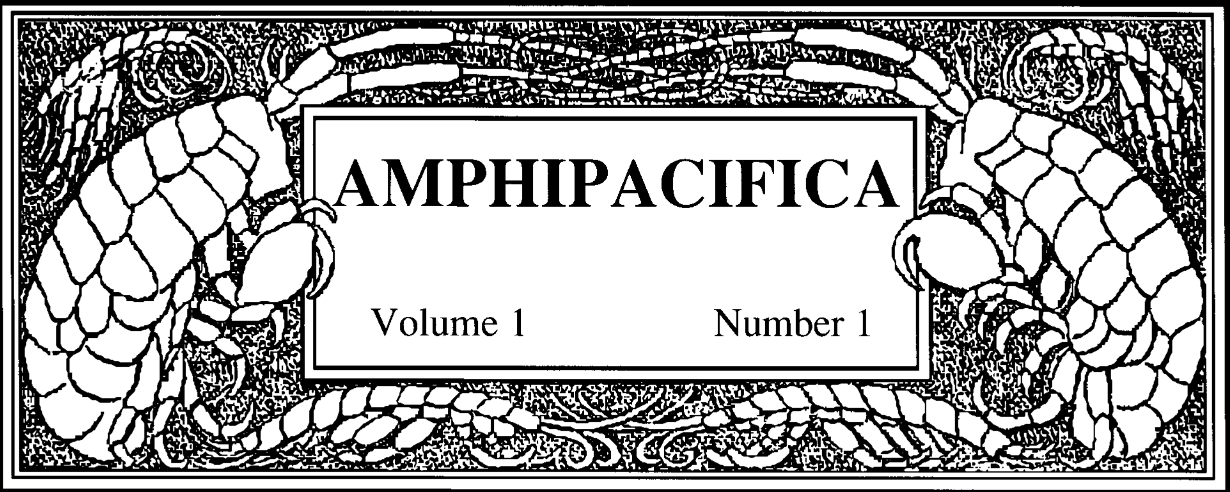


AMPHIPACIFICA

Volume 1 Number 1

Contents

January 7, 1994

National Library of Canada ISSN No. 9946895

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.

The journal appears quarterly, or approximately so, with a run of 300-400 copies per issue, each of about 200 pages, and a volume (yearly) total of 1000 pages (approximately). The printed page size is 8.5 X 11 inches (22 X 27.5 cm). Paper quality accommodates line cuts and half tones at 400-600 d.p.i., and a limited number of colour plates at author cost. Manuscripts are to be submitted in "camera-ready" computerized format (IBM- or MAC-compatible diskettes), and also in hard copy, that have previously been refereed (name to be supplied) and text-edited at the author's instigation. Suitability of manuscripts, based on content and adherence to submission regulations will be decided by the Advisory Board of the Journal.

The cost of printing and mailing of each issue is defrayed by institutional and individual subscriptions to the Journal of $50.00 Canadian funds ($40.00 US) per annum, and by page charges to the authors of $15.00 per printed page (including plates). For more detailed instructions and a subscription form, please see the inside back cover. Further information may be supplied on request.

Publication. AMPHIPACIFICA is published by Amphipacifica Research Publications, Registrar of Companies for the Province of British Columbia No. 0152988, 1993.

Translation Services.
Marjorie A. Bousfield, MSc., Montreal, Quebec.

Sponsoring Agencies.
Canadian Museum of Nature, Ottawa, Ontario, Canada.
Friday Harbor Laboratories, University of Washington, Friday Harbor, WA, USA.
Royal British Columbia Museum, Victoria, B. C., Canada.
Royal Ontario Museum, Toronto, Ontario, Canada.

Offices.
(1) Subscriptions and Correspondence: Dr. E. L. Bousfield, Managing Editor, c/o Natural History Division, Royal B,. C. Museum, Victoria, B. C., Canada. V8V 1X4.
(2) Mailing: Friday Harbor Laboratories, Friday Harbor, WA, USA 98250. Att: Dr. C. P. Staude.
Authorized by the U. S. Postal Service for second class postage paid at Friday Harbor, WA., USA 98250.

Registration.
The journal "AMPHIPACIFICA" is registered at the National Library of Canada, Legal Deposit Office, 395 Wellington St., Ottawa, Canada, as ISSN Number 9946895.

Printing.
Island Blue Print Co. Ltd., Victoria, B. C., Canada.

AMPHIPACIFICA

JOURNAL OF SYSTEMATIC BIOLOGY

Published quarterly by AMPHIPACIFICA RESEARCH PUBLICATIONS,
611-548 Dallas Rd., Victoria, British Columbia, Canada. V8V 1B3

Printed on acid-free paper

POSTMASTER: Please send address changes to AMPHIPACIFICA, Friday Harbor
Laboratories, Friday Harbor, WA 98250, U.S.A. att: C. P. Staude.

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.

WELCOME TO AMPHIPACIFICA

AMPHIPACIFICA is a new journal devoted to the discipline of systematic zoology. As its name implies, the publication treats mainly invertebrate animals, with initial emphasis on the amphipod crustaceans, and on the trans-Pacific regional fauna.

The need for this journal is multifold. The stimulus to its inception at this time, however, results mainly from diminishing funding and reduced publication outlets for taxonomic and whole-organism biology. In the view of many biologists in these disciplines, cutbacks in staff, funding, and publication outlets signify changes in the planning and fiscal priorities of governmental agencies in North America and elsewhere. Also, during the past two decades, university faculties have been cutting back in these areas of training and research with the result that, today, relatively few "whole-organism" departments remain. Comparatively few students are being trained in taxonomy and related scientific disciplines because future employment is becoming increasingly limited. Modern museum and governmental agencies which, in immediate post WWII times, were broadly supportive of the systematic sciences, are moving to the principle of cost-accountability in programs and services involving these sciences. Whatever the monetary justification, these trends appear counter-productive in the short run, and possibly irreparably damaging to the conduct of basic science in the long run. Once the "fly wheel" of activity is stopped, enormous energy and resources, over long periods, are required to get it going again. One might well ask how taxonomic studies and storage of museum research specimens can be made "cost-accountable"? Surely the preservation of its natural history treasures, and communication of information on the country's biota, are primary governmental responsibilities that have traditionally been funded as a service to all its citizens! Should it not remain so?

Environmental studies may be more cost-accountable to governments and ultimately to their electorates. However, scientists have failed to communicate successfully to funding agencies the point that biological communities cannot be assessed meaningfully without accurately identifying the organisms that make up those communities. Such is the essence and importance of taxonomy which, in turn, is part of the broader discipline of systematics - - the science of describing and classifying organisms in an orderly natural fashion. In recent years, cutbacks have been particularly hard on authors of larger monographic studies, where publication charges may be set at $60-100. per printed page. Without institutional or research grant support, many researchers find that publication is often beyond their financial means and their valuable work may remain in manuscript form, largely inaccessible to the scientific community and to the general public. Authors of smaller papers (5-25 pages) may be less severely handicapped since their papers take less space, cost less to edit and print, serve more authors per issue, and are therefore more acceptable to the primary research journals. The inhibition or outright loss of major revisionary studies is doubly damaging to the advancement of science since the larger papers are often basic to our understanding of biological systematics, and in depicting the broader picture of ecological, biogeographical, and evolutionary relationships within groups of organisms. Thus, the need for continued publication of these kinds of comprehensive studies remains paramount.

In recognition of this need, much of it through personal experience, the present editors and advisory panel have launched this new journal. Taxonomic problems remain basic and broadly challenging within several phyla and classes of invertebrates. Thus, within the North Pacific coastal shelf fauna, some invertebrate groups are proving 30-50% new to science, and percentages may be even higher for the deep-water fauna. Many of these shelf species are proving critical to the assessment and monitoring of environmental quality, especially where man-made environmental disturbances are frequent. In addition, some regional aquatic vertebrate animals have not yet been adequately described . Development of knowledge of their biology and life style remains a major challenge to systematic biologists.

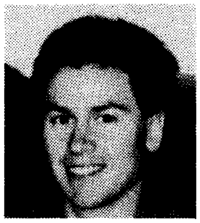
Financially, the present enterprise remains a non-profit "break-even" proposition. The page charges to authors, combined with journal subscription fees , are designed to offset total publishing costs of about $20,000 for an annual 4-issue output of approximately 800-900 pages. Through mandatory submission of pre-refereed, "camera-ready" copy, and elimination of mechanical editing services and page proof, publication costs are reduced mainly to those of printing and mailing copies. Corresponding page charges are thus hopefully well within the financial means of most contributors. The policy should also result in relatively speedy publication, following acceptance of the manuscript by the editorial and advisory boards.

We are optimistic that this new taxonomic journal will fulfill its purpose. The first issue deals mainly with North Pacific regional amphipods in which a surprisingly large number of taxa have proven new to science. Our tribute to the late J. L. (Jerry) Barnard provides insight into his multi-disciplinary approach to Amphipodology, and to his legacy of systematic work on which the "follow-up" studies of many of his friends and colleagues are currently based. We warmly welcome new readers and new contributors and look forward to receiving your commentary and suggestions.

Ed Bousfield, Craig Staude, and Phil Lambert
Editorial Board

About our Authors ....

Norma Jarrett has recently retired as a volunteer Research Associate with the Canadian Museum of Nature, a position in which she served effectively over a period of nearly 15 years. She has authored or co-authored several papers on the systematics and distributional ecology of amphipod crustaceans of the North Pacific region.



Ed Hendrycks is a Research Assistant in the Crustacean Unit of the Canadian Museum of Nature in Ottawa, in collaboration with Drs. C.-t. Shih and Kathleen E. Conlan. His interests in aquatic invertebrate biology include entomology and carcinology, with special reference to the systematics of amphipod crustaceans.

Craig Staude is an operations Biologist at the Friday Harbor Laboratories, University of Washington, with responsibility mainly for computer facilities and field operations. His interests in invertebrate zoology are broad but he specializes in the systematics of amphipod crustaceans. The chapter on Amphipoda: Gammaridea in Kozloff's ""Marine Invertebrates of thePacific Northwest" (1987) is one of Craig's publications.

Phil Lambert is Head of the Invertebrate Zoology Unit, Royal British Columbia Museum, Victoria, B. C. His principal research interest is the taxonomy of the Holothuroidea (Echinodermata). He has broad experience with computer systems, with research museum display methodology, and with SCUBA in coastal waters of Pacific North America.

Ed Bousfield is currently a Research Associate at the Royal British Columbia Museum, Victoria, following a long career in the Zoology Division at the Canadian Museum of Nature in Ottawa. He has published extensively on the systematics and phylogeny of amphipod crustaceans, and has developed more recent interests in Burgess Shale fossil arthropods, and in the biology of sea serpents.

THE IMPACT OF J. L. BARNARD ON NORTH AMERICAN PACIFIC AMPHIPOD RESEARCH: A TRIBUTE

E. L. Bousfield[1] and C.P. Staude[2]

ABSTRACT

From 1947 to 1963, and prior to his association with the Smithsonian Institution and move to Arizona, Dr. J. L. (Jerry) Barnard had conducted extensive field surveys on gammaridean amphipod crustaceans and other marine invertebrates along the Pacific coast of California, northern Mexico, and southern Oregon. During this 17-year period, and in the following 28-year period until his death, he published 65 papers on this rich fauna. These encompassed more than 500 regional species of gammarideans of which 213 species, 45 genera, and 2 families were newly proposed. Jerry Barnard pioneered the taxonomic study of the Phoxocephalidae, Ampeliscidae, Megaluropidae, Haustoriidae, Lysianassidae, and other infaunal or sediment-burrowing families, typically with primitive pelagic mating life styles. He also contributed many new names within the Hyalidae, Liljeborgiidae, Melitidae, Isaeidae, Ampithoidae and other "reptant" or bottom-crawling and tube-dwelling families with advanced pre-amplexing mating style. Especially after 1963, his revisionary studies elevated amphipodology to a new plateau of excellence in a region where fewer than 150 gammaridean species had been known previously. Jerry's popular, well-illustrated keys have introduced at least two generations of students to Pacific coast amphipods. His research publications have greatly facilitated the subsequent monographic studies of Hurley and the SCAMIT group of researchers in California, and of numerous workers on amphipods in the Canadian research group, mostly from the more northerly coasts of Washington state, British Columbia, and Alaska. Barnard's contributions continue to provide a solid framework upon which illustrated guides to the known amphipod fauna of the Pacific coast from Alaska to California, of more than 700 species, can be based. His work has had an equally profound and lasting influence on Russian, Japanese, and Chinese investigations on amphipod crustaceans of the entire North Pacific region and world-wide.

INTRODUCTION

When Jim Thomas invited us to take part in the J. L. Barnard memorial symposium in Washington, we were delighted and honoured to do so. One of us (ELB) was able to attend and present orally the essence of the following tribute. Although Jerry and ELB met only occasionally over the years, mainly at scientific meetings, and once in Washington, their correspondence extended over more than 30 years and involved a very broad range of topics in amphipodology. ELB also had the privilege of reviewing some of Jerry's larger manuscripts prior to publication, as well as a few of his NSF research proposals. These included his pioneering work (with Margaret Drummond) on Australian Phoxocephalidae (1978) and part of his two-volume compendium (with Charlene) on freshwater amphipods of the world (1983). Although Jerry did not always incorporate review suggestions, nor the previously published views of some colleagues, his works were characterized by a scholarly attention to detail, a broad comprehensiveness and thoroughness, and overall excellence of presentation. As most amphipodologists know, his views differed on some aspects of this discipline, most notably and strongly on the overall phyletic positioning and classification of gammaridean higher taxa. The correctness of these views on amphipod phylogeny will be decided eventually by our peers and followers, and are not discussed here. Shortly before his death, Jerry and ELB exchanged pleasant philosophical views on the course of amphipod systematics, and on the need to increase scientific emphasis upon, and financial support for, systematic biology in general. Dr. Barnard had been very helpful to members of our Canadian working group on North American Pacific amphipods, in many ways, not the least of which was his generosity in supplying reprints of his pioneering work there.

Jerry Barnard's life-time impact on Pacific coast amphipod research was profound. His interest in amphipodology was multi-disciplinary. The results of his work continue to affect an increasingly wide circle of scientific colleagues, students, and the general public. He contributed voluminous new information not only on the taxonomy of amphipods, but also on their biogeography, ecology and , to some extent, on their life style and behaviour In this short summary we have attempted to high-light some particularly significant facets of his leadership qualities and creativity. Some colleagues mentioned here are relative newcomers to the world of amphipod research but all have benefitted significantly from his insights. In this tribute to Jerry, we

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[1] **Royal British Columbia Museum, Victoria, B. C., Canada V8V 1X4.**

[2] **Friday Harbor Laboratories, Friday Harbor, WA, USA 98250.**

have looked into details of selected research contributions in an attempt to assess the taxonomic breadth of his work, the etymology of his new taxonomic names, and his role in development of Pacific regional amphipod biogeography. This treatment may therefore appear a bit "diffuse" and perhaps unfocussed, but in this sense it reflects the diversity of Jerry Barnard's impact on Pacific science. We are deeply indebted to his legacy of new information and new ideas on Pacific am-phipods and grateful for his help in facilitating our own work in more northerly Canadian and S.E. Alaskan parts of that faunistically rich and scientifically challenging region.

ACKNOWLEDGEMENTS

This contribution results largely from our personal interaction with Jerry Barnard over the years. We wish to acknowledge helpful commentary on text material from colleagues at the J. L. Barnard memorial symposium in Washington in April, 1992, and from members of the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT), in Los Angeles, CA, where the paper was again presented in November, 1992. We thank P. G. Moore, Millport, Scotland., and Les Watling, Darling Marine Center, Walpole , Maine, for their editorial input on portions of the present text.

THE EASTERN NORTH PACIFIC STUDY REGION

The coastal marine northeast Pacific region, encompassing most of Jerry Barnard's faunistic study areas, may be subdivided, for convenience, into eight "working" sub-regions (see pertinent illustrations and Tables in Conlan and Bousfield (1982), Bousfield (1979b, 1982, etc.)). Clockwise around the North Pacific rim, from the left (as in TABLE III, p. 12) are: (1) the northwestern Pacific (Asiatic) coastal marine subregion; (2) Bering Sea and Aleutian Chain; (3) southern Alaska, Prince William Sound and southeastern Alaska; (4) north-central B. C. and Queen Charlotte Islands; (5) south-central B.C. and Vancouver Island; (6) Washington-Oregon; (7) north-central California; and (8) southern California and Baja California.. Zones 7 & 8 have been combined in the biogeographic subregions of Fig. 1, p. 11.

EARLY REGIONAL RESEARCH ACTIVITIES

Jerry Barnard's early interests in aquatic biology gave almost no clue as to his ultimate career obsession with amphipod crustaceans. His subsequent dedication and personal drive to develop the systematics, biogeography, ecology, and behaviour of these ubiquitous invertebrates was to influence the direction and scope of amphipodology as never before. Following his graduation from Pasadena Junior College in 1947, he took up a Ph.D. program at the University of Southern California, under the late Dr. John Garth, who gently steered him from a limited study of eastern Pacific corals towards amphipod crustaceans. In this challenging but initially frustrating, pursuit he was encouraged by the late R. J. (Bob) Menzies, an isopod specialist, with whom he shared early interests in marine wood-boring crustaceans. With the support also of Dr. John W. Mohr, USC professor, this interest led to a Ph.D. thesis on the wood-boring amphipod *Chelura terebrans*, published in 1955, and soon afterwards, a world-revison of the family (1959). In the concluding year of his thesis he gained initial experience with more northerly eastern Pacific amphipods at Coos Bay, Oregon (1954a). Following three summers' work (as a USC PDF) in arctic coastal marine regions (Pt Barrow, and Ice Island T-3) he returned to the balmy climes of Southern California where he began a major program as a research associate at the Beaudette Foundation, near Pt Conception. The Institute provided facilities which allowed him to penetrate coastal marine environments (especially sedimentary ones), to all depths, up and down the coast, but mainly into the sub-tropical environments, including the rich unexplored amphipod faunas of the Baja region. Contemporaneously, and in later years through participation in international marine expeditions, he pioneered the systematics of the rich unknown faunas of regional submarine canyons and of the deep-sea. Working virtually as a one-man-show, Jerry produced a flood of regional amphipod revisionary studies (1958-1964, and continuing), that established the taxononomic basis for all subsequent studies on amphipods of the Californian and (as his colleagues of today are finding) the entire North American Pacific region.

NORTH PACIFIC REGIONAL PUBLICATIONS

Jerry Barnard's contribution to knowledge of the North American Pacific gammaridean amphipod fauna has been monumental. Of his output of about 220 published papers worldwide (1950-1991: see Rothman, 1992), at least 65 papers (nearly 30%) deal solely or inclusively with the systematics, biogeography, ecology and behaviour of the N.E. Pacific fauna, mostly from Washington-Oregon to Baja California (sub-regions 6, 7, 8 (above)). About half the titles were produced during his active field work in the California-Oregon region from1947-1963 and the remainder during his residence in Arizona, 1964-74, and at the USNM in Washington, 1974 to 1991. Of these 65 titles, some 30% are short descriptive papers at species level, e.g.*Chelura terebrans* (1955); *Dogielinotus loquax*, (1967), and another 30% are larger monographic studies at genus or family level, e.g. Phoxocephalidae (1960); Synopiidae (1972); *Rhepoxynius* (with Charlene, 1982). About 15% are subregional faunistic studies, e.g. "Oregon amphipods" (1954a), "California rocky intertidal" (1969b) and another 15% reveal his special interest in the deep-water and bathyal species, e.g. "Submarine canyon amphipods" (1966), and "Cedros Trench" (1967a). The remaining 10% of titles (and by no means the least important) reflect Jerry's (and Charlene's) unrivalled talent as collators of voluminous data, and include popular works such as "Light's Manual: Amphipoda" (1975); and taxonomic compendia such as "Index to Families, Genera, and Species" (1958); and "Families and Genera" (with Gordan Karman, 1991). This last served to update Jerry's previous alphabetically arranged single-author study (1969a) which, in itself, had replaced Sars (1895), Stebbing (1906) and Gurjanova (1951) as the modern taxonomic "Bible" of gammaridean amphipod research. Many of Jerry's studies on amphipod systematics contain detailed station data, and reveal deep interest in faunal ecological relationships. In his major synthesis with Charlene (1983), the coastal freshwater and terrestrial gammarideans are also treated.

PREVIOUS REGIONAL STUDIES

Prior to Jerry Barnard's initial studies on the Californian and southern Oregon coasts in 1947-54, relatively little work had been done on amphipods of any of these North American coastal marine sub-zones. Chief among a mere two dozen early regional studies were those of Dana and Stimpson in the mid-1800's (Puget Sound to California), S. J. Holmes in the first decade of this century (off Alaska and off S. California), Vimy Stout in 1913 (southern California), A. L. Alderman in 1936 (northern California), Elsa D. Thorsteinson in 1941 (N. Washington State region) and Clarence R. Shoemaker from 1926-1964 (throughout the region). The 19th century records had been encompassed in the major world-wide compendium of Stebbing (1906).

In recent years, and partly in response to Jerry's taxonomic leadership on the Californian fauna, including that of the SCAMIT group directly, the number of North American regional studies by others has more than doubled. More emphasis was placed on the previously unstudied coastal amphipods occurring in Alaska and British Columbia by D. E. Hurley (1963), T. E. Bowman and J. C. McCain (1967), K. O. Coyle (1980-82), P. N. Slattery (1985-86), C. P. Staude (1987, and in prep.), P. G. Moore (1993), and by the "Canadian group" that includes E. L. Mills (1961-62), Diana R. Laubitz (1977), J. J. Dickinson (1982-83), Kathleen E. Conlan (1982-83, 1990), Norma E. Jarrett (1981, 1982, 1994), C.-t Shih (in prep.), E. A. Hendrycks (1994), Jane R. Kendall (in prep.), Andrée Chevrier (in prep.), Phillip Hoover (in prep.) and the present authors (1981-1994).

