 1A2. Manuscripts for consideration should be addressed to Dr. Francis R. Cook, Editor, Canadian Field-Naturalist, RR 3, North Augusta, Ontario, Canada K0G 1R0.

Francis R. Cook

THE PHYLETIC CLASSIFICATION OF AMPHIPOD CRUSTACEANS: PROBLEMS IN RESOLUTION*

by E. L. Bousfield¹ and C.-t. Shih²

ABSTRACT

The phyletic classification of amphipod crustaceans has been a major source of disagreement among principal recent workers. The disagreement results at least partly from the masking effects of convergent or homoplasious morphology not only on superfamily and subordinal recognition, but also on the determination of closest phyletic sister groups to the Amphipoda within the Malacostraca. The most recent attempts at phyletic classification of amphipods (e.g. Schram 1986, and others) are based partly on the work of the present writer, but leave important problems not entirely resolved. As a result, some recent major classifications remain alphabetical (e.g. Ruffo, 1990; Barnard & Karaman, 1991).

Based on new evidence, partly from recent behavioural work of CMN colleague K. E. Conlan, this study takes a morphological-behavioural approach to solving such problems at all levels of classification. Among malacostracan potential sister groups, the Amphipoda appears phyletically least remote from the Mysidacea, but more remote from the Hemiaridea and the Isopoda. Within the Amphipoda, two natural subordinal groups are recognized, viz, the primitive, relict Ingolfiellidea, and the more advanced, dominant Gammaridea, both with extant members in marine and freshwater habitats. Within the Gammaridea, two exclusively marine, infraordinal groups, the Hyperiidea and the Caprelliidea, have possibly arisen from stegocephalid- and podocerid-like ancestors respectively.

The infraorders and superfamilies within the Gammaridea may be organized broadly and semi-phyletically into "Amphipoda Natantia" and "Amphipoda Reptantia", analogous to categories formerly employed within the malacostracan Decapoda. The former category includes reproductively free-swimming groups, with direct mating (usually lacking pre-amplexus) mostly freely in the water column. Typically here, the male is sexually specialized in the antennal sensory organs (e.g. possesses callynophore, calceoli and brush setae), eyes, and tail fan, but seldom in the gnathopods. The mature male stage is also smaller than the female and is a terminal life stage (non-moulting, often non-feeding). Components of the second category are mostly benthic or infaunal in all life stages, mating occurs on/in the bottom, with pre-amplexus (precopulatory grasping of the female and/or agonistic behaviour toward other males). Here also, the male is usually the larger, is usually sexually specialized in the gnathopods but not markedly in sensory organs or tail fan, and is indeterminate in growth (mates during two or more life stages). The very few anomalies within this classification are variously attributable to delayed loss of plesiomorphic structures or to convergent morphology and behaviour, in specialized forms.

INTRODUCTION

The phyletic classification of amphipods has long been fraught with difficulties and much controversy among principal workers. Their views tend to be "colored" by their experiences with various taxonomic and ecological subgroupings, particularly within the Gammaridea (e.g. Bousfield (1979, 1982a, 1983); Barnard and Karaman (1980); Holsinger (1989); Stock (1985); Ruffo (1989); Lincoln (1979); Schram (1986). Contributing to this difficulty is the relatively large size of this crustacean ordinal group (more than 7000 described species in 4 suborders and more than 125 families), and the large number of external morphological characters (100+) employed variously at higher levels of classification. The current state of the problem of classification within the Amphipoda seems analogous to the tale of the three blind men who were asked to describe an elephant based on the part of the beast that each happened to be touching — trunk, leg, or tail — with three widely differing results. An overall, comprehensive, and phyletically

rational picture therefore seems possible only by characterizing all body parts, of all component groups, simultaneously.

Faced with these difficulties and limitations, some authors (e.g. Ruffo et al (1990), and Barnard and Karaman (1991) have expediently adopted a simple, pragmatic, alphabetical listing of families within suborders, as is widely accepted for classifying genera within families and species within genera. However, a useful phyletic "lead" has been provided by major workers within suborder Hyperiidea (e.g. Bowman & Gruner, 1973) and Caprelliidea (e.g. McCain (1970); Laubitz (1970)). Also, in order to avoid being overwhelmed by unwieldy numbers of names and volume of taxonomic detail within the much larger suborder Gammaridea, others (e.g. Lincoln (1979); Schram (1986); and the writer (Bousfield, 1979, 1983) have attempted to reduce the classificatory problem to a manageable "compromise" by utilizing a phyletically defined superfamily concept. Within the Gammaridea, this method reduces a

*Based on the Plenary lecture, First European Crustacean Conference, Paris, August 31, 1992.

¹ Researcher Emeritus, Canadian Museum of Nature, Ottawa, Canada, K1A 6P4

² Research Division, Canadian Museum of Nature, Ottawa, Canada, K1A 6P4

taxonomically unwieldy 90+ families to less than two dozen readily conceptualized and readily manageable super families. Also, the number of statistically significant characters of major taxonomic value is reduced to less than 50, thereby facilitating numerical taxonomic analysis.

The need for a well founded, widely acceptable phyletic classification of amphipods, especially within the Gammaridea, is of increasing concern. Owing to new taxonomic discoveries and revisions of older taxa, species diversity within this subordinal group is increasing at the rate of about 1-2% per year. Correct family and superfamily placement of taxa such as *Aetiopodes* Moore & Myers (1988) remains highly subjective and increasingly difficult.

Without a confirmed phylogeny, character states cannot be "ordered" or polarized at appropriate taxonomic levels, nor can family-level units be properly defined in relation to one another. Lack of a recognized phylogeny severely handicaps students of amphipod behaviour and physiology who require stable ancestral reference points in formulating their conclusions. Today, the Amphipoda remains one of the few major animal groups in which alphabetical classifications appear more widely utilized than phyletic arrangements. Such lack of consensus constitutes an impediment to systematic work within this subdiscipline of crustacean systematics. In our view, this problem merits further close scrutiny and, hopefully, early resolution.

The phyletic position of the other broadly recognized suborders of Amphipoda, the Hyperidea, Caprellidea, and Ingolfiellidea viz-a-viz the Gammaridea, has been unevenly examined by previous workers. In the "pre-ingolfiellid" classical arrangements of Stebbing (1888) and Sars (1895), the hyperiids were considered among the most primitive, and the caprellids among the most advanced higher categories of amphipod crustaceans. Although recent literature on hyperiids contains little "outgroup" phyletic conjecture (e.g. Bowman & Gruner, 1973), the early status quo has apparently been maintained. With respect to the caprellids, the more recent "in-depth" studies of Laubitz (1993) and Takeuchi (1993) confirm, widely acceptably, the highly probable corophioidean origins of the caprellids, whether mono- or poly- phyletically. The morphologically advanced position of caprellids is maintained including, by inference, that of their relatively recently evolved cetacean-parasitic cyanid confreres. The small relict group of highly modified infaunal and hypogean ingolfiellid amphipods is generally considered to be phyletically very old and worthy of maintenance at subordinal level (e.g. Ruffo, 1969; Stock 1977), a view that is amplified here (pp. 120). Bowman and Abele (1982), however, would include the ingolfiellids within the Gammaridea, close to family Gammaridae.

Schram (1986) has provided one of the most recent comprehensive reviews of amphipod classification. Whereas he has acknowledged the relatively primitive phyletic position of the ingolfiellids and hyperiids, and followed phyletic arrangements of superfamilies and families within the Gammaridea proposed earlier (e.g. Bousfield, 1979, 1982a,

1983), he has placed the caprellids in a primitive position, close to the ingolfiellids. He has advocated the use of rigid cladistic techniques (e.g. a Wagner 78 program) in producing a natural classification. However, in agreement with Ridley (1983), we find many basic or "obvious" assumptions about character states to be often flawed by homoplasies; resulting cladograms in which these are not recognized are thus less realistic than phenograms in which homoplasious tendencies are selected out or otherwise minimized.

In this essay, we propose to treat the classification of amphipods phyletically, but with a somewhat semi-pragmatic approach. After the fashion of D. H. Steele (1988, et seq.) who noted that amphipods were primarily swimmers and clingers, and secondarily crawlers and burrowers, we have borrowed from older decapod crustacean classification the terms "Natantia" (for the reproductively swimming and pelagic types) and "Reptantia" (for the reproductively bottom-crawling and benthic categories). This approach utilizes reproductive (mating) morphology and behaviour, in both sexes, as its principal phyletic basis. Whatever the nature of the morphology and life style of mature females and immature stages of both sexes, reproductive morphology tends to be displayed most diagnostically in the mature male stage. Of particular significance there is the form and armature of the antennae, gnathopods, and uropod 3 and, to some extent, in the mechanical coupling organelles of peraeopods, pleopods, and uropods. The approach also facilitates the solution, or near-solution, of some longstanding problems of natural ordering of character states, and their application at proper levels of phyletic classification.

ACKNOWLEDGEMENTS

The work was conducted mainly at the National Museum of Natural Sciences in Ottawa over the past five years, and collated in research association with the Royal British Columbia Museum in Victoria. Officers of the following institutions have contributed significantly to the refinement of ideas in this work: Dr. K. E. Conlan, Canadian Museum of Nature, Ottawa, Canada; Dr. J. R. Holsinger, Old Dominion University, Norfolk, Virginia; Dr. D. H. Steele Memorial University, St. John's, Newfoundland; Dr. Pierre Brunel, Université de Montréal, Québec; Dr. Roger Lincoln, British Museum, London; Dr. J. K. Lowry, Australian Museum, Sydney; and Dr. Les Watling, Darling Marine Center, Maine, USA. We are especially grateful to Dr. D. R. Calder, Royal Ontario Museum, Toronto, who supplied material of a new species of *Valettioopsis*, and to Moira Galbraith, Victoria, who supplied material of pelagic eusiroideans and lysianassids used in these comparative morphological studies. Helpful editorial commentary was provided by Dr. C. P. Staude, Friday Harbor Laboratories, and by Philip Lambert, Royal British Columbia Museum. Preparation of the line illustrations was greatly facilitated by Susan Laurie-Bourque, Hull, Que., and Floy E. Zittin, Cupertino, California. Basic work leading to compilation of the present results was carried out partly under government of Canada NSERC grants (1987-90).

External Morphology of the Amphipod Crustacean.

By way of review, the general external morphology of a gammaridean amphipod has been diagrammed previously in Bousfield (1973), Barnard & Karman (1991), and in several other popular and semi-popular works (e.g. Staude, 1987). In Figs. 1A and 1B, the principal features of representative member of Amphipoda "Natantia" and "Reptantia" respectively, are outlined.

Amphipods are similar to most members of the subclass Malacostraca (large crustaceans) in having a finitely tagmatized body; head with 5 pairs of appendages; thorax with 8 pairs (first pair fused to head as maxillipeds); abdomen with 6 pairs, and terminating in a small supra-anal flap or telson. The order Amphipoda is superficially similar to most other orders within supraorder Peracarida in which the carapace is much reduced or lacking; in having eyes that are sessile or near-sessile; mouthparts that are concentrated in a buccal mass beneath the head; thoracic legs that are uniramous (or nearly so); and lecithotropic (nonplanktonic) development of eggs within a thoracic brood pouch of the female.

Amphipods differ from all other malacostracans in having ambulatory thoracic (peraeonal) legs arranged in two distinct groups: the first four pairs are directed forwards, with the dactyls (claws) backwards, and the last three pairs are directed backwards, the dactyls forwards, hence the name "amphi"+"pod" (both kinds of feet). This contrasts with the "fan-wise" or radiating position of the thoracic legs in isopod crustaceans. A second distinctive feature, unique to amphipods, is the arrangement of abdominal limbs: the first three pairs are biramous swimming legs (pleopods) and the hind three pairs are thrusting legs (uropods). This arrangement of abdominal limbs contrasts with that, which consists of five pairs of pleopods and one pair of uropods in all other eumalacostracan crustaceans. In amphipods, tail thrust drives the animal forwards, whereas in decapods the tail thrust is typically a rearwards "escape reaction".

The diagnostic features of amphipods that mate freely in the water column (Natantia) are shown in Figure 1A, and are described in detail elsewhere. The body is slender, often toothed or carinate above, with large powerful abdomen, large pleopods, and lanceolate, serially spinose uropods. The head is generally short and deep, with rostrum, and eyes variously pigmented or lacking (abyssal forms). The antenna are slender and elongate. Antenna 1, peduncle stout; basal segments of flagellum often fused and strongly armed with aesthetascs (chemo-sensory filaments), forming a callynophore; accessory flagellum short or lacking (in hyperiids). Antenna 2, peduncular segments 3-5 slender, anterior margin (of male) lined with fine filaments (brush setae) and often calceoli; flagellum elongate (esp. in males), often with calceoli. Mouthparts basic, mandibular and maxillipedal palps usually projecting anteriorly.

Coxal plates 1-4 various, usually shallow, similar but often unlike. Gnathopods 1 & 2 usually slender, weakly subchelate, with slender carpus and propod, seldom sexually dimorphic. Peraeopods 5-7 usually slender, usually subsimilar

(homopodous), but peraeopod 6 is often longest; coxae posterolobate (hind lobe larger). Telson usually large, and bilobate (fused and plate-like in hyperiids). Coxal gills large, often pleated, on peraeopods 2-7.

Diagnostic features of benthic amphipods, the Reptantia, that mate on or in the bottom substrata, are shown in figure 1B. The body tends to be short and compact, often flattened dorsventrally, seldom with dorsal teeth or carinations. The head is usually long and shallow, lacking rostrum, eyes usually small. The antenna tend to be short, with stout peduncular segments, especially in males; callynophore and brush setae never present, and calceoli rare. Mouthparts variable, mandibular and maxillipedal palps usually visible.

Coxal plates 1-4 various, from large, deep, overlapping, to small and basally separated. Gnathopods often large, strongly subchelate, strongly sexually dimorphic. Peraeopods with relative short stout segments, and anterolobate coxae (front lobe the larger). Abdomen short; pleopods medium to reduced or highly modified. Uropods short, stout, rami linear, with apical spines. Uropod 3, rami usually short, margins spinose, or highly modified, seldom sexually dimorphic. Telson lobes variously fused, plate-like. Coxal gills plate-like or sac-like, never pleated, often lacking on peraeopod 7.

These diagnoses are intended as a generalized guide to basic amphipod morphotypes. They do not apply to any particular species, nor to immature stages. Within each group are exceptional cases that resemble species of the other group. Such encounters provide one of the frustrating "joys" of attempting to classify amphipod crustaceans.

The phylogeny of the Amphipoda as a group within the Peracarida

The phyletic positioning of the Amphipoda has also been the subject of considerable controversy. The most widely held (classical) view, that amphipods are most closely related to isopods, is held by a number of modern workers including Bowman and Abele (1982), Stock (pers. commun.) and Schram 1984, 1986). Other workers including Dahl (1963), Watling (1981), and Bousfield (1988) have presented evidence that the natural sister group among the Peracarida is the Mysidacea (*sens. lat.*). A few others (e.g. D. H. Steele, and recently Watling (pers. communic.)) have looked for an ancestry outside the Peracarida, and do not rule out the Syncarida as the closest natural outgroup among the Eumalacostraca.

A basis for a possible mysidacean common ancestry is depicted in Figure 2. A typical gammaridean amphipod is represented by the phoxocephaloidean (lower right). At first glance, it appears to have little in common, at least externally, with the various forms of Mysidacea in the upper figures. The Mysidaceans are much more plesiomorphic in possession of a distinct maxillary carapace, and fully biramous thoracic limbs, among other differences. However, the relatively primitive ingolfiellidean amphipod (lower middle

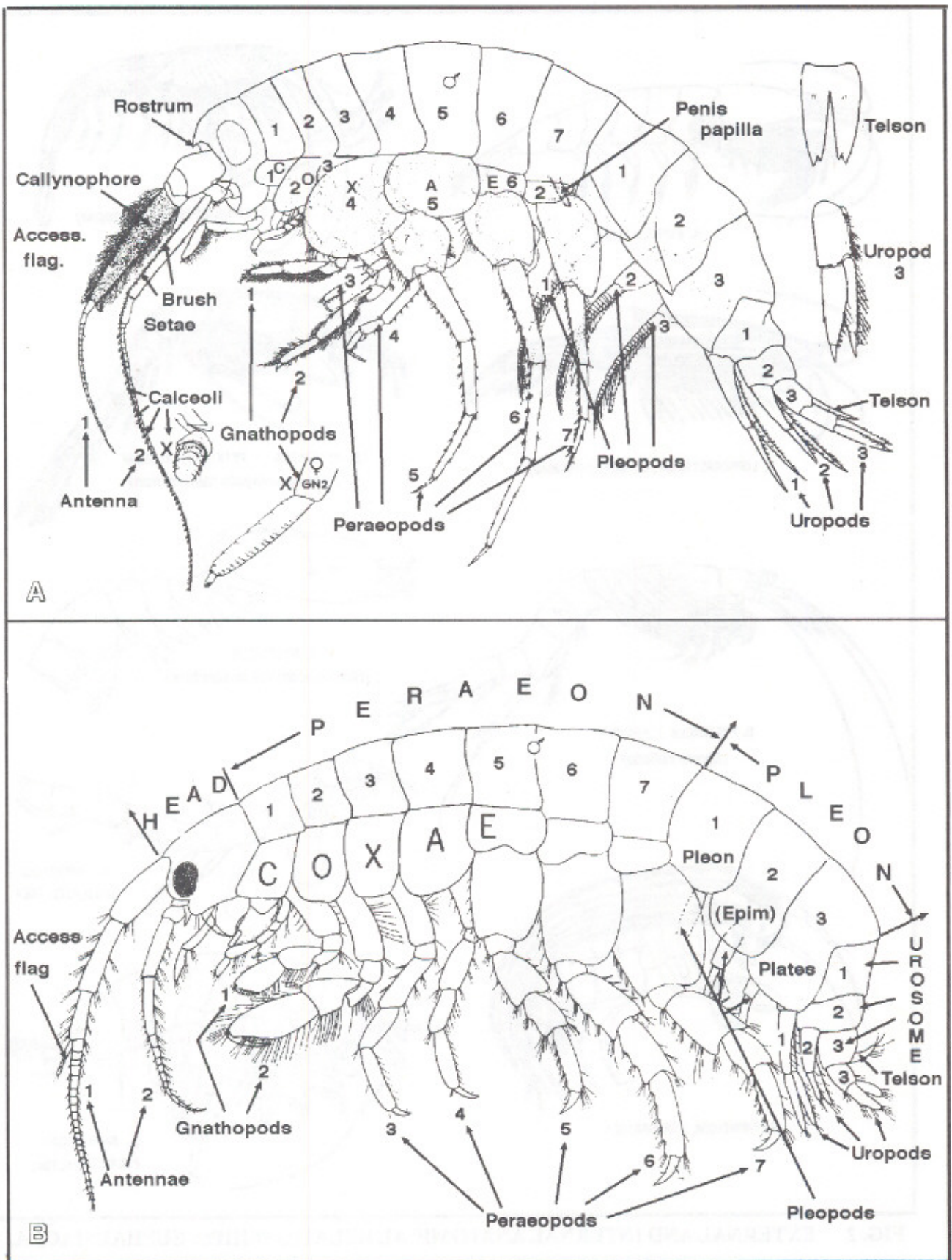


FIG. 1. Basic Morphology of the Amphipod Crustacean.
 A. Natantia (Hyperioptidae) B. Reptantia (Melitidae)

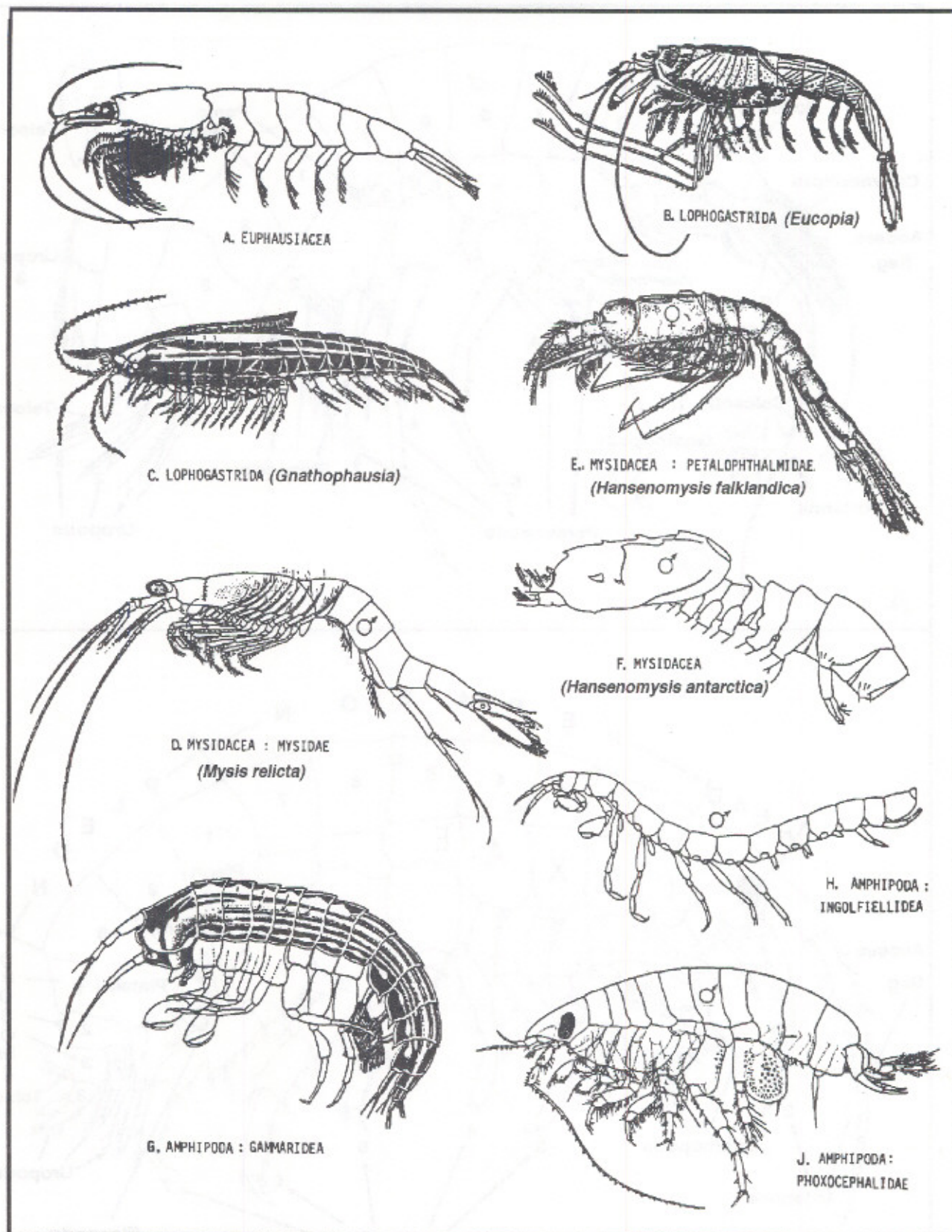


FIG. 2 EXTERNAL AND INTERNAL ANATOMICAL RELATIONSHIPS: EUPHAUSIACEA, LOPHOGASTRIDA, MYSIDA, AMPHIPODA.

(After Watling, 1981, and other sources)

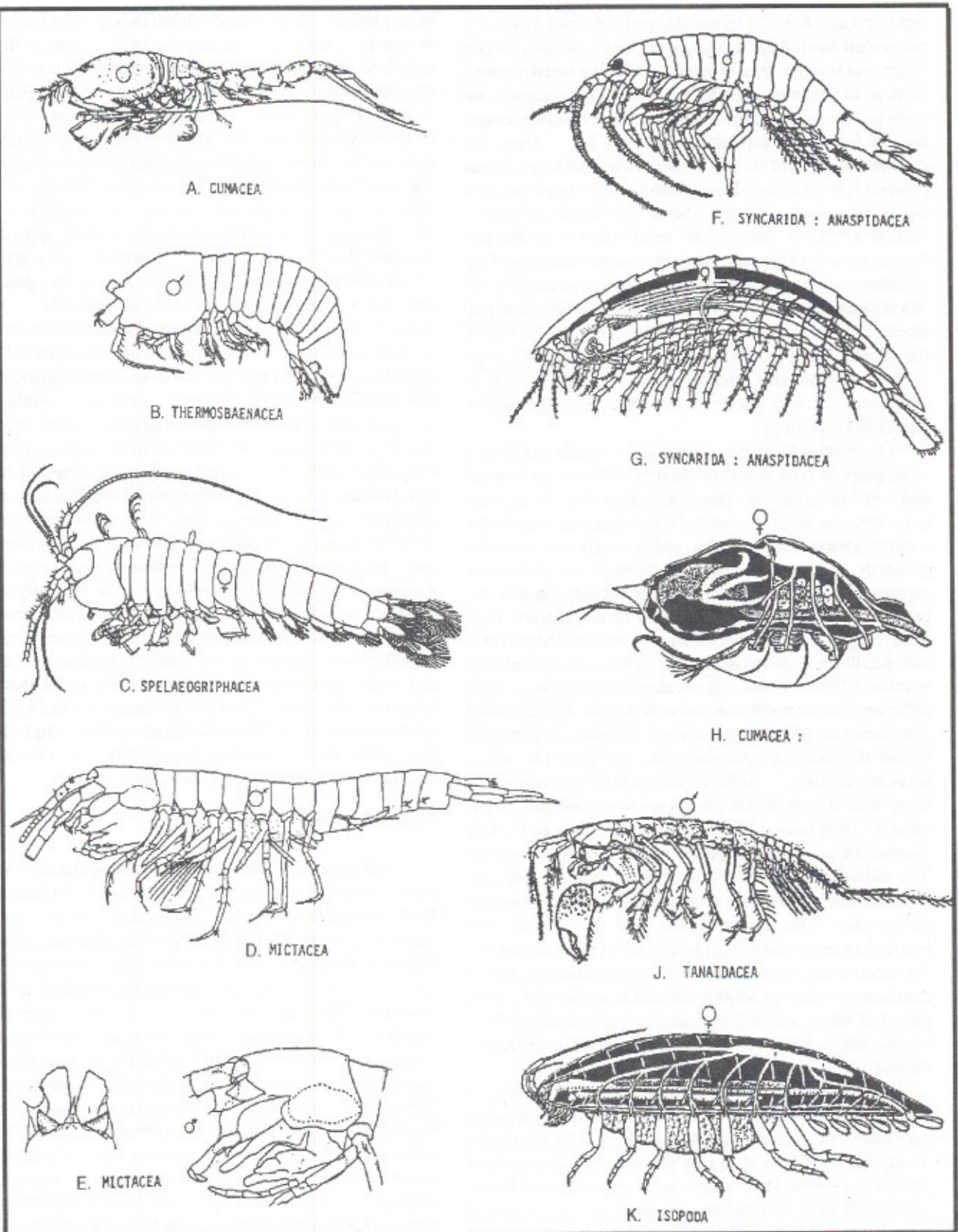


FIG 3. EXTERNAL AND INTERNAL ANATOMICAL RELATIONSHIPS OF MALACOSTRACAN SUPERORDERS SYNCARIDA, CUMACEA, BRACHYCARIDA, MICTACEA AND ISOPODA
(After Watling, 1981, Bowman & Illife, 1985, and other sources)

right, and also Fig. 27) shows (1) vestigial stalked eyes, (2) partly cleft maxilliped basal segment, and (3) uropod 2 much larger and stronger than uropod 1, both with serially setose rami, as in pleopods elsewhere. All of these features are more prominently and functionally present in mysidaceans, esp. in family Petalophthalmidae Fig. 2E. Thus, the enlarged uropod 2 of the ingolfiellidean may be homologous pleopod 5, anomalously longer than the anterior pleopods in this mysidacean family. Members of this family also demonstrate a trend to "fore and aft" subdivision of the thoracic legs, as in the Amphipoda. Also, the internal anatomy of the mysidacean (e.g. Lophogastrida, Fig. 3C), especially of the blood vascular system, with dorsal thoracic ostiate heart and thoracic respiratory vessels, is nearly identical with that of the Amphipoda (Fig. 3G; see also Watling, 1981; Schram (1986). Mysids also possess antennal glands as well as maxillary excretory glands, a very basis and phyletically significant homology).

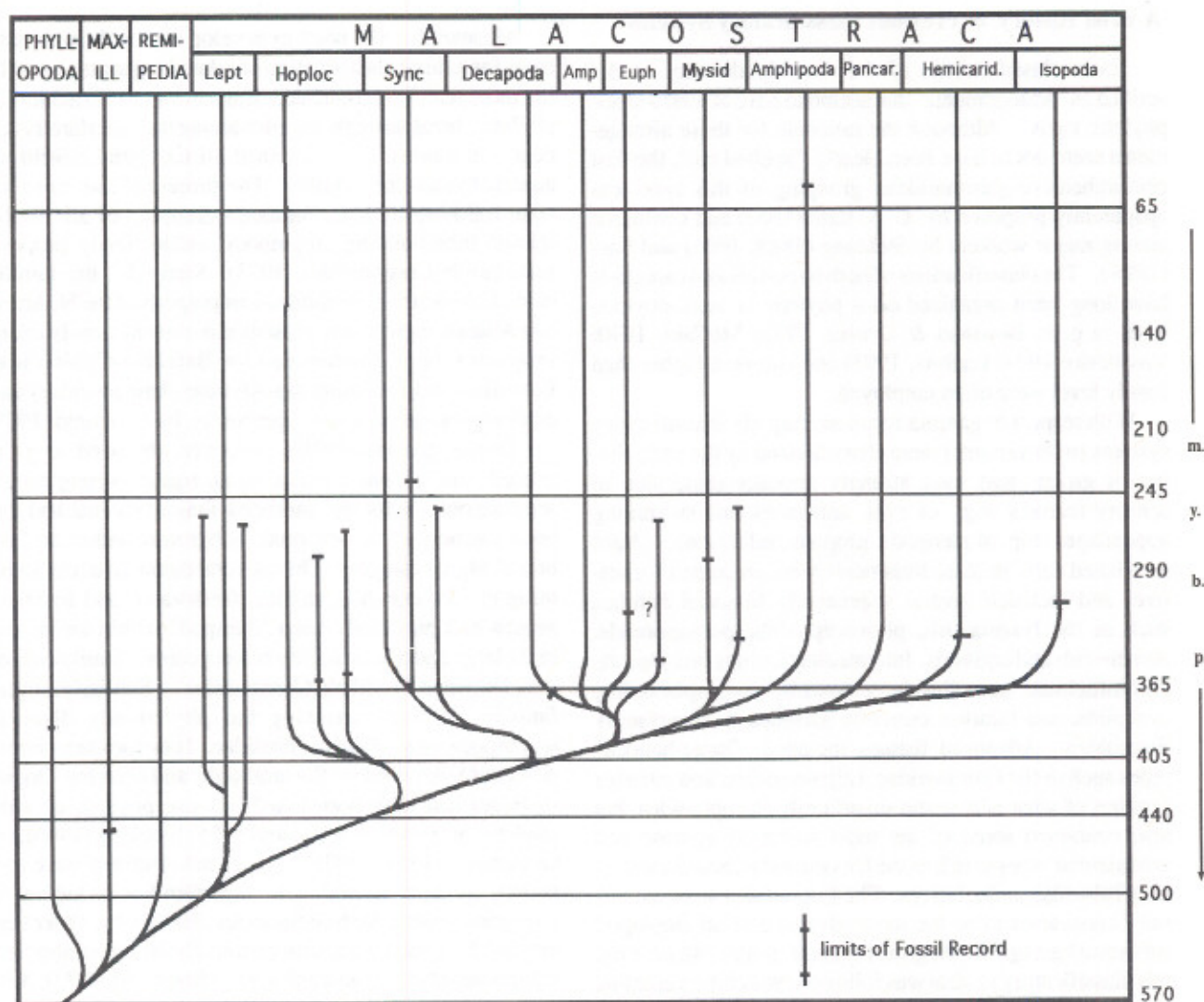
On the other hand, the external and internal morphology of amphipods contrasts very strongly with that of isopods and with brachycaridans (hemicarideans) (Fig. 3). In these latter taxa, the heart is weakly (or non-) ostiate, mainly (or entirely) abdominal in position, and the respiratory system is primarily abdominal, vestigially thoracic (or posteriorly cephalic). Both groups have maxillary glands but lack the primitive antennal excretory glands of amphipods. Here also, components of the buccal mass, especially the maxillae and maxillipeds, are basically differently constructed (see Schram, 1986). Other major features of these two groups, differing from the amphipods, occur in the lack of peraeopodal gill elements, and in the universal presence of flabellate (rather than annular) pleopod rami, and plate-like telson (even in juveniles). Such differences between members of these ordinal peracaridan groups are numerous and fundamental. Their similarities (in general body form and lack of carapace) appear more probably superficial and convergent. The differences probably reflect basic differences in life-style; the amphipods being primitively swimmers, secondarily crawlers (per Steele, 1988), and the isopods and brachycaridans primitively crawlers, secondarily swimmers. All these factors, in combination, suggest a relatively remote common ancestry of amphipods and isopods, and a long period of subsequent differing evolutionary pathways. As we may note below (p. 83), the fossil record of these groups, limited as it is, tends to support such a conclusion.

With respect to the Syncarida, overall similarities (with the Amphipoda) in body form and structure of some appendages cannot be denied (see Schram, 1986). Such includes a body that is cylindrical and carapaceless, eyes that are both stalked and sessile, first thoracic segment that is fused (usually) to the head, mouthparts occurring in a loose buccal mass beneath the head, pleopod rami that are annulate, and telson that is partly cleft (in some juveniles). However, under close scrutiny, several similarities appear superficial, and comprise an anomalous mixture of primitive and advanced characteristics, many probably convergent or

homoplasious. Thus, the cylindrical carapaceless body (e.g. in Anaspidacea) is only weakly tagmatized between thorax and abdomen, and metachronal swimming motion is continuous between thoracic exopods and the five pairs of abdominal pleopods. Although the pleopod rami are plesiomorphically annulate, the pleopods *per se* (except in the ancestral Palaeocaridacea) are apomorphically uniramous and usually anteriorly sexually dimorphic (Schram, 1986). The thoracic limbs (including maxillipeds) are plesiomorphically biramous, and their endopods apparently 8- (rather than 7-) segmented. Internally, although the syncarid heart is cylindrical and dorsal, it is apomorphically few- (or not) ostiate, and strongest abdominally. Also, syncarid respiration is of a more advanced type (abdominal as well as thoracic). Moreover, syncarids possess only maxillary glands and lack the primitive antennal glands that characterize amphipod excretory systems. Although syncarids and amphipods share an advanced lecithotrophic egg development, their reproductive life styles and ontogeny are very different and much less apomorphic in the Syncarida (see Schram, 1986). In combination, these character state differences appear to be at least as great as between the Amphipoda and other higher taxa within the Eumalacostraca, and suggest that a close phyletic relationship between the Amphipoda and the Syncarida has yet to be critically demonstrated. On the other hand, the gross character-state similarities between syncarids and amphipods may reflect modifications required by similarities in benthic, brackish- and fresh-water (possibly cold-water) life styles that are almost certainly convergent within many of the known Syncarida (including the Palaeocaridacea) and the Amphipoda. Regretably, the fossil record reveals little direct evidence bearing on such relationships (see below, p. 83).

Palaeohistorical Model

Although the fossil record of the Amphipoda is relatively limited (since Upper Eocene, Oligocene (Karaman, 1984; Bousfield & Poinar, 1993), much can be deduced indirectly from present geographical distributions and continental drift relationships, and from comparative morphology of component superfamily groups (see Bousfield, 1982b; Karaman, 1984; Schram, 1986; and Derek Briggs, pers. comunic.). Thus, the continental freshwater distribution of component families of the primitive gammaridean superfamily Crangonyctoidea parallels that of the Astacura (Decapoda), where the fossil record is much better documented, and suggests an early Gondwanian (Mesozoic, or earlier?) ancestry. On similar grounds, the world distribution of the small group of more primitive hypogean ingolfiellid amphipods (see Stock, 1981), the gross morphology of whose epigean forebearers can only be hypothesized, would make a late Palaeozoic origin of the Amphipoda (as a whole) seem not unreasonable (see Figure 5, after Bousfield and Conlan, 1990). Such timing would be consistent with the fossil record of other peracaridan groups (e.g. Isopoda, Tanaidacea, and Cumacea) that extend back to the Lower



Carboniferous. It is also not inconsistent with fossil records of other Eumalacostraca, for which primitive stomatopods and syncarids are recorded from various levels of the Carboniferous, and a primitive reptant decapod member (*Palaeopalaemon*, a "proto-glypheaoid") from the Upper Devonian. The earliest and most primitive crustacean groups (phyllopods, maxillipods, and even the leptostran malacostracans), were mostly small, filter-feeding and deposit-feeding marine morphotypes. Their fossil records extend back variously into the early Palaeozoic, and may indicate a possible Pre-cambrian origin for the Crustacea per se. However, the relatively abrupt appearance of major new eumalacostracan morphotypes in the Middle to Late Palaeozoic coincides rather neatly with the contemporaneous evolution and proliferation of new vascular plant groups (e.g. pteridophytes, cycads, *Cordaitales*). These relatively large, higher plant forms, along with attendant and endemic invertebrate faunas, presumably formed a basic and major

new food resource, for larger crustaceans in coastal terrestrial, fresh- and brackish-water environments at this stage of palaeohistory. Ancestral amphipods, with features of a "proto-ingolfiellid" (see p. 121) may have first appeared at that time.

At any rate, the limited fossil record of the Amphipoda might indicate that most superfamily groups are of relatively recent origin and evolution, probably since mid-Mesozoic times, some 200 m.y.b.p. (Bousfield, 1982b). The highly specialized caprellidan Cymaidae cannot be much older than Eocene, when their whale hosts first exploited the food resources of Tertiary Seas. Similarly, terrestrial amphipods (Talitridae) that inhabit rain forest leaf litter of Indo-Pacific and tropical rain forests, are unlikely to be older than the Cretaceous Period when angiosperm forests first evolved. Indeed, fossil talitrids from amber deposits of Mexico and the Dominican Republic are of Eocene Age, well within the predicted time frame (Bousfield & Poinar, Jr., 1994).

A Brief History of Previous Classificatory Systems

Early classifications of the Amphipoda may be described as "arrangements" that seemed to have at least a semi-phyletic basis. Although the rationale for these arrangements seem not to have been clearly "spelled out", the first comprehensive gammaridean grouping of this type was apparently proposed by C. S. Bate (1862) and continued among major workers by Stebbing (1888, 1906) and Sars (1895). The classifications of both hyperiids and caprellids have long been organized on a phyletic or semi-phyletic basis (e.g. in Bowman & Gruner, 1973; McCain, 1970; Vassilenko 1974; Laubitz, 1993) and sub-taxa higher than family level were often employed.

With respect to gammaridean amphipods, classificatory systems (with variants) were characterized by the early listing of groups that were strongly sexually dimorphic in sensory features (e.g. of eyes, antennae), and swimming appendages (esp. of pleopods, uropods and telson). Major taxa listed early in these treatments were presumed "primitive" and included several vegetatively fossorial families such as the lysianassids, phoxocephalids, pontoporeiids, ampelisids and argissids. Intermediate listings included the amphilocheids, stenothoids, pleustids, paramphithoids, synopiids, and families currently assigned to superfamily Eusiroidea. Advanced listings included "large-handed" types such as the Gammaridae, Liljeborgiidae, and member families of what is now the superfamily Corophioidea, but also contained some of the most strikingly spinose and ornamented groups such as the Dexaminidae, and the terrestrial Talitridae and relatives. The Caprellidae were universally considered to be the most advanced of all amphipod subordinal groups. During the first half of the 20th century, this classificatory system was followed, with little variation, by most major workers, including Chevreux & Fage (1925), Shoemaker (1930) and Gurjanova (1951).

In 1958, J. L. Barnard introduced a purely pragmatic alphabetical listing of families and genera within the Gammaridea, upon which he expanded in a later descriptive and annotated compendium of world-wide families and genera (Barnard, 1969a). He informally proposed, at various times, several phyletic systems, most notably based on the "*Gammarus*" prototype, and on the "*Corophium*" (fleshy telson) ancestral type (Fig. 5). However, the "fleshy telson" thesis, expanded and detailed in subsequent papers, and in his major compendium on freshwater amphipods (Barnard & Barnard, 1983) appeared to be inconsistent with the overall morphological evidence developed by other workers. Although others soon adopted the alphabetical system (e.g. Ruffo et al (1983, 1990)), his phyletic thesis received little published support elsewhere. As pointed out by Schram (1994), his co-author (in Barnard & Karaman, 1983) wrote a dissenting opinion in a separate appendix to that paper. Despite these informal phyletic proposals, the classification system of Barnard's subsequent collated works (e.g. Barnard & Barnard, 1983; Barnard & Karaman, 1991) continued to be essentially alphabetical.

Meanwhile, the need to develop a broadly acceptable basis for natural classification of related higher taxa was being more widely recognized. Bulycheva (1957) achieved a phyletic "breakthrough" by introducing the superfamily concept, Talitroidea, that combined all terrestrial talitrid and aquatic hyalid-like families. The success of this move was soon followed by J. L. Barnard's grouping of all "fleshy-telson" tube-building amphipods within newly proposed superfamily Corophioidea (1973). Similarly, the families of shallow-water gammaridean amphipods of the N. American Atlantic region were presented mainly in closely related groupings (e.g. Pontogeneiidae-Bateidae-Calliopidae-Eusiridae, and Dexaminidae-Atylidae-Ampelisidae) each equivalent to an informal superfamily, by Bousfield (1973).

During the mid-1970's, however, the need to group related families was matched by an equally strong need to separate out obviously unrelated major taxa that had long been submerged as informal subgroups within an "umbrella" higher category. Thus, several distinctive free-swimming or free-crawling, marine, freshwater, and hypogean groups had previously been "dumped" within an increasingly large and unwieldy heterogeneous family concept long known as "good old Gammaridae". Similarly, several families of free-burrowing but phyletically disparate amphipods (e.g. Phoxocephalidae, Haustoriidae (Pontoporeiidae), Argissidae, the urothoids, and even the Dogielinotidae) had long been listed in close phyletic or semi-phyletic proximity (e.g. by Sars (1895), Stebbing (1906), and Gurjanova (1951, 1962)). The gammaroideans were soon broken up into several new superfamilies, including the Crangonyctoidea, Melphidippoidea, Melitoidea (later Hadzioidae), Bogidielloidea, with various family allocations (e.g. Gammarellidae) to Eusiroidea, etc. (Bousfield, 1977). With the superfamily concept thus broadened, a phyletic arrangement of all gammaridean amphipods was then formally attempted (Bousfield, 1979a). Encouraged by the acceptance of several of these linkages by Lincoln (1979), Holsinger (1992a) and others, the superfamily and family concepts were further refined (Bousfield, 1982a, 1983). These included a phyletic sorting out of the major sand-burrowing taxa, a reclassification still in progress (e.g. Bousfield, 1989).

In support of the initial formal phyletic arrangement of superfamilies, Bousfield (1979) developed a phylogenetic tree of relationships that is examined again in this study (p. 125). Trees provide a quick "visual" of basic relationships between groups of organisms, and have been widely accepted in eumalacostracan classification (e.g. Siewing, 1963). By employing numerical taxonomic methodology modified from Sneath and Sokal (1973), these relationships became more widely acceptable (Bousfield, 1983). The classification was recognized in principle in Mark Ridley's (1983) explanation of organic diversity, and incorporated in Lowry's (1986) analysis of callinophore distribution and, with some reservations, in Schram's comprehensive book on Crustacea (1986). The chart of Bousfield (1983), summarizing the range of plesio-apomorphy in selected character states within 22

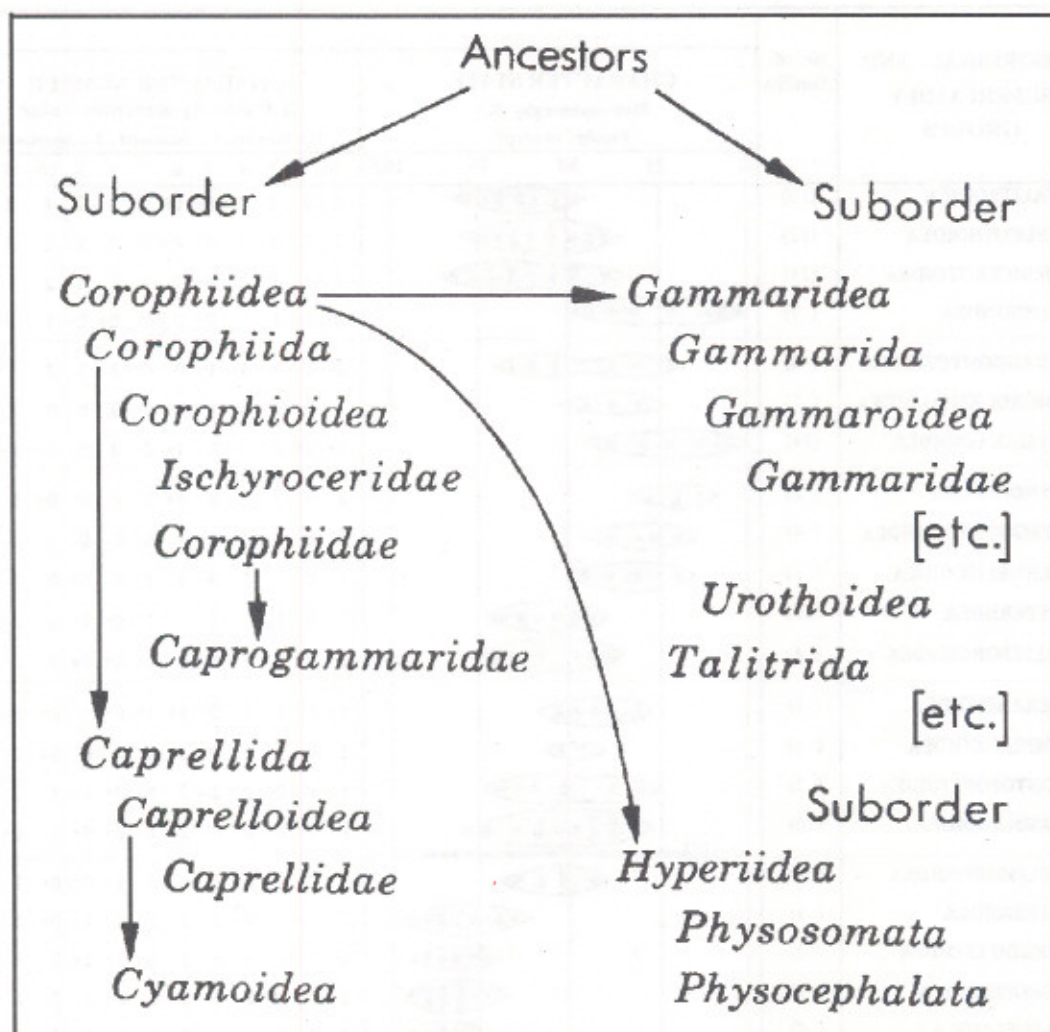


FIG. 5. PHYLETIC RELATIONSHIPS WITHIN THE AMPHIPODA PROPOSED BY J. L. BARNARD (1969).

sub-ordinal and superfamily categories within the Amphipoda is provided in Fig. 6 (p. 86). The character states are ordered, with plesio-apomorphic values of 0, 1, and 2, and the values apply to component families of the almond-shaped envelopes for each superfamily and subordinal taxon. An index of plesio-apomorphy (P/A Index) was derived by adding the values across the 12 characters for each taxon and expressing them as a percentage of 24, the highest total possible. High P/A values denote advanced, and low values primitive, taxa. In terms of present classification orientation, we may note that the envelopes for superfamilies of Natantia range mainly below, and those of the Reptantia mainly above, the 50% P/A level. A certain degree of overlap is not unexpected, where the more advanced groups of Natantia (e.g. Oedicerotidea, Hyperiidea, Pontoporeioidea) range above, and the more primitive groups of Reptantia (e.g. Crangonyctoidea, Gammaroidea) range below, the 50% level.

Recently, computer-based methodology has been more widely employed and the results more widely accepted. However, these results may not necessarily correspond to the

actual route through which a group of organisms evolved. Thus, using a Wagner 78 program, Schram and Brusca had (by 1986, above) produced a cladogram of relationships among amphipod taxa that was "quite at odds with anything (then) currently in the literature". Although apparently yet unpublished, such a result would command respect. Brusca and Wilson (1991) obtained highly credible results in reclassifying the Isopoda, using a number of cladistic analysis packages that included HENNIG86 and PAUP (version 3.0). On the other hand, by means of a Wagner 78 program, Schram (1984) had employed 31 paired character states in developing 4 cladograms of relationships of major taxa within the Eumalacostraca, all of which placed the Isopoda as the phylogenetically closest outgroup to the Amphipoda. However, the character states found to be phylogenetically "synapomorphic" in these two taxa (nos. 13, 14, 21, 22, and 31 - i.e. uniramous thoracopods, pleopods lost or reduced, presence of thoracic coxal plates, eyes sessile, carapace absent) are features that are especially vulnerable to broadly eumalacostracan convergent evolution. In our view, the

SUBORDINAL AND SUPERFAMILY GROUPS	No. of families	CHARACTER STATE					CHARACTER NUMBER & Plesio-Apomorphic Value												Total No./24	P./A. Index (%)	
		Plesio-apomorphy (%)					0 = Plesiom.; 1 = Intermed.; 2 = Apomorph.														
		Family "envelop"																			
		0	25	50	75	100	1	2	3	4	5	6	7	8	9	10	11	12			
1. TALITROIDEA	(10)						2	2	2	0	0+	0+	0	2	2	1	2	0+	13+	55	
2. LEUCOTHOIDEA	(12)						2	2	-	2	1	0	0+	0	1	2	2	2	0	14	58
3. OEDICEROTOIDEA	(2+)						1	1	1	2	0+	2	1	1	1+	2	1+	1+	14+	54	
4. EUSIROIDEA	(7)						0+	0+	1	1	0+	0	0	0+	0+	1	0+	0	3+	15	
5. CRANGONYCTOIDEA	(4)						2	1	1	1	1	0	0	2	2	2	1	0	13	54	
6. PHOXOCEPHALOIDEA	(3)						1	0	0	2	1	2	0	0	0	0	1	2	9	38	
7. LYSIANASSOIDEA	(2+)						0+	0+	0+	0	1	1-	0	0	0	1-	0+	2	5+	21	
8. SYNOPIOIDEA	(2)						1	0	1	1	0	0+	0	0	0	0+	0	1+	4+	17	
9. STEGOCEPHALOIDEA	(4)						2	0	1	0	0+	1	0	0	0	1	1	0+	6+	25	
10. PARDALISCOIDEA	(5)						1	0	1	2	0+	1	1	0	0+	0	0	0	6+	26	
11. HYPERIIDAE	(21)						1	0	1	2	2	1	1	0+	1	2	2	0	13+	54	
12. LILJEBORGIOIDEA	(4)						2	1	2	2	0	1	1	0+	1+	1	2	2	15+	62	
13. DEXAMINOIDEA	(5)						1+	1	1	1	0+	1+	1+	0+	1	0+	0+	1	8+	35	
14. AMPELISCOIDEA	(1)						1	0	1	2	0+	2	1+	0	0	0+	2	2	11+	47	
15. PONTOPOREIOIDEA	(2)						1	1	0+	2	2-	2	1+	0+	1-	1	2	0	13+	54	
16. GAMMAROIDEA	(10)						1	2-	1	0	1	2	2	0+	0+	1	0+	0+	10+	42	
17. MELPHIDIPPOIDEA	(4)						1	1	1	2-	1	1	2	1	0+	0+	1	2-	13	53	
18. HADZIOIDEA	(3)						2	2-	2	2-	1	2	2	2	1+	0+	2	2	20-	83	
19. BOGIDIELLOIDEA	(2)						2	1-	2	2	1	2	2	2	1+	2	2	2	21	86	
20. COROPHIOIDEA	(9)						2	2	2	2	1	2	2	2	2	2	2	0+	21+	88	
21. CAPRELLIDEA	(6)						2	2	2	2	1	2	2	2	2	2	2	0	21	87	
22. INGOLFIELLIDEA	(2)						2	0	2	2	1	1+	2	1	0	2	2	2	17	71	

FIG. 6. RANGE OF PLESIO-APOMORPHY IN SUBORDINAL AND SUPERFAMILIES OF AMPHIPODA (AFTER BOUSFIELD, 1983)

basic differences between isopods and amphipods (e.g., in embryonic development, in mouthpart morphology, and in annulate vs. flabellate pleopods) are more significant and less subject to homoplasy; moreover, such character states of the Amphipoda find much closer parallels within the Mysidacea and Lophogastrida, as noted in the analysis of Brusca and Wilson (1991).

A recent analysis of amphipod classification, using the PAUP Version 3.0k program, has produced 5 cladograms of phylogenetic relationships of amphipod families and suborders considerably at variance within anything previously published (Kim & Kim (1993). However, the validity of these results has been questioned by Schram (1994), since the analysis of the entire amphipod taxonomic assemblage considered only 20 families (about 15% of the total) and only 16 characters (of more than 50 that could be deemed useful). A further review of that study also reveals that 10 (62%) of

the selected characters concern only mouthparts, uropods, and pleopods, of essentially non-reproductive orientation, and thus of probable lesser phyletic significance.

Investigations elsewhere contribute usefully to the solution of problems of amphipod phyletic classification. Conlan (1990, 1991a) is continuing studies on the significance of sexual dimorphism of the gnathopods and of mate-guarding strategies in the phyletic relationships of corophioid amphipods. As we find in the present study, her work applies more broadly across the superfamilies of Reptantia and across the Amphipoda generally.

Other major workers in amphipod phylogeny are investigating potential amphipod-synbranchid relationships (D. H. Steele, L. Watling, personal communication). In present studies, we have yet found little evidence for such a relationship, but applaud their wide and stimulating interest in classificatory aspects of amphipod crustaceans.

A New Approach to Amphipod Phyletic Classification

As outlined previously (p. 77), the current status of phyletic classification of the Amphipoda finds no single system universally accepted or satisfactorily treating all major problems of natural relationship.

The following semi-phyletic approach to classification of amphipod crustaceans is based primarily on reproductive morphology and behaviour, as outlined recently by Conlan (1991a, b: Fig. 7, here). In summary, amphipods that search out and mate freely, usually in the water column, tend to be closely related phyletically, and may be collectively termed *Amphipoda Natantia*. Those that mate on or in bottom substrata, following a period of "mate-guarding" proximity between males and females, are less closely related to each other phyletically, but exhibit such similarity of life style as to be conveniently and pragmatically termed *Amphipoda Reptantia*. The primary features that distinguish these two principal categories are given in Table 1, and treated in greater detail in the following text.

Although this semi-phyletic approach covers all major groups of amphipods, at subordinal and superfamily levels, it does not pretend to solve all problems of natural classification, at all taxonomic levels. In this essay we have attempted to tackle some of the more vexing problems, using the *Natantia-Reptantia* approach in a manner that may point to ultimately correct phyletic solutions. Many problems remain unresolved and await input from yet undiscovered taxa, and broader input from more recent and more basic taxonomic tools such as ultrastructural analysis, electrophoretic serology, and eventually DNA-DNA hybridization. Especially vexing to gross morphological analysis are those taxa whose immediate characteristics are "reptant" (at family and generic level) but which prove more or less closely related to groups that are primarily "natant". We conclude that the problem of convergence is encountered in virtually every facet of phyletic investigation, and allowances for this phenomenon must be made accordingly.

In the following sections we consider the phyletic significance of sexually dimorphic characters and character states, as evidenced in both the *Natantia* and *Reptantia*. In the first part of the analysis, we consider the antennal sensory organelles, reproductively significant features of the gnathopods, and phyletic trends exhibited by uropod 3 and the telson. In the second part, we examine classificatory problems posed by the present status of hyperiid-gammarid and ingolfiellid-gammarid morphological relationships, and the difficulties encountered in the study of fossorial amphipods, and enigmatic hypogean taxa.

In our concluding section we present, in tabular form, a broadly revised listing of subordinal, superfamily, and family level taxa within the umbrella concept of *Natantia-Reptantia*. Because the concept concerning *Reptantia* is essentially pragmatic, and because cladistic taxonomic analysis is especially difficult to apply within the *Amphipoda*, our concept of higher level phyletic relationships is presented in the form of a phyletic tree, revised from previous studies.

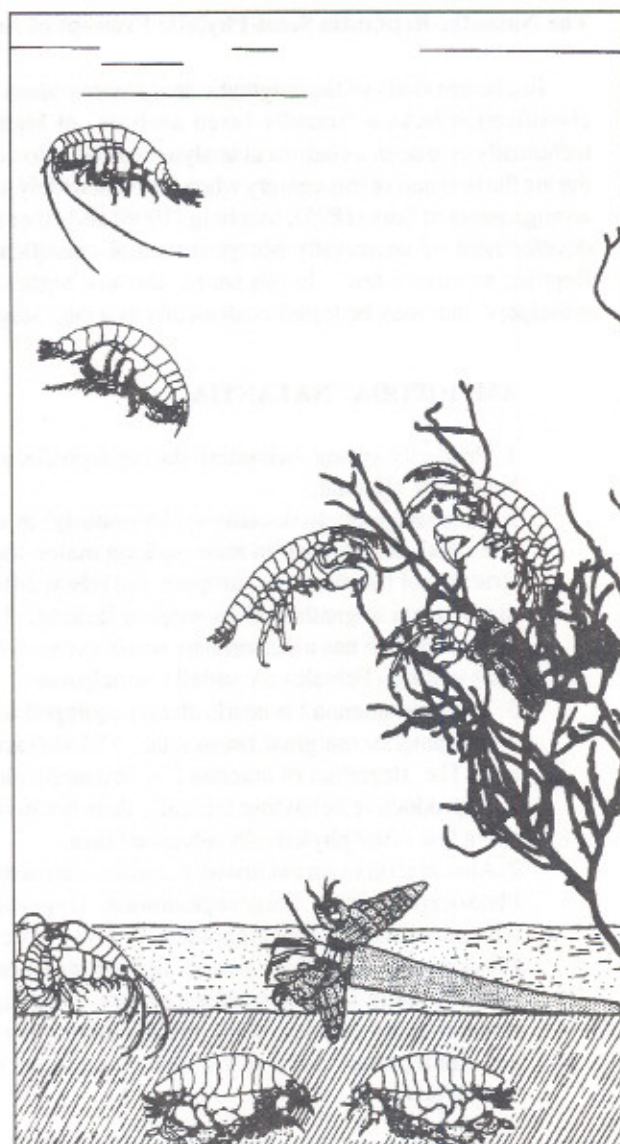


FIG. 7. Natant and Reptant Amphipoda Reproductive Setting (after Conlan, 1991).

In a more complete study, we might have included analysis of other major groups of appendages, especially the mouthparts, pereopods, and pleopods. The significance of mouthpart morphology in the phyletic classification of amphipod crustaceans has been outlined previously for gammarideans by Bousfield (1979, 1982a, 1983, etc.) and Barnard (1969, etc.), for caprellideans by McCain (1970) and others, and for hyperiids by Bowman and Gruner (1973). In general, mouthpart morphology is a direct reflection of food preference and feeding methodology and is significant mainly at the family level of classification. Although their character states seldom mirror reproductive behaviour, certain features, especially of the mandible, are considered basic to phyletic classification. However, for development of more credible phyletic results we would advise caution in utilizing mouthpart morphology to the exclusion of reproductively significant character states.

The Natantia-Reptantia Semi-Phyletic Concept of Amphipod Classification

In a recent study of the enigmatic new gammaridean genus *Aetiopedes*, Moore and Myers (1988) opined that amphipod classification lacks a "soundly based analysis" of higher taxa or a "well founded" phylogeny. Such a comment may technically be true in a cladistical analytical sense. However, it apparently overlooks the long period of systematic stability during the first half of this century when the most widely accepted classification of amphipods was based on the semi-phyletic arrangements of Sars (1895), Stebbing (1906) and other major workers. The lack of cladistic analyses in no way prevented development of universally accepted natural classifications within other major animal groups, e.g. Mammalia, Aves, Reptilia, to name a few. In this study, the new higher classificatory concepts are based on what might be termed "first principles" that may be tested cladistically at a later stage, and are diagnosed and described as follows:

AMPHIPODA "NATANTIA"

1. Primarily strong swimmers during reproductive behaviour, even where the vegetative life style is benthic or infaunal;
2. Sexes mate freely (usually synchronously) in water column, or on/in the substratum.
3. Sexual dimorphism: in mate-seeking males, the body form, antennal size and armature, eye size, and structure of the pleopods, uropods and telson differ, usually strongly, from those of the female. Sexual dimorphism in gnathopods is weak or lacking. The male is typically smaller than the female.
4. Male morph has a determinate moult cycle (6-8 stages); the adult stage is terminal and the male dies after mating. Females are usually semelparous.
5. The male antenna 1 is nearly always equipped with a calynophore; peduncular segments 3-5 of antenna 2, bear anterior marginal brush setae. Calceoli are frequently and variably present on one or both antennae. The flagellum of antenna 2 is frequently elongate in the male.
6. Reproductive behaviour typically does not involve pre-amplexus, except in in some Oedicerotoidea, and a few other phyletically advanced taxa.
7. Almost all taxa are exclusively marine, often with strong representation in the deep sea (Lysianassoidea, Phoxocephaloidea, Stegocephaloidea, Hyperioidea, Synopioidae, Pardausoidea, Dexaminioidea, Ampeliscoidea, Melphidippoidea. A few eusiroideans, melphidippoideans and allied groups (e.g., *Phreatogammarus*, *Sensonator*), and some oedicerotoideans inhabit fresh water, and pontoporeioideans inhabit mainly fresh or brackish waters. The vegetative life style is free-living or commensal; a few lysianassoideans and pardausoideans are ecto-parasitic. Some eusiroidean genera (within Pontogeneiidae and Calliopidae) and a few melphidippoideans (*Phreatogammarus* and *Sensonator*) are hypogean in fresh water.

AMPHIPODA "REPTANTIA"

1. Primarily mate-guarders during reproductive behaviour. Free living forms tend to be carriers, and utilize gnathopods in pre-amplexus with the female until her ovulating moult. Tube builders and semi-sessile groups are mate attenders.
2. Sexes mate on or in the bottom, rarely in water column.
3. Sexual dimorphism of gnathopods is usually strong. The male is typically larger than the female but otherwise not markedly different in form. The antennae may differ in size sexually.
4. Male morph growth stages are indeterminate(8+), with two or more sexual instars; continues to feed and mates continuously after maturity. Females are usually iteroparous.
5. Male antennae lack calynophore and brush setae and are seldom rarely equipped with calceoli, except in some primitive taxa. The flagellum of antenna 2 is not elongated.
6. Mating behaviour involves pre-amplexus and/or mate-attending agonistic displays by males, often of lengthy duration.
7. Most groups are marine (Leucothoidea, Caprellioidea) or mainly so (Haldioidea, Liljeborgioidea, Ingolfiellioidea, Corophioidea) but with relatively limited representation in the deep sea. Nearly all have freshwater representatives. The vegetative life style is free-living or commensal, fossorial or domicolous, and occasionally parasitic (external). The Crangonyctoidea, Gammaroidea, Bogidielloidea and Talitroidea are primarily (or nearly exclusively) freshwater and/or terrestrial. All groups except the Leucothoidea, Corophioidea, and Caprellioidea contain one or more hypogean species, and the Bogidielloidea and Ingolfiellioidea are exclusively so.