The northwestern Pacific gammaridean fauna, much of which overlaps, or is closely related to, the Northeastern Pacific fauna, had been well studied by Russian workers, mostly prior to Jerry's arrival on the scene. Among the most productive systematists were A. I. Bulycheva (1938, 1957); Eupraxie F. Gurjanova (1951, 1962, 1980); J. A. Birstein and M. E. Vinogradov (1958,) and, more recently, N. L. Tzvetkova (1975). Their work was complemented by the studies of Japanese gammaridean specialists such as M. Iwasa (1939), K. Nagata (1965, 1966), and more recently by H. Morino (1979), A. Hirayama (1983, 1986) and others.

In summary, we may gauge the overall impact of Jerry Barnard's publication record on the North Pacific amphipod fauna by noting that it exceeded that of all other workers of the Northeastern region combined (to date), and surpassed all previous work on the Northwestern Pacific fauna, which had been taxonomically broad in scope and extensive in time.

IMPACT OF TAXONOMIC NAMES PROPOSED BY J. L. BARNARD

An indicator of the magnitude of Jerry Barnard's scientific impact is the regional extent of his new taxonomic names. Analysis of these names is here based on the list of North American Pacific amphipod taxa published by Don Cadien on behalf of SCAMIT (1991). In Table I, the numbers of published regional amphipod genera and species are summarized by superfamily, family, and subfamily where applicable (column 1), according to the Cadien List, 1991 (column 2), and to an unpublished "Canada List" (column 3) that includes forthcoming taxa from northern regions of British Columbia, Alaska, and the Bering Sea. The individual sub-columns (of columns 2 and 3) give the ratio of taxa newly described by Jerry Barnard to the total number of that taxon known from the region. Thus, within the "genera" sub-column, a ratio of 4/20 means that Barnard originally described 4 of the 20 known regional genera within the perrtinent subfamily/family/superfamily category of column 1. Within the species sub-column, a ratio of 18/55 means that he originally described 18 of 55 species known from the pertinent larger taxon of column 1.

Although Barnard's listings and arrangements were almost invariably alphabetical, the arrangement of superfamilies here is phyletic, following Bousfield (1979, 1982, 1983, in prep.), and Schram (1986). Such permits a more natural (clearly related) grouping of families and a return to the semi-phyletic arrangements of Sars (1895) and Stebbing (1906). Those early amphipod systematists lacked knowledge of most of today's fauna and numerical taxonomic methodology, yet they were remarkably prescient in their quasi-phyletic arrangements. Following the lead of Don Steele (1988) who demonstrated that amphipods are primarily and primitively swimmers, and secondarily crawlers, burrowers, and tube-builders, we may apply the terms neritic-mating, and benthic-mating for corresponding amphipod superfamily groupings. These categories are roughly analogous to the terms "Natantia" and "Reptantia" that were utilized in earlier pragmatic classification of decapod crustaceans. These terms may be diagnosed briefly as follows (see also Bousfield, 1994, in prep):

"SWIMMERS": Swimming life style (essentially); sexes mate in the water column; mature male stage is terminal, often non-feeding; males are strongly dimorphic in sensory and swimming structures (i.e. possess antennal callynophore and/or brush setae and/or calceoli, and powerful pleopods and tail fan); telson is usually bilobate; gnathopods are usually not sexually dimorphic and not pre-amplexing in function.

TABLE I. NUMBERS OF AMPHIPOD CRUSTACEANS FROM THE NORTH EASTERN PACIFIC COASTAL MARINE REGION DESCRIBED BY J. L.BARNARD, 1952-1991.

TAXON	“SCAMIT LIST” (D. B. Cadien, S. Calif.)		“CANADIAN LIST” (ELB Research Group)	
A. “SWIMMERS” (natants)	Genera New/Total	Species New/Total	Genera New/Total	Species New/Total
I. PHOXOCEPHALOIDEA	**7/16**	**37/56**	**8/19**	**37/76**
1. Urothoidae	0/1	1/3	0/1	1/3
2. Phoxocephalidae				
Metharpiniinae	**3/4**	**20/29**	**3/6**	**20/37**
Parharpiniinae	1/1	0/2	1/1	0/2
Pontharpiniinae	1/1	0/1	1/1	0/3
Harpiniinae	0/4	**11/13**	0/5	**11/19**
Eobrolginae	1/2	2/4	1/2	2/8
Phoxocephalinae	1/2	2/3	1/2	2/3
Coxophoxinae	1/1	1/1	1/1	1/1
3. Platyischnopidae	2/2	2/2	-	-
II. PONTOPOREIOIDEA	1/2	1/6	1/4	1/11
1. Pontoporeiidae	0/1	0/1	0/3	0/4
2. Haustoriidae	1/1	1/5	1/1	1/7
III. LYSIANASSOIDEA	5/33	**21/73**	5/45	**21/112**
1. Uristidae	4/20	**18/55**	4/26	**18/82**
2. Lysianassidae	1/7	3/9	1/8	3/12
3. Cyphocaridae	0/3	0/6	0/4	0/8
4. Hyperiopsidae	-	-	0/2	0/3
5. Conicostomatidae	0/2	0/2	0/3	0/4
6. Trischizostomatidae	-	-	0/1	0/1?
7. Valettiidae	0/1	0/1	0/1	0/2
IV. EUSIROIDEA	3/12	**10/32**	**10/56**	**10/54**
1. Pontogeneiidae	1/3	3/14	1/3	3/16
2. Bateidae	0/1	0/2	-	-
3. Calliopiidae	2/4	**3/5**	2/6	3/12
4. Eusiridae	0/3	2/9	0/7	2/16
5. Gammaracanthidae	-	-	0/1	0/2
6. Amathillopsidae	-	-	0/1	0/1
7. Epimeridae	0/1	2/2	0/1	2/3
8. Paramphithoidae	-	-	0/3	0/4

TABLE I. (Cont'd - 2)

TAXON A. "SWIMMERS"	"SCAMIT LIST" (D.B. Cadien, S. Calif.)		"CANADIAN LIST" (ELB Research Group)	
	Genera New/Total	Species New/Total	Genera New/Total	Species New/Total
V. OEDICEROTOIDEA				
1. Oedicerotidae	1/9	19/30	1/11	19/45
VI. SYNOPIOIDEA	1/6	6/12	3/8	10/17
1. Argissidae	0/1	0/1	0/1	0/2
2. Synopiidae	1/5	6/11	3/7?	10/15?
VII. PARDALISCOIDEA	1/6	6/12	1/12	9/14
1. Pardaliscidae	1/9	9/12	1/10	9/12
2. Stilipedidae	0/2	0/2	0/2	0/2
VIII. STEGOCEPHALOID.	0/1	0/1	0/5	0/6
1. Stegocephalidae	0/1	0/1	0/5	0/6
IX. HYPERIIDEA	0	0	0/12	0/30
1. Physosomata	-	-		
2. Physocephalata	-	-		
X. DEXAMINOIDEA	1/5	3/8	1/5	3/13
1. Atylidae	0/1	1/4	0/1	1/8
2. Lepechinellidae	0/1	1/1	0/1	1/1
3. Dexaminidae	1/3	1/3	1/3	1/4
XI. AMPELISCOIDEA				
1. Ampeliscidae	0/3	19/52	0/3	19/55
XII. MELPHIDIPPOIDEA	3/5	6/6	6/6	
1. Melphidippidae	1/3	3/3	1/3	3/3
2. Megaluropidae	2/2	3/3	2/2	3/3
B. "CRAWLERS" (reptants)				
XIII. CRANGONYCTOIDEA				
1. Crangonyctidae	-	-	0/3	0/5
XIV. TALITROIDEA	1/13	8/28	1/17	8/73
1. Hyalidae	0/2	3/6	0/6	3/30
2. Hyalellidae	0/2	1/5	0/2	1/8
3. Dogielinotidae	0/1	1/1	0/1	1/1
4. <u>Najnidae</u>	0/1	1/2	0/1	1/10
5. Talitridae	0/5	0/12	0/5	0/12
6. Phliantidae	0/1	1/1	0/1	1/1
7. Eophliantidae	1/1	1/1	1/1	1/1

TABLE I. (Cont'd - 3)

TAXON	"SCAMIT LIST" (D. B. Cadien, S. Calif.)		"CANADIAN LIST" (ELB Research Group)	
B. "CRAWLERS" (reptants)	Genera New/Total	Species New/Total	Genera New/Total	Species New/Total
XV. LEUCOTHOIDEA	6/24	**28/52**	6/49	**28/142+**
1. Pleustidae	**4/7**	**8/18**	4/30	8/80
Mesopleustinae	-	-	0/1	0/2
Eosymtinae	-	-	0/2	0/3
Pleusymtinae	1/1	2/2	1/6	2/14
Stenopleustinae	0/1	1/1	0/3	1/3
Pleustinae	0/1	1/5	0/3	1/28
Pleusirinae	1/1	1/1	1/1	1/1
Dactylopleust.	1/1	0/2	1/1	0/2
Pleustoidinae	-	-	0/1	0/1
Neopleustinae	-	-	0/4	0/4
Parapleustinae	1/2	**3/7**	1/7	3/22
2. Amphilochidae	0/3	**3/5**	0/5?	**3/8?**
3. Leucothoidae	0/1	1/2	0/1	1/4
4. Anamixidae ...	0/1	**2/2**	-	-
5. Stenothoidae	2/9	**13/22**	2/14?	**13/40+**
6. Lafystiidae	0/1	0/1	0/3	0/5
7. Acanthonotozomatidae (*s. l.*)	0/3	1/3	0/7	1/8
XVI. LILJEBORGIOIDEA	1/3	**7/10**	0/1?	0/1?
1. Liljeborgiidae	1/2	**7/9**	- ?	- ?
2. Sebidae	- ?	- ?	0/1	0/1
3. Colomastigidae	0/1	0/1	- ?	- ?
XVII. GAMMAROIDEA				
1. Gammaridae	0/1	0/1	0/2	0/2
2. Anisogammaridae	0/5	0/9	0/8	0/18
3. Mesogammaridae	0/1	0/1	0/1	0/1
4. Gammaroporeiidae	0/1	0/1	0/1	0/1
XVIII. HADZIOIDEA	**3/9**	**12/24**	1/8	**10/37?**
1. Hadziidae	**2/2**	**2/2**	- ?	- ?
2. Melitidae	1/7	**10/22**	1/8	**10/37 ?**
XIX. COROPHIOIDEA	7/39	**32/128**	7/51	**32/150**
1. Isaeidae	3/11	**16/50**	3/11	**16/55**
2. Ischyroceridae	2/6	**6/19**	2/7	**6/30**
3. Ampithopidae	0/3	3/18	0/4	3/22? .
4. Biancolinidae	1/1	**1/1**	1/1	1/1
5. Aoridae	1/10	3/18	1/10	3/18

TABLE 1.(Cont'd - 4)

6. Cheluridae	0/1	0/1	0/1	0/1
7. Corophiidae	0/1	0/9	0/1	0/10
8. Podoceridae	0/5	2/11	0/5	2/11
XX. CAPRELLIDEA				
1. CAPRELLIDA	-	-	0/10 ?	0/25+ ?
2. CYAMIDA	-	-	0/6 ?	0/10+ ?
XXI. INGOLFIELLIDEA* (unconfirmed record from Prince William Sound *fide* Cadien)				

"CRAWLERS": Life style mainly crawling,, burrowing,, domicolous, or inquilinous; mate on or in the bottom; mature male with indeterminate growth; males weakly or not dimorphic in sensory structures (i.e.lack callynophore calceoli, or brush setae, except in the most primitive crangonyctoideans and gammaroideans), with normal or weak pleopods and tail fans; telson lobes often fused to a simple plate; gnathopods strongly sexually dimorphic (usually), typically pre-amplexing and/or agonistic in function.

Highlights of Table I. Of the 513 published species listed by Cadien (1991) from S. California to Alaska, Jerry Barnard newly proposed 213 names (about 40% of the total). For ease of analysis, taxonomic groups in which Barnardian taxa are especially dominant or significant are indicated in **boldface.** The table reveals the following:

1. JLB described new taxa in 45/60 regional families and in all but 2 superfamilies of gammaridean amphipods. He did not include hyperiids, caprellids, or ingolfiellids in his regional studies.
2. JLB described about 50% more new taxa from the "natant" superfamilies (126) than from the "reptant" superfamilies (87) although total numbers of species within each group were roughly the same. This difference is probably a reflection of the greater taxonomic challenge among sediment-burrowing species that Jerry faced when he first arrived on the scene. This, in turn may have reflected the concentration of early taxonomic study on the relatively more conspicuous and more easily collected males of epifaunal and tube-dwelling amphipod groups.
3. JLB made major name contributions (ratios of 20- 50% +) in the reproductively "natant" (particularly infaunal or sediment-burrowing) groups such as Phoxocephaloidea, Lysianassoidea, Oedicerotoidea, Synopioidea, Ampeliscoidea, and Melphidippoidea, as well as the Eusiroidea and Pardaliscoidea..

Within the "reptants", JLB's strongest name contributions were in some Talitroidea (Hyalidae), some Leucothoidea (Pleustidae, Amphilochidae, and Stenothoidae), the commensal Liljeborgioidea, the Hadzioidea, and the relatively primitive families within the Corophioidea (Isaeidae, Ischyroceridae, and Ampithoidae). However, he contributed few new names to groups such as the Pontoporeioidea and Gammaroidea (northern and/or freshwater), Crangonyctoidea (freshwater), and talitroideans (semi-terrestrial).

5. The proportion of Barnardian new names is generally lower in taxonomic groups of the "Canadian" list, e.g., in some families of Talitroidea (Hyalidae, Hyalellidae, and Najnidae) and Leucothoidea (Pleustidae) which are proving to be mainly northern in distribution. However, little reduction of his impact is noted within the advan-ced corophioideans, many described previously, and not at all in the Liljeborgioidea, the families of which are almost exclusively southern in biogeographic affinities.

ETYMOLOGY OF NEW GENERIC NAMES BY J. L. BARNARD

Some interesting facets of Jerry Barnard's taxonomic work are revealed by his choice of new taxonomic names. Table II provides a list of all new generic and new family names proposed by Jerry and his co-authors in papers dealing with the North American Pacific gammaridean amphipod fauna. His 45 new generic names represent more than 20% of all those applied to the 500+ species of the SCAMIT regional list (Cadien, 1991). Of the two new family names, one (Najnidae) is apparently endemic to the North Pacific region. His leadership in the development of information on this unique group of talitroidean kelp borers is to be recognized in a forthcoming paper in this journal (Bousfield and Hendrycks, in prep).

Analysis of the etymology of names selected at the generic level reveals a shift in emphasis both temporally and regionally during Jerry's career. In the initial phases, as in the California-Oregon studies, his selection of names was essentially classical or typical. Thus, within the 45 genera of North American Pacific gammarideans containing species described by him, their root-sources may be apportioned thusly: classical Latin or Greek origin (10, or 23% of total); classical prefix-suffix modifications of existing root names (13, or 31%); anagrams (word scrambles) (12, or 28%); native, or aboriginal names (5, or 11%); miscellaneous origins (5, or 11%).

TABLE II. HIGHER TAXONOMIC NAMES OF NORTH AMERICAN PACIFIC GAMMARIDEAN AMPHIPODA PROPOSED BY J. L. BARNARD AND CO-AUTHORS 1950-91

(per D. B. Cadien, SCAMIT taxonomic list, 1991)

I. Superfamily PHOXOCEPHALOIDEA

Mandibulophoxus (gilesi) 1957
Coxophoxus (hidalgo) 1966
Eobrolgus (spinosus) 1979
Eyakia (calcarata) 1979
Foxiphalus (obtusidens) 1979
Grandifoxus (grandis) 1979
Rhepoxynius (epistomus) 1979
**Eudevenopus (honduranus) 1983*
**Tiburonella (viscana) 1983*

II. Superfamily PONTOPOREIOIDEA

Eohaustorius (washingtonianus) 1957

III. Superfamily LYSIANASSOIDEA
**Dissiminassa (dissimilis) 1991*
Ocosingo (borlus) 1969
Fresnillo (fimbriatus) 1969
Pachynella (lodo) 1964
Rimakoroga (rima) 1987
Thrombasia (viscalero) 1966

IV. Superfamily EUSIROIDEA
Accedomoera (vagor) 1964
Oligochinus (lighti) 1969
Calliopiella (pratti) 1954
Callaska (pratti) 1954

V. Superfamily OEDICEROTOIDEA
Finoculodes (omnifera) 1971

VI. Superfamily SYNOPIOIDEA
Garrosyrrhoe (bigarra) 1964

VII. Superfamily PARDALISCOIDEA
Tosilus (arroyo) 1966

VIII. Superfamily DEXAMINOIDEA
Dexamonica (reduncans) 1957

IX. Superfamily MELPHIDIPPOIDEA
Melphisana (bola) 1962
*MEGALUROPIDAE 1986
**Gibberosus (longimerus) 1986*
**Resupinus (syncaudatus) 1986*

X. Superfamily TALITROIDEA

NAJNIDAE 1972
Lignophliantis (pyrifera) 1969

XI. Superfamily LEUCOTHOIDEA
**Dactylopleustes (echinoicus)1979*

Pleusirus (secorrus) 1969
Pleusymtes (glaber) 1959
**Incisocalliope (newportensis) 1959*
Stenula (latipes) 1962

**Zaikometopa (erythrophthalma) 1987*

XII. Superfamily LILJEBORGIOIDEA.
Listriella (goleta) 1959

XIII. Superfamily HADZIOIDEA
Netamelita (cortada) 1969
Dulzura (sal) 1969
Lupimaera 1982 (lupana) 1969

XIII. Superfamily COROPHIOIDEA
Gaviota (podophthalma) 1958

Amphideutopus (oculatus) 1959
Chirimedeia (zotea) 1962
Cedriphotis (malinolea) 1967

Ventojassa (ventosa) 1970

Acuminodeutopus (heteruropus) 1959
Rudilemboides (stenopropodus) 1959

Note:

1. All names listed without regard for subsequent synonymy
2. *: co-authored names
3. TYPE species in parentheses

These proportionalities, in which classical selections comprise more than 50% of the names, contrast rather markedly with those of some later contemporary studies, especially on Australian and New Zealand faunas, where native or aboriginal became predominant. Thus, in his collaborations with Margaret Drummond (1978 et seq.), more than 75% of his new names can be attributed to such roots, but very few to classical origins. The pragmatic significance and usefulness of this change of emphasis remains to be assessed. However, at least a few authors (e.g. Fenwick, 1980; Thurston, 1982) have followed this lead.

BARNARDIAN IMPACT ON NORTHEASTERN PACIFIC AMPHIPOD BIOGEOGRAPHY

Jerry's Barnard's scientific impact on the amphipod fauna of British Columbia and Alaska is very significant, but is less striking than that on the Californian fauna. As one might expect this difference is undoubtedly a function of biogeographical factors within the regional faunules, combined with Jerry's field involvement mainly with the Californian biota.. The overall basis for such a correlation is provided in an overview of the principal coastal marine biogeographical sub-regions from Alaska to Central California (Figure 1), as originally demonstrated by Jarrett, Hendrycks, and Bousfield (1989). The biogeographical affinities of northeastern Pacific amphipods may be clustered into two major subgroupings: (1) those with arctic-subarctic affinities that penetrate variiously southwards to summer-warm limits of survival, and (2) those with boreal and warm-temperate affinities that penetrate variously northward to summer-cold limits of reproductive capability. A few warm-temperate species common in southern California (TABLE I, zone 8) also occur disjunctly in the Strait of Georgia (zone 7 of map). A small enclave in the region from about Dixon Entrance to Cross Sound (southeastern Alaska), termed the N. E. Pacific High Boreal subregion, contains species that occur exclusively there or in closely adjacent waters (zone 5 of map).

It appears from this preliminary biogeographical analysis that a large percentage of the total northeastern Pacific coastal marine fauna terminates in the Alaska-B.C. region and does not reach California. By contrast, although a significant fraction of the Californian fauna reaches British Columbia, it terminates at southeastern Alaska.. For this reason, therefore, Jerry Barnard, working mainly from Oregon southward to Baja California, treated the northern fauna in a peripheral manner. Although he left a major taxonomic challenge for the current Canadian group of amphipod systematists, he did provide numerous published examples of how it might be undertaken.

A detailed basis for the above biogeographic correlation of Barnard's N. American Pacific work is encapsulated in Jarrett and Bousfield's recent treatment of the regional phoxocephlid subfamily Metharpininiinae, (this volume, p. 58). Career-wise, the infaunal Phoxocephalidae was perhaps Jerry"s single most intensively studied family group . In Table III, the distribution of 43 N. American Pacific species within the Metharpiniinae is plotted across 8 subregions from the northwestern Pacific to Baja California. In general we may note that the most primitive species and genera (within *Grandifoxus* and *Beringiaphoxus)* are confined to the most northerly zones, the most advanced species and genera (within *Rhepoxinius* and *Metharpinia)* occur in the south (zones 4-8) and phyletically intermediate species (within *Majoxiphalus* and *Foxiphalus)* are clinally intermediate throughout.