The Callynophore

The possible significance of the callynophore in phyletic classification of amphipods was first introduced by Lincoln and Lowry (1984) and amplified formally by Lowry (1986). This structure consists of a bundle of generally close-set aesthetascs on the posterior, or postero-medial, margin of the fused (or conjoint) basal segments of the flagellum of antenna 1. The callynophore is distributed across a wide spectrum of amphipod taxa, including all Hyperiidea, but is characteristic of superfamily groups within the Natantia (Fig. 8). It also occurs widely across pelagic marine Malacostraca such as the Mysidacea, Lophogastrida, Euphausiacea, and Decapoda Natantia (e.g., Dendrobranchiata, Caridea) (Lowry, 1986). The structure almost certainly occurred in extinct presumably pelagic malacostracan groups such as the Pygocephalomorpha (Mysidacea) and various 'Eocaridacea' and Waterstonellidea, but present interpretation of fossil specimens does not clearly demonstrate this feature (e.g. in Schram, 1986). However, the callynophore occurs only sparsely in reproductively pelagic males of the infaunal Cumacea, and is rare (perhaps secondarily developed?) in isopods. It is apparently lacking in stomatopods, syncarids, and all other essentially benthic, reptant, or freshwater malacostracans.

With respect to function, since the callynophore consists of aesthetascs of various sizes and densities, its primary role is almost certainly chemosensory, but in some decapods may also be tactile or mechanical. In most amphipod groups the callynophore is developed only in the final adult male instar, and would seem to be of direct reproductive significance in the detection of females within the water column. However, in some generic groups (e.g., within Lysianassoidea, Synopioidea), callynophore-like structures may also be present in mature females and subadult stages, perhaps indicating a possible secondary role in detection of food resources.

Representative forms of callynophores, within the Amphipoda, are illustrated in Fig. 8. Lowry (1986) has described a one-field arrangement of the callynophore within families Platyishnoidae, Urothoidae and Phoxocephaloidea (Phoxocephaloidea), a condition he considers primitive, and in some hyperiids (e.g. Archaeoscinidae), perhaps convergently. In all other taxa the arrangement is two-field. The callynophore is especially strongly developed in pelagic carnivores and necrophages, often where calceoli are weak or lacking, such as within the Lysianassoidea, Synopioidea, Pardaliscoidea, Stegocephaloidea, and Hyperiidea. However, with few exceptions, the callynophore is weak or lacking in reproductively pelagic but vegetatively benthic groups such as the nestling Dexaminioidea and tube-building Ampeliscoidea, and the fossorial Phoxocephaloidea and Pontoporeioidea. It is also weak or lacking in several subgroups within Natantia where the total life cycle is essentially benthic and infaunal (e.g. Haustoriidae), or commensal-parasitic (e.g. some Lysianassoidea) and/or where preamplexing reproductive behaviour has secondarily and convergently developed (e.g. in Paracalliopiidae and Exoedicerotidae within Oedicerotoidea). Curiously, the

callynophore is surprisingly infrequent, or weakly developed, in the mainly marine, but mainly acalceolate family Oedicerotidae and, within superfamily Eusiroidea, is apparently restricted to the pelagic, primitive family Eusiridae.

The callynophore is almost totally lacking in the reproductively benthic Reptantia, including the Caprellidea and Ingolfiellidea, even in those that have apparently become secondarily pelagic (e.g., *Macrohectopus*: Gammaroidea). However, callynophore-like structures have been reported from a few Amphilochidae (e.g. *Austropheonoides*, *Peltocoxa*) and Cressidae (*Cressa cristata*) within the primitive subgroups of Leucothoidea (Lowry, 1986).

We may reasonably conclude, therefore, that the callynophore (and its character states) offers one of the potentially most useful criteria of reproductive life style within the Amphipoda. Although its occurrence across the spectrum of amphipod superfamilies is subject to some homoplasious tendencies, such aberrancies may be correlated with non-reproductive life style and are thus predictable. In broader perspective, the presence of a callynophore is a plesiomorphic, or basic feature of malacostracan reproductive morphology, and in our view provides a primary basis for development of a phyletic classification within the Amphipoda.

Antennal Brush setae

The term "brush setae" was first applied by the author (Bousfield, 1979a) to describe the dense tufts or clusters of short brush-like setae that variously line the anterior margins of peduncular segments 3, 4, and 5, of antenna 2. A more refined term "callynosetae" might be coined from the Greek root employed by Lowry (1986) in naming the callynophore. Brush setae may occur also on the posterior (lower) margins of peduncular segments 1-3 of antenna 1 (e.g., in Dexaminioidea). To date, brush setae have been found only in the terminal male stage of pelagically reproductive amphipod superfamilies, and not yet in subadult males, females and/or immatures. They also occur in pelagic males of other peracaridan taxa such as the Cumacea and Mysidacea. Brush setae are weakly to moderately developed in calceolate amphipod taxa such as the Phoxocephaloidea, Pontoporeioidea, Eusiroidea, Oedicerotoidea, and Lysianassoidea. They are almost invariably present, and most strongly developed, in non-calceolate superfamilies of Natantia such as the Pardaliscoidea, Synopioidea, Dexaminioidea, Ampeliscoidea, and Melphidippoidea, but are less well developed or even rare within the Stegocephaloidea and Hyperiidea (Figs. 8, 30).

The function of brush setae is yet unknown and conjectural. Although they have not yet been studied in ultrastructural detail, in gross morphology they appear as modified setae, rather than thin-walled as in aesthetascs. Their role may be tactile, during the process of copulation, when the male is briefly in close contact with the female. The presence of brush setae only in males and only in plesiomorphic taxa (within the Natantia) suggests strongly that their function is of reproductive significance, and thus potentially of primary value in phyletic classification.

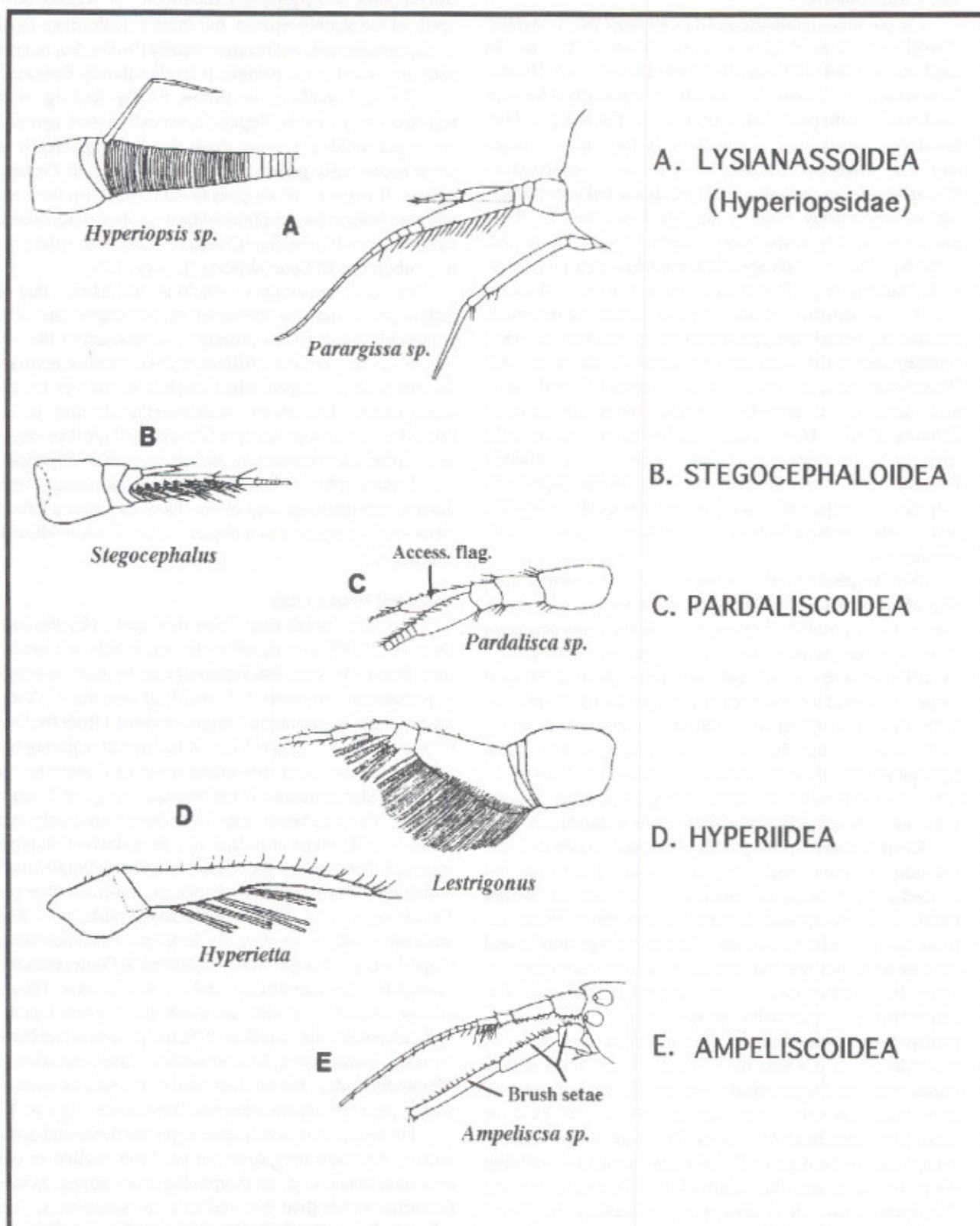


FIG. 8. TYPES OF ANTENNULAR CALLYNOPHORES
[after Barnard (1969), Bowman (1973) and other sources]

The Calceolus: Occurrence within the Amphipoda.

The possible significance of antennal calceoli in the phyletic classification of the Amphipoda has been alluded to variously by Bousfield (1979a, 1983), Lincoln and Hurley (1981), Lincoln (1984) and more recently by Godfrey, Holsinger & Carson (1988), Stapleton, Williams & Barnard (1988), Holsinger (1992), and Steele & Steele (1993).

The principal features of these antennal microstructures have been outlined by Godfrey *et al.* (1988), with special reference to those of genera within the primitive superfamilies Crangonyctoidea and Gammaroidea of the Reptantia. The calceolus is a slipper-shaped membranous microstructure attached variously to the anteromedial segmental margins of the flagella and peduncles of both antenna 1 (antennule) and antenna 2. The combination of its structural form (in advanced forms: similar to that of a parabolic radar "dish"), and its anterior antennal location, may indicate that it functions primarily as a mechanoreceptor for detection of aquatic vibrations. However, its innervation and connection to the brain has not yet been ascertained, nor have micro-acoustical studies yet confirmed its true function. The calceolus is not to be confused with the aesthetasc, a sublinear thin-walled microstructure of mainly chemosensory function, found only on flagellar segments of antenna 1 in nearly all species of Amphipoda. The aesthetasc also occurs widely across malacostracan ordinal subgroups, including the Decapoda. The calceolus is also readily distinguished from brush setae and other seta-like structures co-occurring on antennal peduncular and flagellar segments.

Representative types of amphipod calceoli are illustrated here (Figs. 9 & 10). Calceoli-like structures are found on the proximal flagellar segments of antenna 1 (male) of a few other malacostracans, notably within the Syncarida (Anaspidacea: *Koonunga cursor*) and the Mysidacea (Mysida: *Xenacanthomysis pseudomacropsis*). Such structures are not considered calceoli by Lincoln (pers. communic.) and may be of different function, or convergent in form. However, they are included here as of possible phyletic significance within the Malacostraca and, in our view, merit further detailed comparative micro-anatomical and behavioural study.

Within the Amphipoda, the calceolus of the Crangonyctoidea (Figs. 9, 10) appears to be the most simplified, and probably most plesiomorphic in form (category 9, of Lincoln and Hurley, 1981). It consists only of a basal stalk and elongate (usually narrow, occasionally distally broadened) body that bears numerous (20+) elements of similar simple structure. Holsinger (1992) has distinguished two subtypes of calceoli within the Crangonyctoidea. The calceolus of northern Crangonyctidae is slender and elongate, with an simple branched internal "tree-trunk" configuration. Some separation of basal elements in *Crangonyx richmondensis* (illustrated by Godfrey *et al.*, 1988) are suggestive of "proto-receptacles". By contrast, the calceolus of the austral Sternophysingidae and Paramelitidae is typically broad, paddle-shaped, and its internal tree-trunk con-

figuration has more numerous indistinct branches, a seemingly more primitive condition. In slightly more advanced types of calceoli (Fig. 10: Phoxocephaloidea), the elements are fewer (10-15 in Platyschnopidae; 4-6 in Phoxocephalidae); and the body may be short and spatulate, or barrel-shaped, as in some Phoxocephaloidea.

In more advanced types of calceoli, the basal element is broadened and modified into a receptacle (weakly developed in Pontoporeioidea and Gammaroidea, strongly so in Eusiroidea), and the stalk is distally expanded into a bulla or resonator, weakly and more strongly in those same groups, respectively. In some Pontoporeioidea (Bathyporeiidae), finger-like processes protrude over the proximal elements. In the most advanced types of calceoli (viz., in some Eusiroidea: Gammarellidae, Eusiridae; Fig. 9), and in some pelagic Lysianassoidea (e.g. *Ichnopus* spp., Lowry and Stoddart, 1992), the distal elements are few and widely separated from one or more large, cup-shaped receptacles, and the bulla is prominent.

With respect to the Eusiroidea, Steele & Steele (1993) found two types of calceoli in *Gammarellus angulosus*, viz, a large "pontogeneiid" type and a smaller, but more complex "gammarellid" type. The former occurred singly only on flagellar segments of first and second antennae of mature males. The latter were found encircling the flagellar segments of larger immatures and females as well as mature males. Although Steele & Steele (*loc. cit.*) have urged caution in the use of calceoli in higher classification, their work may be interpreted as directly supportive of such use. Thus, the basic pontogeneiid type, in males only, would directly link the Gammarellidae to other families with similar male-only calceoli, now placed within superfamily Eusiroidea. The smaller, more specialized calceoli of all sexes and stages of *Gammarellus*, are almost certainly not reproductively significant. Instead, these may assist in the detection of pelagic prey organisms by all life stages of these raptorial predators.

The evolutionary morphological sequence within the calceoli portrayed here is believed to match more closely the phylogeny of corresponding superfamily groups, based on other character states (see below), than does the somewhat pragmatic sequence originally provided by Lincoln and Hurley (1981).

A graphical plot of the types of calceoli and their distribution by antennal site, sex, and higher taxon, can be linked by means of a branching arrangement with relationships that, in part, are remarkably similar to phyletic arrangements derived elsewhere from analysis of other character states (Figure 14). In the first two categories, this arrangement goes somewhat beyond the relationships proposed by Lincoln (1984) on the basis of the taxonomic (classificatory) distribution of calceoli. In the present chart, the positions of the major taxa in the various "boxes" are correlated primarily with the distribution (or lack) of calceoli on one or other (or both) antennae, along the horizontal axis and with the morphological type and its sexual occurrence,

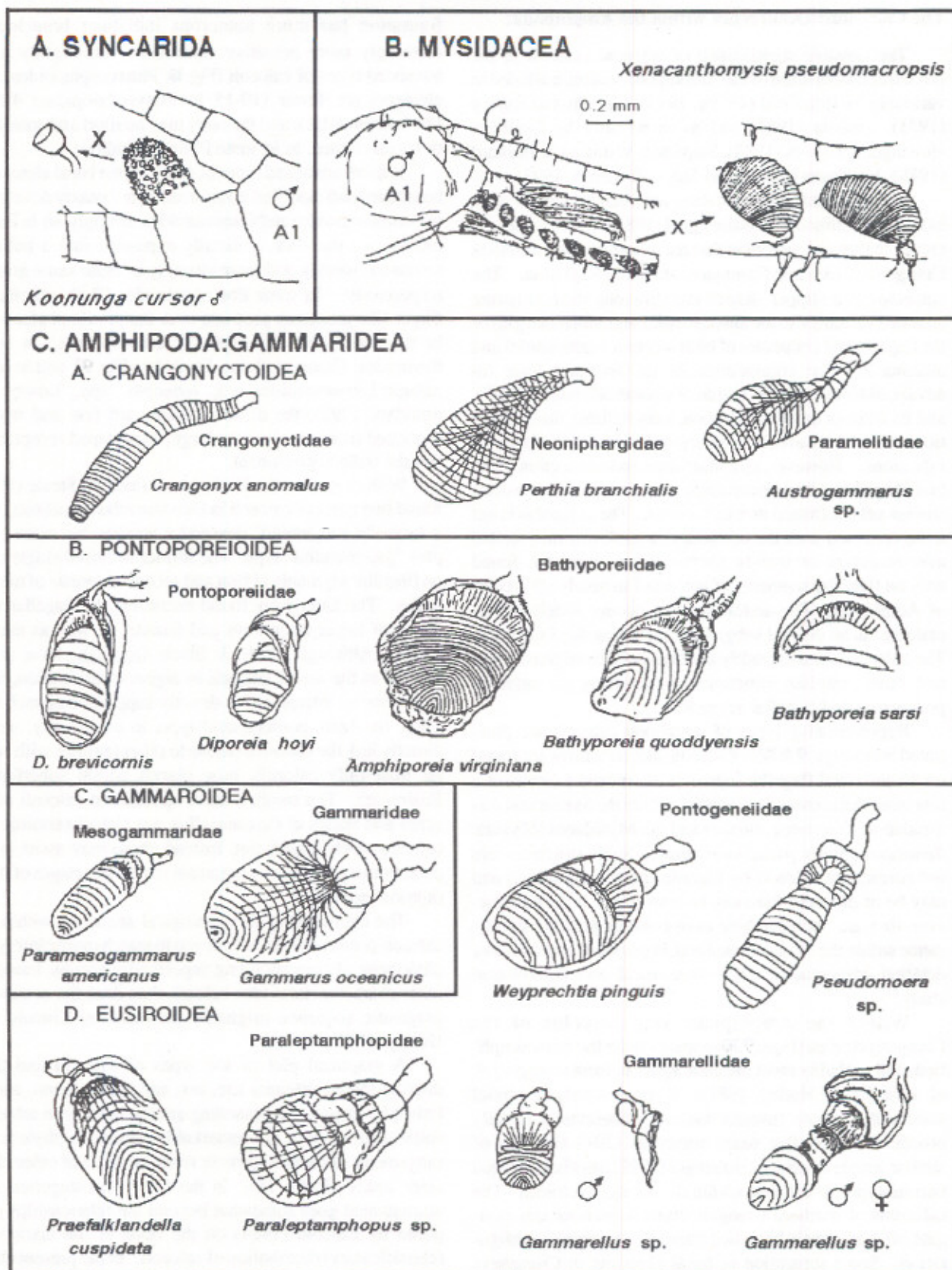


FIG. 9. TYPES OF CALCEOLI IN GAMMARIDEAN AMPHIPODA AND POSITIONALLY SIMILAR ORGANELLES IN OTHER MALACOSTRACANS [modified from Lincoln & Hurley (1981) and other sources]

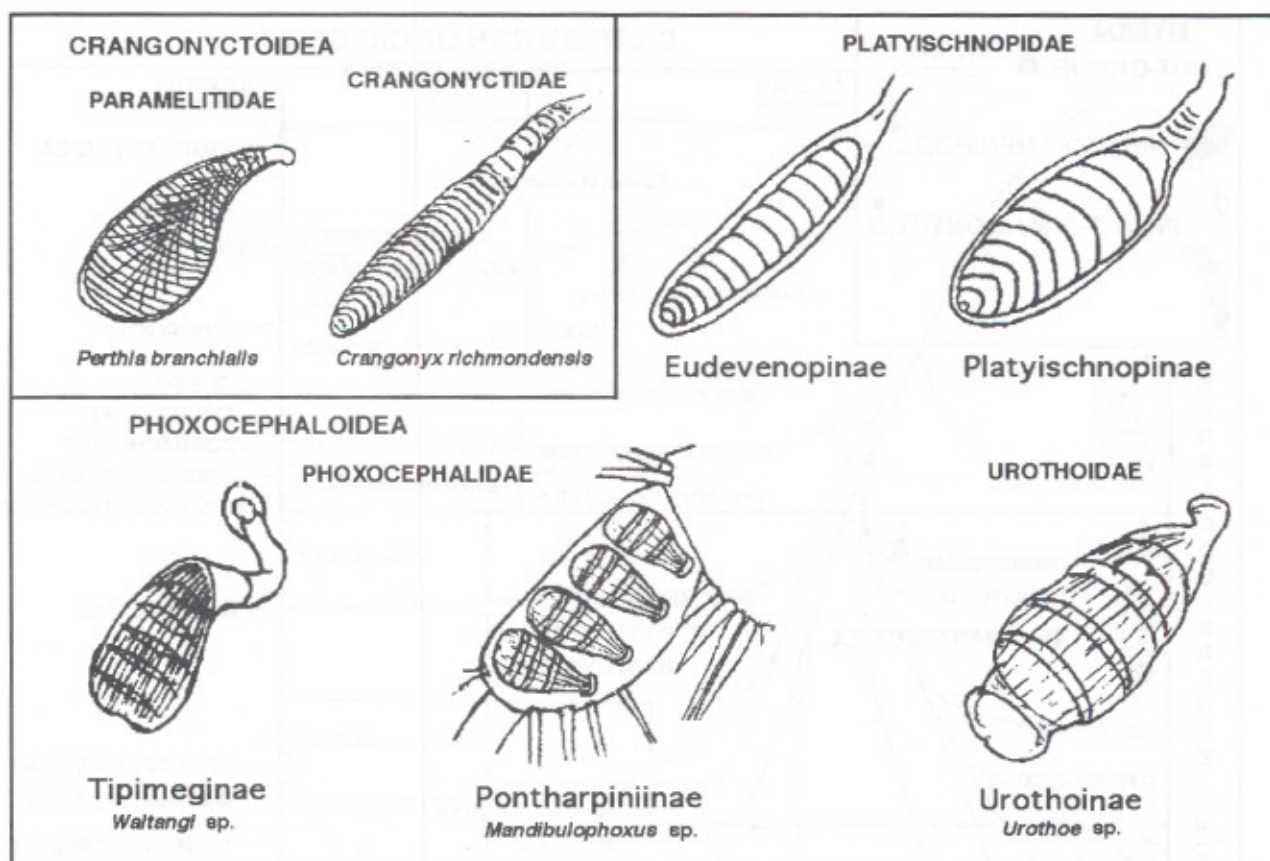


FIG. 10. PLESIOMORPHIC CALCEOLI: REPRESENTATIVE SUPERFAMILIES AND FAMILIES [after Jarrett & Bousfield, (1994 a, b), Godfrey et al (1988), and other sources]

on the vertical axis. The vertical and horizontal axes also simulate, fanwise, an approximate evolutionary time scale for the probable first appearance of the ancestral type of each major taxonomic group.

In this tentative scheme, the arrangement is rooted in a presumed mysid-like out-group in which calceolus-like structures were possible (cf. *Xenacanthomysis*; Fig. 9), at least on antenna 1 of the male. Such structures very probably occurred in presumed former epigean and pelagic marine ancestors of the now hypogean relict suborder Ingolfiellidea, and of the continental freshwater-endemic Crangonyctoidea. Such epigean and marine ancestral types have not yet been found extant, or in the fossil record, but are predicted from this study and from earlier considerations (e.g. Bousfield, 1982b). In this two-dimensional scheme, all members of the seven calceolate superfamilies, and the enigmatic (melphidippoidean?) hypogean calceolate *Sensonator valentiensis* Notenboom (1986), cannot be confined cleanly within any given graphical box. Such variance is attributable to parallel development, diversification, and subsequent loss of calceoli from the antenna of both sexes, presumably in response to changing life styles within the various taxonomic subgroups. Notably, the more strongly calceolate superfamily groups (calceoli on both A1 and A2, left column) are those in which members are primarily pelagic and/or mate

freely in the water column. These include most of the Phoxocephaloidea, Pontoporeioidea, Lysianassoidea, Eusiroidea, and Oedicerotoidea. The less strongly calceolate superfamilies (with rare exceptions, calceoli on A2 only, right column) are found in the most primitive members of benthic superfamilies of the Reptantia, such as the Crangonyctoidea, and Gammaroidea. The position of acalceolate superfamilies is tentative, but is guided partly by the presence or absence of an antennal callynophore and other presumably primitive, often vestigial characters such as male antennal brush setae (see below).

With respect to the sexes, the more primitive types of calceoli occur (with very few exceptions) in the 'males only' category of presumed most primitive superfamily taxa such as the Crangonyctoidea, Phoxocephaloidea, Pontoporeioidea, and most of the Lysianassoidea (upper two rows). Calceolate females are frequent in pelagic (especially raptorial) members of Eusiroidea (e.g. Eusiridae and Gammarellidae), in some large hypogean predators in more primitive groups (e.g. *Crangonyx packardii*, *Sensonator*, p. 123), but rare in the fossorial Oedicerotidae, and benthic Gammaroidea.

With respect to calceolus morphology, the more advanced types occur mainly in the carnivorous family subgroups of the pelagic-mating Eusiroidea and Oedicerotoidea, and in the primitive benthic Gammaroidea (lower two rows).

These distributions suggest that calceoli developed initially (in males only) as a device presumably for detecting species-specific swimming vibrations of females at mating time. The calceoli became have become secondarily adapted, and more complex structurally (in free-swimming raptors), for detection of escape vibrations of free-swimming prey, and thus developed in females and immatures, as well as in reproductive males. As mating styles changed from pelagic to benthic and/or hypogean, lotic to lentic, marine to freshwater, involving pre-amplexus (see below), the primary rôle of calceoli correspondingly diminished or disappeared. The of reduction and disappearance of calceoli from male antennae was apparently first from antenna 1, and then antenna 2; in the latter, the sequence was first from the peduncle, and finally from the flagellum. However, as noted above, calceoli persist (or become secondarily developed) in both males and females of some epigean (e.g., in some Anisogammaridae and Gammaridae) and/or cave pool amphipods (e.g. in *Crangonyx packardii* and *Sternophysinx calceola* of Crangonyctoidea; *Sensonor valentiensis* (Melphidippoidea?), and some large paraleptamphipod eusiroideans of New Zealand) (Bousfield, 1980) where life styles presumably remain free-swimming and raptorial.

Gnathod Structure and Phyletic Significance

Of all morphological characters of amphipod crustaceans, the gnathopods (peracopods 1 & 2 of formal malacostracan terminology) have previously been considered one of the most significant and fundamental indicators of high level phyletic relationships, at least within the suborders Gammaridea (Stebbing, 1906; Barnard & Karaman, 1991); and Caprellidea (Laubitz, 1993; Takeuchi, 1993). Initially, and based on early taxonomic studies on intertidal groups of "good old Gammaridae" of northwestern Europe (J. H. Stock concept), the sexually dimorphic, powerfully subchelate form of the gnathopods, utilized in sexual precopulatory carrying behaviour in the male, was considered by many workers as the basic or ancestral amphipod reproductive form (e.g., Barnard, 1969a). More recently, however, extensive comparative morphological studies have been conducted on gnathopods and other phyletically significant characters (e.g. Bousfield, 1979a, 1982a, 1983, 1986), and the scope of their function in reproductive behaviour (e.g. Borowsky, 1984; Conlan, 1991a). These studies have correlated gnathopod morphology and sexual dimorphism, across a rather broad spectrum of amphipod superfamilies, with a pre-amplexing and/or mate-guarding form of reproductive behaviour. As summarized partly by Schram (1986), this form of reproductive behaviour is now considered by most workers as relatively highly evolved and specialized within the Amphipoda as a peracaridan group.

What then might be the probable ancestral form of the gnathopods, and concomitant ancestral reproductive life style within the Amphipoda? We might first look at gnathopod structure in members of various superfamilies that are classified as primitive on the basis of other

plesiomorphic character states (per Bousfield 1979, 1983, etc.). The Lysianassoidea is one such superfamily group for which the distal portions of gnathopods 1 & 2 of species representative of the more primitive component families (Valettiidae and Uristidae) are detailed in Fig. 12. In the very primitive genus *Valettiopsis* Holmes (see Barnard and Ingram, 1990), the carpus and propod of both gnathopods (in both sexes) are subsimilar, moderately slender and elongate, each with subparallel anterior (upper) and posterior (lower) margins. The propod is weakly but normally subchelate, the dactyl short and closely fitting the slightly oblique palm. In the slightly more specialized genus *Hirondella*, the carpus of gnathopod 1 is relatively short and shallowly lobate below. The propod is slightly narrowed distally, with an excavate palm, overlapped by the tip of the dactyl. In gnathopod 2, the propod is relatively short, and the palm slightly oblique forwards (parachelate). In the genus *Ventiella*, gnathopod 1 is little different, but in gnathopod 2, the propod has become much shortened, and the palm and dactyl much reduced in size to form a micro-subchela that is typical of the more advanced families and genera within Lysianassoidea. Within *Orchomenella* (family Uristidae), in addition to the micro-subchelate form of gnathopod 2, gnathopod 1 has also become structurally modified in having a much shortened carpus, with relatively narrow and deep posterior lobe, and the propod has become broadened, and the palm and dactyl enlarged and slightly parachelate.

In summary, despite minor modifications within an increasingly sophisticated generic series, we may note that the plesiomorphic form of both gnathopods may be described as non sexually dimorphic and weakly subchelate, with slender carpus and propod. Within the Lysianassoidea, characterized by gnathopods of the above type, mating takes place freely and rapidly in the water column, and there is no pre-amplexus or mate-guarding phase.

Gnathopods within Natantia.

If we examine a much broader range of superfamilies in which reproductive or mating style is free within the water column, and the taxa are relegated to the subgroup Natantia, a correspondingly broad range of gnathopod types can be identified (Figs. 12, 13). Within the primitive fossorial Phoxocephaloidea, gnathopod types range from the basically plesiomorphic form outlined in the Lysianassoidea (above), to a eusiroidean form with powerfully sub- or parachelate propod and dactyl, and slender posteriorly lobate carpal wrist. In some specialized lysianassids (hyperiopids), eusiroideans (leptamphopids), stegocephaloideans, pardaliscoideans, synopioideans, dexaminoideans (lepechinellids), ampeliscoideans, and some melphidippoideans (Melphidippidae), the carpus and propod (of both gnathopods) may be secondarily abnormally elongated and slender. In others, especially the highly modified and specialized members of the fossorial, micro-carnivorous family Oedicerotidae, the gnathopods are raptorial or fossorial, but typically unlike in form, and the carpus is often much

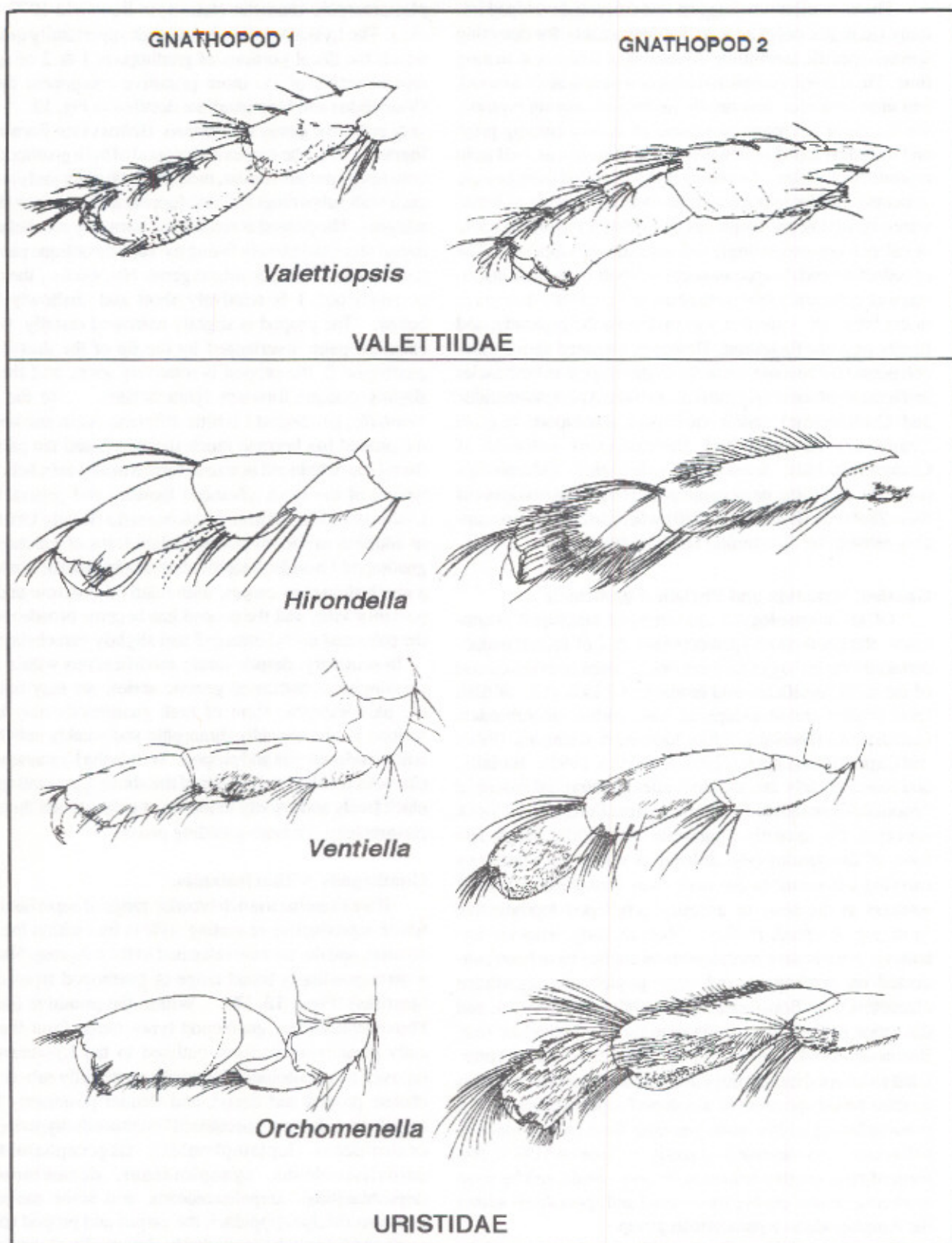


FIG. 12. FORM OF GNATHOPODS 1 & 2 IN LYSIANASSOIDEA
 [after Barnard & Ingram (1990) and other sources]

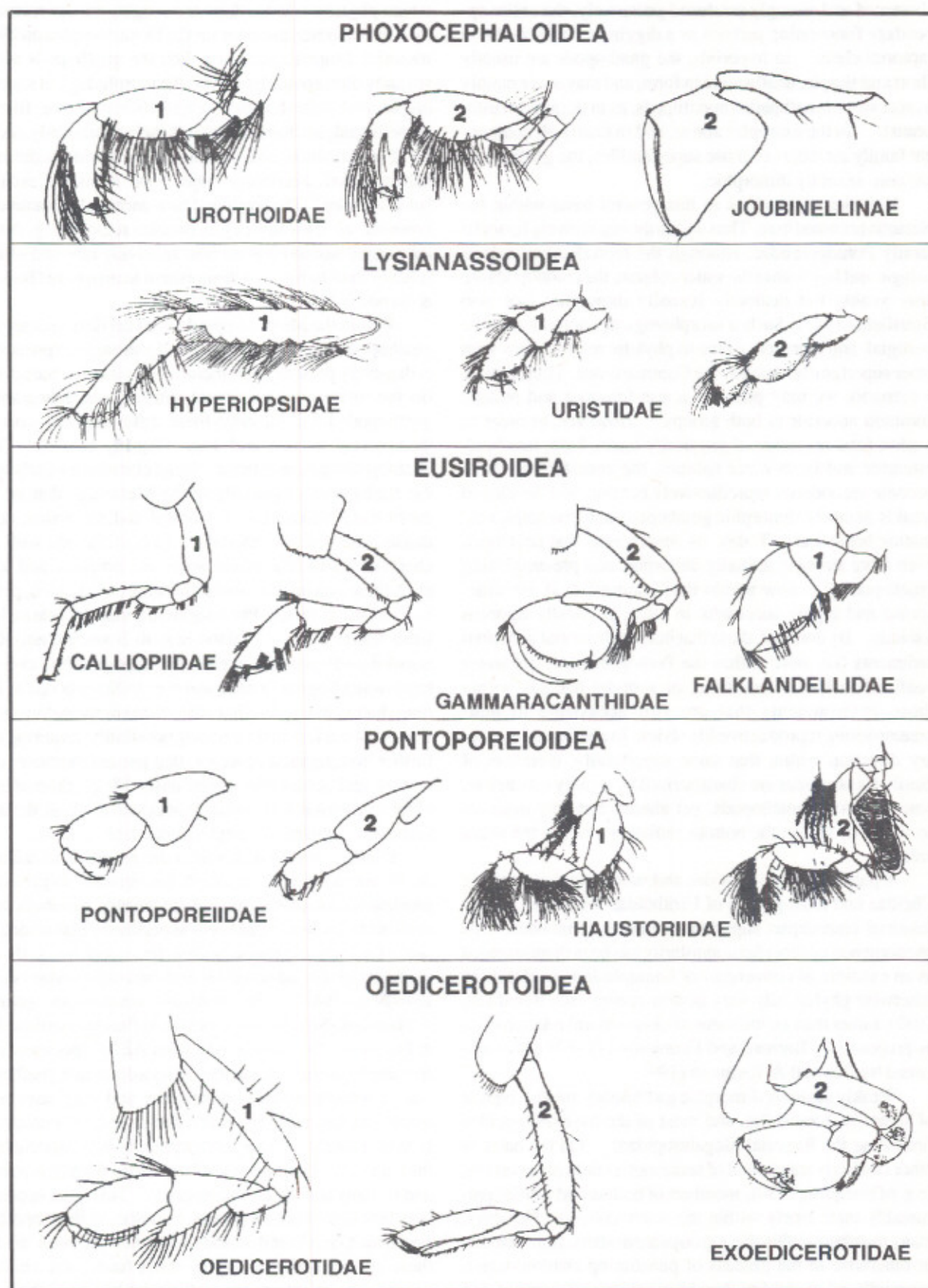


FIG. 13. FORM OF GNATHOPODS 1 & 2 IN SUPERFAMILIES
OF AMPHIPODA NATANTIA (from various sources)

shortened and strongly produced posteriorly, the entire appendage functioning perhaps as a digging tool, as well as a raptorial chela. In hyperiids, the gnathopods are usually short and simple, nearly alike in form, and may serve mainly as accessory mouthparts (maxillipeds, as in decapod crustaceans). In the examples above, and in nearly all component family members of those superfamilies, the gnathopods are non-sexually dimorphic.

However, exceptions to this general trend within the Natantia are noted here. Thus within the vegetatively fossorial family Pontoporeiidae, although the reproductive style is pelagic and free within the water column, the gnathopods are also weakly but distinctly sexually dimorphic (see also Bousfield, 1987). Such a morphological anomaly may be vestigial, and represent a clue to phyletic relationships with other superfamilies such as the Gammaroidea. Thus, in such a scenario, we may presume a non-fossorial and pelagic common ancestor to both groups. However, in order to exploit food resources of physically harsh, lotic, intertidal, estuarine and fresh-water habitats, the ancestor may have become secondarily reproductively benthic, and developed weakly sexually dimorphic gnathopods and pre-amplexing mating behaviour. Today, its descendants that developed even more strongly sexually dimorphic and pre-amplexing gnathopods (i.e. now within the Gammaroidea) are widespread and highly successful in those physically rigorous habitats. By contrast, those that became fossorial in bottom sediments (i.e. now within the Pontoporeiidae) are today confined to lentic, lacustrine, or subtidal habitats within those environments that are still accessible to non-preamplexing reproductive life styles. In another evolutionary direction within that same superfamily, members of family Haustoriidae are characterized by weakly subchelate, non-amplexing gnathopods, yet almost certainly mate directly on or within the bottom sediments, not in the water column.

A parallel set of life styles and morphologies mark the Cheidae and most genera of Urothoidae within the austral fossorial counterpart superfamily Phoxocephaloidea. This phenomenon of superficial similarity has been demonstrated as an example of convergent or homoplasious evolution in otherwise phyletically very distant groups (see Bousfield, 1989), rather than an indicator of close natural relationships as proposed by Barnard and Drummond (1982) and maintained by Barnard & Karaman (1991).

Weakly sexually dimorphic gnathopods are also typical of some Dexaminioidea, and most of the Melphidippoidea (including the fossorial Megaluroidea). On the basis of other character states, and of some earlier field observations (e.g. of Enequist, 1950), members of both superfamilies presumably mate freely within the water column. However, many members within these groups are nestlers, commensals, or otherwise in the process of penetrating shallow-water, especially of anchialine brackish habitats of tropical and warm-water regions, where a pre-amplexing reproductive life style is likely advantageous. In a similar scenario, in

which phyletic relationships are sought, we can reasonably look to a common ancestor for the Dexaminioidea and for the fossorial Ampelicoidea in which the gnathopods are non-sexually dimorphic. However, the morphological specializations and tube-building capabilities of the fossorial ampeliscoideans have resulted in their enormously successful diversification and dominance in marine sedimentary habitats, even becoming major food items for eschrichtid baleen whales. The presumed para-ancestral Dexaminioidea, however, are common in gondwanian regions (e.g. Australian coastal waters) but are now relatively rare and virtually relict in shelf habitats of the northern hemisphere (Bousfield & Kendall, 1994).

Within the Melphidippoidea, sexual dimorphism of the gnathopods is weakly to moderately strongly expressed, but is distinctly present in all members. It is also characterized (in the male) by a consistent similarity in appearance of gnathopods 1 & 2, although these differ markedly (between themselves) in size and form (Fig. 14, bottom). These gnathopod characteristics are found elsewhere widely within the Hadzioidea (especially in the Melitidae) that are now much more widespread in tropical and temperate, coastal marine and brackish habitats. In combination with other character states (e.g. of the antennae, uropods, and telson, etc.), these gnathopod similarities may be extended, perhaps less strongly, to the Phreatogammaridae of brackish and fresh waters of New Zealand (e.g. in Bousfield and Ruffo, unpublished), possibly even to the hypogean brackish- and fresh-water Bogidielloidea, and even to Notenboom's (1986) remarkable, hypogean (but calceolate) *Sensorator*. In this vein, we are left with the exciting possibility, requiring much further investigation however, that present members of the marine and semi-relict superfamily Melphidippoidea are close to a postulated common ancestor to all of the above taxonomic groups (see phylogenetic tree, p. 126).

Finally, we may note within the group of superfamilies of Natantia, sexual dimorphism weakly expressed in gnathopods of certain austral freshwater members within certain freshwater members of superfamily Eusiroidea, but more strongly expressed within fresh and brackish water members of Exoedicerotidae and Paracalliopiidae (see also Bousfield, 1983). The freshwater eusiroidean species of *Falklandella* Schellenberg, 1931, and *Praefalklandella* Stock & Platvoet, 1991 (as in counterpart AZAC species of *Paraleptamphopus*) are characterized by a dominant gnathopod 1 that is weakly sexually dimorphic, and may have a pre-amplexing function. However, pereopod 3 of *Falklandella* is also strongly sexually dimorphic, being carpochelelate in the male (as in some species of *Paramelita* (Crangonyctoidea) and in many aquatic asellid isopods). This latter appendage may function in pre-amplexus, as it does in the isopods, but pertinent behavioural studies have not yet been made on these remote and presumably relict freshwater amphipod groups. In the antipodean oedicerotid families (above), the gnathopods are typically strongly sexually dimorphic, with gnathopod 2 dominant in males. A pre-amplexing carrying

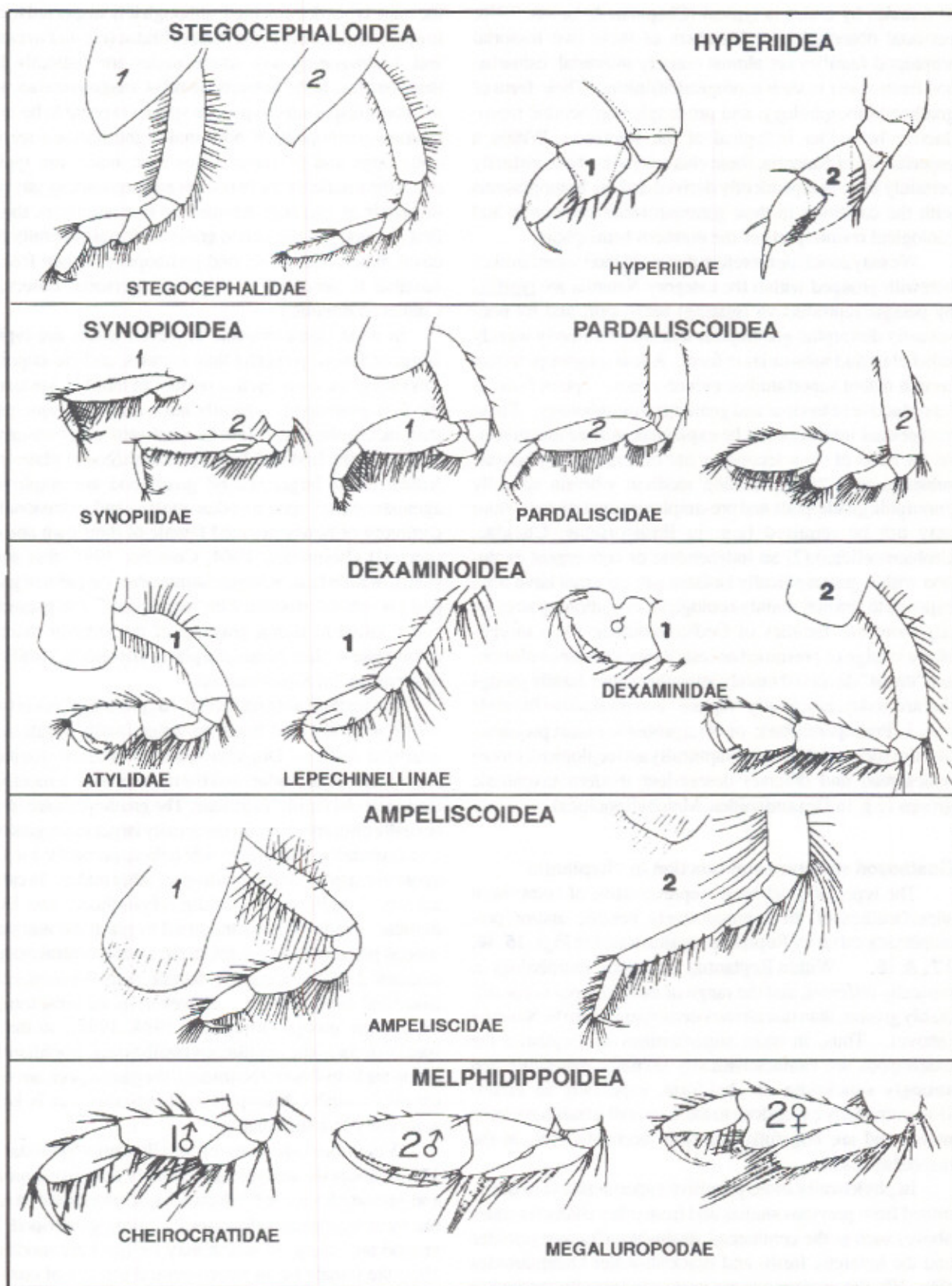


FIG. 14. FURTHER FORMS OF GNATHOPODS 1 & 2 IN SUPERFAMILIES OF AMPHIPODA NATANTIA (from various sources)

of females by males is typical (Chapman & Lewis, 1976; personal observation). Members of these two fossorial amphipod families are almost entirely intertidal, estuarine and fresh-water in their ecological affinities. Their form of gnathopod morphology, and pre-amplexing benthic reproductive behaviour is typical of the Reptantia. Within a superfamily of Natantia, these characteristics have virtually certainly been independently derived and are homoplasious with the condition in their gammaroidean taxonomic and ecological counterparts of the northern hemisphere.

We may conclude therefore that amphipod superfamilies herewith grouped within the category Natantia are typified by pelagic reproductive (mating) behaviour, and by non-sexually dimorphic gnathopods that are primitively weakly subchelate and subsimilar in form. A few subgroups within certain natant superfamilies evince a more reptant form of reproductive behaviour and gnathopod morphology. These exceptional instances can be explained, at least tentatively, on the basis of (1) a secondary use of sedimentary benthic substrata as a "fluid" mating medium wherein sexually dimorphic gnathopods and pre-amplexing mating behaviour may not be required (e.g. in Haustoriidae; Cheidae, Urohaustoriidae); (2) an independent or convergent evolution within geographically isolated sub-taxa that have been exposed to similar, mainly ecological, evolutionary stresses (e.g. southern families of Oedicerotoidea); (3) a morphology vestige of presumed ancestral types whose evolutionary "thrust" devolved mainly into other super-family groups that are, today, essentially "reptant" in reproductive life style (e.g. in Pontoporeiidae); or (4) a probable extant precursor of more successful (biogeographically and ecologically more widespread and diverse) descendent modern taxonomic groups (e.g. in Dexaminoidea, Melphidippoidea).

Gnathopod structure and function in "Reptantia"

The types of gnathopods representative of component superfamilies of the reproductively benthic and/or pre-amplexing category Reptantia are illustrated in Figs. 15, 16, 17, & 18. Within Reptantia, gnathopod morphology is basically different, and the range of morphotypes is considerably greater, than that already demonstrated in the Natantia (above). Thus, in most superfamilies of Reptantia the gnathopods are characteristically sexually dimorphic and strongly subchelate or cheliform, especially in males. However, many exceptions to these overall trends have been noted, and are hopefully plausibly accounted for, in the discourse below.

In phylogenetically more primitive superfamilies (so determined from previous studies and from other character states above) such as the continental freshwater Crangonyctoidea and the holarctic fresh- and brackish-water Gammaroidea (Fig. 10), the gnathopods are variously (usually markedly) sexually dimorphic, with gnathopod 2 usually "dominant". In Crangonyctoidea (as in Natantia), the mature male stage (usually calceolate) is terminal (or subterminal, *vide* Conlan), as in most Natantia. Precopulatory carrying of the female by

the male is not documented, although it is suspected to occur in epigean members of the Paramelitidae (e.g. in *Paramelita*, and *Austrogammarus*), where males are distinctly larger than females. In the holarctic family Crangonyctidae, whose members (especially hypogean species) appear to be mainly raptors, gnathopods of both males and females are often quite large and powerful. However, males are typically much the smaller of the two sexes and presumably physically incapable of carrying females. In true amplexus, the male first gnathopods are used to grasp the female laterally by the coxal plates, and the second gnathopods remain free, presumable to fend off other males (personal observation; Conlan *communic.*).

In most Gammaroidea, however, males are typically larger and more powerful than females, and pre-copulatory carrying is the reproductive norm. In family Gammaridae, the first gnathopods typically have a very oblique palmar margin, enabling the pair to be employed in a "fore-and-aft" seizing of the first and fifth peraeonal (body) plates of the female. The larger second gnathopod are employed in agonistic behaviour to other males (and occasionally in carnivory of newly moulted female of their own and other species!) (Borowsky, 1984; Costello, 1993, this symposium). Within family Anisogammaridae, the palm of gnathopod 1 is vertical, studded with "peg-spines", and presumably better suited to lateral grasping of the anterior margin of coxal plate 4 than peraeonal plates (Bousfield, 1986, *pers. observation* (in *Eogammarus*)).

Within the Talitroidea (Fig. 16) pre-amplexus is typical of the intertidal and brackish-water family Hyalidae, the intertidal fossorial Dogielinotidae, the coastal marine and fresh-water Hyaellidae, and the more primitive members of the supratidal family Talitridae. The gnathopods are strongly sexually dimorphic, and in the usually larger male, gnathopod 2 is especially powerfully subchelate, probably for use in agonistic display, and in fending off other males. In carrying activity within most Hyalidae, Hyaellidae, and Dogielinotidae, gnathopod 1 is modified to grasp the margin of a special pre-copulatory notch in the antero-ventral margin of peraeon 2 of the receptive female (see Borowsky, 1984; Bousfield 1986, 1993). However, in the most terrestrial landhopper groups (Bousfield, 1984, 1988), in the most specialized aquatic inquilinous families (e.g. Eophliantidae), and in the kelp-borers (Najidae), the gnathopods are weakly (or not) sexually dimorphic, and pre-amplexus is lacking, apparently lost secondarily.

Within the Hadzioidea (especially family Melitidae) (Fig. 17), gnathopods are typically strongly sexually dimorphic, and pre-amplexing reproductive style prominent in all but the most hypogean subgroups. Using gnathopod 1, the propod and dactyl of which may be specially modified to clasp the female by an antero-ventral process of coxa 6 (in *Abludomelita* and relatives) (Borowsky, 1984, Bousfield, *pers. observation*). The much larger male gnathopod 2 is held freely, and functions in agonistic behaviour toward other males. In the tropical and warm-temperate marine

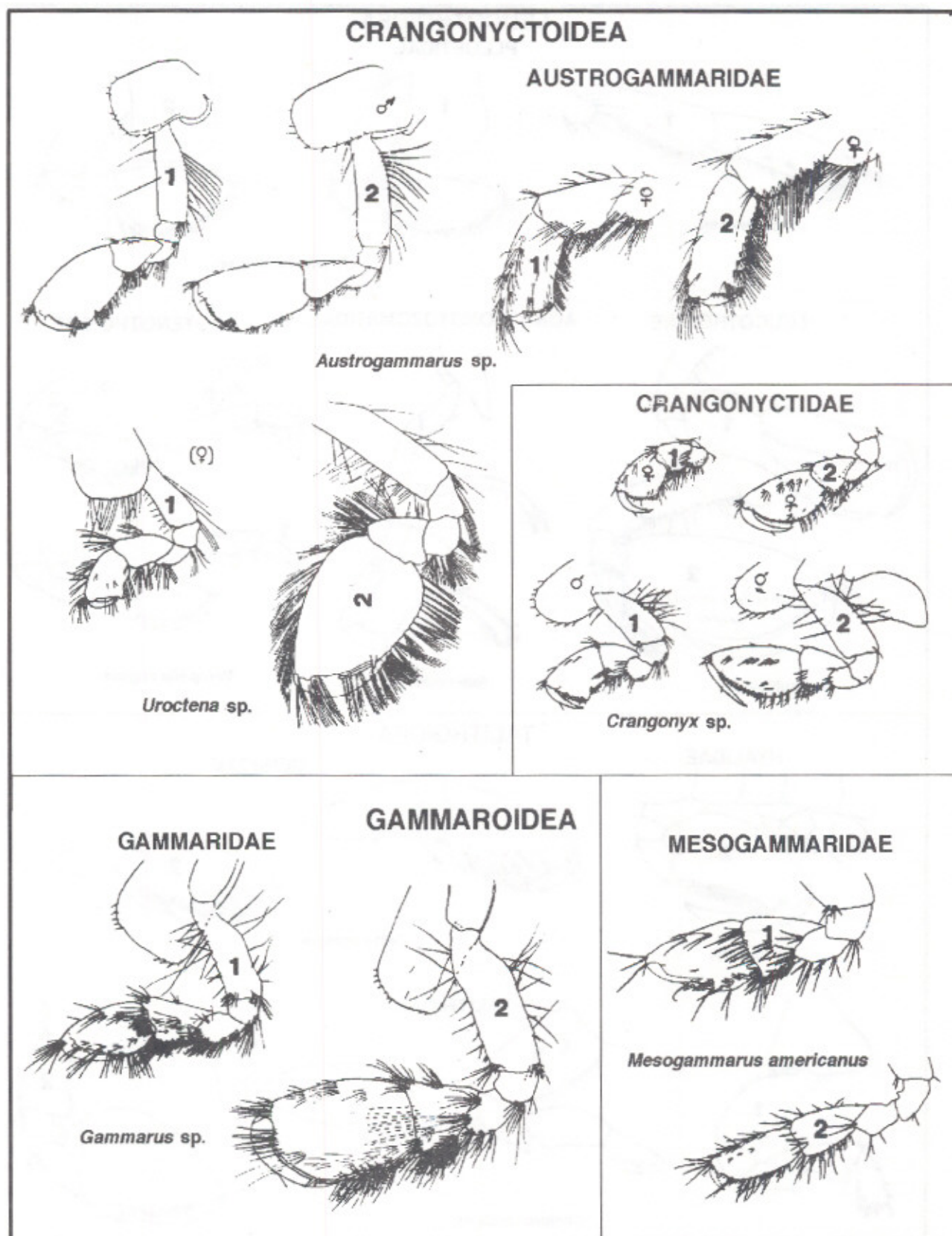


FIG. 15. GNATHOPODS 1 & 2 IN PRIMITIVE SUPERFAMILIES OF AMPHIPODA REPTANTIA [after Bousfield (1958; 1979) and other sources]

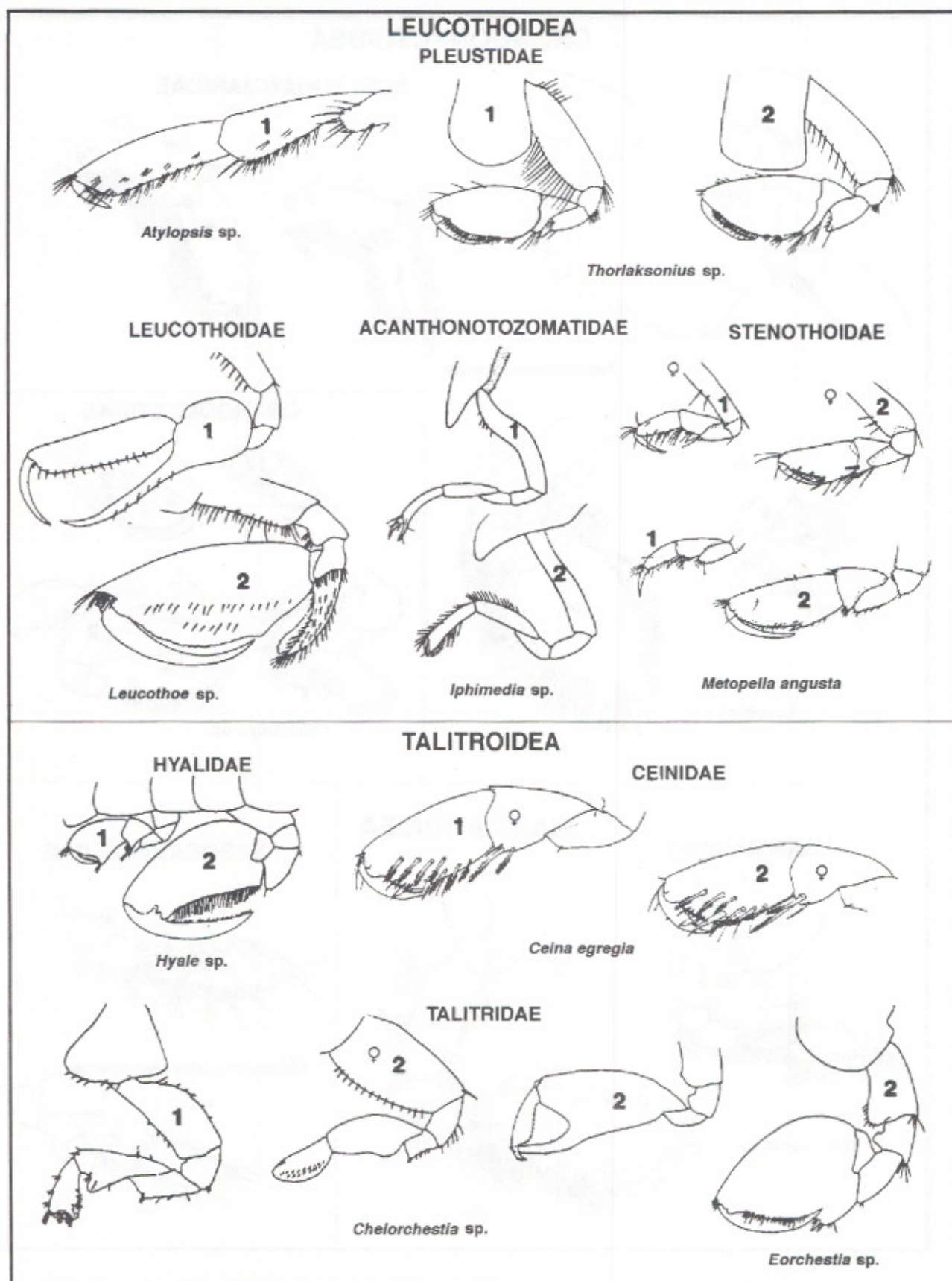


FIG. 16. GNATHOPODS 1 & 2 IN MEDIUM ADVANCED SUPERFAMILIES OF AMPHIPODA REPTANTIA [All males except where indicated] (from various sources)

genus *Dulichella*, either the right or left gnathopod 2 of the male is enormously developed (Fig. 17). The dactyl is greatly enlarged, and its tip fits into a socket in the antero-ventrally produced palmar angle of the propod. Its overall form is grossly similar to the morphology of the gnathopod of the decapod "snapping shrimp" (genus *Alpheus*?) suggesting that it functions in percussive sound production, either to attract receptive females or to warn away other males. However, in most of the hypogean hadzioideans (e.g. weckelids, metaniphargids, metacrangonyctids, etc.), whether the gnathopods are strongly or weakly raptorial, sexual dimorphism is weak or lacking (Stock, 1985; Holsinger, 1992b).

Within the tube-building Corophioidea occurs perhaps the greatest range of gnathopod sexual dimorphism of any reptant amphipod superfamily (Fig. 18). In the male, the gnathopods are typically strongly subchelate or carpochele, but very unlike in form and size. The second gnathopods are usually very much the larger, more complex, and dominant, except in the Aoridae and Cheluridae where gnathopod 1 is the larger. Since corophioideans are sequestered in open-ended tubes of their own construction, they have become, effectively, semi-sessile, and stray little from a fixed location. Such a life style may have resulted in secondary loss of precopulatory "carrying" of the female. Instead, the male "guards" the female in her tube and employs the enlarged gnathopod 2 mainly in agnostic behaviour towards competing males who might approach his reproductive territory (Borowsky, 1984; Conlan, 1988, 1991a). However, pre-amplexus is retained in the free-clinging family Podoceridae and in the presumed descendent Caprellidae, (including Cyamidae) in nearly all species of which the gnathopods are variously strongly sexually dimorphic (see Laubitz, 1970, 1979, 1993; Takeuchi, 1993).

Across the reptant classificatory board, however, some important exceptions to this general picture should be noted. Within the relatively plesiomorphic reptant superfamily Liljeborgioidea (Fig 17, top), sexual dimorphism of the gnathopods is most strongly pronounced in the free-living families Liljeborgiidae, Sebidae, and the sponge-dwelling Colomastigidae, but is weak or virtually non-existent within the hypogean Salentinellidae and Paracrangonyctidae. Within other hypogean superfamily groups, especially those believed to be micro-predators (e.g. Bogidielloidea, Ingolfiellidae), the gnathopods are powerfully subchelate or

carpochele and raptorial, but appear weakly (or not) sexual dimorphic. Finally, within the diverse and possibly polyphyletic assemblage of families currently assigned to the exclusively marine superfamily Leucothoidea, a correspondingly immense diversity of gnathopod types may be seen. Gnathopods 1 & 2 are often much enlarged and of unusual or bizarre form, and often very different from each other in form and size. Taxa within families Leucothoidae, Amphilochidae, and Pleustidae, etc., whose vegetative life styles are commensal, inquilinous, or parasitic, exhibit virtually no sexual dimorphism of the gnathopods. However, in free-living groups such as the Stenothoidae and some of the Pleustidae, especially those of intertidal and brackish habitats (e.g. "*Parapleustes*" *den*), the gnathopods are variously (often strongly) sexually dimorphic.