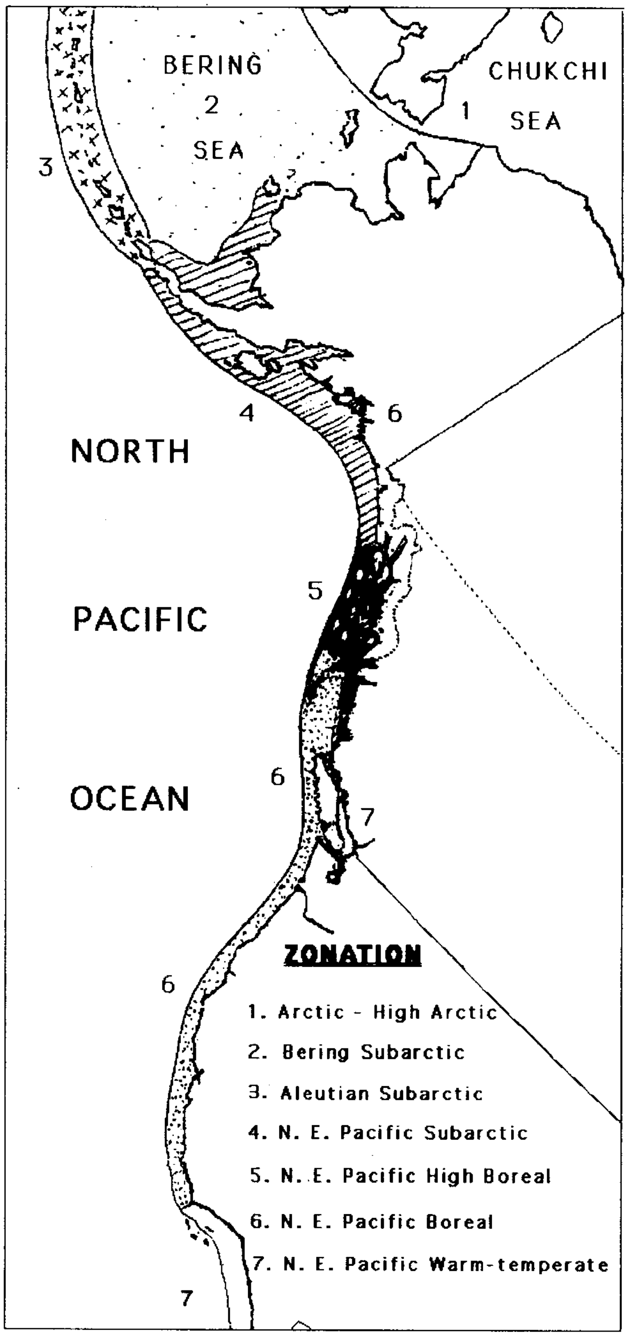

FIG.1. Coastal Biogeographical Sub-Regions

Remarkably, Jerry Barnard is the author of half (3/6) of the regional generic names (as well as half the species within the southerly genus *Microphoxus*), and slightly more than

TABLE III. DISTRIBUTION OF NORTH AMERICAN PACIFIC METHARPIINAE.

(* Barnardian named taxa)

SPECIES	NORTH PACIFIC SUBREGION							
	1	2	3	4	5	6	7	8
I. *GRANDIFOXUS**								
robustus	X							
westi	**X**							
constantinus		X						
pseudonasutus		X						
nasutus		X						
vulpinus		X	x					
aciculatus		X	x	?				
acanthinus		X	X					
lindbergi	X	X	X	**X**	**X**			
longirostris		X	X	X	X			
dixonensis				X				
grandis			X	X	X	X		
II. *BERINGIAPHOXUS*								
beringianus		**X**						
III. *MAJOXIPHALUS*								
maximus		X	X	X	x			
*major**			x	X	X	X	x	
IV. *FOXIPHALUS**								
*aleuti**		X						?
slatteryi		X						
*similis**			x	X	X	X	X	
*xiximeus**			**X**	X	X	X	X	X
fucaximeus						**X**		
falciformis				X	X	X		
obtusidens						x	**X**	**X**
*cognatus**								**X**
*golfensis**								**X**
*apache**								**X**
*secasius**								**xS**
V. *RHEPOXYNIUS*								
*pallidus**				X	X	x		
*vigitegus**				X	X	X		
boreovariatus				**X**	X	X		
*fatigans**				X	X	X	X	x
*daboius**				**x**	?	X	X	X
*variatus**				X	?	?	x	X
*abronius**				X	X	X	X	X
barnardi					**X**	**?**		
*tridentatus**					X	?		
*bicuspidatus**						x	X	x
*lucubrans**							x	X
*stenodes**							?	X
*homocuspidatus**								X
*heterocuspidatus**								X
*menziesi**								xS
*gemmatus**								xS
VI. *METHARPINIA*								
*jonesi**								X
VII. *MICROPHOXUS**								xS

LEGEND FOR TABLE III.

I. Occurrence
  X - abundant in region (or presumed so)
  x - marginally in region.
  xS - essentally south of this region (tropical)
II. Coastal Regions (Progression: North-west to South-east)
  1. Japan Sea and Western Pacific
  2. Bering Sea and Aleutian Chain to Kodiak I.
  3. Prince William Sound & South-eastern Alaska (N. of Dixon Entrance.)
  4. North central B. C. coast and Queen Charlotte Ids.
  5. Southern B.C. coast and Vancouver Island.
  6. Washington and Oregon
  7. Northern and Central California
  8. Southern and Baja California

half (23/43) of the total species within subfamily Metharpiniinae throughout this 8000-mile coastal continental region. On closer examination, we may note that he named 87% (14/16) of species in the most southerly large genus *Rhepoxynius* and 93% of all species (of 5 genera) that range into California. By contrast, he named only 10% (2/20) of species that do not occur in California, and none in the most northerly genera, *Grandifoxus* and *Beringiaphoxus*.

From this example we might expect a similar north-south distribution of Barnardian nomenclatural influence within other major gammaridean taxa, especially those having relatively strong geographical endemism of both species and genera. Such indications have already been noted by one of us (ELB, in preparation) within the Pleustidae, the Melitidae, and some Talitroidea..

QUALITY OF REGIONAL GUIDES AND KEYS

An especially noteworthy feature of Jerry's impact on students of amphipod crustaceans is the exemplary quality of his popular guides and illustrated reference compendia. His chapter on gammaridean amphipods in Light's Manual (1975) remains one of the most useful and best illustrated guides of its type. The keys consist of simple one (or two-) character couplets for which the pertinent illustrations are clear, and the lines clean and uncluttered. The illustrations of his monographic studies and compendia, especially after 1963, are characteristically clean, and the format simple, and provide ample space between individual figures within the plate. These are identified by referenced symbols of a complexity endemic to his own publications. Illustrations of series of mouthparts, gnathopods, telsons, and other taxonomic characters permit ready comparison of critically distinctive character states that are difficult to envisage from the text alone.

Barnard's textual accounts underwent an evolution from generality and brevity in early papers,e.g. Oregon amphipods (1954), to highly specific, and perhaps overly detailed, voluminous descriptions in later monographs (e.g. *Rhepoxyxinius* , 1982). To date, relatively scant diagnostic or numerical phyletic use has been made of many of these character states, either by Jerry or by others. However, he literally left few stones unturned in revealing species taxonomic characters, many previously unnoticed, of possible or potential significance to future amphipod systematists. His originality in coining new descriptive epithets, many of which are now acceptably standard in the discipline, has been noted in other tributes paid to Jerry at the Washington symposium (e.g. by Tom Bowman and Rick Brusca).

We may conclude here by noting that Jerry Barnard's illustrated compendia have facilitated the introduction of at least two generations of students to North American Pacific amphipods. They have proved an exemplary model for Craig Staude's later regional illustrated key (in Kozloff, 1987; see below). Unquestionably also, his impact will continue to be amplified by forthcoming and future illustrated guides, including that planned by Craig and myself, as outlined in the Washington symposium.

CONCLUDING TRIBUTES TO J. L. BARNARD.

Jerry Barnard's leadership in North American Pacific Amphipodology has had a profound and lasting impact, both professionally and personally, on contemporary regional faunal workers. This effect is perhaps most appropriately encapsulated in the personal tribute provided by one of us (CPS), which is our privilege to include here:

"Shortly after I entered graduate school at the University of Washington in 1974, I was faced with the task of identifying amphipods from Puget Sound as part of a large project to assess the impact of Seattle's sewage treatment facilities. It soon became obvious that nearly all of the publications that would shed light on that fauna were the work of Jerry Barnard. His "Amphipods of Oregon", "Amphipoda" in "Light's Manual" (1975, 2nd edition), "Rocky Intertidal Amphipoda of California", Pacific Naturalist series, Allan Hancock papers, and, of course, his "Families and Genera"(1969) became the text-books for my self-taught class in amphipod identification. I also fell heir to the specimens and personal communication he had exchanged with John A. Houghton, a graduate student who preceded me in the College of Fisheries. Once I had developed sufficient confidence, I wrote to Jerry, who kindly responded to my many sophomoric questions.

The serendipitous events that brought me to Friday Harbor Laboratories and insured that I would focus my career on amphipods, also hinged on Jerry's work. I had heard of a "barrel" of specimens from the Pacific Northwest, which Jerry had identified, collecting dust at the Lab. I was eager to examine this collection to confirm my Puget Sound material, so I arranged a visit. During our brief stay, my wife Krispi and I organized the specimens in a manner that impressed its caretaker, Carl Nyblade. Carl offered both of us jobs in his baseline survey project, and we shortly moved to Friday Harbor.

While at Friday Harbor, I decided to pursue a PhD, examining the systematics and biology of amphipods. In this doctoral research, I was again generously assisted by Jerry Barnard. He invited me to work in the visitors' lab at the Smithsonian during two brief visits to the east coast. We discussed my work, and he offered hard-to-find references for me to photocopy. In preparing my keys to the Gammaridea for Kozloff's (1987)"Marine Invertebrates of the Pacific Northwest", Jerry permitted me to use several of his earlier illustrations, and offered helpful advice. I continued to receive reprints of his valuable publications up until his passing.

In short, my life would be very different, and I believe less rewarding and enjoyable, were it not for the impact of Jerry Barnard. My career and even my home have been affected by his life. I would like to add my thanks to the many tributes offered at the meeting in Washington."

In conclusion, we feel certain that Craig's tribute to Jerry Barnard is warmly echoed by all members of the "Canadian Working Group" of amphipod systematists. These include present staff members of the Canadian Museum of Nature in Ottawa: Mark Shih, Diana Laubitz, Kathleen E. Conlan, Ed Hendrycks, and Fahmida Rafi; taxonomic associates of the CMN: Norma Jarrett, and Jane Kendall, both of Ottawa; John Dickinson, Kingston, PA; Andree Chevrier, and Marjorie Bousfield, Montreal, Que.; Patrick Shaw, Regina, Sask.; Eric Mills, Halifax; N.S.; Phillip Hoover, Victoria, B.C.; Craig Staude, Friday Harbor Laboratories, WA, USA; P. G. Moore, Scotland; Gordan Karaman, Yugoslavia; Hiroshi Morino, Japan; and zoological illustrators Susan Laurie-Bourque, Hull, Quebec, and Floy E. Zittin, Cupertino, California. All of these workers have benefitted greatly from Jerry's professional taxonomic leadership and,published record which he has shared most generously with everyone concerned. Their appreciation of his contribution to North American Pacific Amphipodology and to the success of their own work can never be fully expressed. It will be reflected, however, at least in token manner, by several "Barnardian" patronyms, many planned for inclusion in subsequent issues of this journal, to be added to those already in his honour listed by Jim Thomas (1993).

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A REVISION OF FAMILY PLEUSTIDAE (AMPHIPODA: GAMMARIDEA) PART I. SYSTEMATICS AND BIOGEOGRAPHY OF COMPONENT SUBFAMILIES

E. L. Bousfield[1] and E. A. Hendrycks[2]

ABSTRACT

The amphipod family Pleustidae is revised on the basis of extensive material obtained from the North American Pacific coastal marine region and from other sources, and of the pertinent world-wide literature. The world fauna now totals 145 species and subspecies in 38 genera and 12 subfamiliesof which 43 species,18genera, and all 12 subfamilies are new . The family Pleustidae is redefined on the basis of taxonomic characters both newly recognized and previously utilized, and the subfamily components are diagnosed.

The previous heterogeneous assemblage of genera and species is herewith grouped in subfamilies that are both internally consistent, and externally interrelated. The new subfamilies are: Atylopsinae (TYPE species - *Atylopsis emarginatus* Stebbing, 1888); Austropleustinae (TYPE species - *Austropleustes cuspi-datus* K. H. Barnard, 1931); Stenopleustinae (TYPE species - *Stenopleustes malmgreni* Boeck 1871); Mesopleustinae (TYPE species - *Mesopleustes abyssorum* Stebbing, 1888); Pleustoidinae (TYPE species - *Pleustoides carinatus* Gurjanova, 1972); Eosymtinae (TYPE species - *Eosymtes minutus*, new genus, new species); Pleusymtinae (TYPE species - *Pleusymtes glaber* Boeck, 1871); Dactylopleustinae (TYPE species - *Dactylopleustes echinoicus* Tzvetkova, 1975); Pleustinae (TYPE species - *Pleustes tuberculatus* Bate, 1858); Pleusirinae (TYPE species*Pleusirus secorrus* J. L. Barnard, 1969); Neopleustinae TYPE species - *Neopleustes pulcheuus* Kroyer, 1842); and Parapleustinae (TYPE species - *Parapleustes gracilis* Buchholz, 1874).

Principal taxonomic characters utilized in diagnosing subfamilies are described and figured. Phyletic ordering of character states was determined mainly by comparison with those of presumed ancestral "outgroup" members of superfamily Eusuoidea, and by accepted precedent within the literature. The phyletic relationships of the subfamilies were analyzed on both phenetic and cladistic bases. The two results were somewhat similar over all but, in detail, the cladistic groupings appeared to be more natural and more consistent with corresponding biogeographic characteristics. Full descriptions of component genera and species and details of their distributional ecology, are being published in a series of monographic papers elsewhere (proposed for subsequent issues of this journal).*

Morphological and biogeographical analyses of the world-wide fauna revealed two major groups within the Pleustidae: (1) an older, more primitive, and deeper water Mesozoic fauna that is now relict in Indo-Pacific and southern oceans with an outlier in the North Atlantic, and (2) a younger, more advanced, and more eulittoral fauna that is richly diverse in the Holarctic and is centred in the cold-temperate North Pacific marine region. Indirect evidence suggests an early Mesozoic origin and evolution of family Pleustidae, and a post-Tethyan evolution and dispersal of the more advanced subfamilies within the holarctic region. A few members of both primitive and advanced groups have also penetrated the deep sea.

INTRODUCTION

The gammaridean amphipod family Pleustidae was proposed by T. R. R. Stebbing (1906) to encompass several genera that had previously been referred to the family Paramphithoidae. The new family included about 22 species, in the genera *Pleustes* Bate, 1858; *Parapleustes* Buchholz, 1874; *Stenopleustes* Sars, 1895; *Mesopleustes* Stebbing, 1899; *Sympleustes* Stebbing, 1899; and *Neopleustes* Stebbing, 1906. As a result of revisionary work during the next 60-70 years (e.g. Gurjanova, 1951, 1972; Barnard & Given, 1960; Barnard, 1969a) the recognized world fauna has more than tripled, to about 71 species in 13 genera. The additions included *Austropleustes* K. H. Barnard, 1931; *Parepimeriella* Schellenberg, 1931; *Pleusymtes* J. L. Barnard, 1969a; *Pleusirus*, J. L. Barnard, 1969b; *Pleustoides*, Gurjanova, 1972; *Pleustomesus* Gurjanova, 1972; and *Pleustostenus* Gurjanova, 1972. From then until the commencement of this study in 1984, about a dozen new species and the genera *Dactylopleustes* Karaman & Barnard, 1979 and *Tepidopleustes* Karaman & Barnard, 1979, have been added, for a combined total of about 82 species in 15 genera.

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*Units include: Part II, Subfamilies Pleustinae, Dactylopleustinae and Pleusirinae; Part III, Subfamilies Atylopsinae, Austropleustinae and Stenopleustinae; PartIV, Subfamilies Mesopleustinae, Pleustoidinae, Eosymtinae and Pleusymtinae; and Part V. Subfamilies Neopleustinae and Parapleustinae.

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1 **Royal British Columbia Museum, Victoria, B. C. Canada V8V 1X4**
2 **Canadian Museum of Nature, Ottawa, Ontario, Canada K1P 6P4**

Thus, until very recently, the family Pleustidae was viewed as a relatively small to medium-sized group of benthic detritivores and micro-predators, occurring mainly in arctic and cold-temperate seas of the northern hemisphere (see Bousfield 1982a). The group is characterized by a generally dorsally toothed or carinated, deep-plated body morphology, and mouthparts and gnathopods trending to specialization for carnivory and raptorial feeding behaviour. The Pleustidae was positioned initially as the most primitive member of superfamily Leucothoidea by Bousfield (1979, 1982a, 1983). However, in several important respects the component members of family Pleustidae, especially the more primitive types, retain some characters that are little modified beyond those of families of the Eusiroidea; that superfamily is possibly ancestral to the Pleustidae and the other leucothoidean families.

Examples of plesiomorphic character states, common to some members of eusiroidean families and the Pleustidae are: rostrate heads, homopodous peraeopods, slender and subequal gnathopods, and lanceolate rami of the uropods. These character mixes also contributed to earlier difficulties in placing some genera (e.g. *Harpinioides, Atylopsis, Parepimeriella* and *Pleustoides)* within the proper family and superfamily (e.g., in Barnard, 1969a; Barnard & Karaman, 1991).

Since 1955, collecting expeditions of the National Museum of Natural Sciences (e.g.Bousfield, 1958, 1963, 1968, Bousfield & McAllister, 1963; Bousfield & Jarrett, 1981) have resulted in a wealth of new pleustid material from the Pacific coast of Canada and adjacent regions. This material has since been studied in detail by the present authors. It yielded 54 species in 25 genera of which 41 species and 15 genera are new.

In order to classify (in natural and manageable fashion) these new and previous world-wide taxa, now consisting of about 145 species and subspecies in 38 genera, the present authors have followed the model of Barnard and Drummond (1978). Their single-volume treatment of a large, mainly new fauna of phoxocephalid amphipods from south-eastern Australia necessitated the formal subdivision of family Phoxocephalidae into several subfamily units. These have since been expanded and modified to accommodate the world-wide fauna.

The present monographic treatment of family Pleustidae will appear in a five-part series. This paper (Part I) redefines the family Pleustidae, diagnoses the subfamilies, analyses their taxonomic and biogeographic relationships, and reconstructs probable evolutionary pathways to account for their present diversity and distribution. Diagnoses of generic and species components, and distributional-ecological data. for the individual subfamilies are presented elsewhere (Bousfield and Hendrycks, in prep., parts II, III, IV, and V).

ACKNOWLEDGEMENTS

A great many institutions and interested colleagues contributed to the success of this undertaking. For the loan of specimens on which the revision is based, the authors are greatly indebted to the following: the British Museum of Natural History (courtesy Dr. R. L. Lincoln, and Joan Ellis); the Zoological Institute, Leningrad (courtesy Dr. N. L. Tzvetkova); the Friday Harbor Marine Laboratories (courtesy Dr. C. P. Staude); the United States National Museum (courtesy Dr. T. E. Bowman and the late Dr. J. L. Barnard); the University of British Columbia (courtesy Mr. Patrick Shaw); the Pacific Biological Station (courtesy Drs. Z. Kabata and P. Beamish); the Moss Landing Marine Laboratory, California (courtesy Mr. Peter Slattery and colleagues); the Natural History Museum, Los Angeles County (courtesy Dr. H. G. Kuck); the University of Cape Town (courtesy Dr. Charles Griffiths); the Amakusa Marine Biological Laboratory, Kumamoto, Japan (courtesy Dr. Akira Hirayama) and the Zoological Institute, HokkaidoUniversity (courtesy Dr. Shin-ichi Ishimaru).

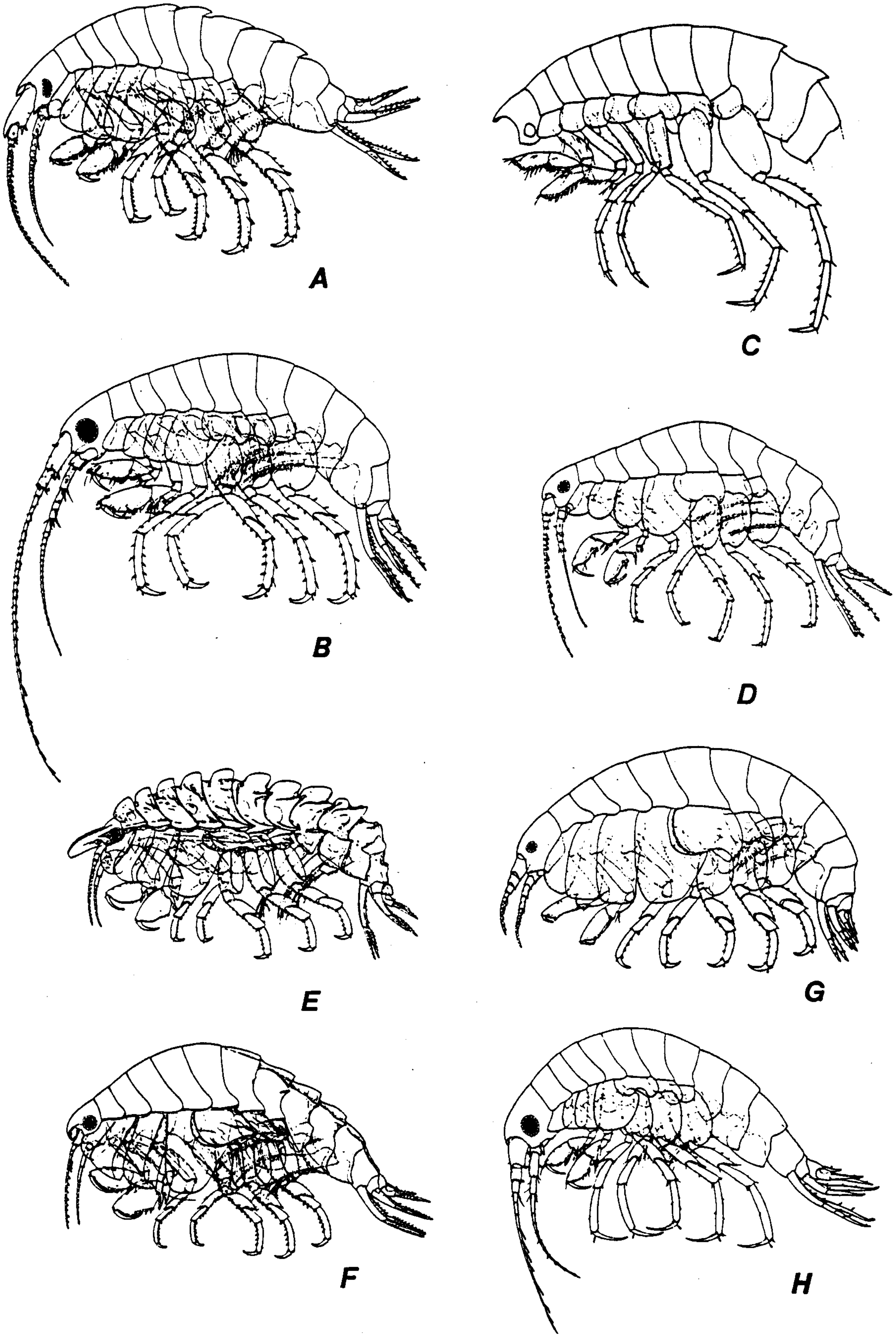
The following colleagues provided commentary on earlier drafts and parts of the text: Dr. Wim Vader, Tromsø Museum, Norway; Dr. Pierre Brunel, Universite de Montréal, Canada; the late Dr. J. L.(Jerry) Barnard, Smithsonian Institution, Washington, D. C., USA; Patrick Shaw. Regina, Sask., Canada; and museum colleagues Drs. Kathleen. E. Conlan, C.-t Shih, and Diana. R. Laubitz, Ottawa, Canada. Drs. Jean Just, Copenhagen, and Roger Lincoln, British Museum of Natural History, London, examined specimens of austral material, especially of the genera *Tepidopleustes* and *Austropleustes,* and provided morphological information critical to the study, for which we are most grateful.