In summary, within component superfamilies of Reptantia, we may conclude that sexual dimorphism of the gnathopods, and benthic pre-amplexing reproductive styles are dominant and characteristic of member groups that are vegetatively free-living and epigean in physically rigorous habitats such as coastal shallows, estuaries, and freshwaters. Conversely, in members that have become (presumably secondarily) symbiotically associated with other animals or plants of marine environments, or penetrated into hypogean brackish- and fresh-water, or fully terrestrial habitats, sexual dimorphism of the gnathopods is expressed weakly or not at all. As a group, the reptants include the most derived amphipod morphotypes, that exploit unusual or restricted food resources under physically rigorous or unusually specialized environmental conditions. In the corresponding reproductive evolutionary sequence, a pre-amplexing reproductive (mating) style is presumed to be an effective means of ensuring species continuity. Thus, at the precise time of ovulation during the female moult cycle, the newly laid eggs (within the female brood pouch) must be fertilized by the male. Without the ensured presence of the male at that time the species could not remain in place within the specialized habitat nor remain viable as a species. However, where such a mechanism is no longer needed to ensure such close contact (as in lentic hypogean habitats, or under confined symbiotic conditions), or the carrying mechanism become physically impossible to maintain (as in terrestrial habitats), the gnathopods lose (presumably secondarily) the sexually dimorphic form, and neotenually revert to a morphology suited to the vegetative life style of both sexually mature adults and immature stages.

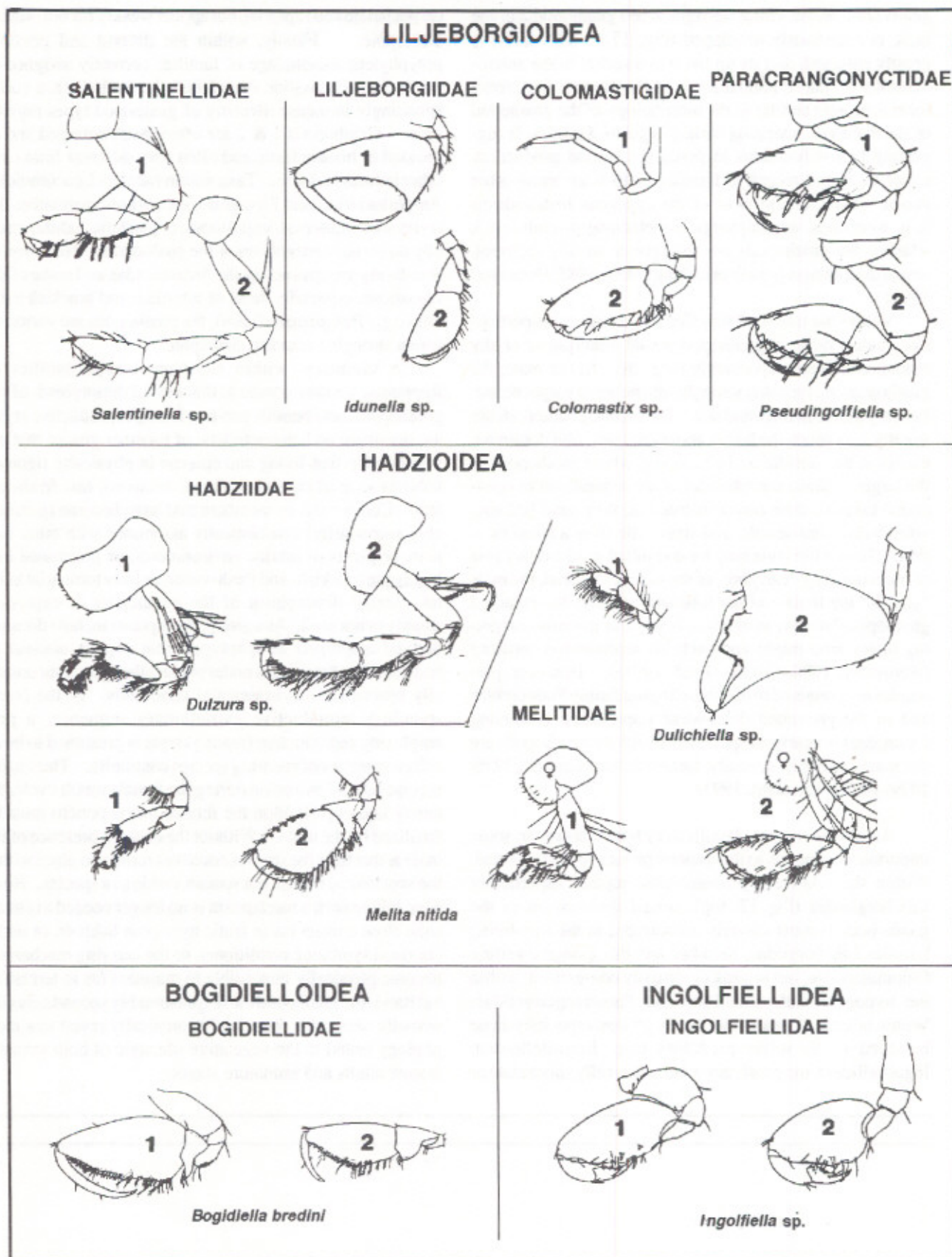


FIG. 17. GNATHOPODS 1 & 2 IN ADVANCED SUPERFAMILIES OF AMPHIPOD REPTANTIA [Males unless specified] (from several sources)

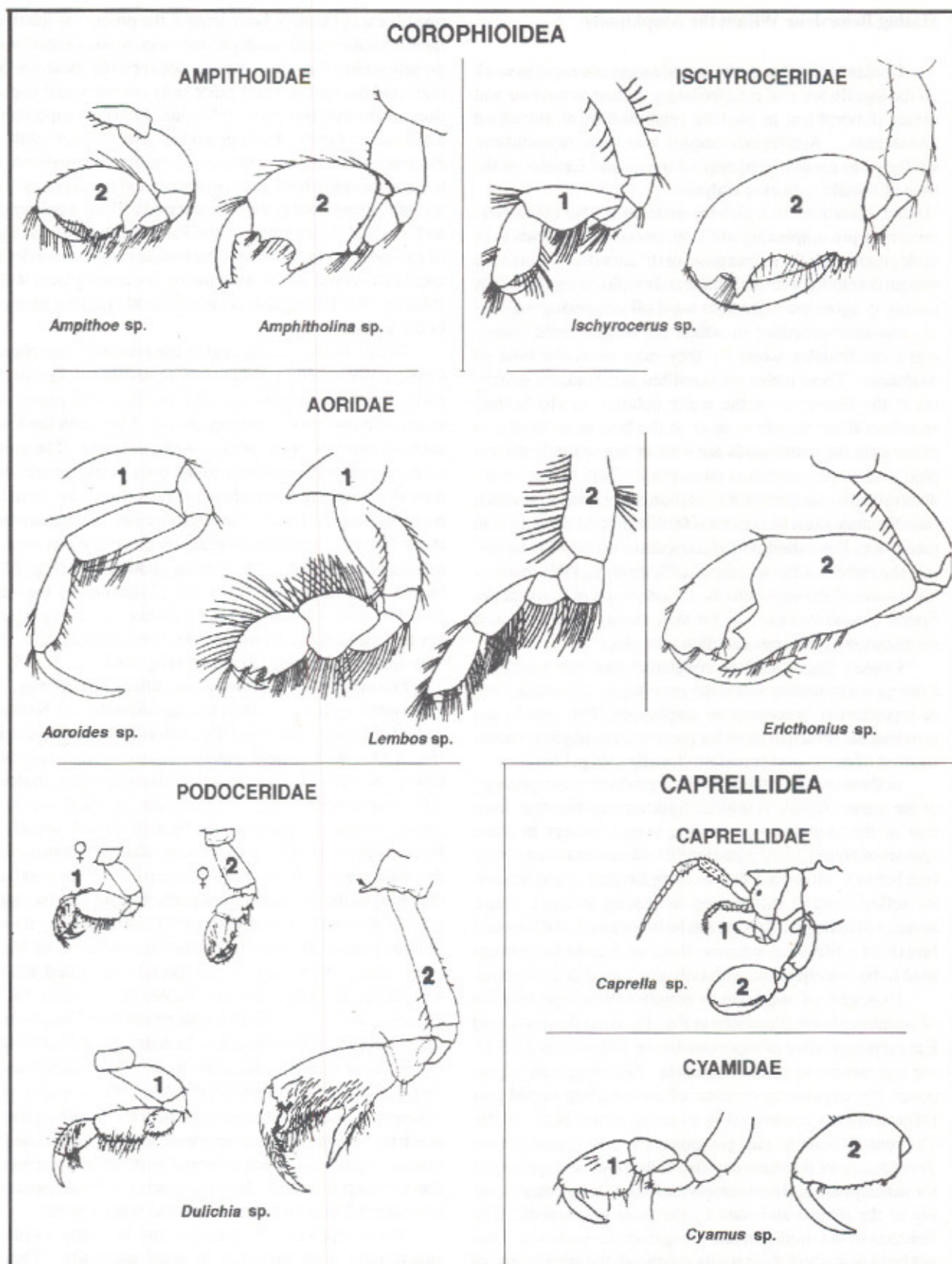


FIG. 18. GNATHOPODS 1 & 2 IN COROPHIOIDEAN AND CAPRELLIDAN AMPHIPODA [males unless specified] (from several sources)

Mating Behaviour Within the Amphipoda

Conlan (1991) has summarized recent advances in work on the significance of precopulatory mating behaviour and sexual dimorphism in phyletic relationships of amphipod crustaceans. Amphipods employ two basic reproductive strategies to ensure proximity of males and females at the time of female ovulating ecdysis:

(1) mate-guarding, in which the males are either (a) carriers involving pre-amplexing and concomitant modification of male gnathopods for the purpose, or (b) attenders, where they remain domiciled with the female and employ the gnathopods mainly in agonistic manner to ward off competing males. (2) non-mate-guarding in which the mature male simply seeks out females wherever they may be at the time of ovulation. These males are classified as (a) pelagic searchers if the female is in the water column, or (b) benthic searchers if the female is on or in the bottom substrata. In either case the gnathopods are little or not sexually dimorphic, and no pre-amplexus takes place. Both strategies are determined by the period of ovulation of the female, at which time the male must be present if fertilization of the eggs is to take place. For a short period immediately following moulting, the cuticle of the female is sufficiently flexible to allow for release of the eggs into the brood pouch or marsupium. Sperm is deposited there by the male during copulation, and fertilization of the eggs can then take place.

Conlan (*loc. cit.*) has concluded that the searching strategy is a primitive, and mate-guarding an advanced, form of reproductive behaviour in amphipods. This conclusion provides the principal basis for present semi-phyletic classification of amphipod superfamilies (fig. 30, p. 126).

In these mating strategies, the reproductive morphology of the mature female is seldom significantly different from that of the vegetative or feeding stages, except in some species of *Melita*, some aquatic talitroideans and a few others (see below). However, the breeding frequency and fecundity reflect overall differences in mating strategy. Thus, females of mate guarders tend to be iteroparous, with several broods in a life time, whereas those of non-mate-guarders tend to be semelparous, with only one brood in a life-time.

Examples of amplexus or copula within superfamilies of Amphipoda are illustrated in Fig. 19. Inset figures C and E are representative of superfamilies of Natantia; B, D, F, G, are representative of the Reptantia. For comparative purposes, the copulatory position of an outgroup mysid pair (*Mesopodopsis orientalis*) is included (from Nair, 1939). The ventral "head-to-tail" position of the male mysid permits direct access of the penis papillae to the posterior opening of the marsupium, and presumably facilitates temporary clasping of the female abdomen by the male pereopods. The function of the modified and elongated pleopods 4 & 5 has not been described; their position beneath the anterior end of the female would suggest a tactile, rather than sperm-transfer role.

The mating position in amphipods contrasts with that in

mysids except that, in both groups, the process is relatively rapid and takes place usually in darkness. In most superfamily groups within Natantia, contact between the mate-seeking male and the female takes place only during actual copulation, and its duration is brief (Conlan, 1991). In superfamily Eusiroidea, family Pontogeneidae, the smaller male of *Paramoera columbiana* lies across the thoracic region of the female, grasping her by the pereaeon and coxal plates "fore and aft", using both pairs of gnathopods. Within the benthic and less mobile members of the Paramphithoidea, the male of *Epimeria cornigera* holds the female crosswise under the specially curved lower margins of his coxal plates 4 & 5 (Moore, 1981), the gnathopods apparently playing little part in the action.

Within the Reptantia, and in the primitive superfamily Crangonyctoidea (e.g. *Synurella chamberlaini*), the smaller male grasps the female sideways by the coxal plates, and inserts the dactyls of gnathopods 1 & 2 between the lower anterior margins of coxae 3 & 4 respectively. The paired antennae are pressed closely to the body of the female, with the calceoli nearly everywhere in contact with the female's body surface. In family Anisogammaridae (Gammaroidea) the dorsally positioned male grasps the female by the anterior margin of coxal plates 4 & 5, using gnathopod 1 (Fig. 19D). In the semi-terrestrial Talitridae (Talitroidea), the male crouches across the female, lying on her side, and positions her by means of his gnathopods and the enlarged peduncles of antenna 2 working in concert (Fig. 19D).

Pre-amplexing positions are illustrated in Fig. 20. Preamplexing is rare within the superfamilies of Natantia, and where it does occur, briefly, differs little from amplexus (Fig. 19A). Within the Reptantia, however, pre-amplexus is nearly the rule. In the primitive Gammaroidea, males of Anisogammaridae (e.g. *Eogammarus oclairi*) carry the smaller female by grasping the base of coxa 4, usually by means of gnathopod 1. In *Gammarus* (family Gammaridae), the male carries the female by means of a "fore-and aft" clutching of the anterior edge of pereaeon plate 1 and posterior edge of pereaeon 5, using gnathopod 1, facilitated by its very oblique palms. Within the Hadzioidea, the male of *Melita nitida* grasps the female by the specially modified anterior lobe of her coxa 6, using the smaller gnathopod 1 for the purpose. The much enlarged male gnathopod 2 may be used in fending off competing males. In many aquatic Talitroidea, especially in *Hyaella* and *Allorchestes* (Hyalellidae) and in *Hyaella* and *Parallorchestes* (Hyalidae), the dorsally positioned male inserts the dactyl of gnathopod 1 in a precopulatory notch in the lower anterior margin of pereaeon 2 of the smaller female. Again, the much enlarged gnathopod 2 apparently functions agonistically. In some species of *Hyaella*, however, gnathopod 2 may be inserted into the female notch.

These reproductive strategies are basically similar at superfamily level but differ in detail internally. They do demonstrate the widespread phenomenon of convergent evolution of similar mating strategies, with differing tactics and morphologies at the family and subfamily levels.

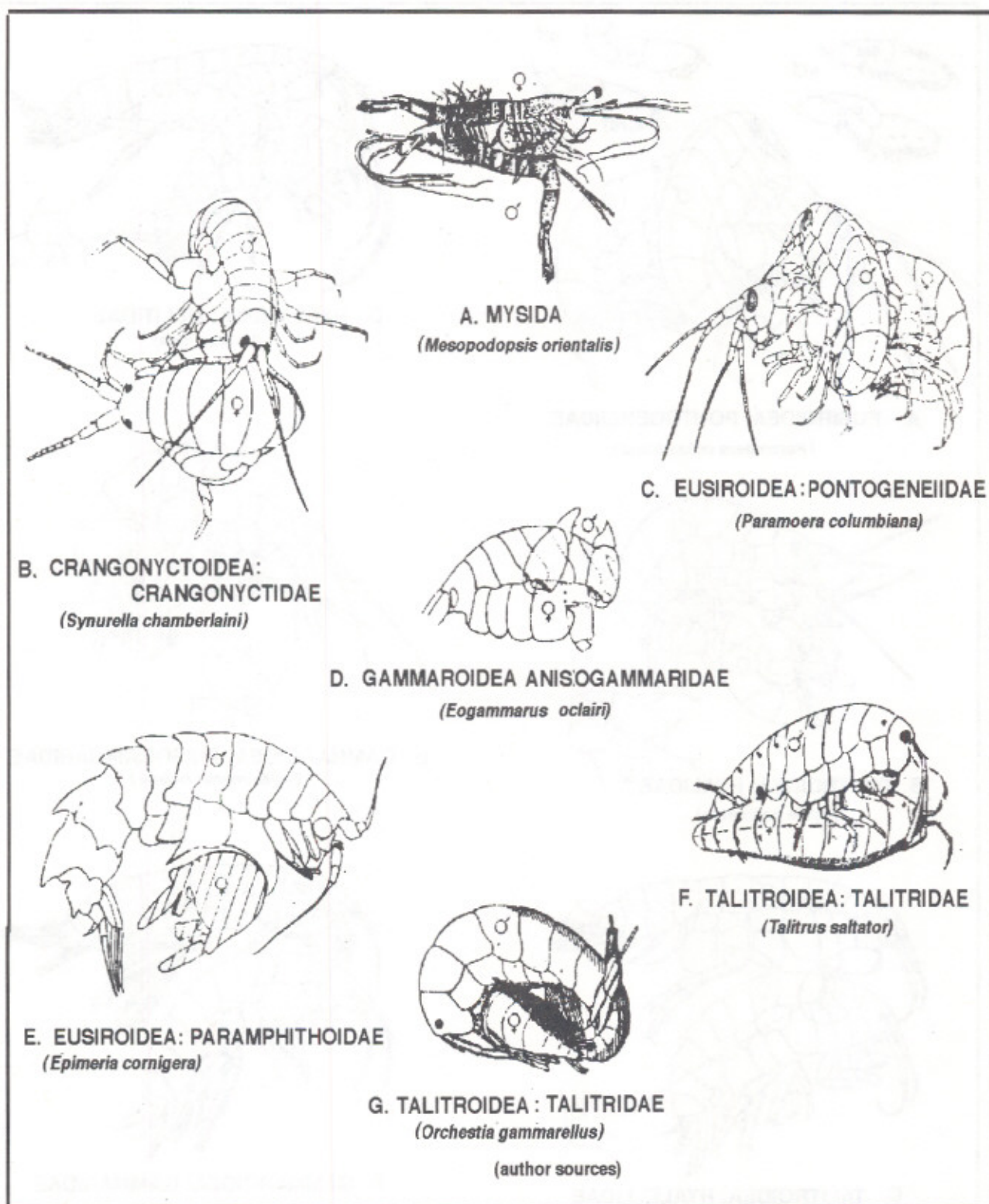


FIG. 19. AMPLEXING POSITIONS IN REPRESENTATIVE SUPERFAMILIES
OF AMPHIPODA, AND MYSIDA

A. (after Nair, 1939) E. (after Moore, 1981) F. (after Williamson, 1951) G. (after Williamson, 1951) B. D. C. (authors sources)

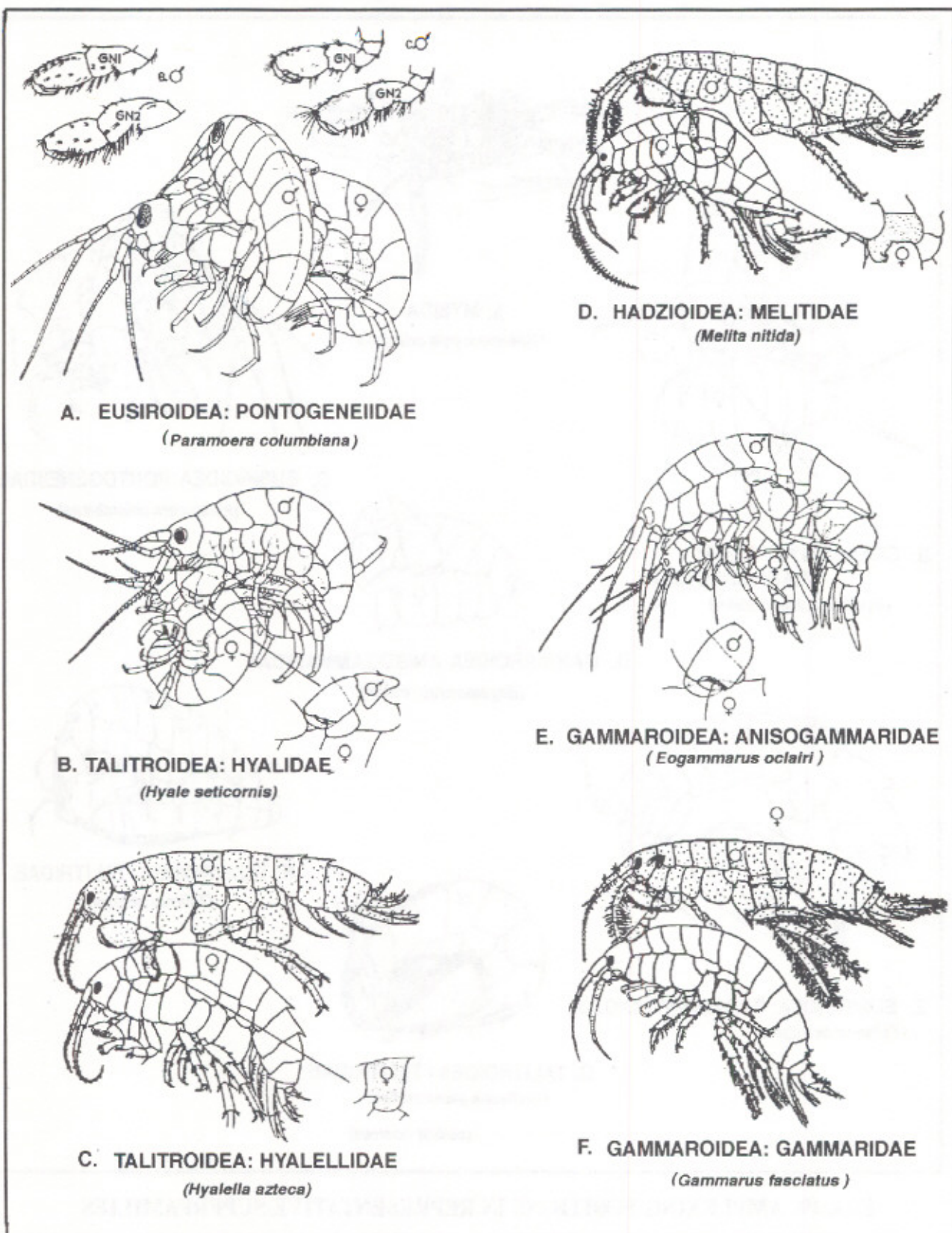


FIG. 20. PRECOPULA IN REPRESENTATIVE SUPERFAMILIES OF
AMPHIPODA "REPTANTIA" (after Borowsky (1984) and authors sources)

Phyletic Significant of Uropod 3.

The significance of uropod 3 in the general description and classification of amphipod crustaceans has always been primary (Stebbing, 1906; Gurjanova, 1951; Barnard, 1969a; Barnard and Karaman, 1991). Its character states have proven especially valuable in preparing taxonomic keys to regional and world faunas, at generic and family levels (e.g. Staude, 1987; Barnard & Barnard, 1983). Its rôle in phyletic and semi-phyletic classification of amphipods (except in some Corophioidea, and the Caprellidea where the abdomen is variously reduced and uropod 3 vestigial or lacking) has been considered previously (e.g. Lincoln, 1979; Bousfield, 1979a, 1982a, 1983; Bowman and Gruner, 1973). However, more detailed study of its form and function in relation to broader aspects of phyletic classification would seem fruitful, and therefore forms a principal part of this overview study.

In the Amphipoda, uropod 3 forms the terminal set of paired body appendages. It is distinguished from uropods 1 & 2 by its form and function. Uropod 3 is primarily a swimming appendage, whether functioning in propulsion or steering. The rami are typically broadened or flattened, and the margins lined with long plumose setae that provide a large surface area for effective paddling or steering action. Uropods 1 & 2 are used mainly in strengthening the caudal portion of the body to permit jumping or flipping, by rapid flexion of the urosome (Barnard & Karaman, 1991); they are secondarily modified for copulatory or tactile function in specialized habitats but are seldom modified for swimming.

The most plesiomorphic and generalized form of uropod 3 is typical of the Natantia and more primitive Reptantia (Figs. 21, 22 upper). The paired rami are large, lanceolate, and typically subequal in length (aequiramous condition), and the inner and outer margins variously lined with plumose setae and/or short spines (Figs. 21A-D). The terminal segment of the outer ramus is present (plesiomorphic condition) in the more primitive superfamilies such as the Phoxocephaloidea, Lysianassoidea, and Pandaliscoidea (Figs. 21A-D), but trends to loss or fusion with the proximal segment in advanced callinophorates (e.g. Stegocephaloidea, Fig. 21N, O) or in vegetatively benthic forms such as Pontoporeioidea (Fig. 21G,H). In many pelagic groups (within Eusiroidea, Oedicerotoidea, Synpioidea, Hyperioidea, Melphidippoidea and pelagic males of Dexaminoidea and Ampeliscoidea), the terminal segment is totally lacking (Fig. 21E, F, L, M, P, Q, T, V, X). In more advanced, especially abyssal-benthic forms (e.g. Lepechinellinae), both rami may be reduced in size and swimming setae lost, or nearly so (Fig. 21U).

Within the Natantia, especially the Pandaliscoidea, and Hyperioidea having a pelagic life style, sexual dimorphism of uropod 3 is generally slight, the rami being scarcely more strongly setose in the male than in the female. However, in vegetatively benthic and reproductively pelagic taxa such as Phoxocephaloidea and Pontoporeioidea, sexual dimorphism of uropod 3 is often pronounced. In female and immatures the appendage is much smaller, the inner ramus is often

reduced in size (parviramus condition, Fig. 21B, J), and ramal margins usually lack swimming setae. Exceptionally, in some of the Pontoporeioidea (e.g. Haustoriidae) and many of the Oedicerotoidea (Oedicerotidae), mature males may be secondarily infaunal and/or mate within the substratum, and show little or no retention of the natatorial form of uropod 3 (Fig. 21K, L).

Apomorphic conditions of uropod 3 characterize the more advanced superfamily groups within the Reptantia (Fig. 22, lower, Fig. 23). Only within primitive crangonyctoideans, gammaroideans, hadzioideans and liljeborgioideans is the fully biramous and/or marginally setose condition encountered (Fig. 22A-F; Fig. 22L). In the hypogean Bogidielloidea, the rami remain essentially aequiramous and not sexually dimorphic, despite overall reduction in size, general lack of marginal setae, and loss of the terminal segment of the outer ramus (Fig. 22O, P). This feature suggests a close natural relationship of the Bogidielloidea to the epigean Melphidippoidea. In more advanced hypogean forms, the terminal segment of the outer ramus may be much enlarged and especially distinctive in males (as in *Eriopisa* Fig. 22H, *Gininiphargus* (Williams and Barnard, 1988), in several species of *Allocrangonyx* and *Pseudoniphargus* and in many Niphargidae (Barnard & Barnard, 1983). In these forms, the primary function may be tactile, as in the elongate antennae and elongate, setose peraeopods. More often, however, one or both rami are reduced, often markedly so, with total loss of marginal setae, and/or spines, as in infaunal or hypogean crangonyctoideans, hadzioideans, gammaroideans and liljeborgioideans (Fig. 22E, G, J, K, M, N).