LEGEND FOR FIGURES (The following attributes to unpublished work are employed:

* Bousfield & Hendrycks, Part II, in prep.
! Bousfield & Hendrycks, Part III, in prep.
Bousfield & Hendrycks, Part IV, in prep.
\+ Bousfield & Hendrycks, Part V, in prep.

Fig. 1. Subfamilies of Pleustidae: Representative Species (SEE PAGE 19 - OPPOSITE)

A, B: PLEUSYMTINAE (New genus, new species, #; *Pleusymtes,* new species, !)
C : ATYLOPSINAE (*Atylopsis procerus*) (after Andres, 1986)
D : PLEUSIRINAE (*Pleusirus secorrus*) (after *)
E, F: PLEUSTINAE (*Pleustes,* new species *; new genus, new species *)
G : PARAPLEUSTINAE (New genus, new species +)
H : EOSYMTINAE (*Eosymtes,* new species#)


A
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The illustrations were prepared with the very capable assistance of Mrs. Susan Laurie-Bourque, Hull, Quebec and Mrs. Floy E. Zittin, Cupertino, California. Marjorie Bousfield provided translations of the pertinent Russian literature.

The work was supported through funding and facilities provided by the National Museum of Natural Sciences (now Canadian Museum of Nature), Ottawa, the Royal Ontario Museum, Toronto, Canada, and an operating grant from the Natural Sciences and Engineering Research Council of Canada (NSERC), all of which is gratefully acknowledged.

SYSTEMATICS

TAXONOMIC CHARACTERS AND CHARACTER STATES OF THE PLEUSTIDAE

The amphipod family Pleustidae has been viewed previously as a relatively small to medium-sized group of species. Taxonomically usable or diagnostic characters were relatively few, and character states of the general body, appendages, and mouthparts varied little (e.g. Barnard, 1969a, andp. 20 below). The present study reveals, however, that the family is one of the larger sub-units of suborder Gammaridea (145 species and subspecies) with such rich diversity of taxonomic characters, and breadth of pertinent character states, that 38 genera and 12 subfamilies are required to encompass them. This diversity compares favourably with that found by Barnard and Drummond (1978) in their comprehensive taxonomic analysis of the Phoxocephalidae, a primitive fossorial family of comparable size. In particular, the mouthpart morphology of these two groups of detritivores and micro-carnivores varies in remarkably similar ways (form of the mandibular molar, lower lip, maxillipedal palp) even though they occupy essentially different habitats. Granted, part of this diversity is attributable to the expanded definition of Pleustidae (herein). This definition encompasses genera and higher units that are either aberrant and/or new (e.g. within Eosymtinae) or had previously been included in other superfamilies (e.g.*Atylopsis* within Eusiroidea). Also, some were not clearly allocated at family or superfamily level (within *Incertae Sedis).* However, the main factors accounting for this diversity are: (1) the incorporation of many new pleustid genera and species from the North Pacific region, and (2) the more comprehensive description and analysis of all body parts as detailed below and in subsidiary publications (Bousfield & Hendrycks, in prep., Parts II-V). The diversity of some of the principal taxonomic characters is indicated in figures 1-7.

The use of taxonomic characters in diagnosing and phyletically relating subgroups within Pleustidae is complicated by the phenomenon of morphological convergence. As Barnard and Drummond (1978) discovered, this factor more than any other had led to the previous unsatisfactory state of classification within the northern phoxocephalids. This was rectified by full analysis of the more primitive groups of the southern hemisphere, especially of the Australian region. Although the phoxocephalids and pleustids appear to be of comparable diversity and antiquity, the modern pleustid groups of the northern hemisphere have revealed the extent of morphological convergence, and led to the development of a more realistic natural classification of the world fauna of Pleustidae. However, these general conclusions may require modification as new information comes to hand. Further study of the aberrant and primitive pleustids of Indo-Pacific marine regions, and of northern pleustids with specialized habitats and life styles, are much needed in this regard.

Sexual Differentiation

Within the Phoxocephalidae, the sexes are strongly dimorphic; they swarm and mate synchronously in the water column (Bousfield, 1979, 1982a). Within the Pleustidae, however, sexual dimorphism is little evident. There is apparently no reproductive swarming phase, and mating within most subfamilies takes place probably on or near the bottom. Pre-amplexus *(sensu* Borowsky, 1984), possibly of short duration, may take place in some pleustid taxa in which the gnathopods are conspicuously sexually dimorphic (as in some Parapleustinae). Such inference, however, requires confirmation from actual behavioural studies.

Males tend to differ only slightly from females in superficial characters such as body size, head structures, gnathopods, and other appendages. Thus, in males, the body is generally smaller and more slender, but the eyes are usually larger, the rostrum stronger, antenna 1 has more sensory aesthetascs, antenna 2 is often more setose, and the gnathopods are relatively larger and more powerful. In addition, the peraeopods (segments, especially dactyls) are more slender, pleopods 2 and 3 are occasionally modified, the uropod rami are more slender, and the telson is often longer and more slender than in corresponding females. Since these differences are relatively slight, and because the female is usually larger, and more frequently encountered in

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Fig. 2. Subfamilies of Pleustidae: Representative Species. (SEE PAGE 21 - OPPOSITE)

I, J: STENOPLEUSTINAE *(Sympleustes latipes* - after Lincoln, 1979; Sars, 1895; S. *malmgreni* - after Barnard, 1969a; Sars, 1895).

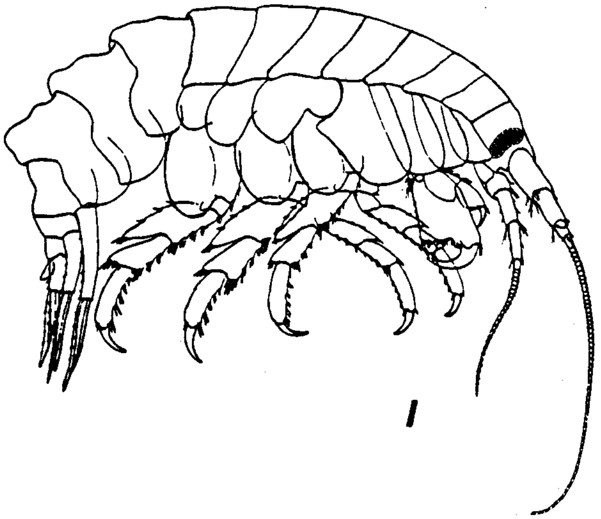
K, L: PARAPLEUSTINAE *(Parapleustes,* new species +; New Genus, new species, +)

M: AUSTROPLEUSTINAE *(Tepidopleustes honomu* - after Barnard, 1971)

N: DACTYLOPLEUSTINAE *(Dactylopleustes,* new species*)

O: PLEUSTOIDINAE *(Pleustoides carinatus* - after Gurjanova, 1972)

P: MESOPLEUSTINAE *(Mesopleustes,* new species, #)



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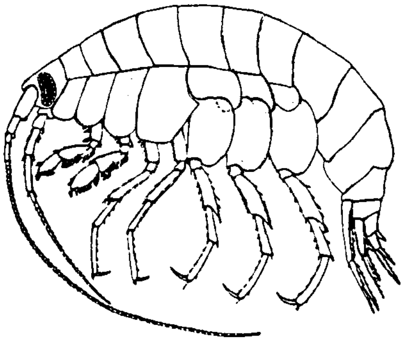

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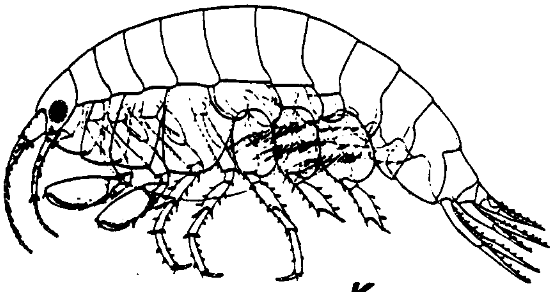

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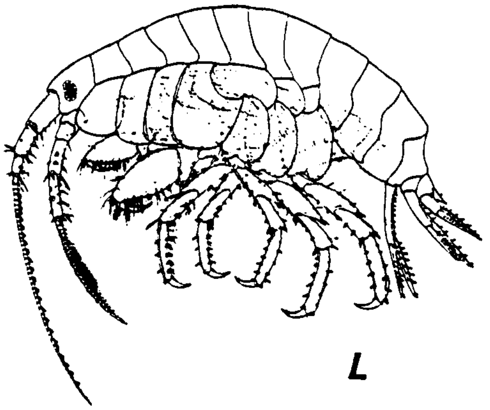

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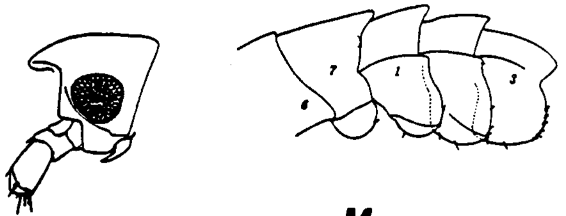

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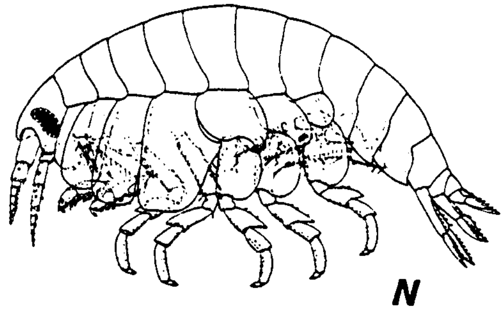

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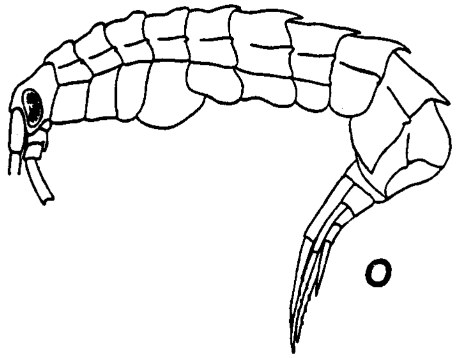

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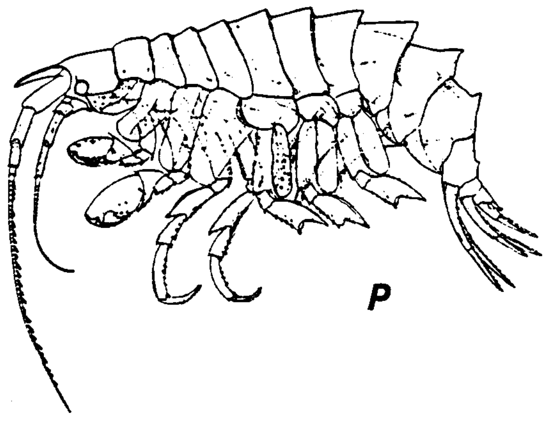

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field samples, the following diagnoses (and more detailed descriptions elsewhere) are based on the female sex, unless otherwise designated.

Body Form

Pleustids are small to medium-sized (2.0 - 30.0 mm) amphipods in which the dorsal and/or lateral surfaces of the peraeon and pleon are often variously carinated, toothed, or mucronate (Figs. I A,C,E,F; Figs. 2I,M,O,P). Only in Eosymtinae, Pleusirinae, and most Parapleustinae and Pleusymtinae are surface processes lacking. In pleustids, the dorsal margin of urosome 2 is narrow, and often totally occluded by segments 1 and 3, especially in more advanced subfamilies (Figs. I A,B,D,G; Figs. 2K,L). This feature, like the median posterior cusps on coxae 2-4 of some Pleustinae, and the plumose inner marginal seta(e) of maxilla 2, are reminiscent of many Talitroidea.

Body Colour

Pleustids are among the most beautiful and strikingly pigmented amphipods (Bousfield, 1985). At least two species in two different subfamilies bear the appellation ' "pulchellus". Subcutaneous pigmentation provides ground colouration that may range from almost black to pure white; on such background may be superimposed the changeable colour and size of epicuticular chromatophores that contribute to the mottled and speckled appearance of certain sand and gravel-dwelling species within the Pleusymtinae and Parapleustinae. The striking body colouration of members of Pleustinae and Parapleustinae that occupy bottom sites open to easy fish predation, may function in warning potential predators of distasteful or poisonous body compounds.(e.g. terpenes) of types recently investigated in eastern Pacific invertebrate animals by Andersen (1988). Pleustids members of the amphipod community are not heavily preyed upon (Nagata, 1966). Other types of body colouration (banding) combined with specialized body form and posture (e.g. in Pleustinae), enable the amphipods to imitate mitrellid snails in classical Batesian mimicry (Crane, 1969; Field, 1974).

Rostrum

The rostrum is generally medium, down-curved distally, but does exceed the antero-lateral head lobe (Figs. 1A,C,D,F,H; 2I,J,M,N; 3E). In some of these (e.g. in Neopleustinae), the rostrum appears as a short extension of the mid-dorsal head crest.

In a few, mainly advanced groups, the rostrum is shorter than the lateral head lobe (e.g. Figs. I B,G; 2K,L,O; 3D). However, in Mesopleustinae, Pleustinae, and some Pleusymtinae *(Pleustomesus)* the rostrum is strongly developed, its length more than half that of the dorsal margin of the head itself (Figs. IE, F; 2P; 3A-C). In Pleustinae, the rostrum is typically sexually dimorphic, and is longer and more slender in the male than in the corresponding female.

Lateral Head Lobe

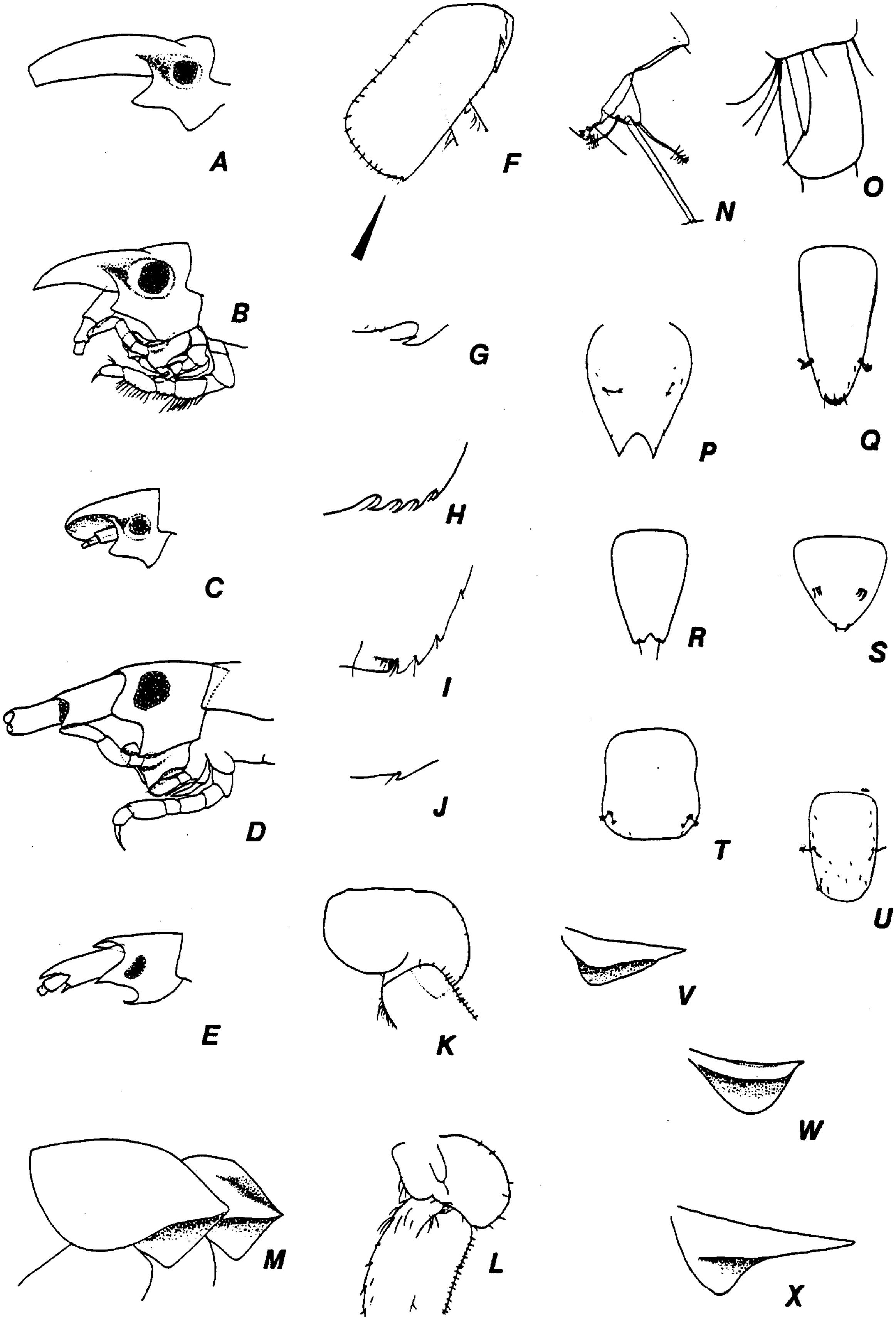
Usually acute (Fig. IA,G; 2K,O,P) but may be sub-acute or rounded (Figs. ID,H; 2L,N). Its anterior margin is usually smooth and even, but may be weakly incised, with even a faint trace of the "pontogeneiid" cleft (Fig. 2I - some Stenopleustinae). The inferior antennal sinus is often long and shallow (Figs. I H; 20,P), but may be deep and the lower cusp acute (Figs. I A, 1 B, 2L - in Pleusymtinae, Parapleustinae).

Eyes

The paired lateral eyes are typically large, ommatidial, and pigmented. They may be sub-rectangular or sub-rhomboidal in outline (Fig. 1B,H,2M), reniform (Figs. 21,J,N,O), oval or roundish (Figs ID,G), or unpigmented (Fig.2P).

Fig. 3. Subfamilies of Pleustidae: Heads (A-E); Coxal Plates, (F-M); Accessory flagellum (N,O); Telson (dorsal and lateral aspects: P-X) (SEE PAGE 23 - OPPOSITE)

Heads (lateral view)
A,B : PLEUSTINAE *(Pleustes,* new species *; *Pleustes,* new species *)
C : PLEUSTINAE (New genus, new species *)
D : PARAPLEUSTINAE (New genus, new species +)
E : PLEUSYMTINAE (New genus, new species *)
Coxal Plates
(Coxae 1-3: F-J; coxa 5: K; coxa 6: L; coxae 6-7: M)
F : PLEUSYMTINAE *(Pleusymtes coquillus* - after Barnard, 1971)
G : PLEUSYMTINAE (New genus, new species #)
H : EOSYMTINAE *(Eosymtes,* new species #)
I, J: PARAPLEUSTINAE (New genus, new species +; *"Parapleustes" oculatus* Holmes, 1908 +)
K, L: PLEUSYMTINAE *(Pleusymtes coquillus* - after Barnard, 1971)
M : PLEUSTINAE *(Pleustes* sp. *)
Accessory Flagellum
N : PARAPLEUSTINAE (New genus, new species +)
O : INCERTAE SEDIS *(Harpinioides drepanocheir*- after Stebbing, 1888)
Telson
P : ATYLOPSINAE *(Atylopsis procerus* - after Andres, 1986)
Q : PARAPLEUSTINAE (New genus, new species +)
R : INCERTAE SEDIS *(Harpinioides drepanocheir* - after Stebbing, 1888)
S : AUSTROPLEUSTINAE *(Tepidopleustes honomu* - after Barnard, 1970)
T : PLEUSTINAE *(Pleustes* sp. *)
U : PLEUSYMTINAE (New genus, new species #)
V : PARAPLEUSTINAE *("Parapleustes" oculatus* Holmes, 1908 +)
W : STENOPLEUSTINAE *(Stenopleustes pulchellus* Sars, 1895 !)
X : PLEUSTINAE *(Pleustes* sp. *)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Antenna 1

Usually elongate and longer than antenna 2, with slender flagellum, the segments of which bear short, slender aesthetascs, more richly so in the male (Figs. 1 A,B; 21,J,L,P). Very rarely (in some Atylopsinae, Stenopleustinae) the basal flagellar segments are conjoint and may bear a few short transverse rows of aethetascs, forming what may be a vestigial callynophore (Lowry, 1986). Peduncular segment 1 is normally elongate, often with antero-distal or postero-distal processes (Figs. 40, P). Peduncular segments 2 and 3 are long, plesiomorphically (Figs. 21,J,L,P) but become variously shortened apomorphically (Figs. lD, F,G). The accessory flagellum is typically minute (Fig. 3N), vestigial, or totally lacking, rarely l-segmented and distinct (Fig. 3).

Antenna 2

Usually slender, and shorter than antenna 1, with slender, weakly spinose (rarely setose) peduncle and flagellum. The basal segment is large, rounded anteriorly, and the gland cone of segment 2 is usually large, distinct, and subparallel to the posterior margin of segment 3. In a few instances (Figs. lE, F. G; 2N) the antennae are short, few-segmented, and subequal.

Buccal Complex

The buccal mass of most pleustids is retrogressed somewhat posteriorly beneath the head (Figs. 3B,D; Fig. 7). The buccal complex is shallow in most primitive subfamilies (Fig 7) but medium-deep in higher subfamilies (Figs. 3B,D).

Upper Lip

In higher subfamilies, the upper lip is variously deeply cleft, with sloping sides; the lobes are distinctly asymmetrical (Figs. 4E-G). In primitive subfamilies, the distal margin is shallowly notched (depth less than width), nearly smooth, and the lobes are subequal (Figs. 4A-D). The epistome is usually ridged medially, but it is rounded in front, not acutely produced (Fig. 4C).

Lower Lip

In higher subfamilies the inner lobes are flat and shallow; the outer lobes are small, rounded, oblique. and widely separated (Figs. 4M, N). In lower subfamilies, the inner lobes are indistinct or small and narrow, and the outer lobes are large and closely approximated (Figs. 4H,I). In all instances, the mandibular lobes are relatively short and the wings rounded. Intermediate conditions occur in the intermediate families (Figs. 4J-L).

Mandible

The pleustid mandible exhibits a variety of biting and grinding surfaces, indicating a corresponding diversity of feeding types. The mandibular body is of medium size, slender, and generally tapers distally to the multi-cuspate cutting incisors. The bite is guided by the lacinia mobilis, the right incisor fitting and locking between the left incisor and left lacinia mobilis, in the manner indicated by Dahl and Hessler (1981).

Lacinia Mobilis

The left lacinia is multi-dentate; the usual number of teeth ranging from 6-12 (Figs. SA,F,H), rarely as few as 5 (some Atylopsinae), but may be more than 20 (in some Parapleustinae). The teeth may be regular (Figs. SA,H) or uneven (Fig. SF). The right lacinia is present only in the in the primitive subfamilies. It may be tricuspate (Atylopsinae), blade-like, or bicuspate (Fig. SD inset), spike-like, or otherwise reduced (Stenopleustinae).

Spine-Row

The blades of the spine-row serve primarily to push food particles toward the grinding molar, and/or mouth opening K: (Dahl and Hessler, 1981). In many pleustids, the blades are numerous (6-15), slender, distally simple or weakly pectinate (Figs. SA,B,E). The distal blades of the spine-row are usually largest and most strongly modified. In some groups, especially those in which a true right lacinia is lacking (e.g. Pleusymtinae) the distal-most blade(s) may be broad and chisel-shaped, and serve as a false lacinia. In some groups (Figs. 5B,H), the supernumerary slender setae (between the blades) may form small clusters next to the left lacinia. In other groups, particularly those with modified or non-triturating molar surfaces, the blades are fewer and often thickened, stiffened, and heavily pectinate distally (Figs. 5B,C,D,H). In the most specialized feeding types (within

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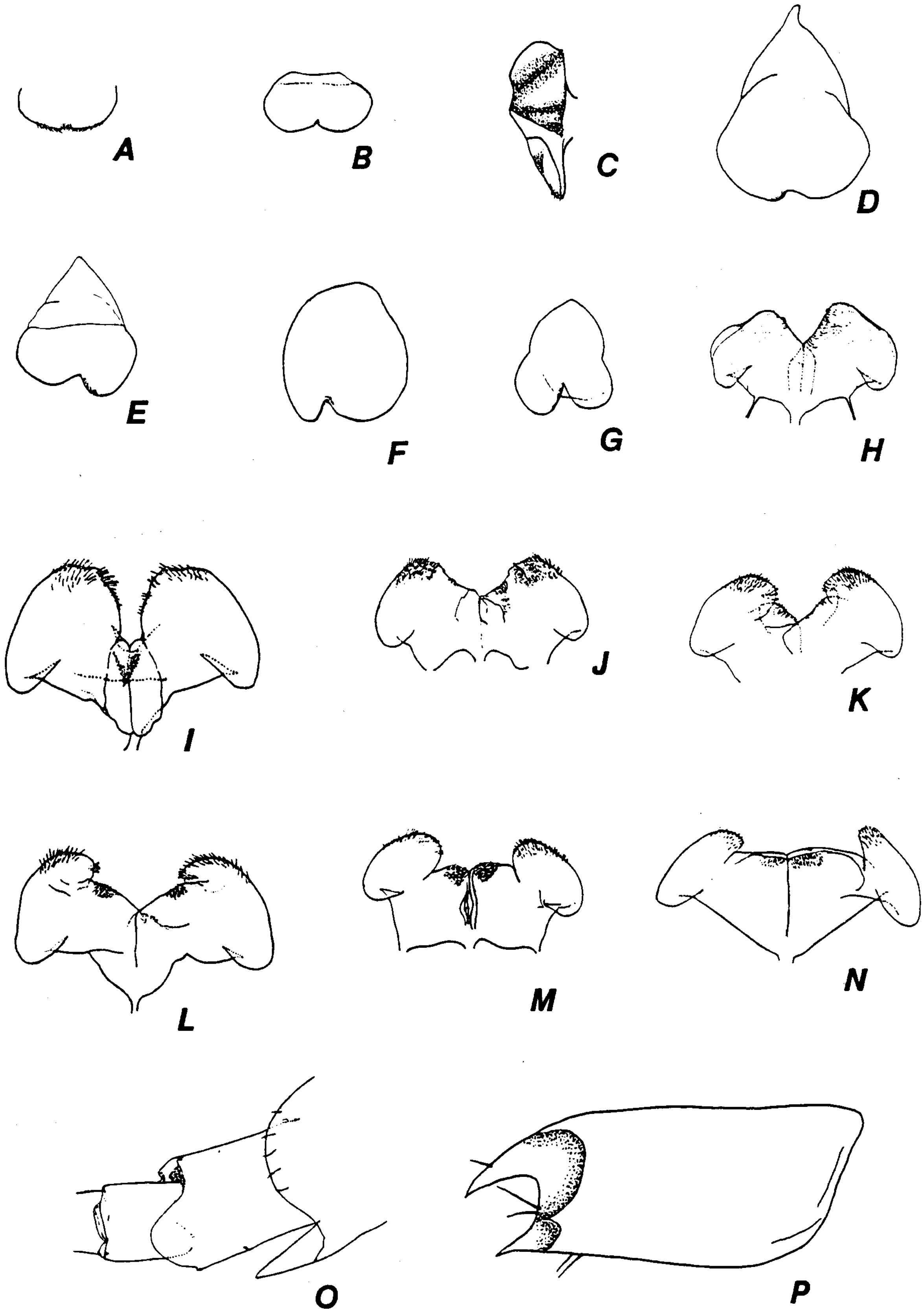
Fig. 4. Subfamilies of Pleustidae. Mouthparts: Upper Lip (A-G); Lower Lip (H-N); Antenna 1, peduncle 1 (O-P). (SEE PAGE 25 - OPPOSITE).

Upper Lip
A : ATYLOPSINAE (*Atylopsis procerus* - after Andres, 1986)
B : DACTYLOPLEUSTINAE (*Dactylopleustes*, new species *)
C : PLEUSTINAE (*Pleustes* sp. *)
D : EOSYMTINAE (*Eosymtes*, new species #)
E : PLEUSYMTINAE (New genus, new species #)
F : STENOPLEUSTINAE (*Stenopleustes monocuspis* Barnard and Given 1960 !)
G : PARAPLEUSTINAE (*"Parapleustes" oculatus* Holmes,1908 +; new genus new species +)
Lower Lip
H : MESOPLEUSTINAE (*Mesopleustes* sp. #)
I : EOSYMTINAE (*Eosymtes*, new species #)
J : PLEUSTINAE (*Pleustes* sp. *)
K, L : PLEUSYMTINAE (New genus, new species #)
M, N: PARAPLEUSTINAE (*"Parapleustes" oculatus* Holmes,1908 +)
Antenna 1, peduncle 1
O : PLEUSYMTINAE (New genus, new species #)
P : EOSYMTINAE (*Eosymtes*, new species #)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Parapleustinae) the blades may be very short, stout and heavily chitinized or mineralized, with a flattened apex forming an effective "molarized" grinding surface (Fig 5F). Intermediate forms of this type occur within the Parapleustinae.

Molar

The mandibular molar provides one of the principal bases for differentiation of pleustid subfamilies. Six principal types are recognized: (1) large, columnar; triturating (grinding) surface fully ridged (Fig. 5A); (2) large, columnar. triturating surface with smooth (unridged) central core, and ridged or spinose periphery (Figs. 5C,D); (3) compressed or narrowing distally; grinding surface "cobbled", or granular, with or without marginal spines (Figs. 5G,H); (4) columnar, with smooth or pavement-like grinding surface, and uniformly sharp edges (Fig. 5B); (5) non-triturative; apex inflated, margin rounded, smooth, with no trace of ridges or teeth (Fig. 5E); (6) non-triturative; apex small, conconical, stub-like, setulose (Fig. 5F). In plesiomorphic variants of (6) (e.g. some Neopleustinae), the molar body is less reduced, and the apex may retain minute spines and non-functional ridges. In variants of (1) and (2) above, the molar bears a chitinized distal molar hump (or knob), and antero-medially a plumose flagellum, both typical of eusiroidean and talitroidean molars, but lacking in most leucothoidean molars. A distal molar setal tuft (primordial molar flake of Conlan, 1983; Lincoln & Lowry, 1984) is variously present in the primitive subfamilies (above), and in the Stenopleustinae (Figs. 5A,D).

Palp

The mandibular palp is 3-segmented, the segments typically slender and elongate (Fig. 7 - Eosymtinae). In some groups (Neopleustinae, Pleusirinae, some Parapleustinae) the palp is elongate, more than double the length of the mandibular body, but it is of normal size (to 1.5 times MD body) in most subfamilies. Segment 3 is usually as long as, or longer than, segment 2, slightly curved, with blunt apex bearing 4-5 long setae, and the posterior margin lined with a variable number of short to medium, pectinate setae and/or occasionally longer simple setae (Fig. 7). The "A" setae (Cole, 1980) are inserted very near the base of the segment and typically are restricted to a single seta (Fig. 7 - Eosymtinae). In the apomorphic condition, "A" setae are lacking entirely. In the plesiomorphic condition, two or more setae may occur in small basal clusters (e.g. in Atylopsinae, some Austropleustinae), or in clusters of up to 12 long setae (some Pleustinae). Segment 2 is slender, rarely broadened (as in eusiroideans) and the inner margin (especially distally) is armed with variable numbers of slender setae. Segment 1 is typically short, but occasionally elongate (as in Pleusirinae, some Neopleustinae).

Maxlla 1

The outer plate is medium short, not very broad, and typically bears 9 stout apical pectinate spines (Fig. 7 detail - Eosymtinae, most subfamilies). In the plesiomorphic condition, there are 11 spines (e.g. Atylopsinae, Mesopleustinae). In the apomorphic condition there are either few (6-7 in most Stenopleustinae) or many (15-20+ in some Dactylopleustinae and Parapleustinae); in the latter case the spine-teeth tend to be tall, simple, slender, and curved. The inner plate is small, ovate or triangular, and usually bears 1-2 (plesiomorphically 3-4, or apomorphically 0) apical setae. The palp is 2-segmented, typically slender, the apex exceeding the outer plate. The distal segment is armed apically with short stout spines and sub-apically with slender spines, and facially (often) with setules or pilosity. The proximal segment is short, but may have a disto-lateral wing-like expansion that may bear short setae (e.g. Pleustinae, some Stenothoinae, Neopleustinae).

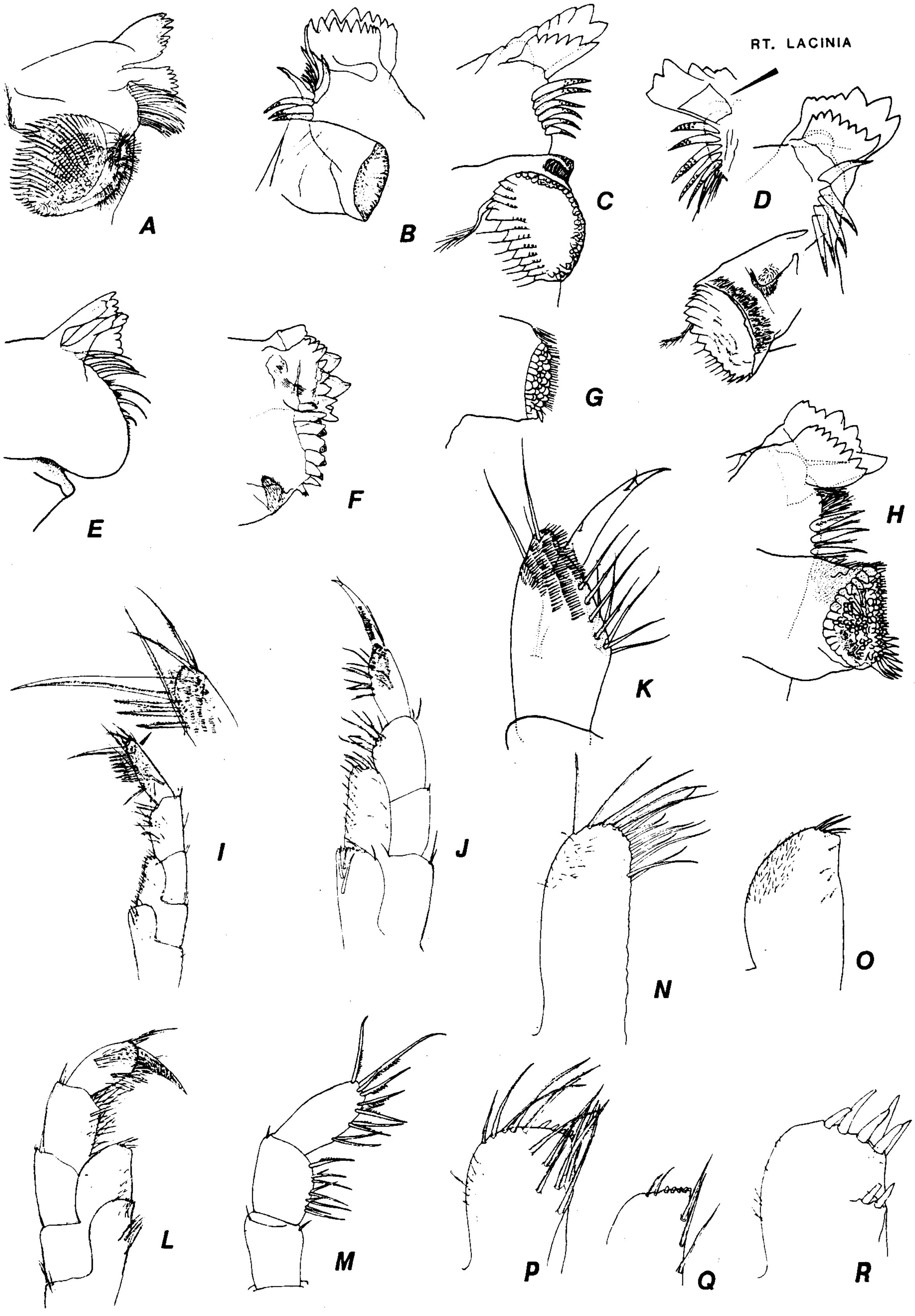
Fig. 5. Mouthparts. Mandible (A-H); Maxilliped Palp (I-M); outer plate (N-O); Inner plate (P-R)
(SEE P. 27 - OPPOSITE)

Mandible
A : MESOPLEUSTINAE *(Mesopleustes,* new species #)
B : PLEUSYMTINAE (New genus, new species #)
C, D: EOSYMTINAE *(Eosymtes,* new species # showing left lacinia; New genus, new species # showing right lacinia)
E : DACTYLOPLEUSTINAE *(Dactylopleustes,* new species *)
F : PARAPLEUSTINAE (New genus, new species +)
G : STENOPLEUSTINAE *(Stenopleustes monocuspis* Barnard & Given, 1960); *Stenopleustes pulchellus* Sars, 1895 !)

Maxilliped palp
I : NEOPLEUSTINAE *(Neopleustes,* new species +)
J : PLEUSYMTINAE *(Pleusymtes coquillus,* - after Barnard, 1971)
K: STENOPLEUSTINAE *(Stenopleustes monocuspis,* Barnard & Given, 1960 !)
L : MESOPLEUSTINAE *(Mesopleustes,* new species #)
M : AUSTROPLEUSTINAE *(Tepidopleustes honomu* - after Barnard, 1970

Maxilliped outer plate
N : PARAPLEUSTINAE (New genus, new species +)
O : MESOPLEUSTINAE *(Mesopleustes,* new species #)

Maxilliped, inner plate
P, Q : PARAPLEUSTINAE (New genus, new species +; *"Parapleustes"oculatus* Holmes, 1908 +
R : PLEUSTINAE *(Pleustes sp: *)*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Maxilla 2

The plates are relatively small, the inner typically slightly shorter than the outer plate, and variously broadened medially (Fig. 7 detail - Eosymtinae). Both plates are apically armed with medium long stiff setae. The inner plate lacks the row of facial setae so conspicuous in eusiroidean family members; however, one or two large plumose inner marginal or submarginal setae occur in nearly all pleustid subfamilies. They are similar to those of talitroidean family members and may represent dislocated remnants of the presumed ancestral facial row.

Maxilliped

Characters of the maxilliped plates and palp are very important in pleustid classification. Three main types of outer plates are distinguished here: (1) broad, having the outer margin strongly arched and broadest medially (Fig. 5O); (2) narrow, columnar, having both inner and outer margins essentially straight and subparallel (Fig. 5N); and (3) intermediate, having the outer margin arched or curved distally but broadest basally (Figs. 5I,J). The inner margin is typically smooth and sharp and forms a cutting edge; although normally straight, it may be scalloped (some Stenopleustinae) or incised and bowed (as in Dactylopleustinae). It may be armed submarginally with few to many short setae (Figs. 5N,O).

The inner plate is typically shorter and broader than the outer, exceeding the base of the outer plate segment mainly in primitive subfamilies (Fig. 5L). The apex is typically subtruncate, and bears variable numbers of spines of two types: (1) heavy and stout (Fig. 5R); or (2) small, short, "button-like" (Figs. 5J,L,Q). Intermediate types also occur (Fig. 5P). The anterior face and inner margin bear few to several slender masticatory setae (Figs. 5J, L,P,Q) or 2-3 stiff, heavy, spines (Fig. 5R).

The palp is normally 4-segmented; segment 2 is normally longest. The dactyl is long, slender, and possesses micro-pectinate (Figs. 5J, L) but these are lacking in the austral group (Atylopsinae to Stenopleustinae) (Fig. 5K). The dactyl is occasionally small or lacking (Fig. 5M).

Segment 3 is of two main types: (1) apex oblique, extending distally beyond the base of the dactyl (Figs. 5K,I), or (2) apex truncate or gently rounded, not extending distinctly beyond the base of the dactyl (Figs. 5J,L). In several genera within Neopleustinae and Parapleustinae, the inner distal margin of segment 3 may be armed with stiff pectinate spines and short serrate teeth (Fig. 5(I) - detail). The distal medial surface usually bears numerous micro-pectinations arranged in short rows (Fig. 5 (I)).

Coxal Plates 1-4

The anterior coxal plates of pleustids are typically deeper than wide, and increase regularly in size posteriorly (Figs.1B,D,F; 2 I-L). Rarely are the plates small and shallow (Fig 1C). However, coxa 1 varies considerably in form. It may be markedly smaller than the others (Fig. 2N). The distal portion may be expanded broadly (Figs. 1E,F; 2L) or narrowing and bent forward (Figs. 2K,P). The lower margins of coxae 2-4 are often straight or nearly so (Figs. 1A,B,E-H; 2I, K,L,N) but may be rounded (Fig. 1D, 2J). In coxae with straight margins, the posterodistal corners of plates 1-3 bear one or more cusps or notches that are usually small (Fig. 3J), occasionally multiple (Figs. 3F,H,I), but may be conspicuous (Figs. 1A; 2K; 3G). Coxa 4 is normally strongly excavate posteriorly, shallowly (Figs. 1A,B,E; 2X, L,P) or occasionally deeply (Fig. 1G - some Parapleustinae), and may be produced as a distinct posterior process (Figs. 1 E,F; 2I,N).

Gnathopods 1 & 2

Typically they are strongly subchelate and subsimilar in form and size. Gnathopod 2 is usually slightly larger, the propod stronger, and the carpus shorter and deeper than in gnathopod 1 (Figs. 6G,H; J,K; Q,R). The basal segment of each gnathopod is relatively long and slender and protrudes below the coxal plates (Figs. 1 B,C; 2J). The posterior margin is nearly smooth, but the anterior margin is often heavily (Figs. 1E,F; 2J,N), setose distally or nearly bare (Figs. 1D,H; 2X,P). The ischium (segment 3) is always short, as in eusiroideans. The merus (segment 4) is also short; the postero-distal margin is usually rounded and setose (Figs. 6A,B; D,E; N; O,P) but may be produced in a sharp tooth or cusp (Figs. 6 G,H; J,K; L,M; Q,R).

Fig. 6. Subfamilies of Pleustidae: Representative types of gnathopods, and pleon plates 1-3. (SEE PAGE 29).

Gnathopods 1 & 2

A,B : DACTYLOPLEUSTINAE (*Dactylopleustes*, new species,)
D,E : PLEUSIRINAE (*Pleusirus secorrus*) (After *)
G,H : MESOPLEUSTINAE (*Mesopleustes*, new species #

J,K : PLEUSTINAE (*Pleustes* (new subgenus) sp.)