Within Amphipoda Reptantia, sexual dimorphism of uropod 3 is variously expressed, often strongly so, depending to large degree on reproductive life style. In primarily benthic taxa, with pre-amplexing or benthic reproductive style, uropod 3 is moderately sexually dimorphic in freely ambulatory groups, both epigean and hypogean (e.g. in primitive Crangonyctoidea and Gammaroidea, less so in primitive Hadzioidea and marine Liljeborgioidea). In groups that have apparently become secondarily aquatic (non terrestrial Talitroidea), the rami have are very short, vestigial or lacking (Fig. 23D, E). Sexual dimorphism of uropods is entirely lost (or nearly so) in tube-building, inquilinous, commensal, advanced hypogean, and saltatory groups (e.g. most Corophioidea, Leucothoidea, Liljeborgioidea, and Talitroidea). Here the appendage is often highly modified or specialized, in both form and function, in both sexes (Fig. 23A, B, C). Within the domicolous Corophioidea, uropod 3 is much reduced, with rami typically short and slender, but remains biramous (even with terminal segment of outer ramus in some primitive Iseaeidae) in all but the most advanced Aoridae and Corophiidae (Fig. 23H, J). In the Ampithoidae and Ischyroceridae, the outer ramus is equipped distally with hooks and spines for the purpose of retaining hold of its tube while foraging from the entrance or repelling invaders (Figs. 23F, G, J). In the advanced Podoceridae, uropod 3 is vestigial (Fig. 23L). Within suborder Caprellidea,

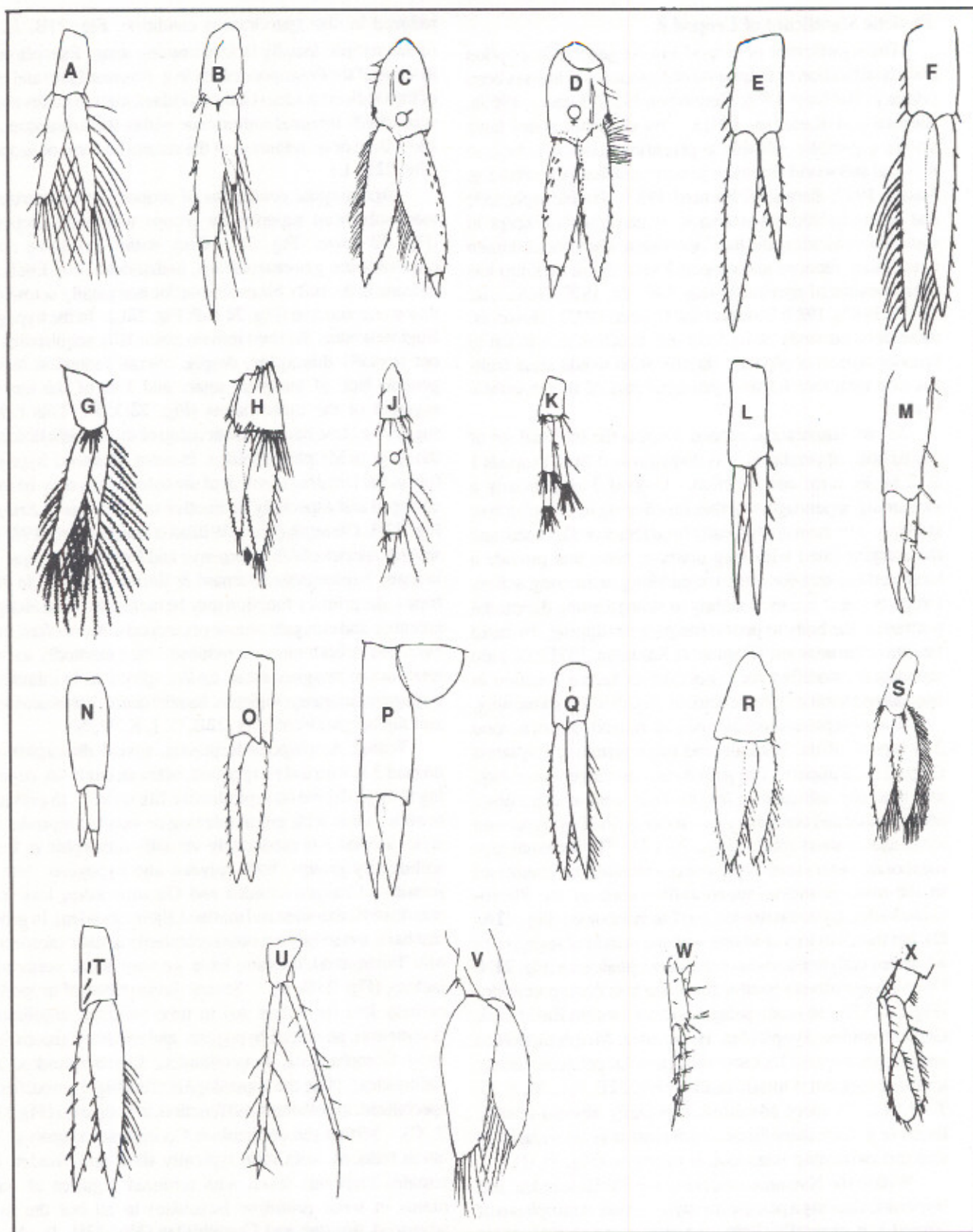


FIG. 21. FORM OF UROPOD 3 IN SUPERFAMILIES OF AMPHIPODA "NATANTIA"
 A, B - PHOXOCEPHALOIDEA; C, D - LYSIANASSOIDEA; E, F - EUSIROIDEA; G, H, J - PONTOPOREIOIDEA;
 K - HAUSTORIOIDEA; L, M - OEDICEROTOIDEA; N, O - STEGOCEPHALOIDEA; P - HYPERIIDAE;
 Q - SYNOPIOIDEA; R, S - PARDALISCOIDEA; T, U - DEXAMINOIDEA; V - AMPELISCOIDEA;
 W, X - MELPHIDIPPOIDEA. [after Barnard, 1969, and other sources]

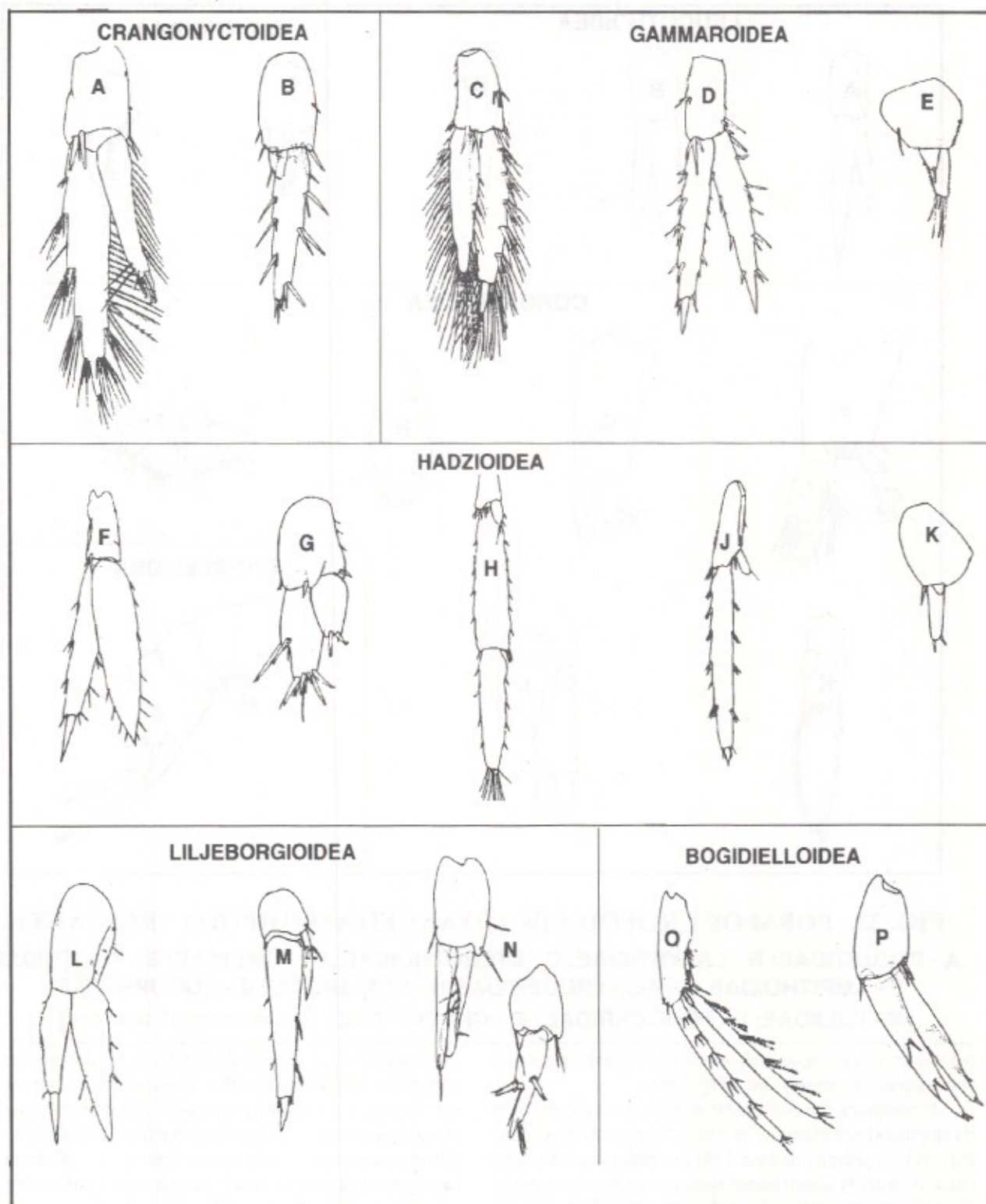


FIG. 22. FORM OF UROPOD 3 IN PRIMITIVE AND INTERMEDIATE AMPHIPODA "REPTANTIA" (from several sources)

A, B - *Austrogammarus*, *Crangonx* C, D, E - *Gammarus*, *Mesogammarus*, *Gammaroporeia*

F, G, H, J, K - *Hadzia*, *Elasmopus*, *Eriopisa*, *Melita*, *Metacrangonyx*

L, M, N - *Listriella*, *Salentinella*, *Pseudingolfiella* O, P - *Bogidiella*, *Kergueleniola*

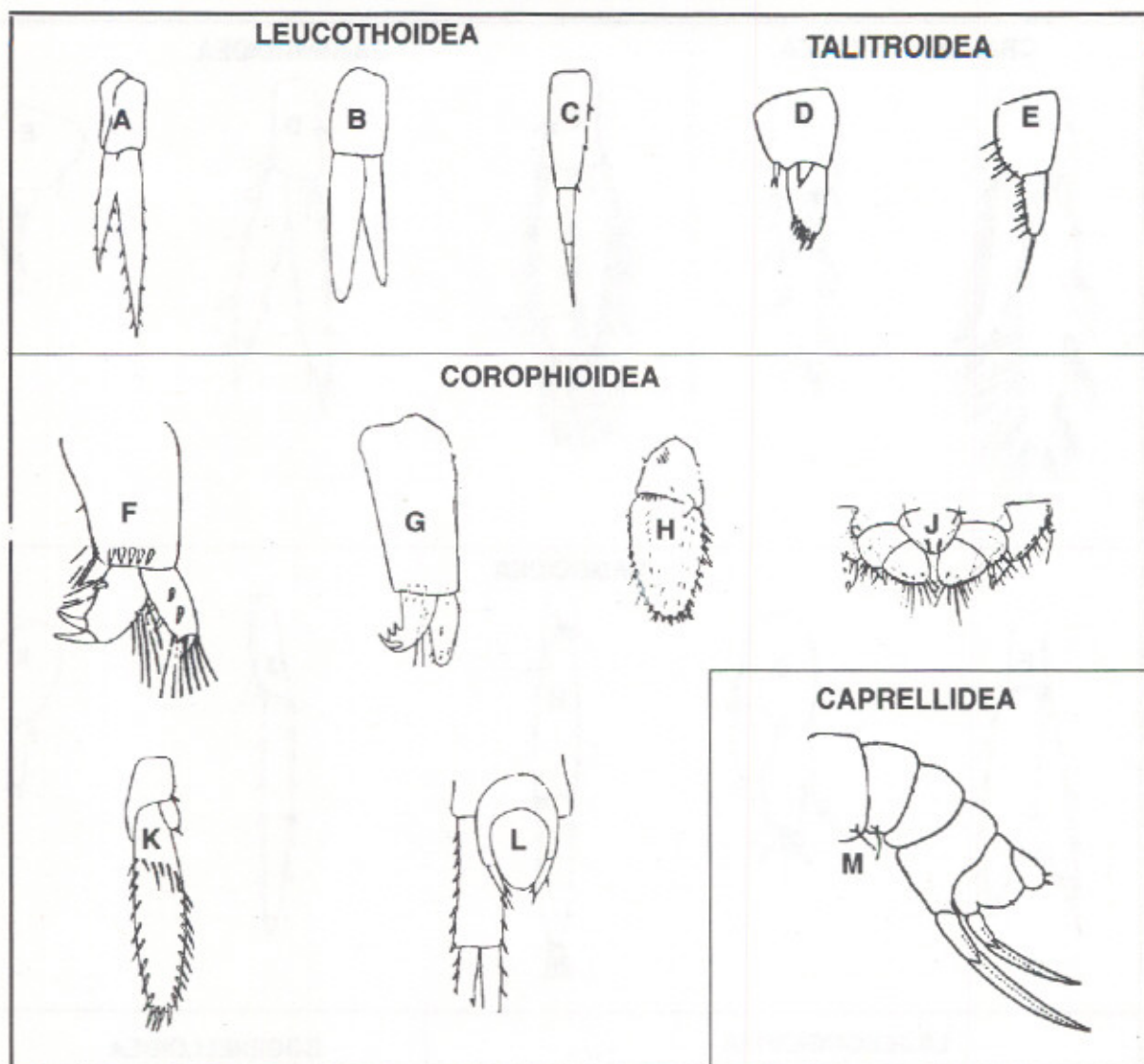


FIG. 23. FORM OF UROPOD 3 IN ADVANCED AMPHIPODA "REPTANTIA"
A - PLEUSTIDAE; B - LAFYSTIIDAE; C - STENOTHOIDAE; D - HYALIDAE; E - TALITRIDAE;
F - AMPITHOIDAE; G - ISCHYROCERIDAE; H - CHELURIDAE; J - COROPHIIDAE;
K - ICILIIDAE; L - PODOCERIDAE; M - CERCOPIIDAE [from several sources]

the abdomen is vestigial in all but the most primitive species, and uropod 3 is entirely lost (Fig. 23M).

In summary, we may note that, with few exceptions, in all amphipod superfamilies in which the reproductive (mating) style is pelagic, uropod 3 (in the male) is of the large natatory, usually aequiramous type, even where the vegetative life style is benthic and/or infaunal. This plesiomorphic form of uropod 3 is diagnostic of the phylogenetically primitive, gammaridean and hyperiidean superfamily groups, within the Natantia. By contrast, in all superfamily groups that have become secondarily benthic or infaunal, and reproductively benthic or pre-amplexing, the form of uropod 3 is typically of the non-swimming, tactile form. Here the rami are secondarily, and thus apomorphically, reduced or modified in form

and function. Only in vegetatively benthic or infaunal forms within the Natantia and within free-living, pre-amplexing superfamilies of Reptantia is uropod 3 found to be strongly sexually dimorphic. Extreme reduction and/or modification of uropod 3 is associated with domicolous, commensal, fossorial, hypogean, or nearly sessile aquatic life styles, or with colonization of supratidal and terrestrial environments. In these forms, the original natatory function of the appendage has been lost and/or modified for secondary functions that have presumably enabled the species to penetrate new environments, new niches and utilize new food resources. Thus, the form of uropod 3 may be utilized as a valuable and useful indicator of phyletic classificatory relationships within the Amphipoda.

PHYLETIC SIGNIFICANCE OF THE FORM OF THE TELSON.

As analyzed previously (Bousfield 1979, 1983, 1986), the deeply bilobate form of the telson is deemed the plesiomorphic condition within amphipodan, peracaridan, and indeed, all malacostracan crustaceans. Conversely, the entire, platelike, or "fleshy" form of the telson is concluded to be the typical apomorphic state, as in Leucothoidea and Corophioidea subfamilies, and represents (typically) a distal fusion of the two primary lobes. A very advanced condition is seen in the Thaumatothoidea, and many Hyperioidea, where the plate-like telson is fused with the urosome. A less frequent, presumably apomorphic, condition occurs where the lobes become separated throughout their entire length (as in most Gammaroidea and certain Hadzioidea) and attains an extreme separation dorsally on urosome 3 (abdominal segment 6) in the advanced fossorial genus *Eohaustorius* (Pontoporeioidea).

A panoramic view of telson types across the spectrum of higher amphipod taxa is provided in Figure 24. The prototype amphipod is depicted with a bilobate telson, the apex of each lobe having a "notch and spine" configuration. This state may be derived from a pelagic peracaridan (or primitive malacostracan) ancestral outgroup in which the tips of the telson lobes may actually represent vestiges of primordial caudal furcae, as in the phyletic relict Lophogastrida and Euphausiacea. Following evolutionary lines outwards from this base, through each superfamily group, we find that member species and genera having the great-est number of plesiomorphic character states (those nearest the base) also tend to have fully or partially bilobate telsons. Conversely, member species and genera with the most apomorphic or derived character states, in balance, usually show the most strongly fused or plate-like form of the telson. The totally bilobate apomorphic form may be noted in advanced members of the Gammaroidea and in some members of the Pontoporeioidea (family Haustoriidae).

Derivation of a phyletically "critical" significance to the overall form of the telson is not straightforward, however, because of the obvious independently homoplasious development of the plate-like telson within nearly every superfamily group. Thus, to derive a superfamily group based solely on a plate-like telson would embrace members of at least ten different major groups, and be totally artificial. However, if we look more closely at these evolutionary trends, we may note that within "natant" pelagically mating superfamilies, e.g. Lysianassoidea, Eusiroidea, Pardaliscoidea, Synopioidea, etc., the clearly dominant (typical) form of the telson is deeply bilobate. Conversely, within the more advanced "reptant" superfamilies such as the Leucothoidea, Talitroidea, Bogidielloidea, and Corophioidea, the dominant state is distally notched or plate-like. Perhaps in confirming these general phyletic trends, we may note that the form of the telson in some of the most advanced superfamilies of Natantia (e.g. the Stegocephaloidea, Oedicerotoidea, and the Hyperioidea) is predominantly (or entirely) plate-like.

Hyperioidea, however, are basically parasitoid, at least for part of their life cycle, and employ salps, medusae, and other pelagic invertebrates as host sub-strata; in this sense they are "reptant" in life style. In the more primitive families within selected superfamilies of Reptantia (e.g. Crangonyctoidea, Gammaroidea, and Liljeborgioidea), retention of the deeply or partly bilobate condition is common.

Undoubtedly, the function of the telson has an important bearing on both its overall, and detailed, form. In pelagic, free-swimming groups, the flexible, bilobate telson may function in balance and in aileron-like stabilization, taking over this function (partly from the antennal squame that is lacking in amphipods (see Watling 1983)). In "thruster-swimmers" such as the oedicerotids and hyperiids, the plate-like telson is part of the entire forward-thrusting tail-fan in which the urosomal segments may be fused and strength-ened. Here, the rôle of the telson may be subordinate to that of the larger and presumably more effective component uropods, the rami of which are effectively bilobate and flexible.

On the other hand, within the "reptant", primarily benthic, infaunal, tube-building, commensal, and/or hypogean amphipod superfamilies, hydrodynamic functions of the telson are presumably gradually lost. Other functions such as grooming (see Bowman, 1971), tube-dwelling (see Barnard, 1969; Myers (1988); Conlan (1990), or saltation (as in Talitridae), appear better served by a short plate-like form, with various specialized spinose marginal and apical modifications. A certain degree of sexual dimorphism is retained in the form of the telson, especially within hypogean groups such as the neoniphargid and stygobromid crangonyctoideans, allocrangonyctids, niphargoideans, etc. Here, the telson of the mature male is often relatively elongate and more deeply cleft or notched distally than in the female (vestige of its primordial natatory function?). Unfortunately, detailed and well-documented information on the precise rôle of the telson is lacking for many of the "reptant", as well as more-difficult-to study "natant" groups.

In summary, the present view of evolutionary and phyletic trends in the form of the telson contrasts directly with the views of some others, in which the "fleshy" entire telson was considered plesiomorphic, and led to postulating the Corophiidae as a probable ancestral amphipod type (see Barnard 1969, 1973, Barnard and Karaman, 1980) (Fig. 5). However, the broader more comprehensive studies on the malacostracan telson by Bowman (1974), Schminke (1977), and Schram (1986), while controversial and conflicting, lend little support to the Barnardian view.

At this point we may safely conclude, from an overwhelming array of evidence, that the plesiomorphic or primitive condition of the amphipod telson is bilobate, and that the apomorphic or advanced condition is typically plate-like or apically entire. However, the form of the telson is so fraught with life-style modifications at lower taxonomic levels that, per se, it may be phyletically significant only at family, subfamily, or even generic levels, or not at all.

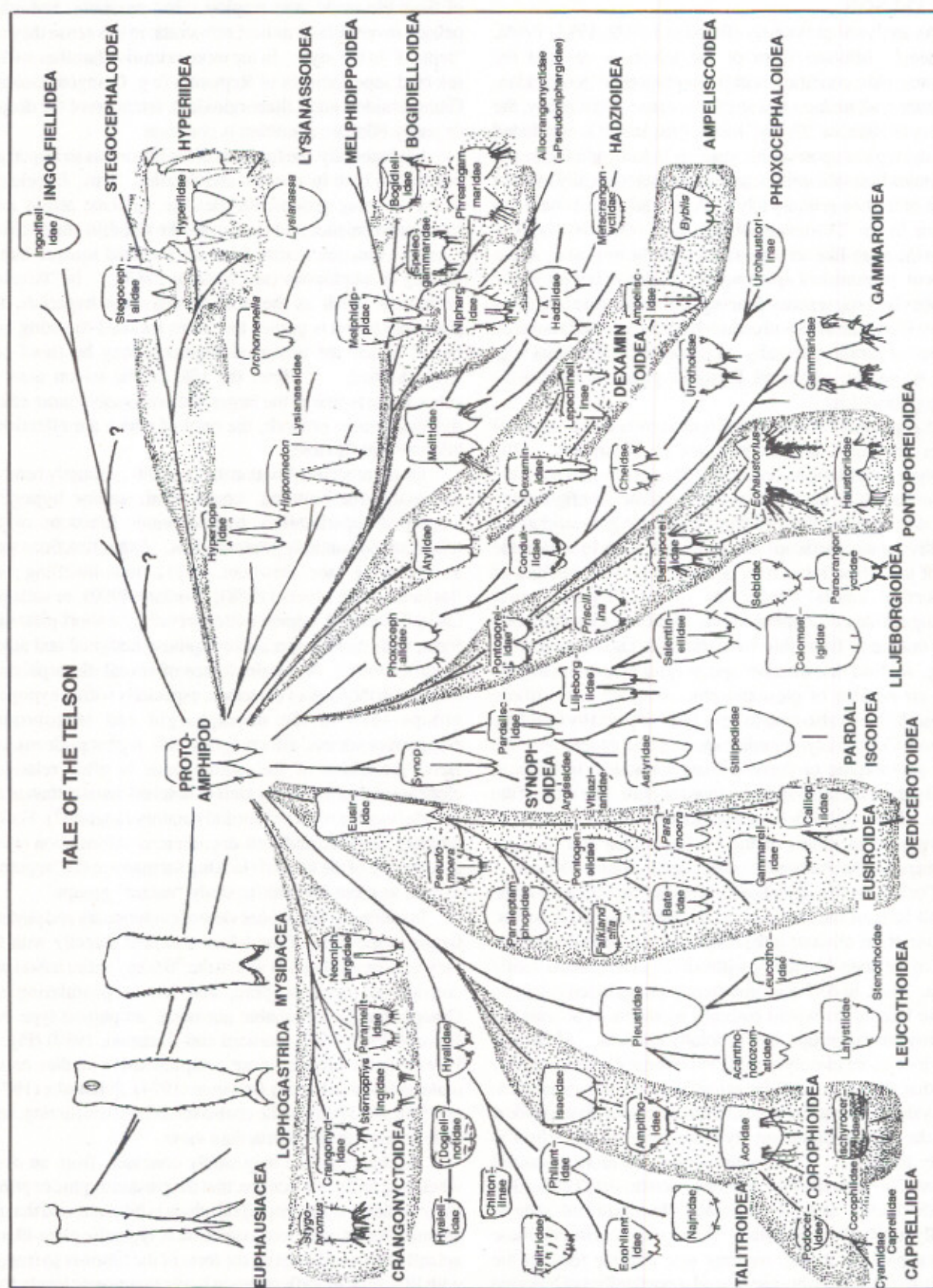


FIG. 24. EVOLUTION OF THE TELSON WITHIN AMPHIPOD SUPERFAMILIES

SPECIAL TAXONOMIC AND PHYLETIC PROBLEMS WITHIN THE AMPHIPODA

The phyletic classification of amphipod crustaceans is rendered especially difficult by the widespread occurrence of character convergence in unrelated taxa of similar life styles, and by the difficulty of selecting suitable outgroup taxa, with or without the use of numerical taxonomic methodology. Assuming natural monophyly of the Amphipoda as an ordinal group within the Malacostraca, an attempt is made here to establish closest phyletic relationships of:

- (1) Suborder Hyperiidea
- (2) Suborder Ingolfiellidea
- (3) Selected hypogean genera of uncertain classification having character states of potential ancestral significance.

(1) Systematics and phylogeny of the Hyperiidea

The Suborder Hyperiidea is divided into two infraorders, 6 superfamilies, and 21 families (Bowman & Gruner, 1973). Infraorder Physosomata is generally regarded to be more primitive (showing more plesiomorphic character states) and is thus closer to the presumed ancestral hyperiid than is infraorder Cephalosomata (Bowman & Gruner, 1973). In many respects some members of the Physosomata resemble some non-calceolate callinophorate members of Gammaridea-Natantia, including the broad peraeonal body region, shortened head that often telescopes into peraeon 1, small peraeopod 7, and usual presence of a mandibular palp. The fused urosome segments 1, 2 & 3, the fused inner ramus and peduncles of uropods 1-3, the 1-segmented outer ramus of uropod 3, and plate-like telson are advanced character states that are only occasionally met with (and never totally in combination) in only a few gammarideans (e.g. cyphocarid lysianassids) that tend to have pelagic and neritic life styles that are similar to the hyperiideans.

Sveshnikov & Vinogradov (1987) considered the suborder Hyperiidea to consist of a heterogeneous and apparently polymorphic group of pelagic carnivorous crustaceans. All are hyperiids are pelagobionts; none are benthic. Member species can be grouped into two life form classes of which about 35% are free-swimming predators, and the other 65% exclusively parasites and commensals of gelatinous animals. The former are all members of the advanced Physocephalata whereas the parasitoids encompass all of the Physosomata and several groups within the Cephalosomata. Of the former, the primitive sciniform family members are commensals and strict ectoparasites. These animals have a well developed pleon and urosome, but the grasping adaptations of the appendages are poorly developed or absent. Since the scinid physosomatids are among the most primitive forms of hyperiids, we might reasonably look for ancestral types among the gammaridean amphipods that are similarly free-swimming and weakly parasitoid.

Table II presents a character-state matrix pertinent to physosomatid hyperiids, and to non-calceolate callinophorate superfamilies of Gammaridea-Natantia. The closest (or least different) match (score of 28/40) with the scinid hyperiids is

that of superfamily Stegocephaloidea. Similarities with other gammaridean superfamilies (Lysianassoidea and Pardaliscoidea) are smaller, in the 40-50% range. These levels are higher, however, than with advanced members of the benthic Reptantia, including the Corophioidea, considered by some to be directly ancestral to the Hyperiidea (see p. 85). Some similarities with stegocephaloideans are conspicuous. Synapomorphies include a telescoped head, an asymmetrically notched upper lip, slightly dissimilar but mainly simple gnathopods, a weakened or shortened maxillipedal palp, shortened peraeopod 7, and nearly plate-like (apically notched) telson. However, stegocephaloideans are much less advanced in retaining an accessory flagellum, deep coxal plates, unfused urosome segment 2 & 3, sometimes 2-segmented outer ramus of uropod 3, and the invariable presence of coxal gill on peraeopod 7, among other plesiomorphic features.

Figure 25 is a resulting phenogram of character state similarities between physosomatid hyperiids and non-calceolate gammaridean Natantia. This phenogram, derived through simple cluster analysis, shows an overall average similarity of hyperiids to callinophorate gammarideans of about 55%. Character state differences that contribute to the relatively low morphological similarity include, in the hyperiids, lack of antennal calceoli and accessory flagellum, absence of a maxillipedal palp, and total fusion of urosome segments 2 & 3, and telson lobes.

Conclusions. These observations suggest that hyperiids may have evolved from a gammaridean ancestral type that was nearest to the present stegocephaloidean body form. Bousfield (1982b) has hypothesized a probable mid-Mesozoic most recent time of origin for callinophorate gammaridean groups, a thesis which, if reasonably correct, would suggest an earlier common ancestry for hyperiid amphipods. The fact that hyperiids exhibit several major differences from closest gammaridean relatives would also suggest that hyperiids have diverged from a common ancestor over a considerable period of geological time. However, despite the remarkable diversity of form, function, and life style shown by members of the Hyperiidea, their derivation from a common ancestor within the much more primitive Gammaridea might justify consideration of their classificatory status as infraordinal within the Gammaridea Natantia. By analogy within the world of vertebrate animals, might the hyperiids be to the gammarideans what the birds are to the dinosaurian euryapsid reptiles?

By similar analysis, members of suborder Caprelliidea can be derived from a corophioidean ancestral type (Podoceridae, Laubitz, 1979, 1982) and thus justify reduction of its current subordinal status to infraordinal level.

By contrast, however, the Ingolfiellidea (see also p. 120) possesses unique character states that are more plesiomorphic than anything occurring within the Gammaridea (*sens. lat.*). These include the short unpigmented eye lobes, elongate peduncular segment 3 of antenna 2, partially divided (in-

TABLE I. CHARACTERS AND CHARACTER STATES OF SUBORDER HYPERIIDEA.

CHARACTER	CHARACTER STATE
1. Callynophore (A, male)	1. Present
2. Calceolii (A, male)	2. Absent
3. Accessory flagellum (male, female)	3. Absent
4. Maxilliped palp	4. Usually absent, rarely 1-segmented rudiment
5. Gnathopods 1 & 2 (sexual dimorphism)	5. If present, not significant
6. Brood plates slender (female)	6. No, all broad, bowed margins, smooth
7. Coxal plates 1-4 large	7. If larger, usually significant
8. Pereopod 7 > Pereopod 6	8. Usually smaller to subequal (<i>Mimonectes</i> excepted)
9. Coxal gill of pereopod 7	9. Always lacking
10. Pleopods (male) rel to pleopods of female	10. Always more powerful
11. Sexual dimorphism in pereopods	11. Slight, if any
12. Sexual dimorphism of pleopod rami	12. Never
13. Sexual dimorphism of uropods	13. Usually slight (strong in <i>Lycaeopsis</i>)
14. Lower lip, inner lobes	14. No, never seen
15. Mandible, left lacinia dentition	15. 8- to 15-dentate
16. Urosome segments	16. Urosomites 2 and 3 fused
17. Telson	17. Entire
18. Upper Lip	18. Notched
19. Maxilla 1, inner plate.	19. Usually not present
20. Uropod 3, outer ramus, segments	20. Always 1-segmented

TABLE II. CHARACTER STATE MATRIX: HYPERIIDEA AND GAMMARIDEAN SUPERFAMILIES

MAJOR TAXON	C H A R A C T E R N U M B E R																				P/A IND
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
A. Hyperiidea	0	2	2	2	0	0	1+	1+	0	0	2	0	0	0	1	2	2	2	2	2	21+
B. Stegocephaloidea	0	2	0	0	0	1	0+	2	0	1-	1	0	0	0+	0	0	1	1	1	2	12
C. Lysianassoidea (Hyperlopsiidae)	0	1	0	0+	0	2	0	1	0	0	2	0	0	0	1	0	0	0+	0	0	7+
D. Lysianassoidea (Trischizostomatidae)	0	0+	0	0	1	1	1-	2	0	1	0	0	0	0	1	0	0	2	0	1	10
E. Pardaliscoidea	0	2	0+	0	0	0	1	0+	0	1-	1	0	1	1+	1	0	0	2	0	1	11+
F. Synopioidea	0	2	0	0	0	1	1	0	0	0	0	0	0	1+	0	0	0+	0	0	1	6
G. Dexaminoidea	1	2	1+	1	1	1+	0+	0	1-	0	1	0	1	1	2	0	0	0	0	1	14+
H. Stenothoidea	2	2	2-	0	2	0	0	1	2	1	2	2	0	2	1+	0	2	0	1	2	24
J. Corophioidea	2	2	1	0	2	0	1	0	2	2	2	2	2	2	2	1	2	0+	0	2	27
LEGEND FOR CHARACTER STATES: 0 - PLESIOMORPHIC; 1 - INTERMEDIATE; 2 - APOMORPHIC.																					

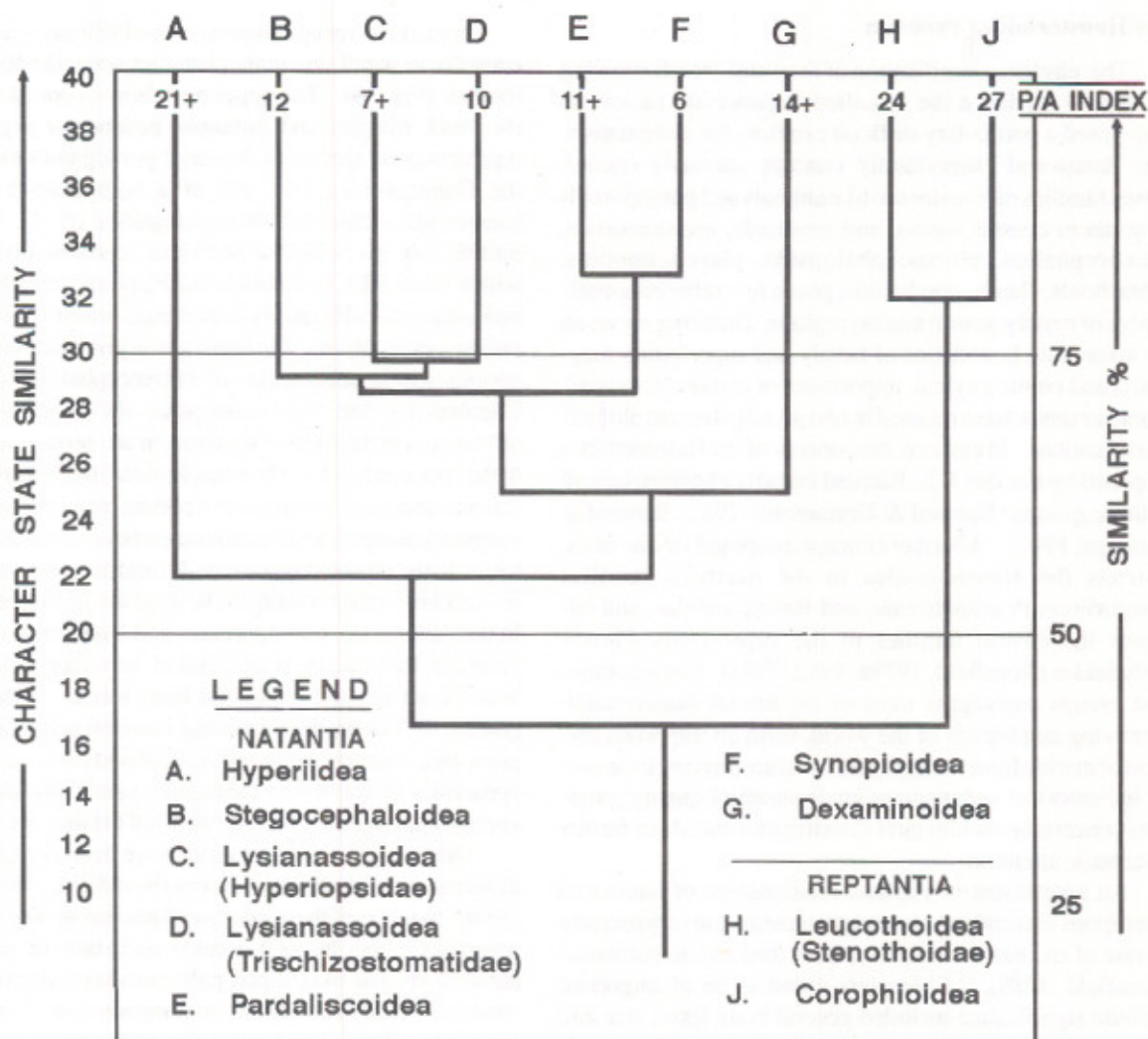


FIG. 25. PHENOGRAM: HYPERIIDAE AND GAMMARIDEAN CALLYNOPHORATE AND NON-CALLYNOPHORATE SUPERFAMILIES

completely fused) segment 1 of the maxillipeds, subsimilar carpocheate gnathopods, and large uropod 2. All of these unique features strongly support continued full subordinal recognition of the Ingolfiellidae.