O,P : AUSTROPLEUSTINAE (*Tepidopleustes homonomu* - after Barnard, 1970)
Q,R : PLEUSYMTINAE (New genus, new species, !)

Gnathopod 1

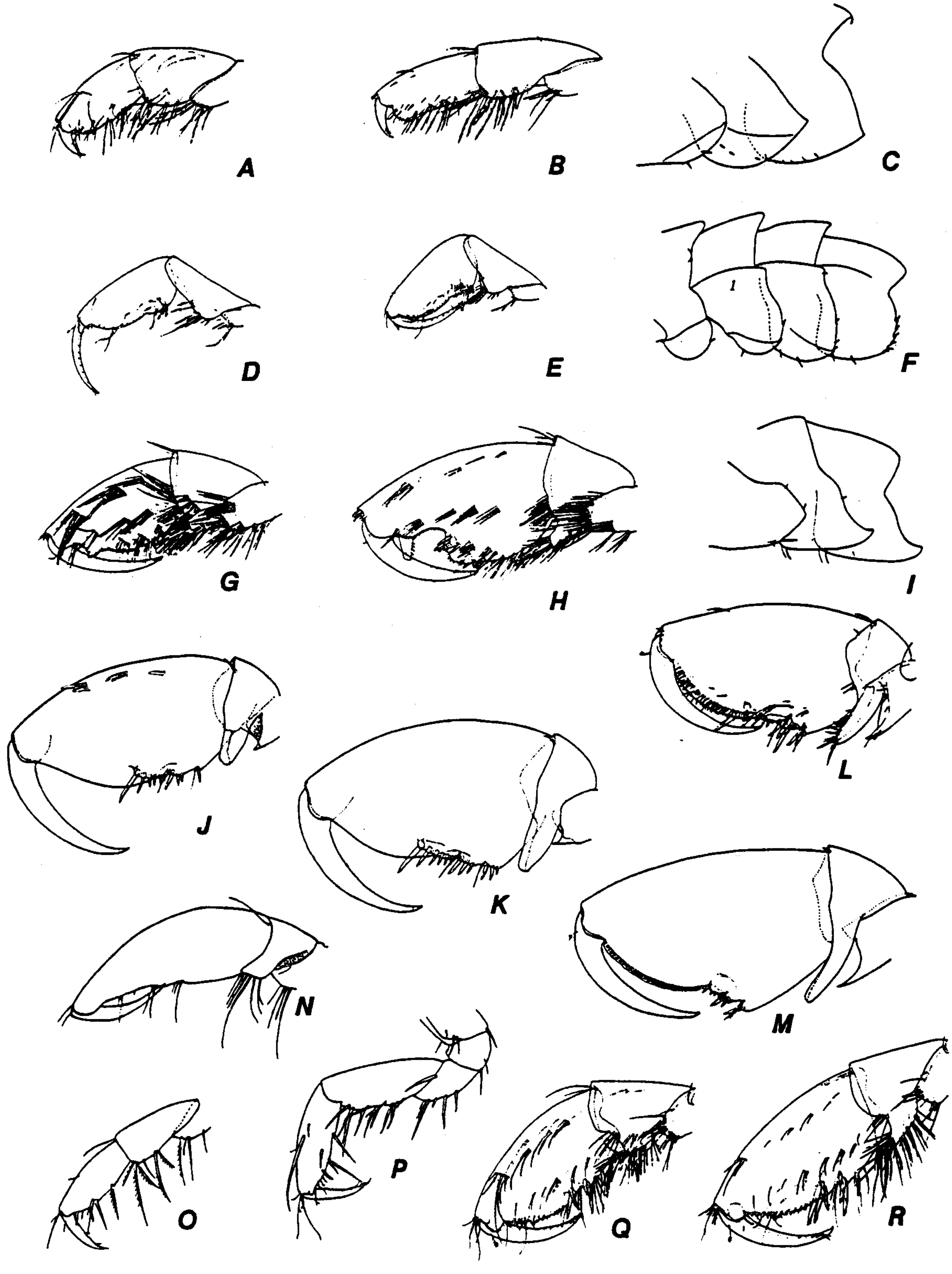
N : *INCERTAE SEDIS*: (*Harpinioides drepanocheir* - after Stebbing, 1888)

Gnathopod 2

L,M : PLEUSTINAE (New genus, new species. *; *Pleustes*, new species *)

Pleon plates 1-3

C : PARAPLEUSTINAE (*"Parapleustes" derzhavini* - after Barnard, 1970)
F : AUSTROPLEUSTINAE (*Tepidopleustes honomu* - after Barnard, 1971)
F,I : PLEUSYMTINAE (*Pleusymtes coquillus* - after Barnard, 1971)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The plesiomorphic condition of the carpus is shallow and elongate, subequal to the propod, with long, shallow, setose or spinose posterior lobe (Figs. 6A,B; O,P). In the apomorphic condition, the carpus is short and deep, with a deep, narrow hind lobe that is often densely armed apically with rows of stiff setae and occasionally with pectinate spines (Figs. 6J,K; 3L,M). Intermediate stages are frequent (Figs. 1A,B; 2H; 6 Q,R - in many subfamilies). A second apomorphic condition is the "eusiroidean" form in which the carpus is long and very slender, with a small, shallow, weakly setose posterior lobe (Figs. 6D,E).

The plesiomorphic condition of the propod is also shallow and elongate, with a small, smooth, convex palm, and setose posterior margin (Figs. 1C,G; 6A,B). This condition is conceivably secondarily derived or convergent in one genus of Parapleustinae (Fig. 6G). In the presumed plesiomorphic or "detritivore" condition, the inner (median) face bears several groups of superior lateral and inferior lateral setae (Figs. 6G,H; Q,R): These setae are presumably reduced or lost in the apomorphic or "raptorial" condition. One apomorphic condition of the pleustid propod is large and deep, the palm smooth, convex, and bearing a median tooth or cusp, and 1-2 groups of spines at the postero-distal angle (Figs. 6A,B; 6Q,R). Typically, the palm is lined submarginally on each side with a row of short setae. In another type of apomorphic condition (in strongly raptorial groups) the propod is very deep, the palm may be strongly toothed and/or incised, and the posterior angle armed with several groups of strong spines (Figs. 2I; 6J,K). In the latter instance, the posterior margin may become relatively short, and devoid of setae (or nearly so). In a third type of advanced condition, the propod becomes even more slender, and the palmar margin very oblique or merging imperceptively with the posterior margin (Figs. 6N,O,P).

The dactyl is usually large and strong, smoothly fitting the palmar margin (6J,K,M); its posterior margin is usually smooth, but may be serrated or dentate (Fig. 6P); here the palm is short and weak, the dactyl may exceed the spines at the palmar angle (Figs. 6A,B; 0,P).

Peraeopods 3-4

Typically slender, subequal (4 slightly shorter), with bases extending below the lower margins of all but the deepest coxal plates. Anterior and posterior margins of the basis are weakly (occasionally strongly) setose. The anterior and posterior margins of the distal segments (4-6) are typically spinose (Figs. 1A, F; 2K), rarely setose (Fig. 2L), or nearly bare (Fig. 1 H). Segment 5 is invariably shorter than 4 or 6, and is typically overhung proximally by the anterodistal process of segment 4 (Fig. 2P). The dactyl is usually strongly curved and powerful (Figs. 1 A, B; 2 I,L,P) but may be long and slender (Fig. 1 H), short and curved (Fig. 1 D,F), or short and minutely pectinate on the posterior margin (Fig. 2N).

Peraeopods 5-7

Primarily and classically homopodous. similar in form and size, although peraeopod 5 is usually the shortest, and peraeopod 6 slightly the longest (Figs. 1A,D,F; 2L). Rarely are they heteropodous, differing markedly in form and size (Fig. 1C). The coxae of peraeopods 5 & 6 are typically posterolobate and rounded behind (Figs. 3K,L) but may be angular both posteriorly and/or laterally (Fig. 3M - in Pleustinae). The anterior and posterior margins of distal segments (4-6) are usually spinose, with variations similar to those of peraeopods 3 and 4 noted above. Segment 5 is always shortest, and is variously overhung posteriorly by the postero-distal process of segment 4 (Figs. 1G; 2I). The dactyls are generally longer and stouter than those of peraeopods 3 and 4, except when short and pectinate on the anterior margin, as in the Dactylopleustinae (Fig. 2N).

Pleon plates 1-3

Generally deep and broad in form, the hind margins are usually smooth and the hind corners quadrate (Fig. 6C), acutely produced, hook-like (Figs, 1A,B; 2(O); 6I), or round and the hind margin serrated (Fig. 6F). Proximo-lateral cusps or teeth are present in some highly sculptured Pleustinae (Fig. 1E). The ventral margins, especially of plates 2 and 3, typically bear small spines, rarely setae (Fig. 6C).

Pleopods

All three pairs of pleopods are typically well developed and strongly natatory in both sexes. Pleopod 3 is slightly theshortest. The peduncles are long, nearly smooth or weakly setose laterally, and bear two serrated coupling spines (retinacula) on the medio-distal margin. The rami are long, subequal, multi-segmented, and richly plumose-setose. The inner margin of the proximal segments of the inner ramus are armed with 4-5 slender 'clothespin ' spines *(sensu* Barnard & Drummond, 1982). Within the Pleusymtinae, pleopod 2 is sexually dimorphic in one species *(Pleusymtes brachypalmus* Ishimaru, 1985) and pleopod 3 of a new genus and species from the North American Pacific coast is also sexually dimorphic.

Uropods

Uropods 1 and 2 are typically slender, with peduncle and both rami marginally and apically spinose (Figs. 1A, F; 2L,P). The peduncle of uropod 1 bears a disto-lateral ecdysial spine, best developed in the more advanced groups (Figs. 1A,B; 2X). The outer ramus of both uropods is shorter than the inner, often conspicuously so (Figs. 1B,G; 2P). Uropod 3 is shortest, the tips of the rami seldom extending beyond those of the other uropods. Both rami are longer than the peduncle. The outer ramus is usually distinctly shorter than the inner but may be subequal in some primitive species (within Atylopsinae, Austropleustinae).

Telson

The telson is typically plate-like, with an entire apical margin and a ventral mid-rib or keel. It varies in shape from short, subquadrate, even broadening distally, with a truncated apex (Fig. 3T), to elongate, tongue-like, or narrowing distally to a subacute apex (Figs. 3Q,S,U). In primitive groups, the apex may be cleft or incised, a situation that presumably represents incomplete fusion of the ancestral separated telson lobes (Figs. 3P,R). The apex bears paired notches, widely or narrowly separated, within each of which is based a small sensory seta or spine . The lateral margins and dorsal surface may bear small supernumerary setules, but true spines are lacking. Paired twin groups of sensory penicillate setae are located about midway dorsolaterally on each side; these may be slightly proximal (Fig. 3U) or distal (Figs. 3Q,T). The dorsal surface may be slightly hollowed or depressed.

The ventral keel of the telson is a feature almost unique to the Pleustidae. In most subfamilies it forms a deep, median, longitudinal rib, presumably of strengthening function. It is deepest centrally in Stenopleustinae and related subfamilies (Fig. 3W), but proximally in most others (Figs. 3V,X). In some primitive subfamilies (e.g. Atylopsinae), it may be shallow and weakly developed. It is lacking in Lafystiidae, Laphystiopsidae, and all groups relegated to the category of *Incertae Sedis.*

Coxal Gills

These are simple (unpleated or unlobed), sac-like or plate-like respiratory appendages attached to the posterior margin of the coxal segment of peraeopods 2-6. A small coxal gill may also be found on peraeopod 7 in a few primitive subfamilies (Atylopsinae, Austropleustinae (fide Just, Lincoln)) and in at least one species of Stenopleustinae. In most subfamilies, the gills are narrowly sac-like on peraeopods 2-4 but more broadly sac-like or plate-like on peraeopods 5-6. All gills are essentially narrowly saclike in primitive subfamilies (e.g. Atylopsinae, Eosymtinae and most Stenopleustinae) but are mainly broadly sac-like or plate-like in the others. The condition of the coxal gills of Pleustoidinae has not yet been noted or formally described.

Brood plates

Also known as oostegites, or brood lamellae, the brood plates are large, thin, lamellate structures attached to the hind margins of the coxal segments of peraeopods 2-5 of mature females. The first three pairs are large and broad, and the margins armed with numerous long simple brood setae. The fourth pair is typically smaller and broadly linear in form, the margins bearing relatively few setae.

Cuticle

Little is known of the surface microstructures of pleustid amphipods. No pleustids were formally included in the studies of Halcrow and Bousfield (1987), but unpublished authors' photographs reveal (in a species of Parapleustinae) regular surface polygons within which are irregular rows of micropores, and macropores; from some of the latter protrude prominent blade-like macrotrichs or microspines. Barnard (1964) has shown shallow pits and thickenings that cover the body of Mesopleustinae; these are common in many species within the Pleustinae (Bousfield and Hendrycks, in prep:, Part II).

SYSTEMATICS OF FAMILY PLEUSTIDAE

The family Pleustidae was initially defined by Stebbing (1906) and updated by Gurjanova (1951) and Barnard (1969a). These early diagnoses were relatively brief and encompassed about a dozen major character states, mainly of mouthparts, antennae, gnathopods, coxal plates, and general body form. The more recent diagnoses of Gurjanova (1972), Bousfield (1973, 1982a), and Lincoln (1979) encompassed a greater number of characters and character states that included features of gills, brood plates, and mouthparts not previously treated. The present diagnosis continues the trend towards increasingly broad coverage of morphological characters, and greater precision in treatment of character states. This format accommodates the much greater number and diversity of pleustid taxa revealed in this study, and more fully meets the requirements of numerical taxonomic methodology.

PLEUSTIDAE Buchholz, 1874

Paramphithoidae Sars, 1895 (partim): 343.
Pleustidae Stebbing, 1906: 870.—Barnard, 1969: 421.—Gurjanova, 1972: 634.—Bousfield, 1982a: 266.—Barnard & Karaman, 1991: 644.

Type Subfamily. Pleustinae Stebbing, 1906.

Subfamilies. Atylopsinae, new subfamily [p. 34]; Stenopleustinae, new subfamily [p. 35]; Austropleustinae, new subfamily [p. 34]; Mesopleustinae, new subfamily [p. 36]; Pleustoidinae, new subfamily [p. 37]; Eosymtinae, new subfamily [p. 37]; Pleusymptinae, new subfamily [p. 37]; Dactylopleustinae, new subfamily [p.38]; Pleustinae, new subfamily (p. 39]; Pleusirinae, new subfamily [p.39]; Neopleustinae, new subfamily [p. 40]; and Parapleustinae, new subfamily [p. 41].

Diagnosis. Body small to medium large, often broadened anteriorly, usually toothed or carinated dorsally, especially on the pleon; surface often strikingly coloured or maculated. Urosome 2 short, often dorsally occluded by segments 1 and 3. Head deep, variously (often strongly) rostrate; anterior head lobe pronounced, acute or rounded. rarely incised; inferior antennal sinus distinct, inferior lobe acute, or produced. Eyes typically large, well pigmented. subrotund to subrectangular. Antennae short to medium-long, slender, lacking calceoli. Antenna 1 longer than 2, peduncular segment 1 large, often produced distally; segments 2 and 3 often short; accessory flagellum minute or lacking. Buccal mass shallow to medium deep, regressed slightly behind head.

Upper lip apically notched or incised; lobes usually asymmetrical; epistome with rounded median anterior ridge. Lower lip, inner lobes varying from tall and narrow to broad and squat; outer lobes: from large and closely approximated to small, rounded and widely separated.

Mandible well developed. Molar present, basically with strong, apical, triturating surface, secondarily reduced, setulose or smooth, non-triturative. Spine-row strong, blades often thickened, pectinate, blade-like, or "molarized" (p. 29). Left lacinia multi-dentate (6-12+ teeth); right lacinia present in primitive subfamilies, lacking in advanced groups; incisor strongly toothed. Maxilla 1, inner plate small, with few (0-4) apical setae; outer plate with 9 (6-17) tall pectinate spines; palp large, 2-segmented, apically spinose and setose. Maxilla 2, inner plate shorter, often broader than outer, lacking facial row of setae, but inner margin usually with 1-2 large plumose setae. Maxilliped strongly developed; outer plate basically large, with convex outer margin, secondarily reduced, slender, columnar in form;inner plate often short, apex subtruncate, bearing setae and spines of large or small types , inner margin with masticatory setae or spines; palp large, semi-raptorial, segment 2 largest, segment 3 often produced apically beyond base of slender dactyl.

Coxae 1-4 usually large, deeper than corresponding peraeonal plates, increasing posteriorly; mid-point of hind margins occasionaly weakly processiferous; lower hind corner usually with small cusp(s); coxa 1 often short, modified; coxa 4 excavate behind.

Gnathopods 1 and 2 variously (often strongly) subchelate, occasionally simple, usually subsimilar (2 larger), occasionally sexually dimorphic; palm often with median tooth, postero-distal angle with stout spine cluster(s); carpus not longer than propod, hind lobe often narrow, deep; basis with setose anterior margin; dactyls with short unguis.

Peraeopods 3-7 normal, little modified, segments spinose, rarely setose, dactyls strong. Peraeopods 3 and 4 subequal (3 longer). Peraeopods 5-7 regularly homopodous (similar in size and form); coxae postero-lobate, usually rounded behind, occasionally ridged laterally; bases expanded, rounded behind, not distally narrowing, segment 4 variously overhanging shorter segment 5 behind.

Pleon side plates large, overlapping, hind corners usually acuminate, hind margin smooth or serrated. Pleopods large. Uropod 3, rami lanceolate, margins spinose (lacking plumose setae), inner ramus the longer, both rami longer than peduncle. Telson short to medium, with mid-ventral keel; margins smooth or setulose (not spinose); apex variously rounded, rarely incised.

Coxal gills primarily small and sac-like, secondarily large and plate-like, on peraeopods 2-6, rarely on peraeopod 7.

Brood plates on peraeopods 2-4 large, broad, on 5 small, margins with numerous simple setae.

Mature male typically smaller than mature female.

Taxonomic Commentary. Bousfield (1979, 1982a, 1983) established superfamily Leucothoidea to encompass the Pleustidae and other deep-plated, mostly smooth-bodied, micro-carnivorous, benthic inquilines and commensals, of fully marine environments. All have variously reduced or modified mouth-parts, non-glandular, prehensile, weakly ambulatory peraeopods with postero-lobate coxae 5-7; lanceolate, non-foliaceous uropod rami; and short, plate-like (usually keeled) telsons.

Originally included in the superfamily were the Pleustidae, Laphystiopsidae, Amphilochidae, Leucothoidae, Anamixidae, Maxillipiidae, Colomastigidae, Pagetinidae, Nihotungidae, Tulearidae, Stenothoidae, Thaumatelsonidae, and Cressidae. Subsequently, the family Colomastigidae was transferred to the Liljeborgioidea (near Sebidae - see Barnard, 1971); the Anamixidae was found to consist entirely of males of the genus *Leucothoides,* and may require submergence within Leucothoidae (see Thomas and Barnard, 1983). The status of Laphystiopsidae is uncertain; it is proving closely related to Lafystiidae, now transferred from superfamily Stegocephaloidea to the Leucothoidea (Bousfield, 1992).

In most character states, however, the Pleustidae appears to be the most plesiomorphic of all leucothoidean families and the most closely related, through a series of intermediate, isolated genera, to the superfamily Eusiroidea (see below; Shaw, personal comunic). In this regard, pleustid genera had originally been placed within the Paramphithoidae, one of the most advanced families of superfamily Eusiroidea, by Sars (1895) and earlier authors. However, despite these clinal linkages, the present study confirms the correctness of Stebbing's original decision (1906) to give formal recognition to this assemblage as a fully distinctive family, the Pleustidae.

Biogeographic commentary. The family Pleustidae consists of two main distributional entities, each of which exhibits strong internal taxonomic and phyletic relationships. One group (consisting of most subfamilies) is essentially Holarctic in distribution; its strongest diversity is centred in the North Pacific with its most primitive member confined to the deep sea (p. 53). By contrast, members of the group comprising the Atylopsinae, Austropleustinae, and Stenopleustinae, are mainly austral or confined to the North Atlantic and adjacent Arctic region. Of these, subfamily Stenopleustinae is most like some advanced northern subfamilies. However, some of the apparent similarities are homoplasious (p. 52). Evolutionary processes within family Pleustidae appear to be very complex and still not fully understood.

SUBFAMILIES OF PLEUSTIDAE

ATYLOPSINAE, new subfamily

Calliopiidae Stebbing, 1906: 299 (partim).—J. L. Barnard 1969a: 167.

Eusiridae H. G. Andres, 1986.—Barnard & Karaman, 1991: 284.

Type genus. *Atylopsis* Stebbing, 1888: 294.—Barnard & Karaman, 1991: 308. (Type species - *Atylopsis emarginatus* Stebbing, 1888).

(CONT'D ON P. 34)

KEY TO SUBFAMILIES OF PLEUSTIDAE

1. Coxal gill present on peraeopod 7 in some or all members; maxilliped palp segment 3, apex oblique, more or less produced beyond base of dactyl (Fig.S K); dactyl slender, non-pectinate (Fig. 5 K) or weak or lacking (Fig. 5 M); pleon plate 3 often rounded and/or serrated behind (Figs. 2m; 6 F); telson keeled keeled centrally (Fig. 3 W), often cleft or notched apically .... 2.

—Coxal gill lacking on peraeopod 7; maxilliped palp segment 3 apically truncate or rounded (Fig. 5 L), if oblique and produced, dactyl is straight, pectinate [Fig. 5 (1)]; pleon plate 3 subquadrate, hind corner usually acuminate or produced, hind margin not serrated (Figs. 6 C, 1): telson keeled proximally (Fig. U. V, X), or if centrally, rostrum elongate (Fig. 3 B)A, B) .... 4.

2. Upper lip with shallow notch, lobes subsymmetrical (Figs. 4A,B)); lower lip, inner lobes small, narrow, outer lobes large, little separated (Fig. 4I); maxilla 2 inner plate with 2-3 stout facial setae; mandibular blades slender, weakly pectinate (Fig. 5A) .... **Atylopsinae** (p. 34).