The distributional-ecological occurrence of the Ingolfiellidae, world-wide in marine and hypogean in continental freshwater, supports not only their classificatory distinctiveness but their probable great antiquity (late Paleozoic, per Bousfield & Conlan, 1990)

Distributional-Ecology of hyperiid amphipods

Both hyperiids and stegocephaloideans are exclusively marine, in fully saline (> 30‰) waters, well away from the immediate influence of land run-off. Both groups are present over the shelf and slope, and in the abyss, or exhibit vertical diurnal migrations from below the euphotic zone.

Stegocephaloideans are mainly epibenthic, but *Parandania boeck* is mesopelagic (Moore & Rainbow, 1989), and lives in association with medusae (e.g. *Atolla parva*). Also stegocephaloideans are found mainly in cold-water regions, as are the more primitive members of the Hyperiidea, the Physosomata, and some of the more primitive members of the Cephalosomata (of family Hyperiidae).

As noted above, at some stage in their life history, most hyperiids are parasitoid, usually in relationship with the Coelenterata, Tunicata, and other jelly-like pelagic animals. Stegocephaloideans are symbiotic with sponges, tunicates, sessile coelenterates, and other cnidarians (Moore and Rainbow, 1984, 1989). Such associations indicate lengthy evolutionary development, and classificatory stability, further underscoring the suitability of stegocephaloideans as a phyletic outgroup taxon for the Hyperiidea.

The Haustorioidea Problem

The phyletic classification of fossorial, free-burrowing amphipods having a the so-called "haustoriid" facies has long posed a particularly difficult problem for systematists. The "haustoriid" superfamily concept variously encompasses families of *Haustorius*-like animals and pontoporeiids of northern coastal waters, and urothoids, urohaustoriids, phoxocephalids, phoxocephalopsids, platyischnopids, zobrachoids, cheids, condukiids, plus a few other enigmatic genera of mainly austral marine regions. Differing views on the taxonomic boundaries of family and superfamily diagnoses, and on the phyletic importance of certain "fossorial" character states, have resulted in two principal recent phyletic classifications. In essence, the concept of the Haustorioidea proposed by the late J. L. Barnard broadly encompasses all of those groups (Barnard & Drummond, 1982; Barnard & Karaman, 1991). A further concept, proposed by one of us, restricts the Haustorioidea to the northern families Haustoriidae, Pontoporeiidae, and Bathyporeiidae, and relegates the austral families to the superfamily Phoxocephaloidea (Bousfield, 1979a, 1982, 1983). Since component groups encompass most of the littoral marine sand-burrowing amphipods of the world, form an important element of marine food energy cycles, and are proving to be useful indicators of sedimentary environmental quality, problems concerning their natural classification merit our further systematic attention.

An assessment of phyletic relationships of haustoriid amphipods was undertaken and presented relatively recently by one of us, but the results remain formally unpublished (Bousfield, 1989). Characters found to be of important phyletic significance included general body form, size and shape of the rostrum, presence of antennal sensory organs, structure and "dactylation" of the posterior peraeopods and maxillipedal palp, form of the pleopods, type of mouthparts, and differences in character states of the telson, uropods, and other appendages. The major difficulty in sorting out the phylogeny of fossorial animals is the "look-alike" problem, i.e. the high incidence of convergent evolution within nearly every character and character state, of all the family groups investigated. However, close and careful examination of these character states, in relationship to those that tend to be relatively independent of fossorial life style (e.g. significant in reproduction, feeding, and swimming), in combination, provides a more reliable basis for sorting out homoplasious similarities from true phyletic similarities. On this methodological premise, evidence from the evolutionary direction, or trending, within pertinent character states suggested a basic phyletic difference between the two major groups. Thus, the northern haustoriids appeared to be more closely related to gammaroidean amphipods, and of relatively recent origin, perhaps associated with the opening of the Atlantic Ocean during the Mesozoic Era. The southern group was found phyletically more primitive and isolated from other major taxa, and of greater antiquity, originating probably prior to the Gondwanian continental breakup.

In this brief recapitulations of the 1989 analysis, we here consider in detail one main character state, the form of the rostrum (Fig. 26). The upper row shows a dorsal outline of the head, rostrum and proximal peduncular segments of representative species of fossorial pontogammarids within the Gammaroidea (A), and of a bathyporeiid and two haustoriids within the Pontoporeioidea (B, C, D). The middle row gives similar views of representative species within urothoid (E), urohaustoriid (F), phoxocephalopsid (G), and zobrachoid (H) family complexes, within urothoid type phoxocephaloideans. The bottom row gives similar views of species within subfamilies of Phoxocephalidae (H, J, K), Cheidae (L), and Platyischnopidae (M). Trends and key differences in the form of the rostrum are pronounced. Thus in the "hooded heads" (Phoxocephalidae) and "shark-snouts" (cheids and platyischnopids) (bottom row) the rostrum is variously elongate and extends much beyond the lateral head lobes. In the urothoid type animals (middle row), the rostrum is short but extends distinctly beyond the lateral head lobes. In the gammarids, pontoporeiids, and haustoriids (top row), however, the rostrum is vestigial or very short, and extends little or not beyond the lateral head lobes. In these latter groups, the substrate-penetrating function performed by the prow-like rostrum of the phoxocephalids and urothoids is apparently performed by the distally narrowing and closely approximated peduncular segments of the first antennal pair.

Other major character states have been correlated with differences in form of the rostrum (Bousfield, 1989). Thus, family members of the upper row all possess strongly deflexed urosomes ("bent backs"), weakly dactylate (or adactylate) peraeopods and maxillipedal palp, variously dissimilar and weakly sexually dimorphic gnathopods 1 & 2, unreduced (gammaroidean) mouthparts, pleopods reproductively non sexually dimorphic, broad to medium broad brood plates, and advanced, gammaroidean-type antennal calceoli (when present), among other differences. Family members of the middle and lower rows, all possess weakly deflexed urosomes ("straight backs"), strongly dactylate peraeopods and maxillipedal palp, subsimilar and non sexually dimorphic gnathopods 1 & 2, strongly reduced or modified (carnivorous) mouthparts, high incidences of reproductively sexually dimorphic pleopods, linear or sublinear brood plates, and primitive crangonyctoidean-type calceoli (when present).

In all these instances, these differences are here considered of major phyletic significance rather than of convergent similarity. Accordingly, members of the family Haustoriidae are included here with the phyletically related Pontoporeiidae and Bathyporeiidae, within superfamily Pontoporeioidea, and allied with superfamily Gammaroidea of the northern hemisphere (Fig. 30, Table III). Members of the southern fossorial family groups are here maintained within superfamily Phoxocephaloidea, that is phyletically isolated from other marine superfamily groups, but exhibits character states that perhaps indicate distinct relationships to the Crangonyctoidea, now restricted to continental freshwaters of the world.

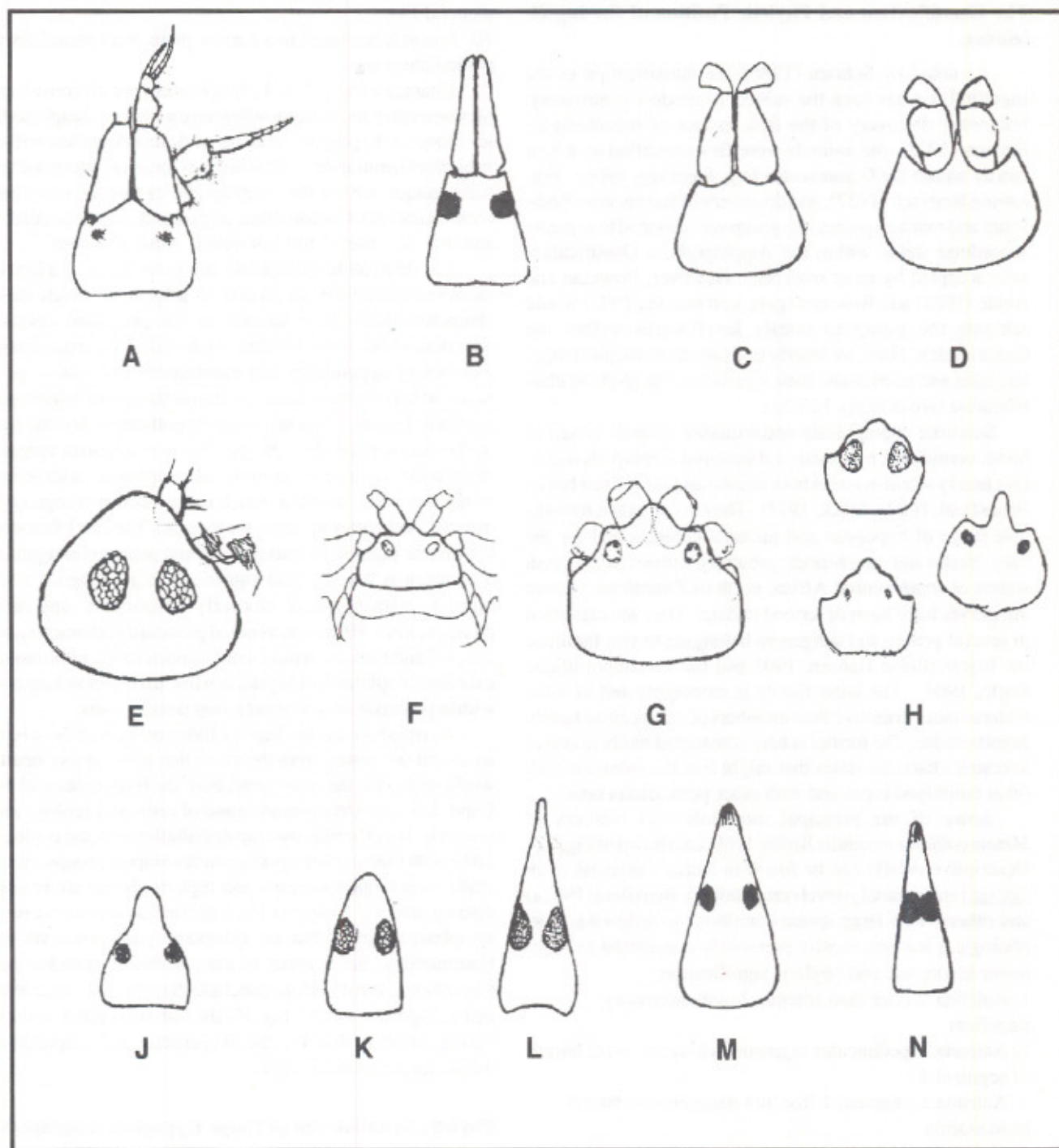


FIG. 26. SIGNIFICANCE OF ROSTRUM IN SUPERFAMILY RELATIONSHIPS

TOP	A Pontogammaridae	B Bathyporeiidae	C Haustoriidae (<i>Protohaustorius</i>)
ROW	D Haustoriidae (<i>Haustorius</i>)		
MIDDLE	E Urothoinae	F Urohaustoriinae	G Phoxocephalopsinae
ROW	H Zobrachoinae		
BOTTOM	Phoxocephalidae: J Tipimeginae	K Brolginae	L Phoxocephalinae
ROW	M Cheidae	N Platyschnopidae	

The Classification and Phyletic Position of the Ingolfiellidea.

As noted by Schram (1986), the classification of the Ingolfiellidea has been the subject of modest controversy. Following discovery of the first species of *Ingolfiella* by Hansen (1903), the animals were first classified as a new family within the Gammaridea (e.g. Stebbing, 1906). Following Reibisch (1927), and discovery of further new freshwater and marine species, the group was elevated to separate subordinal status within the Amphipoda, a classification now accepted by most workers. However, Bowman and Abele (1982) and Bowman (pers. communic., 1992) would relegate the group to family level status within the Gammaridea. Here, we briefly re-examine its major character states and re-evaluate their significance in phyletic classification (see also pp. 125-26).

Suborder Ingolfiellida encompasses a small group of blind, vermiform, hypogean and fossorial amphipods occurring nearly world-wide in both marine and freshwater habits (Bousfield, 1982a; Stock, 1977). They occur over a remarkable range of hypogean and infaunal habitats, and are the only freshwater amphipods presently known from fresh waters of south-central Africa, north of Zimbabwe. About 40 species have been described to date. They are classified in several genera and subgenera belonging to two families, the Ingolfiellidae Hansen, 1903 and the Metaingolfiellidae Ruffo, 1969. The latter family is monotypic and in some features more primitive than members of the speciose family Ingolfiellidae. The former is here considered likely to reveal ancestral character states that might link the suborder with other amphipod types and with other peracaridan taxa.

Some of the principal morphological features of *Metaingolfiella mirabilis* Ruffo, 1969, are shown in Fig. 27. Descriptive details can be found in Ruffo's original work (loc. cit.) and in family-level compendia by Bousfield (1982a) and others. This large species exhibits the following morphological features mostly previously considered to be of major taxonomic and phyletic significance:

1. Antenna shorter than antenna 2, with accessory flagellum
2. Antenna 2, peduncular segment 3 elongate, $>1/2$ length of segment 4
3. Antenna 2, segment 1 free, not concealed by lateral head margin
4. Unpigmented ocular lobes present, at the lateral anterior head process.
5. Paired maxillipeds with distally separated (unfused) basal segments
6. Gnathopods large, dissimilar, raptorial, strongly carpocheleiform (carpus with palm, against which closes the combined propod and dactyl), not sexually dimorphic.
7. Peraeopods 3-7, dactyls very short.
8. Pleopods biramous, rami annulate, pleopod 1 complexly sexually dimorphic.
9. Uropod 2 much larger and longer than uropod 1, almost

pleopod-like

10. Telson lobes fused to a narrow plate, with paired distal penicillate setae

Character states 2, 3, 4, 5, 6, 8, and 9 are all considered plesiomorphic and found nowhere else within the Amphipoda, let alone in hypogean families and superfamilies within suborder Gammaridea. This taxon is therefore morphologically unique within the Amphipoda, cannot be classified within suborder Gammaridea, as presently conceptualized, and therefore merits full subordinal status of its own.

It is difficult to extrapolate character states of a highly modified vermiform amphipod to a form in which these characters might have existed in the presumed epigean ancestors of the Ingolfiellidea. Homoplasious reduction of locomotory appendages and mouthparts, and loss of pronounced sexual dimorphism, is almost the rule in fully hypogean amphipods. As noted in the hypothetical phyletic tree of the Amphipoda (Fig. 30, p. 126), the ancestral epigean ingolfiellid was almost certainly calynophorate, with primitively calceolate antenna, much as in modern crangonyctoids, and with a terminal male stage. The eye lobes may have borne pigmented stalked eyes, and peduncular segment 3 of antenna 2 a vestigial squame. The gnathopods were almost certainly non sexually dimorphic and non preamplifying. However, as noted previously, character nos. 2, 3, 4, 5 and 8 occur, in more conspicuous form, within some extant petalophthalmid Mysidacea but, to date, nowhere else within potential ancestral outgroup peracaridans.

As noted above, the Ingolfiellidea occur widely in both fresh and salt water, from the shore line to the abyss, nearly world wide. On the other hand, both the Hyperiidea and the Caprelliidea are strictly marine and of restricted ecology and life style. Ingolfiellids overlap distributionally and ecologically with many other hypogean amphipod groups, especially with bogidielloids and niphargids but are readily distinguishable. Whereas the ingolfiellids possess several symplesiomorphies but no synapomorphies vis-a-vis the Gammaridea, the reverse is true of the Hyperiidea and Caprelliidea. We therefore conclude that the case for continued recognition of the Ingolfiellidea at subordinal level is strong whereas that for the Hyperiidea and Caprelliidea merits further consideration.

Phyletic Relationships of Large Hypogean Amphipods

As in the fossorial amphipods, the phyletic placement of hypogean amphipods is subject to problems of convergent evolution because of the specialized but relatively uniform nature of the phreatic environment. However, such problems tend to be evidenced in rather different and mainly non reproductively related aspects of their systematics. Holsinger (1993) has comprehensively reviewed the distribution of the world fauna of 740 hypogean amphipod species that are distributed among 36 families and 12 superfamilies or equivalent groups. Most of these occur in the northern hemisphere, but diversity is relatively high among groundwater amphipods

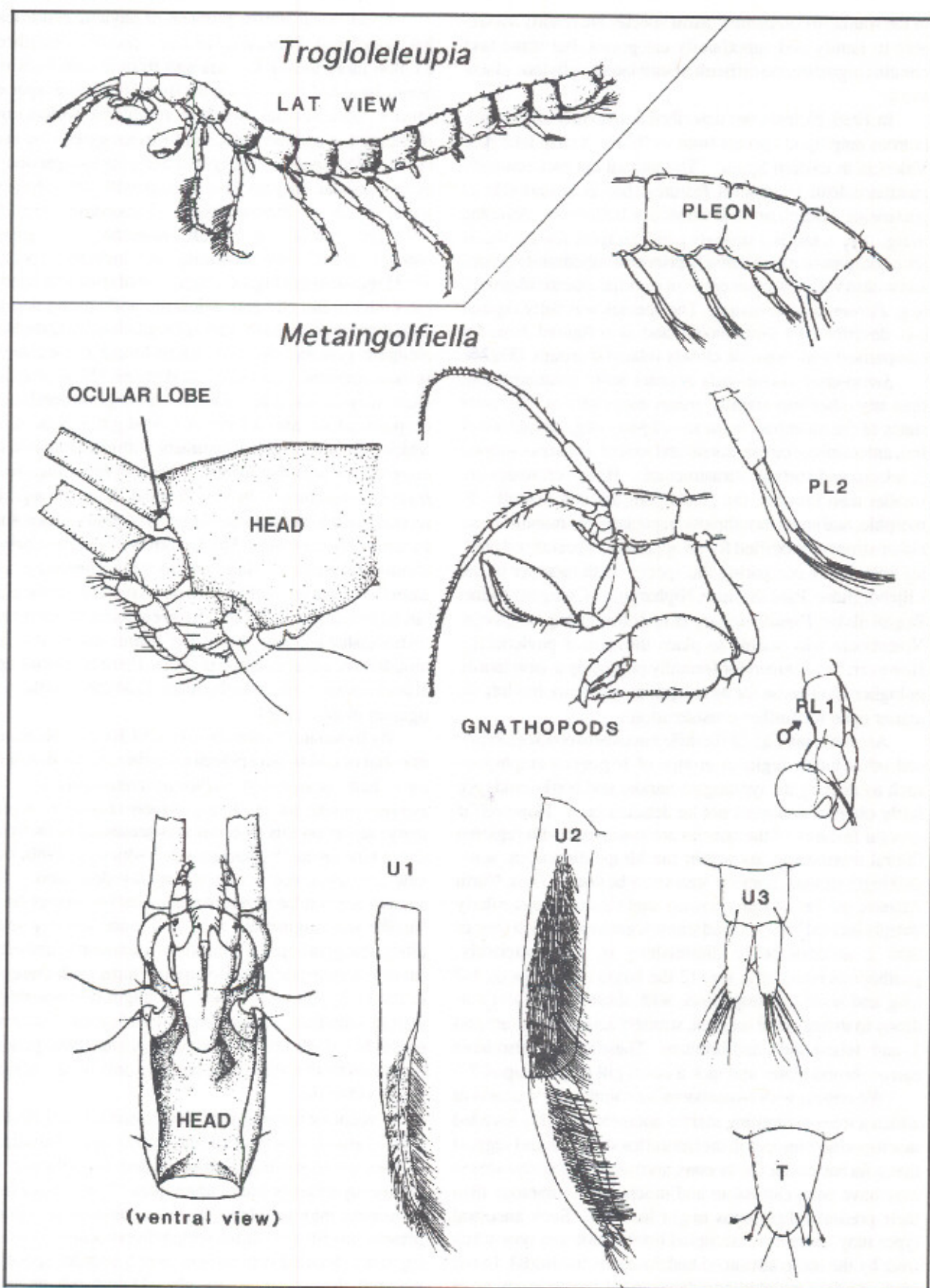


FIG. 27 MORPHOLOGICAL FEATURES OF INGOLFIELLIDEA (mainly after Ruffo, 1969)

of the southern continents. Most species are readily assignable to family and superfamily categories, but some taxa remain enigmatic and difficult of satisfactory phyletic placement.

In 1986, Notenboom described a relatively large, carnivorous amphipod species from wells and a cave lake near Valencia in eastern Spain. The animal appears basically gammaroidean in general features, but is remarkable in possessing calceoli on both antenna of both sexes. As noted in fig. 11, this is a strongly plesiomorphic feature that is found only among the relatively primitive superfamily groups and within very few other epigean gammaroidean subgroups (e.g. *Paramesogammarus*). The species was fully figured and described by Notenboom and is refigured here for comparison with possible closely related ingroups (Fig. 28).

Sensonator valentiensis appears more gammaroidean than any other superfamily group, especially in character states of the antennae, some mouthparts (e.g. simple lower lip), anterolobate coxae, dorsal abdominal spination, uropod 3, telson, and surface ultrastructure. However, males are smaller than females, the gnathopods are non sexually dimorphic, and some mouthparts, especially the mandible, are rather strongly modified for an apparently specialized feeding role. After comparing the species with member of the Liljeborgiidae, Pardaliscidae, Niphargidae, Crangonyctidae, Bogidiellidae, *Pseudoniphargus*, and other hypogean groups, Notenboom was unable to place the animal phyletically. However, he refrained from formally proposing a new family or higher level taxon for its reception, and hence has left the matter open for further consideration.

As seen in our Fig. 28 the differences between *Sensonator* and other major regional groups of hypogean amphipods such as niphargids, typhlogammarids, and bogidiellids are fairly obvious and need not be detailed here. However, if general features of the species are compared with regional littoral marine species within the Melphidippoidea, some strikingly similar character states may be noted. Thus, North Atlantic species of *Cheirocratus* and *Casco* have similarly sharply incised inferior head sinuses, antenna 1 much shorter than 2, anterior coxae diminishing in size posteriorly, gnathopods unequal in size (2 the larger), peraeopods 5-7 long and nearly homopodous, with short dactyls and tendency to strong distal setation, strongly aequiramous uropod 3, and telson short and bilobate. These species also have narrow brood plates and lack a coxal gill on peraeopod 7.

We concur with Notenboom's evolutionary scenario in which a free-swimming marine ancestor probably invaded macroporous biotopes in the littoral karst. We would suggest that as far back as the Cretaceous, ancestral melphidippoideans may have been calceolate and much more numerous than their present relict status might indicate. Such ancestral types may once have occupied littoral biotopes now taken over by the more advanced hadzioideans (melitids). In our view, modern melphidippoideans merit further study as an extant relict group that may well have sprung from the same common ancestor as *Sensonator*.

A somewhat similar problem of phyletic classification has concerned *Phreatogammarus fragilis* described by Chilton more than 100 years ago from stream beds in the South Island of New Zealand. He assigned the species to family Gammaridae where it remained following its redescription and the addition of further species by Hurley (1954). The species is refigured here, for comparison with other regional epigean species and with other hypogean world genera of possible phyletic relationships (Fig. 29).

The animals superficially resemble some gammaroideans of the northern hemisphere, including species of *Typhlogammarus* (Fig. 29). Characters of strongest similarity are found in the elongate antennae, with strong accessory flagellum, large, sexually dimorphic gnathopods (2 the larger), elongate peraeopods with antero-lobate coxae, dorsally spinose urosome, and large brood plates. However, differences may be noted in the mouthparts, peraeopod dactyls, uropods, telson, and a form of sternal gill is present, all of which precludes direct assignment within any known modern group of gammaroideans. Although *Phreatogammarus fragilis* in continental New Zealand, it bears a superficial resemblance to medium and large hypogean species such as *Pintaweckelia grandis* Stock from wells in the Caribbean continental island of Haiti, and to *Carnarimelita janstocki* Bousfield from anchialine cave pools in the volcanic Hawaiian Islands (Fig. 29). Although *Phreatogammarus* is readily distinguishable from these two forms, especially in the mouthparts, coxal gills and uropods, these two forms appear at least remotely phyletically related and merit further investigation in this regard.

By fortunate chance, one of us (ELB) was able to collect material of additional epigean estuarine and freshwater species, here designated as *Phreatogammarus* sp. 1 and *Phreatogammarus* sp. 2 respectively (Fig. 29). A preliminary report on this material was presented at the International Crustacean Symposium in Sydney, in 1980, but the new taxa have not yet been formally described. These species are similar to the phreatic species, except for their smaller size, pigmented eyes, and more strongly sexually dimorphic gnathopods. They form a taxonomic and ecological series, from marine and estuarine, through fluvial epigean to fluvial hypogean biotopes. We might reasonably conjecture, therefore, that this series reveals a direct pathway of egress by which littoral marine organisms have penetrated hypogean fresh waters in the past, not only in austral regions, but world-wide.

Except for the relatively short telson lobes, the estuarine species also demonstrates a remarkable overall similarity to species of *Hornellia*, a tropical and Indo-Pacific genus within superfamily Melphidippoidea. The genus *Phreatogammarus* may well have shared a common ancestor with present-day littoral marine melphidippoideans. Thus, pending more detailed comparison over a broader spectrum of material, the two groups are placed tentatively on the same major evolutionary branch of the revised and updated amphipod phyletic tree (Fig. 30).

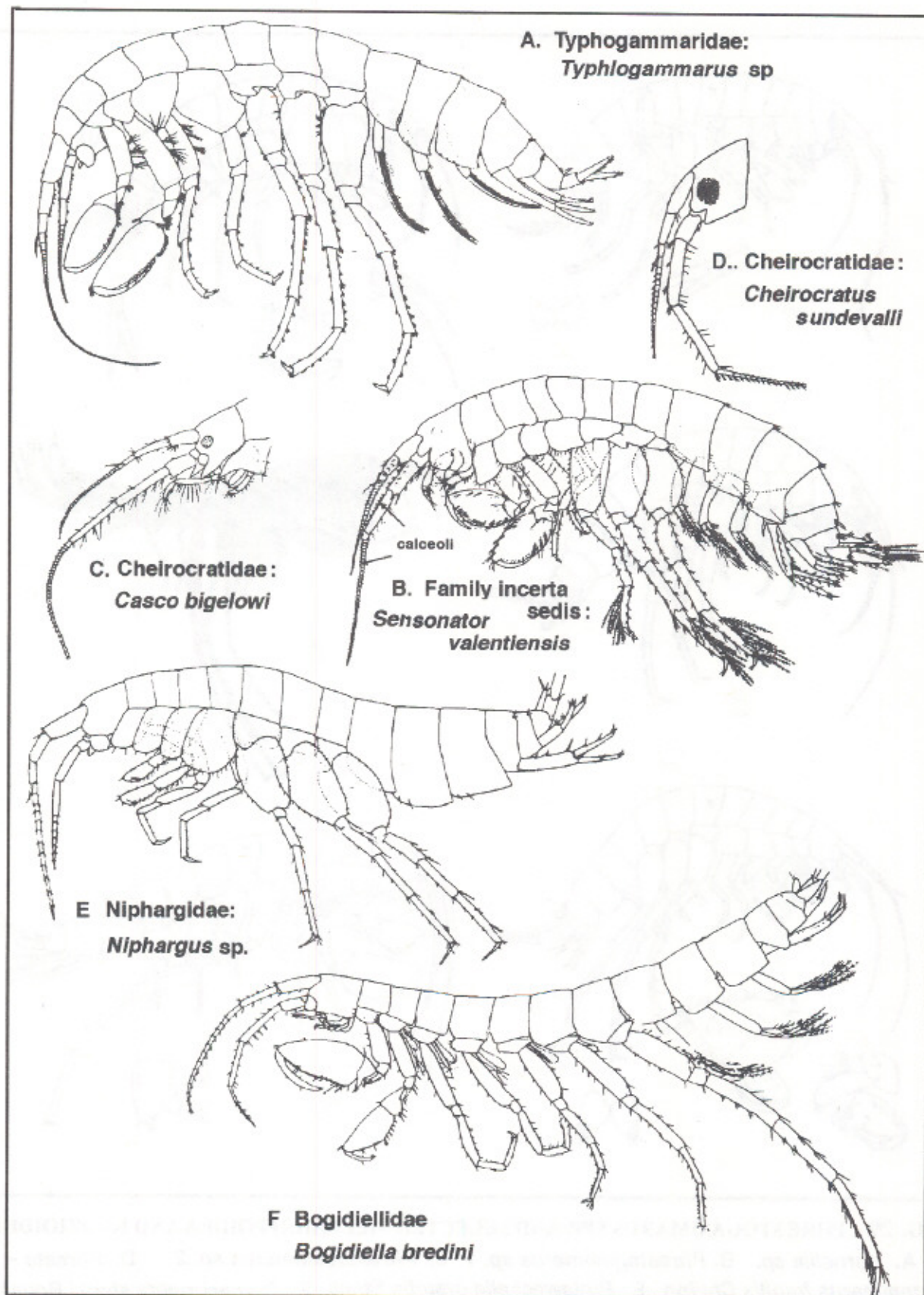


FIG. 28 CONVERGENT MORPHOLOGIES IN LARGE HYPOGEAN AMPHIPODS [from Notenboom (1986) and various sources]

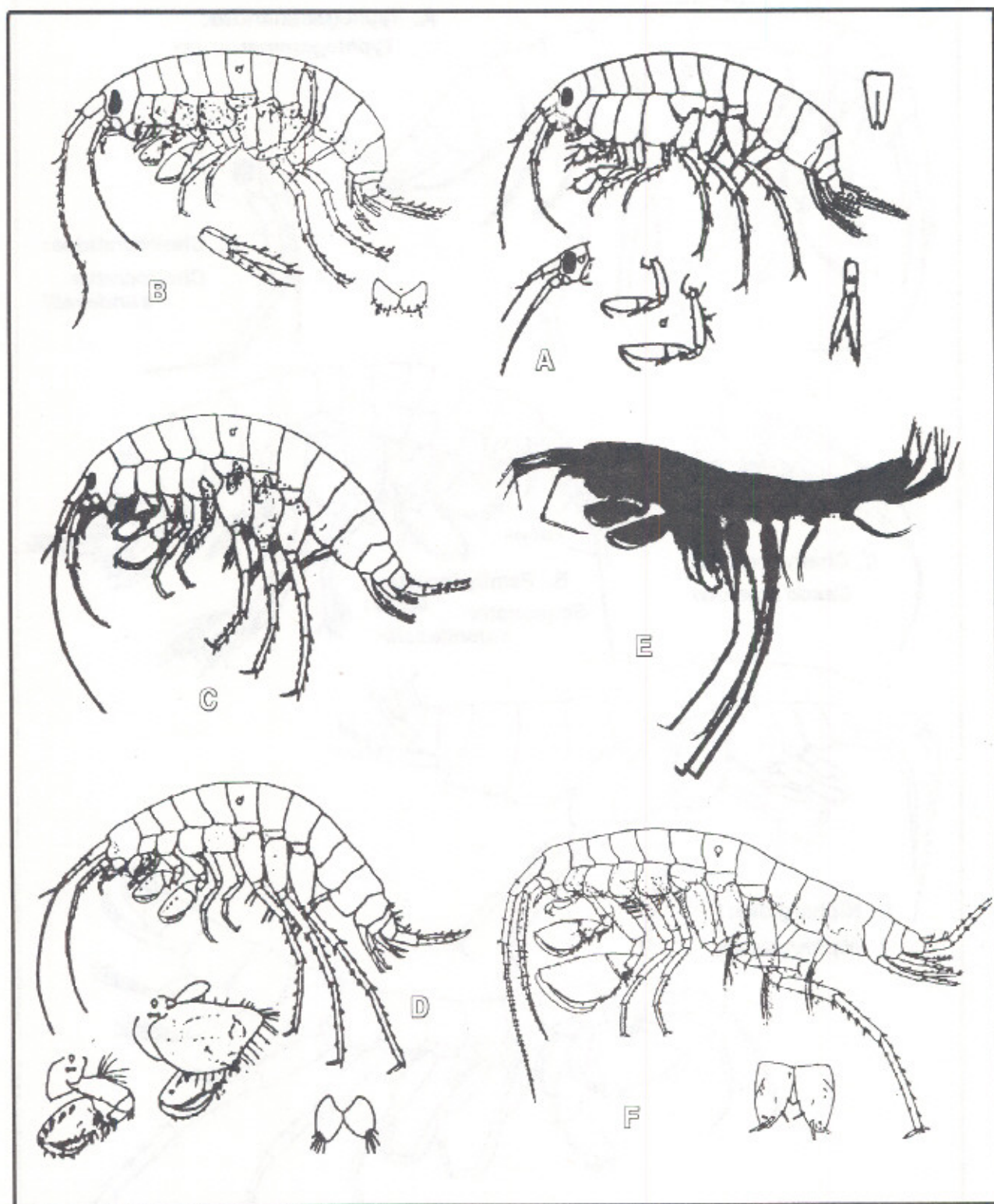


FIG. 29 PHREATOGAMMARUS SPP. AND SELECTED MELPHIDIPPOIDEA AND HADZIOIDEA
 A. *Hornellia* sp. B. *Phreatogammarus* sp. 1 C. *Phreatogammarus* sp. 2 D. *Phreatogammarus fragilis* Chilton E. *Pintaweckelia grandis* Stock F. *Carnari melita stocki* Bousfield

Phylogenetic tree.