—Upper lip deeply notched, lobes asymmetrical (Fig. 4 E); lower lip, inner lobes large, wide, outer lobes small, widely separated (Figs. 4 L,M); maxilla 2, inner plate lacking stout marginal plumose setae; mandibular blades short, pectinate (Fig. 5 H) .... 3.

3. Gnathopods weakly subchelate or simple, subequal IFigs. 6 A, B; 6(0), P); carpus and propod elongate, palm of propod , median tooth lacking; telson often apically cleft .... **Austropleustinae** (p. 34)

—Gnathopods often strongly subchelate, rarely subequal (2 larger. often of different form) (Figs. 6 G, H); carpus of gnathopod 2 not elongate, deep (Figs. 6 J, M), palm of propod with median tooth (Figs. 6 Q, R); apex of telson entire (Fig. 3S) .... **Stenopleustinae** (p. 35)

4. Mandibular molar normal, with strongly triturative apex (Figs. 5 A-D); coxa 1 bent forwards distally, apex often acute (Fig. 2P); antenna 1, peduncular segment 1 often with acute distal process (Figs. 40, P) 5.

—Molar reduced, apex smooth or setulose, non-triturative (Figs.4 E, F); coxa 1 normal, not bent forwards distally (Fig. 1 D, 2 L); antenna 1, peduncular segment 1 not produced distally as acute process .... 8.

5. Mandibular right lacinia present, blade-like (Fig.S D); left lacinia with few (6-8) teeth (Fig. 5 A, C, D); urosome segment 2 not occluded dorsally (Fig. 7); maxilliped, outer plate broad, outer margin convex (Figs. 5 L, O); lower lip, inner lobes narrow, deep. (Figs. 4 H, I, J) .... 6.

—Right lacinia lacking; left lacinia with many (8+) teeth; urosome 2 occluded dorsally (or nearly so); maxilliped outer plate narrow, columnar (Figs.S J, N); lower lip, inner lobes squat, wide (Fig. 6 N) .... **Pleusymtinae** (p. 37)

6. Telson keeled proximally (Figs. 3 V, X); rostrum medium extending little beyond lateral head lobe (Figs. 3 E; 7); mandibular molar medium, apex with triturative ridges marginally only (Figs. 5 C,D); gnathopods subsimilar in form and size; palm of propod lacking median tooth (Figs.6 A, B; 6 J,K) . . 7.

—Telson keeled centrally (Fig. 3 W); rostrum strong, extending well beyond lateral head lobe (Fig. 2 P); mandibular molar strong, apex with full triturative ridges (Fig. 5A); gnathopods strongly dissimilar in form and size (Figs.6G, H); propod palms with median tooth .... **Mesopleustinae** 36)

7. Body medium to large, mid-dorsally and dorso-laterally ridged or carinated (Fig. 2O); gnathopods "melphidippoidean" in form (lower margin of carpus straight); antenna 1, peduncle 1 distally truncate, unproduced ....**Pleustoidinae** (p. 37)

—Body small, smooth above (Fig. 7); gnathopods ordinary, carpal lobe rounded below (Fig.7 detail); antenna 1, peduncle 1 usually with acutely produced distal process (Figs. 7 detail; 40,P). . **Eosymtinae** (p. 37)

Key to Subfamilies (cont'd)

8. Gnathopod propods lacking median palmer tooth; upper and lower lips of intermediate type (Figs. A D; 4K, L); uropod 1 with strong disto-lateral peduncular spine . . . . 9.
—Gnathopod propods with median palmar tooth; upper and lower lips of advanced type (Figs. 4E-G; 4M, N); uropod 1 with strong disto-lateral penduncular spine . . . . 11.

9. Body strongly carinated (Figs. 1 E, F); rostrum strongly developed (Figs. 3A-C); mandibular molar reduced to stub, setulose (Fig. 5 F); mandibular palp segment 3 usually with many (5+) basal "A" setae . . . . **Pleustinae** (p. 39)
—Body smooth above; rostrum little exceeding lateral head lobe (Figs. 3 D, E); mandibular molar inflated, apex smooth (Fig, SE); mandibular palp segment 3 lacking basal "A" setae . . . . 10.

10. Urosome 2 dorsally occluded (or nearly so) (Fig. 10); peraeopod dactyls normal, simple; gnathopods powerfully subchelate, "eusiroidean" in form (Figs. 6 D, E); uropod I with weak disto-lateral spine . . . . **Pleusirinae** (p. 39)
—Urosome 2 not occluded dorsally (Fig. 2N); peraeopod dactyls small, inner surface finely crenulated; gnathopods weakly subchelate, propod and dactyl elongate, shallow (Figs .6 A, B); uropod 1 lacking disto- lateral peduncular spine . . . . **Dactylopleustinae** (p. 38)

11. Body usually dorsally carinate or mucronate, especially on pleon (Fig. 2 (I)); rostrum medium, extending beyond lateral head lobe (Fig. 2M); mandibular blades normal, slender; urosome 2 not fully occluded dorsally; coxae 1-3, lower hind cusps strong (Figs. 3G, H . . . . **Neopleustinae** (p. 40)

—Body dorsally smooth; rostrum short, not extending beyond lateral head lobe (Fig. 3 D); mandibular blades often strongly thickened or molarized (Fig. 5 F); urosome 2 dorsally occluded; coxae 1-3, hind cusps very weak or lacking (Fig. 3 J) . . . . **Parapleustinae** (p. 41)

(ATYLOPSINAE - CONT'D FROM P. 32))

Genera. One new genus based on *Pleustoides mediterraneus* Ledoyer, 1986; to be described (Bousfield & Hendrycks, in prep., Part III).

Diagnosis: Body smooth or dorsally mucronate. Urosome 2 not dorsally occluded. Antennae slender; antenna 1, peduncular segments 2 and 3 short; basal flagellar segments weakly conjoint, possibly callynophorate (*sensu* Lowry, 1986). Accessory flagellum minute.

Upper lip, median notch shallow, lobes subsymmetrical. Lower lip, inner lobes small, outer lobes large, little separated. Mandible, molar large, triturating surface fully ridged, medial marginal plumose, flagellum strong; left lacinia 5-6 dentate; right lacinia present, tricuspate or chisel-like; blades of spine row slender, weakly pectinate; palp segment 2 widened, segment 3 basally with 1-2 "A" setae. Maxilla 1, outer plate with 9-11 apical spines; inner plate with 1-4 apical seta(e); palp segment 1 narrow, segment 2, subapically setulose. Maxilla 2, inner plate little expanded, with 2-3 stout facial setae. Maxilliped, outer plate large, medially broadest and convex; inner plate tall, apex with "button" spines; palp segment 3, apex oblique, typically extending beyond base of smooth, slender dactyl.

Coxal plates 1-4 shallow, 4th weakly excavate behind, lower hind corners lacking cusps. Gnathopods slender, weakly subchelate or simple; carpus and propod slender, hind margins shallow, setose; palmer margin lacking median tooth; dactyls often serrate.

Peraeopods 3-7 slender, segment 4 little overhanging segment 5 proximally, dactyls slender. Peraeopods 5 to 7 homopodous or heteropodous, 7 longest.

Pleon plates 1-3, hind corners, obtuse or subquadrate, little produced. Uropods 1 and 2 slender; uropod 1 lacking latero-distal peduncular spine. Uropod 3, rami slender, elongate, subequal or unequal.

Telson apically cleft, notched, or entire; keel not described in any species (weakly present?).

Coxal gills on peraeopods 2-7 slender, sac-like. Brood plates large, broad on peraeopods 2-4, smaller on peraeopod 5 (Stebbing, 1888).

Taxonomic Commentary. The plesiomorphic character states are best retained in species of *Atylopsis*. *"Pleustoides" mediterraneus* Ledoyer, 1986, appears to consist of two species, both in a genus distinct from *Pleustoides* Gurjanova, 1972. The genus is to be described elsewhere (Bousfield and Hendrycks, in prep., Part III). Although not quite complying with the typical form of the maxilliped palp, peraeopods 5-7, and telson, the generic group is provisionally placed within the Atylopsinae until the types can be fully redescribed.

AUSTROPLEUSTINAE, new subfamily

Type Genus. *Austropleustes* K.H Barnard, 1931: 428. (TYPE species - *A. cuspidatus* K.H Barnard, 1931: 428).

Genera. *Tepidopleustes* Karaman & Barnard, 1979: 113. (TYPE species - T. *barnardi* [Ledoyer, 1972]: 262).

Diagnosis. Body small to medium. Pleon and posterior peraeonal segments toothed dorsally. Urosome 2 not occluded dorsally. Rostrum medium, slightly exceeding lateral headlobe, weakly keeled. Eyes large, subtriangular or rhomboidal. Antennae long, slender; antennae 1, peduncular segments 2 and 3 short; accessory flagellum very small but distinct, 1-segmented (fide Lincoln).

Upper lip deeply notched; lobes asymmetrical. Lower lip, inner lobes shallow, wide; outer lobes oblique, rounded.

Mandible, molar reduced, apex with small grinding surface or minutely spinulose and setulose; spine-row short to medium, with 3-12 slightly modified blades; left lacinia normally 8-12 dentate; right lacinia present, bidentate (multicuspate - fide Lincoln); palp segment 3 with 2 basal "A" setae segment 2 weakly setose. Maxilla 1, outer plate with 9 apical spines; inner plate with single apical seta; palp slender . Maxilla 2, inner plate not broadened, lacking inner submarginal plumose seta(e). Maxilliped outer plate widest basally, outer margin convex distally, inner margin setose; inner plate short, apex with few "button" spines; palp segment 3 elongate, apex oblique, produced beyond base of slender, non-pectinate dactyl that may be reduced or lacking.

Coxal plates 1-4 small, shallow, regularly increasing, not covering leg bases; lower margins rounded, hind cusp small or lacking, Gnathopods weakly subchelate or simple, subsimilar in form and size, (not sexually dimorphic?); bases weakly setose antero-distally; carpus shallow, elongate (>1/2 propod); propod shallow, palm short, oblique, lacking median tooth, hind margin setose.

Peraeopods 3-7 slender; segment 6 longest, 4 weakly overhanging 5, dactyls strong. Peraeopods 5-7 variably heteropodous, longest posteriorly; bases somewhat dissimilar in size and form, lobate.

Pleon plates subquadrate or rounded behind, posterior marginfinelyserrate. Uropods 1 and 2, outer ramus distinctly the shorter; uropod 1 with disto-lateral peduncular spine usually lacking. Uropod 3, outer ramus variably shorter than inner; peduncle may be produced distally beneath inner ramus. Telson short, apically cleft or rounded, keeled centrally.

Coxal gills on peraeopods 2-7, small, sac-like. Brood plates undescribed.

Taxonomic Commentary. Despite some plesiomorphic character states, subfamily Austropleustinae consistently clusters with the advanced pleustid subfamilies (p. 88). Its closest affinities are with the Stenopleustinae, linked via the genus *Arctopleustes,* especially in the rounded coxal plates, produced form of the maxilliped palp, and slender, nonpectinate dactyl, rounded and serrated pleon plates, and centrally keeled telson. Within subfamily Austropleustinae, the genus *Tepidopleustes* is distinguished by its reduced maxillipedal dactyl and by the lack of a distal peduncular process on uropod 3.

STENOPLEUSTINAE, new subfamily

Type Genus. *Stenopleustes* Sars, 1895: 354. (TYPE species - *S. malmgreni* (Boeck, 1871).

Genera. *Sympleustes* Stebbing, 1899: 209. (TYPE species - *S. latipes* (M. Sars, 1858); *Arctopleustes* Gurjanova, 1972. (TYPE species - *A. rasmyslovi* (Gurjanova, 1951). Two other genera, one based on *Sympleustes olriki* Hansen, 1887, and the other on *Stenopleustes gracilis* Holmes, 1905, to be described (Bousfield & Hendrycks, part III, in prep.).

Diagnosis. Body small to medium, pleon occasionally dorsally mucronate or toothed. Urosome 2 not occluded dorsally. Rostrum medium (p. 19). Anterior head lobe acute or subacute, rarely notched. Eyes large, subrectangular. Antennae slender, elongate:antenna 1, basal flagellar segments often conjoint; peduncular segment 3 short. Accessory flagellum minute or lacking.

Upper lip deeply notched, lobes asymmetrical. Lower lip, inner lobes shallow; outer lobes moderately separated, oblique. Mandible, molar weakly to strongly triturative, narrowing distally and/or compressed, grinding surface with "cobbled" core and marginal ridges or projecting teeth; spine-row short, blades normal or thickened and pectinate, inter-blade setae numerous; left lacinia multi-dentate (8+ teeth); right lacinia present, but reduced blade-like, or vestigial; palp large, segment 3 often lacking "A" setae. Maxilla 1, outer plate with 6-7 apical spines; inner plate with 1(0-3) apical seta; palp normal. Maxilla 2, inner plate narrow, lacking marginal plumose seta(e). Maxilliped, outer plate medium, broadest basally, distal outer margin and apex convex, inner margin of a cutting type, scalloped or indented in one genus; inner plate medium, apex with "button" spines; palp segment 3, apex oblique, extended acutely beyond base of slender, non-pectinate dactyl.

Coxae 1-4 medium deep, lower margins rounded, weakly (or not) cusped behind; coxa 1 normal or expanded distally. Gnathopods of three main types: (1) subsimilar, slender, weakly to moderately subchelate, carpus and propod shallow (*Stenopleustes* type), (2) strongly subchelate, but dissimilar in size (*Sympleustes* type) and (3) grossly dissimilar in size and form, gnathopod 1 weakly subchelate (*Arctopleustes* type). In all three types the bases are setose anteriorly; the merus has an acute postero-distal process, the carpus of gnathopod 1 is elongate (>2/3 propod); the propod palm has a median tooth; and the posterior margin is setose.

Peraeopods 3-7 slender to strong, dactyls slender. Peraeopods 5-7 homopodous; coxae deep; bases broad;

segment 4 often strongly overhanging 5; dactyls distinctly larger than in peraeopods 3 & 4.

Pleon plates normal, hind corner acuminate, hind margins smooth or serrated. Uropods 1 and 2 long; uropod 1, rami subequal, latero-distal peduncular spine small or lacking. Uropod 3, rami long unequal. Telson rounded behind, keeled centrally.

Coxal gills on peraeopods 2-6, occasionally on peraeopod 7, small, sac-like. Brood plates large, broad.

Taxonomic commentary. This medium-sized subfamily (about a dozen species in 5 genera) is marginally included in the advanced group of subfamilies (p. 45). Members retain several important plesiomorphic traits, notably the triturative molar, the right lacinia, the convex form of the maxilliped outer plate, the conjoint proximal flagellar segments of antenna 1, the unoccluded urosome 2, and the sac-like coxal gills, present on peraeopod 7 in one genus. The subfamily is closely related to the Austropleustinae (p. 51), yet apparently shares an atylopsinid ancestry (p. 52). Stenopleustinids also share some characteristics with neopleustinids but the form of the maxilliped palp is apparently convergent.

Biogeographical commentary. Members of all five genera are restricted to intermediate shelf waters of the North Atlantic and adjacent Arctic regions. One species (of the most southerly genus) also occurs off the coast of California.

MESOPLEUSTINAE, new subfamily

Pleustidae Stebbing, 1906 (partim): 315.—Gurjanova, 1951 (partim): 634.—Barnard, 1969a (partim): 422.—Barnard & Karaman, 1991 (partim): 648.

Type genus. *Mesopleustes* Stebbing, 1899: 209. (TYPE species - M. *abyssorum* [Stebbing, 1888].

Diagnosis. Body robust, weakly carinated. Urosome 2 not occluded dorsally. Rostrum strong. Antenna 1, peduncular segments 2 and 3 elongate. Accessory flagellum minute. Eyes unpigmented.

Upper lip shallowly notched, lobes weakly asymmetrical. Lower lip, inner lobes indistinct; outer lobes large, little separated. Mandibular molar strong, triturating surface fully ridged, medial marginal plumose setae present; distal molar process or hump weak; blades of spine-row simple; left lacinia 6-dentate, right lacinia present, bifid; palp medium, segment 3 lacking "A" setae. Maxilla 1, outer plate with 10-11 apical spine-teeth; inner plate with 4 apical setae; palp segment 1 with lateral wing-like process. Maxilla 2, inner plate not expanded, with 1 (normally) submarginal plumose setae. Maxilliped, outer plate large, broadest medially, with convex outer margin; inner plate tall, with 3-6 apical spines; palp segment 3, apex subtruncate, not produced beyond pectinate dactyl.

Coxae 1-3 narrow, deep, hind corners with cusps; coxa 1 sharply bent forward distally. Gnathopods strongly subchelate, dissimilar in size and form (2 larger); bases setose anteriorly; carpus short, deep; propod posterior margin strongly setose and/or spinose, palmar margin with proximo-median tooth, that of gnathopod 2 medially excavate.

Peraeopods 3-7 stout, spinose; bases of 5-7 with strong postero-distal lobes; segment 5 short, strongly overhung proximally by segment 4; dactyls strong.

Pleonal plates, hind corners acuminate, hind margins smooth. Uropods 1 and 2 strong, spinose; uropod 1 lacking disto-lateral peduncular spine. Uropod 3, outer ramus distinctly the shorter. Telson short, keeled centrally, apex weakly incised or entire, penicillate setae distally inserted.

Coxal gills plate-like, on peraeopods 2-6, lacking on P7. Brood plates unknown.

Taxonomic commentary. This monotypic group retains a number of plesiomorphic character traits including the elongate peduncular segments of antenna 1, complete triturating molar ridges and plumose flagellum, 6-dentate left lacinia and bifid right lacinia, 11 apical spines of maxilla 1 outer plate; and broad maxilliped outer plate and of Pleustoidinae (see phenogram and cladogram (pp. 51-52). However, its advanced character states, including the form of coxa 1, gnathopods, uropod 3, telson, and coxal gills combine some features of both the Pleusymtinae and Stenopleustinae.

Distributional Commentary. Abyssal; mainly Indo-Pacific. A phyletic and biogeographically relict group.

PLEUSTOIDINAE, new subfamily

Type Genus. *Pleustoides* Gurjanova, 1972: 134. (TYPE species - P. *carinatus* Gurjanova, 1972).

Diagnosis. Body dorsally and laterally carinated. Urosome 2 not occluded above. Rostrum short. Eyes reniform. Antennae slender; antenna 1, segment 3 short. Accessory flagellum unknown.

Upper and lower lips not described but presumed plesiomorphic. Mandibular molar strong, grinding surfce with smooth central core and radiating ring of triturating ridges; plumose flagellum not described (probably present?); spine row short, blades slender; left lacinia 6-7 dentate?; right lacinia bifid, blade-like (?); palp segment 3 apparently with one basal "A" seta; posterior marginal setae elongate. Maxilla 1, outer plate with 9 apical spines(?); inner plate with 1-2 apical plumose setae; palp broad, outer margin setose. Maxilla 2, inner plate small, little broadened, with 2(3) submarginal plumose setae. Maxilliped, outer plate large, broadest proximally, outer margin convex distally, inner margin spinose; inner plate tall, apex with stout spines; palp segment 2 elongate, segment 3, apex rounded, unproduced.

Coxae 1-4 medium deep, lower margins straight; coxa 1 distally bent forward, subacute. Gnathopods of "melphidippoidean" type (i.e. strongly subchelate, closely subequal, carpus and propod elongate, carpus with shallow, straight, setose hind lobe, propod palm oblique, untoothed, exceeded by dactyl); basis weakly to moderately setose anteriorly.

Peraeopods strong, segments elongate, segment 4 strongly overhanging segment 5. Peraeopods 5-7, bases slightly heteropodous, increasing posteriorly. Dactyls not described.

Pleon plates deep, broad, hind corners acute, hind margin smooth. Uropods I and 2, rami elongate, unequal; uropod 1 apparently lacking disto-lateral peduncular spine. Uropod 3, rami slender, unequal. Telson elongate, notched apically, keeled proximally.

Coxal gills and brood plates undescribed.

Taxonomic commentary. Although original material has not been re-examined, Gurjanova' s descriptions and figures of species of *Pleustoides* suggest a unique genotype that cannot be placed within the other 11 subfamilies here described. No other subfamily group exhibits the combination of dorso-laterally ridged or carinated body, small rostrum, elongate maxilliped palp, short basal segment of the maxilliped outer plate, and "melphidippoidean" gnathopod. As far as can be determined, features of the mouthparts are basically plesiomorphic (Table I) and ally it most closely with subfamilies Eosymtinae and Mesopleustinae.

As noted elsewhere (p. 33), the Mediterranean genus *Pleustoides* of Ledoyer (1986) differs from Gurjanova's western Pacific genus in several major character states, notably the heteropodous condition of the peraeopods, form of the gnathopods, and various peculiarities of the mouthparts. Ledoyer' s form is tentatively given new generic status within subfamily Atylopsinae.

EOSYMTINAE, new subfamily

Type Genus. *Eosymtes,* new genus [p. 43]. (TYPE Species - *Eosymtes minutus,* new species [p. 43].

Genera. One additional new genus and new species, to be described in Bousfield & Hendrycks, Part IV, in prep.

Diagnosis. Small, smooth-bodied, pleustids exhibiting mainly plesiomorphic character states. Urosome 2 not dorsally occluded. Rostrum medium. Anterior head lobe rounded to subacute; inferior sinus shallow to medium deep. Eye medium, reniform or round. Antenna 1 slender, flagellar segments few (10-17); peduncle 1 distally processiferous, segments 2 & 3 not markedly reduced. Accessory flagellum minute.