Long before the advent of numerical taxonomic analysis, hypothetical phylogenetic relationships between higher categories of classification of organisms had classically been presented in a branching tree-like arrangement. In a morphological treatment, the plesiomorphic character states are most strongly evinced in taxa, extant or extinct, that are closest to the trunk and main branches, and the apomorphic or advanced and specialized features are best developed in taxa placed near the branching extremities. In effect, the phylogenetic "tree" may be viewed as a form of cladogram in which the character states are ordered and arranged "parsimoniously", but without numerical basis. Brusca & Wilson (1991) have employed cladistic methodology in phylogenetic analysis of the Isopoda, resulting in major classificatory recommendations for the 10 suborders within this very diverse, primarily benthic, and relatively ancient group of peracaridans. However, the universality applicability and adequacy of cladistic analyses for this purpose has been questioned by some (e.g. Gosliner & Ghiselin, 1984). A full cladistic analysis of the Amphipoda is beyond the scope of this paper. Serious problems concerning character state homoplasy, and the status of so-called "intermediate" taxa have yet to be resolved. However, a phyletic tree based on "first principles" is here provided as a useful visual basis for eventual numerical establishment of a true phyletic classification of the Amphipoda.

In this respect, Bousfield (1979a) has proposed a tree-like arrangement for amphipod suborders and superfamilies that is here refined and updated on the basis of new information and expanded analysis of major characters and character states (see Fig. 30). The thickness of the branches was roughly proportional to the number of extant species in each subtended major category. In the early version, the "stem" taxa lay within a boundary or envelope of those possessing a pelagic reproductive and terminal male stage. Envelopes of selected plesiomorphic character states such as the presence of postero-lobate coxae of pereopods 5-7, and calceolate antennae also encompassed superfamilies, closer to the tips of the branches, in which mature males were benthic, precomplexing, and of indeterminate life stage.

The present version of the tree (Fig. 30) is essentially similar. During the past 15 years the number of species in each group has increased, variously, by only about 5-10%, few major new taxa have been discovered, and the ordering of character states has remained basically unchanged. However, the callynophore (Lowry, 1986), calceoli (Lincoln and Hurley, 1981), brush setae, and other sensory and swimming structures of reproductive males (p. 88) have since been developed as significant indicators of phyletic relationships. Emphasis on such parameters has here altered the position of the main trunk which now centrally subtends superfamilies of Natantia leading to the most highly advanced and modified *Hyperidea*. These taxa are marked by the plesiomorphies of Table I (p.) that include, in the male, a more slender and flexible urosome, powerfully natatory pleopods, and well-

developed, usually plumose-setose uropod 3 and tail fan. Calceolate antennae are restricted to the more primitive members of Natantia and to more advanced subfamilies that have variously penetrated lotic-water environments of coastal estuaries and freshwaters (e.g. some pontogeneiids and calliopids within Eusiroidea; paracalliopiids and exoedicerotids within Oedicerotoidea). The Lysianassoidea is the only group within Natantia to retain callynophore, calceoli, and brush setae, thus remaining closest to the presumed gammaridean ancestral type, and confirming the classical ancestral position set forth by Sars (1895) and Stebbing (1906). The pelagic males of nestling and tube-building Dexaminioidea and Ampeliscoidea have virtually lost the callynophore, but retain antennal brush setae, powerful tail fan, and bilobate telson. In this respect, the Melphidippoidea are similar, but in their development of weakly sexually dimorphic gnathopods, appear transitional to members of the Reptantia. The monotypic genus *Sensorator* (of Notenboom, 1986) is here proposed (p.) as a primitive early offshoot that still retains antennal calceoli of the presumed marine ancestral melphidippoidean. Primitive members of the fossorial Pontoporeioidea (excluding *Haustoriidae*) and the Phoxocephaloidea (most) have totally lost the antennal callynophore but have retained brush setae and calceoli. As noted previously, natant superfamilies with calceoli are primarily cold-temperate and arctic in distribution, those without are primarily tropical and warm-temperate. The coxal gill of pereopod 7 is retained widely within the Natantia, and is plesiomorphically pleated or dendritic in pelagic males of Lysianassoidea, Eusiroidea, Dexaminioidea, and Ampeliscoidea.

The superfamilies of Reptantia are placed nearer to the branch tips. Those on the right side of the tree tend to possess more plesiomorphic character states such as homo-podous pereopods 5-7, with postero-lobate coxae, and generally lack an ecdesial (baso-facial) spine on uropod 1. Among fresh-water members, the occurrence of various types of sternal gills is widespread (e.g. most crangonyctids, hyalellin talitroideans, pontogeneiid eusirids and *Falklandella*, and paracrangonyctid liljeborgiids). Categories of Reptantia on the left side of the tree are advanced in those same character states and, in fresh water members (e.g. of Gammaroidea, Hadzioidea, Bogidielloidea), sternal gills are lacking or very rare. The coxal gill of pereopod 7 is retained only in the most primitive members of Reptantia (e.g. most Gammaroidea and Crangonyctoidea) and that of pereopod 2 is lost in many corophioideans and all caprellidans.

On the left side of the tree, the primitive hypogean and fossorial Ingolfiellidea (p. 126) diverged early from the many evolutionary trunk. Its presumed epigean free-living ancestors were almost certainly callynophorate and calceolate but little except some mysid-like character states can be deduced from comparative morphology (p. 80) and no trace remains in the very limited amphipod fossil record. The hadzioidean and corophioidean superfamilies underwent progressive reduction of antennal sensory structures, diminu-

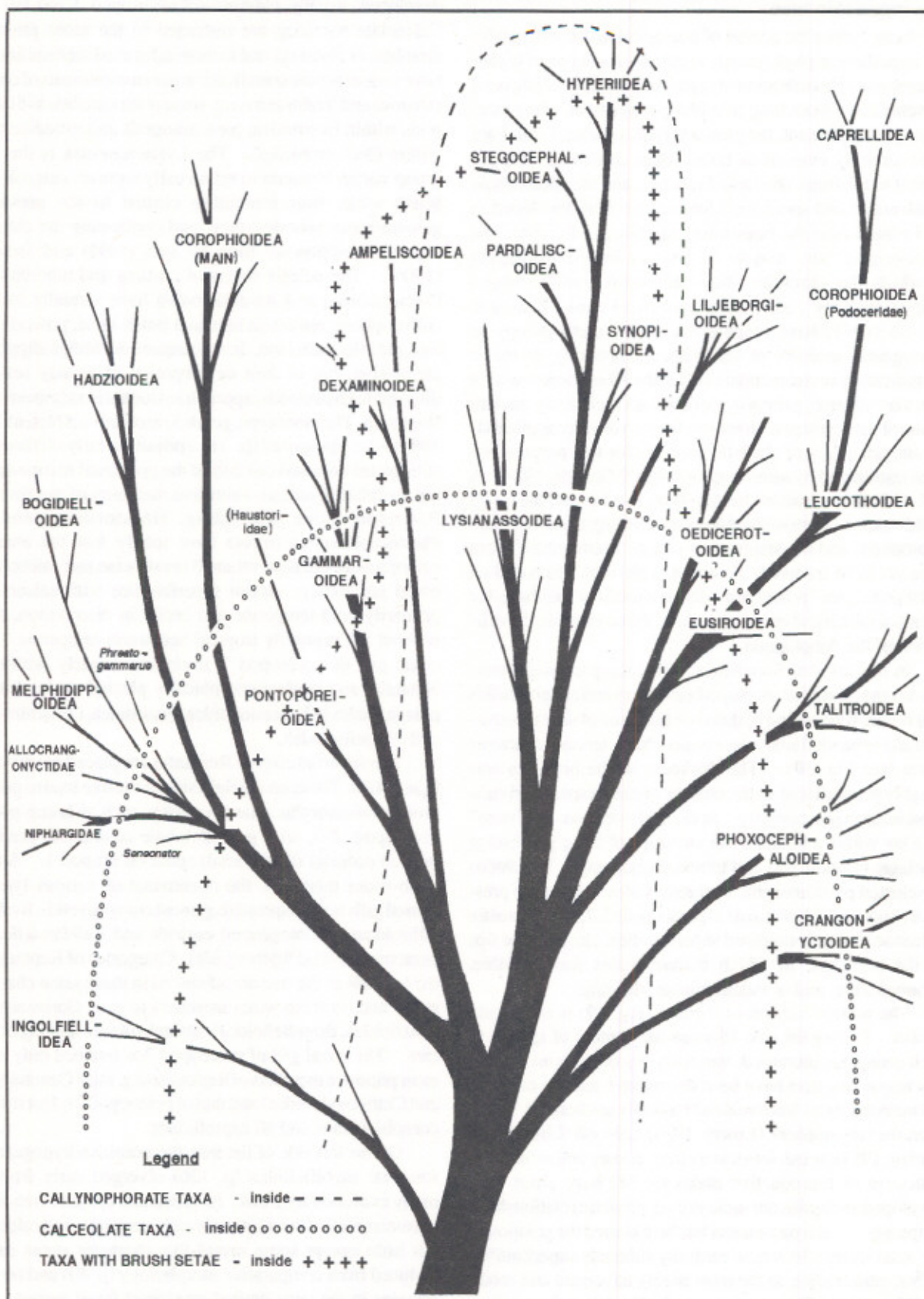


FIG. 30. REVISED PHYLOGENETIC TREE OF AMPHIPOD SUPERFAMILY RELATIONSHIPS

tion of pleopods, uropod 3 and tail fan, and fusion of telson lobes, but enormous development of pre-amplexing and mate-guarding gnathopods in the male (p. 105), apparently associated with benthic and domicolous life styles. The relatively primitive, mainly freshwater gammaroideans have lost callynophore and brush setae, but many have retain antennal calceoli, and fairly strong development of uropod 3, tail fan, and bilobate telson. Gnathopods of the male function in pre-amplexus, rather than in agonistic mate-guarding. Presumably related to the natantian melphidippoideans are the allocrangonyctids and pseudoniphargids, on the one hand, and the phreatogammarids and bogidielloideans on the other (p.126).

On the right side of the tree, the crangonyctoideans are clearly reptant, having lost the callynophore and brush setae, undergone strong reduction of pleopods, uropod 3, and fusion of telson lobes, and are predominantly hypogean in life style. The Crangonyctoidea ranks as the most primitive of reptant superfamilies in which males are typically smaller than females, with non-preamplexing gnathopods, and terminal in life stage. Their widespread retention of calceoli, of a very plesiomorphic form, provides a plausible link with the marine Phoxocephaloidea. Indeed, *Perthia* (the most primitive crangonyctoidean) possesses a natatory uropod 3, strongly bilobate telson, primitively calceolate antenna 1 (male only), specialized carnivorous mouthparts, squarish coxal plates, sexually non-dimorphic raptorial gnathopods, and elongate pereopod 6, features that are reminiscent of many Australian Phoxocephalidae (see also Williams & Barnard, 1988). In association with their freshwater and terrestrial evolutionary thrust, and ability to saltate in air, the talitroideans have undergone very marked reduction of the antennae and sensory structures, of pleopod and uropod 3, and fusion of telson, and powerful development of agonistic and/or pre-amplexing gnathopods, but have otherwise remained generalized and primitive in general body form. Marine members of the Liljeborgioidea (e.g. of Liljeborgiidae, Sebidae, Colomastigidae) are variously specialized for commensal life style, with strongly sexually dimorphic gnathopods. The freshwater members (of Sebidae, Salentinellidae, and Paracrangonyctidae) are hypogean and gnathopods may have become secondarily weakly or not sexually dimorphic. Within the marine leucothoideans, however, members that are morphologically modified in commensal association with tunicates, sponges, and other sessile marine invertebrates (e.g. most Leucothoidae, Vicmusiidae, some Pleustidae, etc), show little or no sexual dimorphism of the gnathopods, except in the microcarnivorous Stenothoidae, and the Anamixidae where modification is extreme (Thomas & Barnard, 1983). Within the Pleustidae, the neopleustinid branch, may have given rise to the Podoceridae (and perhaps the Iciliidae), currently classified within the Corophioidea. These in turn, having strong sexual dimorphism of gnathopods and substrate-clinging life style, have probably given rise directly to the "mainstream" form of the Caprellidea (Laubitz, 1979, 1993).

However, the possibility of a polyphyletic origin of the Caprellidea remains investigative (e.g. Laubitz, 1993; Takeuchi, 1993), as is the origin of the Corophioidea (as presently defined). The leucothoid-podocerid-caprellid clade has remained strictly marine, with strong reduction of abdominal and locomotory appendages, and a strong tendency to semi-sessile, commensal, or ectoparasitic life styles.

Conlan (1991) has utilized the earlier version of the phyletic tree to illustrate the taxonomic distribution of mate-guarding and non-mate-guarding behaviour in the Amphipoda. Mate-guarding behaviour had then been formally described within the Gammaroidea, Talitroidea, Hadzioidea, Corophioidea, and Caprellidea, here categorized within the Reptantia. Non mate-guarding behaviour had been observed within the Lysianassoidea, Eusiroidea, Phoxocephaloidea, Pontoporeioidea, and Ampeliscoidea, all categorized here within the Natantia. She also found that species of *Crangonyx* (Crangonyctoidea) and *Haustorius* and *Amphiporeia* (Pontoporeioidea) did not leave the bottom in mate searching, yet also did not mate-carry or mate-guard. Such behaviour, overlapping between Natantia and Reptantia, is not unexpected, and may reveal how similar mating strategies evolved convergently in phylogenetically unrelated groups exposed to similar environments and edaphic conditions.

Revised Semi-phyletic Classification of the Amphipoda

Phyletically oriented classifications of the Amphipoda proposed by Bousfield (1979a, 1982a, 1983) and embodied in Schram (1986) are revised and updated here (Table 11). A closely similar version was published recently by Bousfield and Staude (1994). Although the subordinal and superfamily concepts remain essentially the same, their semi-phyletic arrangement has been altered significantly to conform with the concept of "Natantia-Reptantia" relationships developed in previous sections, and graphically presented in Fig. 30. As we may note below, the families encompassed within several superfamilies have been expanded or modified in the light of recent discoveries and taxonomic advances.

Within the "Natantia" superfamily Lysianassidae is restored to the basic, ancestral position of earlier authors (Sars, 1895; Gurjanova 1951). The list of member families is expanded to include: (1) the Hyperioptidae and Cyphocaridae, all members of which are neritic, pelagic, and bathypelagic, and the primitive Valettiidae of deep coastal and offshore waters; (2) the fish-parasitic Trischizostomatidae; and (3) the benthic commensal, and modified Conicostomatidae. All of these possess, variously, in combination, the typical lysianassid character states of short swollen peduncular segments and strongly callynophorate flagellum of antenna 1; short rostrum; mouthparts variously modified for carnivory or necrophagy; weakly subchelate, long wristed gnathopod 2 (often with elongate ischium); pleated or convoluted coxal gills; slender or linear brood plates; and (variously) calceolate antennae. Although the Phoxocephaloidea possess more primitive calceoli, and are strongly rostrate, they are ranked phyletically higher because

TABLE III. SEMI-PHYLETIC CLASSIFICATION OF THE AMPHIPOD CRUSTACEANS. [Gammaridea and Ingolfiellidea after Bousfield 1982a, 1983; Hyperidea after Bowman & Gruner, 1973; Caprellidea after McCain, 1970]

<p>I. AMPHIPODA "NATANTIA"</p> <p>Superfamily LYSIANASSIDAE (Gammaridea)</p> <ol style="list-style-type: none"> 1. Valettiidae 2. Hyperipsidae 3. Cyphocaridae 4. Uristidae 5. Lysianassidae 6. Conicostomatidae 7. Trischizostomatidae 8. Incerta sedis <p>Superfamily PHOXOCEPHALOIDEA</p> <ol style="list-style-type: none"> 1. Urothoidae* 2. Platyschnopidae 3. Cheidae 4. Phoxocephalidae 5. Condukiidae <p>Superfamily SYNOPIOIDEA</p> <ol style="list-style-type: none"> 1. Synopiidae 2. Argissidae <p>Superfamily PARDALISCOIDEA</p> <ol style="list-style-type: none"> 1. Stilipedidae (incl. Astyridae) 2. Pardaliscidae 3. Vitjazianidae <p>Superfamily STEGOCEPHALOIDEA</p> <ol style="list-style-type: none"> 1. Stegocephalidae <p>SUBORDER HYPERIDEA</p> <p>INFRAORDER PHYSOSOMATA</p> <p>Superfamily SCINOIDEA</p> <ol style="list-style-type: none"> 1. Archaeoscinidae 2. Mimonectidae 3. Proscinidae 4. Scinidae <p>Superfamily LANCEOLIDEA</p> <ol style="list-style-type: none"> 1. Microphasmidae 2. Chuncolidae 3. Lanceolidae <p>INFRAORDER PHYSOCEPHALATA</p> <p>Superfamily VIBILIOIDEA</p> <ol style="list-style-type: none"> 1. Vibiliidae 2. Cystosomatidae 3. Paraphronimidae 	<p>Superfamily PHRONIMOIDEA</p> <ol style="list-style-type: none"> 1. Hyperiidae 2. Dairellidae 3. Phronimidae 4. Phrosinidae <p>Superfamily LYCAEOPSOIDEA</p> <ol style="list-style-type: none"> 1. Lycaeopsidae <p>Superfamily PLATYSCELOIDEA</p> <ol style="list-style-type: none"> 1. Pronoidae; 2. Anapronoidae 3. Lycaeidae; 4. Oxycephalidae 5. Platyscelidae; 6. Parascelidae <p>Superfamily DEXAMINOIDEA (Gammaridea)</p> <ol style="list-style-type: none"> 1. Atylidae (+ Lepechinellinae) 2. Dexaminidae (+ Prophliantidae) <p>Superfamily AMPELISCOIDEA</p> <ol style="list-style-type: none"> 1. Ampeliscidae <p>Superfamily PONTOPOREIOIDEA</p> <ol style="list-style-type: none"> 1. Pontoporeiidae (incl. Bathyporeiidae) 2. Haustoriidae <p>Superfamily EUSIROIDEA</p> <ol style="list-style-type: none"> 1. Pontogeneiidae 2. Eusiridae 3. Bateidae 4. Calliopiidae 5. Paraleptamphopidae (incl. Falklandellidae) 6. Gammarellidae 7. Amphithopsidae 8. Gammaracanthidae 9. Paramphithoidae <p>Superfamily OEDICEROTOIDEA</p> <ol style="list-style-type: none"> 1. Paracalliopiidae 2. Exoedicerotidae 3. Oedicerotidae <p>Superfamily MELPHIDIPPOIDEA</p> <ol style="list-style-type: none"> 1. <i>Sensonator</i> group (monotypic) 2. Cheirocratidae (=Hornelliidae) 3. Melphidippidae 4. Megaluropidae 5. Niphargidae? (incert. sed.) 6. Phreatogammaridae? (incert. sed.)
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of their loss of callynophore, and their more highly modified mouthparts (lower lip with inner lobes), and unpleated gills. The Synopioidea, Pardaliscoidea and Stegocephaloidea form a non-calceolate core group within Natantia leading to the

advanced, parasitoid Hyperidea, the internal classification of which has been established by Bowman & Gruner (1973).

The weakly or non-rostrate dexaminids and ampeliscids are yet more highly advanced in near loss of callynophore,

TABLE III. (cont'd).

II. AMPHIPODA "REPTANTIA" SUBORDER INGOLFIELLIDEA	3. Mesogammaridae 4. Typhlogammaridae 5. Gammaridae 6. Pontogammaridae 7. Acanthogammaridae 8. Macrohectopidae 9. Caspicolidae? 10. Incert. sed.
1. Ingolfiellidae 2. Metaingolfiellidae Superfamily CRANGONYCTOIDEA 1. Neoniphargidae (+ Perthiidae) 2. Paramelitidae 3. Sternophysingidae 4. Eocrangonyctidae 5. Crangonyctidae	Superfamily BOGIDIELLOIDEA. 1. Artesiidae 2. Bogidiellidae 3. Kergueleniellidae ?
Superfamily LILJEBORGIOIDEA 1. Liljeborgiidae 2. Paracrangonyctidae 3. Sebiidae 4. Colomastigidae 5. Salentinellidae	Superfamily HADZIOIDEA 1. Hadziidae (+ sev. subf.) 2. Metacrangonyctidae 4. Nuuanidae 5. Melitidae 6. Carangoliopsidae 7. Aetiopedidae (transfer from Corophiidae) 8. Allocrangonyctidae (= Pseudoniphargidae)
Superfamily TALITROIDEA 1. Hyalidae (incl. Hyaellidae?) 2. Dogielinotidae 3. Najnidae 4. Ceinidae 5. Eophliantidae 6. Phliantidae 7. Kuriidae 8. Talitridae (4 subgroups) 9. Temnophliantidae	Superfamily COROPHIOIDEA 1. Ampithoidae* 2. Biancolinidae* 3. Aoridae 4. Cheluridae 5. Isaeidae 6. Ischyroceridae 7. Neomegamphopidae 8. Corophiidae 9. Podoceridae*
Superfamily LEUCOTHOIDEA 1. Vicmusiidae 2. Pleustidae (12 subf) 3. Acanthonotozomatidae (incl. 3 subf) 4. Lafystiidae 5. Laphystiopsidae 6. Ochlesidae 7. Amphilochidae (2 subf.) 8. Stenothoidae 9. Cressidae 10. Thaumatesonidae 11. Maxillipiidae 12. Nihotungidae 13. Pagetinidae 14. Leucothoidae (incl. Anamixidae)	SUBORDER CAPRELLIDEA INFRAORDER CAPRELLIDA Superfamily PHTISICOIDEA 1. Phtisicidae 2. Dodecadidae
Superfamily GAMMAROIDEA) 1. Anisogammaridae 2. Gammaroporeiidae	Superfamily CAPRELLOIDEA 1. Caprogammaridae 2. Paracercopidae 3. Caprellidae 4. Aeginellidae
INFRAORDER CYAMIDA Superfamily CYAMOIDEA 1. Cyamidae	

* Possibly convergent within Corophioidea

and weak development of sexually dimorphic gnathopods. The Pontoporeioidea have retained elongate calceolate antennae (male), but lack coxal gill of pereopod 7, and are allied to the reptant Gammaroidea in possessing sexually

dimorphic gnathopods and arostrate head. Freshwater members possess sternal gills. Members of the true Haustoriidae exhibit many character states that are homoplasious with phoxocephaloidean genera (Bousfield, 1989). Despite the

lack of calceoli and (with rare exceptions) loss of gnathopod sexual dimorphism, family Haustoriidae continues here to be classified within the Pontoporeioidea on the basis of head form, mouthpart morphology, adactylate pereopods, strongly deflexed urosome and close similarity of its most primitive members to the sympatric pontoporeiid genus *Amphiporeia*.

Within the Eusiroidea may be recognized two main groups: (1) an essentially pelagic, small to medium sized animals that mostly retain brush setae, calceoli, and strongly natatory pleopods and tail fan, and (2) an essentially benthic group of medium to large-sized animals, including the Paramphithoidae, Amphithopsidae, and Gammaracanthidae Bousfield, 1989, have become benthic but lack sexually dimorphic gnathopods and remain essentially marine. Within subgroup (1) the calceolate pontogeneiids and calliopids have apparently give rise to various groups of Paramoera and allied genera, and to the paraleptamphopid and falklandellid family groups of austral fresh waters. These all tend to have a much reduced uropod 3 and tail fan, but males (in many genera) have developed a pre-amplexing gnathopod 1. Within the closely related but distinctive superfamily Oedicerotoidea, some marine members have retained both calceoli and callynophore, but within estuarine and fresh water exoedicerotids and paracalliopids (southern hemisphere), males have become larger than females and have convergently (to gammaroideans of the northern hemisphere) developed strongly preamplexing gnathopods and the reproductive "carrying" habit, features convergent with those of gammaroideans of the northern hemisphere. As outlined above, the superfamily Melphidippoidea now encompasses the free-swimming marine Cheirocratidae, the fossorial Megaluroidea, and the primitive para-ancestral freshwater hypogean genus *Sensorator*. The phyletic status of the freshwater hypogean family Niphargidae, endemic to the European-Mediterranean region, is considered peripherally melphidippoidean, but remains essentially enigmatic.

The order of listing of superfamilies and suborders of Reptantia is essentially that previously arranged in the family tree (p. 126). The primitive Ingolfiellidae are here considered fully subordinally distinct from the Gammaridae (see also p. 129). Within the Crangonyctoidea, the rationale of Holsinger (1992a) in separating the Sternophysingidae from the Paramelitidae is recognized here, but family Perthiidae, proposed by Williams and Barnard (1988), is readily encompassed within family Neoniphargidae. The sponge-dwelling Colomastigidae is here formally transferred from the Leucothoidea to the Liljeborgioidea. Family composition within the Talitroidea remains unchanged, although the freshwater Hyalellidae have proven to be closely allied with *Allorchestes* and other marine genera and may soon be relegated to subfamily status within the Hyalidae.

The concept of superfamily Leucothoidea has been broadened to encompass the Lafystiidae, Acanthozomatidae, and Ochlesidae (all transferred from Stegocephaloidea), and the unique pleustid-like Vicmusiidae Just, 1990, recorded from Bass Strait Canyon, Australia.

Despite considerable recent taxonomic work on both superfamilies, the family composition of the Gammaroidea and Bogidielloidea remains little changed. The taxonomic refinements within the Hadzioidea have resulted in several new family proposals of which Allocrangonytidae Holsinger, 1989; Nuuanidae McKinney & Barnard, 1977; and Metacrangonytidae Boutin & Missouli, 1988, are provisionally listed here. The family Aetiopedidae Moore and Myers, 1988, based on an enigmatic new form from the Bass Strait region of Australia, was originally placed within the Corophioidea, but is here transferred to the Hadzioidea. The type species, *Aetiopedes gracilis*, possesses a number of strongly melphidippoidean-hadzioidean and non-corophioidean character states. These include a short antenna 1, posteriorly decreasing size of coxae 1-4, elongate carpus of gnathopods, non-glandular bases and unguiform dactyls of pereopods 3 & 4, fully biramous and plumose-setose uropod 3, and linear brood plates. The mouthparts appear hadzioidean, and non-corophioidean, especially in the form of maxilla 2 and maxilliped, and in the notched and slightly asymmetrical form of the upper lip.

The concept of superfamily Corophioidea has remained stable following numerous studies by A. A. Myers (*loc. cit.*) but, under closer numerical taxonomic scrutiny, the concept may prove to be polyphyletic. Thus, amphitoid-biancolinids may form one group, aorid-chelurid-corophiids a second, isaeid-ischyrocerids a third, and the podocerids a fourth, all related more closely to outgroup families within other superfamilies than to each other. Superfamily and family concepts within the Caprellioidea accepted here are basically those of McCain (1970) that also take account the high probability of polyphyletic ancestries proposed by Laubitz (1993) and Takeuchi (1993).

In this presentation, we have delved into the pertinency and usefulness of some morphological features for phyletic classification of amphipod crustaceans. A more comprehensive study might have included the classificatory significance of sexual dimorphism of the pleopods, of the form of the rostrum, of segmentation of pereopods, and of several other major characters. We look to eventual establishment of a data base of non-homoplasious character states sufficiently large to employ cladistical analytical methodology with confidence. We urge further study on the significance of surface ultrastructure in amphipod phylogeny, currently being advanced by Kevin Halcrow (Halcrow & Bousfield, 1987; Halcrow and Powell, 1992; Halcrow, 1993). The protein electrophoretic approach that is now providing answers to species level relationships (Bulnheim & Scholl, 1981; Stewart, 1993) might prove applicable at much higher taxonomic levels. Finally, the fundamental work of Sibley and Ahlquist (1983, *et sequ.*) in which DNA-DNA hybridization techniques were utilized in major phyletic reorganization of avian classification, may eventually be adapted to providing genetic data of exceptional value for the phyletic classification of amphipod crustaceans.

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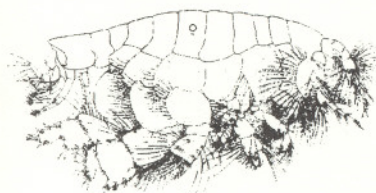
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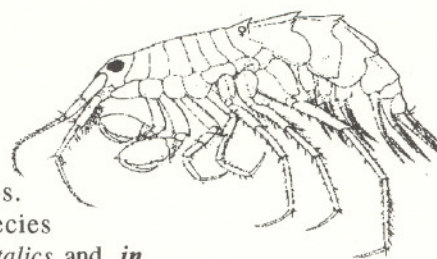
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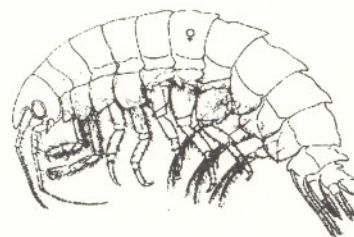
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