Buccal mass shallow, regressed beneath head. Upper lip shallowly notched, lobes weakly asymmetrical. Lower lip, inner lobes narrow; outer lobes large, not widely separated. Mandible, molar strong, triturative face with smooth core and peripheral ridges or teeth, medio-distal plumose flagellum, and distal medial hump; spine-row short, blades acute, distally pectinate; left lacinia 6-8 dentate, right lacinia present, bifid, blade-like; incisor irregularly dentate; palp medium, slender; segment 3 with single basal "A" seta, and simple or weakly pectinate distal marginal setae. Maxilla 1, inner plate with 12 apical plumose setae; outer plate with 9 apical spines; palp slender, segment 1 regular. Maxilla 2, inner plate slightly broadened, submarginally with 2 stout plumose setaea. Maxilliped, outer plate medially widest and convex; inner plate tall, apex with outer slender spines and inner stout spines; palp slender, segment 2 longest, segment 3, apex rounded, not produced distally.

Coxal plates 1-3 medium shallow, hind corners cuspate; coxa 1 shortest, distally bent forwards. Gnathopods strongly subchelate subequal (2 larger); margins of bases nearly bare; carpus medium short, hind lobe deep; propod longer than carpus; palmar margin smooth, convex, lacking median tooth, hind margin bare.

Peraeopods 3-7 slender, segment 4 weakly overhanging 5; dactyls elongate. Peraeopods 5-7 basically homopodous, coxae medium to deep, posterolobate; bases broad, subsimilar.

Pleon plates broad, hind corners square or acuminate. Pleopod 3, outer margin of peduncle setose. Uropods 1 and 2 slender, rami narrow, unequal to subequal; uropod 1 with a small disto-lateral peduncular spine. Uropod 3, rami markedly unequal. Telson medium long, apex slightly incised or entire; keeled proximally.

Coxal gills on peraeopods 2-6, small, slender, sac-like. Brood plates 2-5 broad, deep, margins with few long setae.

Etymology. From the Greek root *"Eo"* (dawn or early) and *"symtes"* (suffix of *pleusymtes*), in reference to its plesiomorphic character states, many of which appear ancestral to those of subfamily Pleusymtinae.

Taxonomic commentary. This small generic grouping is readily placed within the primitive group of pleustid subfamilies, close to Mesopleustinae and Pleustoidinae (p. 36). Many of its features e.g. of antennal peduncle, mouthparts, coxal plates, uropods, and telson would seem antecedent to subfamily Pleusymtinae of the advanced subgroup of families within Pleustidae (Table II, Fig. 9).

PLEUSYMTINAE, new subfamily

Type Genus. *Pleusymtes* Barnard, 1969a: 425. (TYPE species *Pleusymtes glaber* (Boeck, 1861).

Genera. *Pleustomesus* Gurjanova, 1972. [TYPE species - *Pleustomesus medius* (Goes, 1866). Six new genera, mostly monotypic, are to be described in Bousfield and Hendrycks, Part IV, in prep. One genus is based on *Incisocalliope karstensi* Barnard, 1959a (Arctic); another on *Pleusymtes coquillus* Barnard, 1971 (North Pacific); and the other four genera on new species from the western North Pacific shelf region.

Diagnosis. Body small to medium, slender, dorsally smooth, rarely toothed. Urosome 2 dorsally occluded (or nearly so). Rostrum short (rarely long). Anterior head lobe typically acute; inferior sinus produced acutely below antenna 2. Eye large, subrotund or rhomboidal. Antennae slender; antenna 1, peduncular segment 1 elongate and distally processiferous; segments 2 and 3 short. Accessory flagellum minute or lacking.

Upper lip deeply notched, lobes asymmetrical. Lower lip squat, inner lobes shallow, wide, outer lobes oblique, rounded. Mandible, molar strong, triturating surface nearly smooth (rarely pebbled), pavement-like, margins sharp, even; blades of spine row few (5-10), stout, pectinate, distal blade(s) occasionally chisel-shaped; left lacinia 6-11 dentate, right lacinia lacking; palp slender, segment 3 with single basal "A" seta. Maxilla 1, outer plate with 9 apical spines; inner plate small, with 1 (rarely 2) apical seta; palp medium to broad, segment 1 with weak outer marginal lobe and seta(e). Maxilla 2, inner plate broadened, with single marginal plumose seta. Maxilliped, outer plate broadest basally, outer margin curved distally, apex subtruncate, slender-spinose; inner plate short, apex with "button spines", inner marginal setae numerous (4-9). Palp segment 3 apically rounded or truncate, not produced; dactyl long, micropectinate.

Coxal plates 1-4 large, covering leg bases, increasing posteriorly, subquadrate below, hind corners of 1-3 cuspate; coxa 1 distinctly smallest, distally narrowing and often bent forward. Gnathopods relatively strongly subchelate, subequal, weakly sexually dimorphic; bases variously setose anteriorly; merus (segment 4) with acute postero-distal process; carpus usually short, hind lobe deep; propod as deep as carpus, median palmar tooth small (rarely lacking); hind margin short, weakly setose, or bare.

Peraeopods 3-7 generally slender; segment 4 distinctly overhanging 5; dactyls slender, long. Peraeopods 5-7 homopodous; coxae deep, bases broad, lobate behind.

Pleon plates deep, hind corners usually acuminate, produced, or upturned, hook-like, hind margins smooth. Pleopod 2 or 3 may be sexually dimorphic. Uropods 1 & 2 slender, spinose; rami of uropod 1 subequal or unequal; uropod 1 with a strong disto-lateral peduncular spine. Uropod 3, rami unequal, narrow, spinose. Telson rounded or subacute apically, keeled proximally.

Coxal gills large, sac-like on peraeopods 2 & 3, plate-like on peraeopods 4-6. Brood plates normal.

Taxonomic Commentury. This large subfamily (about 30 species in 8 genera, half in *Pleusymtes*) is clearly a member of the advanced group of subfamilies (p. 47), although several important character states (e.g. of mandibular molar, maxilliped outer plate) are intermediate. Its immediate ancestry within the group of primitive subfamilies would seem closest to the Eosymtinae, with which it shares a number of similarities of the antennae, mouthparts, coxal plates, peraeopods, and telson.

Biogeographical Commentary. Of the eight genera within subfamily Pleusymtinae, five are endemic to the North Pacific region. The other three genera (especially *Pleusymtes*), containing most of the species, are mainly arctic and subarctic, penetrating southwards mainly in the North Atlantic region.

DACTYLOPLEUSTINAE, new subfamily

Pleustidae Barnard & Karaman, 1991 (partim): 544.

Type Genus. *Dactylopleustes* Karaman & Barnard, 1979: 112. (TYPE species - *Parapleustes echinoicus* Tzvetkova, 1975, original designation.)

Diagnosis. Body small, smooth, deep-plated. Urosome 2 not dorsally occluded. Rostrum medium. Lateral head lobe rounded. Eyes reniform. Antennae short, subequal, subpediform; antenna 1, peduncular segments 2 and 3 short. Accessory flagellum lacking.

Upper lip shallowly notched, lobes weakly asymmetrical. Lower lip, inner lobes deep, outer lobes oblique. Mandible, molar large, inflated, apical surface non-triturative; blades of spine-row slender, unmodified; left lacinia 6-7 dentate, right lacinia lacking; palp slender, segment 3 lacking "A" setae. Maxilla 1, outer plate short, broad, apical spines 9-16, variable in type; inner plate with one apical seta; palp broad, segment 1 large. Maxilla 2, plates little broadened, outer plate with strong apical spines; inner with 1 marginal plumose seta. Maxilliped, outer plate narrow, basally broadest, outer margin distally convex, inner margin concave; inner plate shon, apex oblique, with 1-2 "button" spines; palp segment 2 shon; segment 3 distally rounded.

Coxae 1-4 deep, covering leg bases; lower margins quadrate, with multiple hind cusps; coxa 1 distinctly the shortest. Gnathopods small, slender, weakly subchelate; basis setose anteriorly; carpus elongate (= propod), lobe shallow; propod palm short, smooth, hind margin setose; dactyl short, stout, overlapping palm.

Peraeopods 3-7 short, margins finely spinose; dactyls short, inner margins finely crenulate or pectinate. Peraeopods 5-7 homopodous but trending to heteropody in one species; coxae very deep postero-lobate; bases variably broadened.

Pleon plates broad, hind corners acuminate. Pleopods relatively weak, rami few-segmented (<10). Uropods 1 and 2 short, rami broad-lanceolate, subequal, inner ramus appearing sexually dimorphic in two species; uropod 1 lacking disto-lateral peduncular spine. Uropod 3 short, rami broadly lanceolate, unequal.

Telson apically rounded, keeled proximally.

Coxal gills sac-like on peraeopods 2-4, plate-like on peraeopods 5 and 6. Brood plates medium broad and relatively small.

Taxonomic Commentary. This monotypic group contains three known species that may represent two or more distinct genera (Bousfield and Hendrycks, Part II, in prep.). The antennae, mouthparts, and peraeopods are specialized, apparently for commensal relationship with echinoids (Tzvetkova, 1975). The overall body plan, however, is plesiomorphic. The peculiar mixture of plesio- and apomorphic character states of subfamily level characters (above) prevents assignment of the group to any of the other subfamilies here defined. Cladistically, it appears remote from most other groups, although its affinities are closest to the Pleustinae and Pleusirinae (Figs. 8, 9).

Biogeographic Commentary. Member species occur in association with echinoids in littoral habitats of the North Pacific region.

PLEUSTINAE, new subfamily

Pleustidae Stebbing, 1906: 310 (partim).—Barnard, J. L., 1969: 421 (partim).—Gurjanova, 1951: 634 (partim).—Barnard & Karaman, 1991: 644 (partim).

Type Genus: *Pleustes* Bate, 1858: 362.—Stebbing, 1906: 309.—Gurjanova, 1951: 635.—Barnard & Karaman, 1991: 650.

Genera. The subfamily is presently monotypic. However, three subgenera of *Pleustes* (each possibly of full generic status) are to be described by Bousfield & Hendrycks, Part 11., in prep. The nominate subgenus is based on the TYPE species, *Pleustes tuberculata* Bate, 1858. A second subgenus is based on *Pleustes angulatus* Shoemaker, 1955, and a third is based on *Pleustes depressus* Alderman, 1936.

Diagnosis. Body stout, broadest between peraeon segments 3-5, and carinate or toothed variously on peraeon, pleon, and urosome. Urosome 2 nearly dorsally occluded. Rostrum strongly developed, often sexually dimorphic. Eyes large, roundish, protruding from head surface. Antennae medium, slender. Antenna 1, peduncular segment 3 very short. Accessory flagellum lacking.

Upper lip, median notch shallow, lobes slightly asymmetrical. Lower lip, inner lobes medium, deep, outer lobes large, oblique, moderately separated. Mandible, molar very small, conical, apex pilose, non-triturative. Spine-row long, blades numerous (14-30+), slender to medium, tips pectinate; left lacinia 7-8 dentate right lacinia lacking; incisor irregularly toothed; palp relatively short, segment 3 with two basal clusterof "A" setae, rarely none. Maxilla 1, outer plate with 9 apical spines; inner plate with 1 subapical seta; palp medium, segment 1 with prominent setose lateral process. Maxilla 2, inner plate broadened, short, with 1 submarginal plumose seta or lacking. Maxilliped, outer plate narrow, basically columnar (outer margin may be slightly convex), inner margin setose, apex rounded, spinose; inner plate short, broad, apex oblique, with stout spines; palp stout, apex of segment 3 rounded, slightly extending beyond base of short dactyl, armed medially with pectinate spines.

Coxal plates 1-4 very deep, broad, covering leg bases; lower margins truncate or scalloped, hind cusps small; coxa 1 hatchet-shaped, covering lower head; coxa4 with posterior process. Gnathopods large, powerfully subchelate, subequal, not sexually dimorphic; basis slender, anterior margin setose; merus with acute postero-distal process; carpus very short, hind lobe narrow, deep; propod, palm smoothly convex, lacking median tooth, often with outer marginal spines, inner marginal spines few (3-5), subequal, clusters of spines at posterior angle; hind margin short, bare.

Peraeopods 3-7, segment 4 strongly overhanging 5; dactyls short to medium, stout. Peraeopods 5-7 stouter than 3-4, homopodous; coxae acute behind, laterally ridged; bases narrowed, ribbed.

Pleon plates deep, hind corners acute, hind margins smooth. Uropods 1-2, rami long, serially spinose; uropod 1, rami subequal disto-lateral peduncular spine very small. Uropod 3 long, rami unequal. Telson short, broad, subtruncate, keeled proximally.

Coxal gills large, pallet-like on peraeopods 2 and 3, platelike on 5 and 6. Brood plates normal.

Taxonomic conunentary. The Pleustinae is a moderately advanced and very distinctive subfamily group (p. 47). The mouthparts embrace both plesiomorphic and apomorphic character states (Tables I & II). The latter include a non-triturative mandibular molar, columnar outer plate of the maxilliped, powerfully subchelate gnathopods with short, deep carpus, and strongly modified coxae and bases of peraeopods 5-7. However, the strongly rostrate head and carinated body, weakly modified upper and lower lips, and strong apical spines of the inner plate of the maxillipeds are considered plesiomorphic. The sexually dimorphic rostrum, dissimilar sizes of peraeopods 3-4 and 5-7 and the bicarinate urosome are apomorphies unique to the Pleustinae. However, they are remarkably congruent with corresponding features of the enigmatic Lafystiidae (p. 48) that live in ectoparasitic relationship with cold-temperate benthic fishes of the region.

Distributional Ecology. To date, members of this subfamily have been recorded only from high-salinity, summer-cold waters of the North Pacific, North Atlantic, and Arctic seas. Shallow-water species are associated with rocky coastlines where they cling to large kelps and benthic algae, or to sponges and colonial invertebrates. Many are beautifully maculated, in all colours from nearly pure white to almost black (Bousfield, 1985). Some mimic the shells of mitrellid snails (Crane, 1969; Field, 1974). The thick, heavily armoured bodies and slow rate of ecdysis (of larger instars) render these animals attractive substrata for temporary settlement of barnacles and other fouling organisms (Slattery & Oliver, 1987).

PLEUSIRINAE, new subfamily

Pleustidae Barnard, 1969b: 198-204 (partim).—Gurjanova, 1972:135 (partim).—Barnard & Karaman, 1991: 644 (partim).

Type Genus. *Pleusirus* J. L Barnard, 1969b: 204.—Barnard & Karaman, 1991: 650. (Type species - P. *secorrus* Barnard, 1969b).

Diagnosis: Body small, smooth. Urosome 2 dorsally occluded. Rostrum medium. Lateral head lobe broadly rounded. Eyes rounded. Antenna slender, short to medium in length; antenna 1, peduncular segments 2 & 3 short. Accessory flagellum minute.

Upper lip moderately incised, lobes asymmetrical. Lower lip, inner lobes weakly defined, deep; outer lobes large, rounded, moderately separated. Mandible, molar large, inflated, apex broadly rounded, surface smooth, nontriturative; spine-row short, blades thickened, pectinate; left lacinia multi-dentate (9+ teeth); right lacinia lacking; palp long, segment 1 elongate, segment 3 lacking "A" setae. Maxilla 1, outer plate with 9 apical spines; inner plate bare; palp slender, segment 1 with small lateral process. Maxilla 2, plates small, weakly setose. Maxilliped, outer plate small. columnar; inner plate small, apical spines stout; palp stout, raptorial, apex of segment 3 oblique, but not produced beyond base of pectinate dactyl.

Coxae 1-4 regularly deep, rounded below, lacking hind cusps. Gnathopods slender, eusiroidean in form (p. 31); propod palmar margin oblique, convex, smooth, with cluster of strong posterodistal spines; hind margin short, lacking basis, anterior margin weakly setose.

Peraeopods 3-7 slender, segment 4 little overhanging 5, dactyls short, weak. Peraeopods 5-7 homopodous, bases lobate behind.

Pleon plates broad, hind corners, acuminate. Uropods 1 & 2 slender, rami unequal; uropod 1 with a weak disto-lateral spine. Uropod 3, inner ramus elongate, outer ramus short. Telson apically rounded, keeled proximally.

Coxal gills small, sac-like on peraeopods 2 & 3, plate-like on 4-6. Brood plates of peraopods 2-4 normally broad, marginally setose; that of peraeopod 5 small, sparsely setose.

Taxonomic Commentary. This small, nearly monotypic group also has a unique mixture of apomorphic and intermediate character states (Tables I & II). The form of the mouthparts, especially the upper and lower lips, maxilla 1, and maxilliped, the medium-length antennae, with short peduncular segments, and the large raptorial form of the gnathopod propods, are basically similar to those of subfamily Pleustinae. However, the short rostrum, uncarinated body, rounded coxae, slender peraeopods, and heterogeneous coxal gills resemble those of the Parapleustinae, and the inflated but non-triturative molar is similar to that of the Dactylopleustinae.

Biogeographical Commentary. The taxon is pan-Pacific in the North Pacific region where it is common in the shallows and along rocky outer coasts. The genus *Pleusirus* contains only two species; one is of restricted occurrence in the western Pacific, but the other is common and widespread in sublittoral habitats of the eastern Pacific, from Alaska to California.

NEOPLEUSTINAE, new subfamily

Type genus. *Neopleustes* Stebbing, 1906: 311.—Gurjanova 1972: 133.—Barnard & Karaman, 1991: 649. (TYPE species - *N. pulchellus* (Kroyer, 1846).

Genera. *Pleustostenus* Gurjanova, 1972:136. (Type species - P. *displosus* Gurjanova, 1972). Four additional genera (to be newly described by Bousfield and Hendrycks, Part V., in prep) are based on: *Neopleustes boecki* Hansen, 1887; *Sympleustes cornigerus* Shoemaker, 1964; *Parapleustes bicuspis* (Kroyer, 1838); *Parapleustes assimilis* (Sars, 1895).

Diagnosis: Medium to large pleustids. Body (especially pleon) dorsally toothed. Urosome 2 narrowed but not occluded dorsally. Rostrum short to medium; head may have mid-dorsal crest. Lateral head lobe acute or rounded. Eyes large, subrectangular. Antennae slender; antenna 1 elongate, basal flagellar segments often weakly conjoint; peduncle 3 short. Accessory flagellum minute or lacking.

Upper lip deeply notched, lobes asymmetrical. Lower lip, inner lobes medium broad, outer lobes oblique, rounded. Mandible, molar much reduced, apical surface pilose or weakly spinose, nontriturative; spine-row medium long, blades thick, pectinate; left lacinia multi-dentate (8+ teeth), right lacinia lacking; palp large (to twice mandibular body length), segment 3 with single basal "A" seta. Maxilla 1, outer plate with 9 apical spines; inner plate with 1 apical seta; palp slender, segment 1 with small lateral process and seta. Maxilla 2, inner plate not broadened, with a single (rarely 2 submarginal plumose seta. Maxilliped, outer plate narrow, subcolumnar, outer margin distally convex; inner plate short, subtruncate, apex with "button" spines; palp strong, segment 3 long, apex oblique, variably produced beyond base of slender pectinate dactyl, and armed with stout pectinate setae.

Coxal plates 1-4 medium deep, increasing regularly posteriorly, rounded below. cuspate behind. Gnathopods of three types: (1) small, weakly subchelate, subsimilar, carpus and propod slender, palm short, median tooth present, hind margin setose (*Neopleustes* type); (2) medium subchelate, subsimilar; carpal lobe narrow, propod palm long, lacking median tooth, hind margin short, nearly bare (*N. bicuspis* generic type, above); (3) large, strongly subchelate, unequal in size and form, carpus short, deep, propod palm with median tooth, hind margin long, setose (*N. cornigerus* generic type, above). In all gnathopod types, the antero-distal margin of the basis is setose.

Peraeopods 3-7 stout, margins spinose, segment 4 strongly overhanging 5; dactyls medium, slender. Peraeopods 5-7 regularly homopodous; coxae posterolobate, rounded; bases rounded behind.

Pleon plates broad, hind corners acuminate or mucronate. Uropods 1 and 2 slender, spinose, rami subequal; uropod 1 with distinct disto-lateral peduncular spine; rami unequal to subequal. Uropod 3 elongate, rami distinctly unequal spinose.

Telson short, apex rounded, keeled proximally (nearly centrally).

Coxal gills broadly sac-like on peraeopods 2-4, plate-like on peraeopods 5 & 6. Brood plates normal.

Taxonomic Commentary. Neopleustinids are readily placed within the advanced group of pleustid subfamilies (p. 47). The group is not strongly distinctive, and combines a number of charactistics of both the Parapleustinae and, to lesser extent, the Stenopleustinae. The tendency for maxilliped palp segment 3 to be distally oblique and produced beyond the base of the dactyl is convergent to such development in the Stenopleustinae. The different form and armature of palp segment 3 and the dactyl, and of the inner and outer maxilliped plates, suggests that the similarities are homoplasious. On the other hand, the nearly centrally keeled telson of the neopleustinids may indicate some phyletic affinity with the stenopleustids, and possibly also the austropleustinids.

The enigmatic genus *Pleustostenus* Gurjanova, 1972, is tentatively placed within the Neopleustinae. The incompleteness of the original description (abdomen missing in the type specimen), some aberrancies in the mandibular molar (described as triturative but figured otherwise by Gurjanova (1972)), and unusual form of coxa 1 (smaller than, and partly masked by, coxa 2) negate firmer classification. As noted elsewhere (Bousfield and Hendrycks, Part V, in prep.), *Pleustostenus* is closest to the genus *Neopleustes.*

Biogeographic Commentary. The 13 component species described to date are confined to medium-deep offshore waters, or in coastal fiords, of Arctic, North Atlantic, and North Pacific marine regions. Little is known of their life style and general biology.

PARAPLEUSTINAE, new subfamily

Type Genus. *Parapleustes* Buchholz, 1874: 337.—Barnard & Karaman, 1991: 649. (TYPE species - *P. gracilis* Buchholz, 1874).

Genera. *Incisocalliope* Barnard & Reish, 1959: 21. [TYPE species - I. *newportensis* Barnard & Reish, 1959]. Five additiona genera are being newly described by Bousfield and Hendrycks, Part V. (in prep.) based on the following TYPE species: *Parapleustes pugettensis* (Dana, 1853); *Parapleustes oculatus* (Holmes, 1908); *Parapleustes commensalis* (Shoemaker, 1952); *Parapleustes nautilus* (Barnard, 1969b); and a fifth new genus that embraces a complex of new species, with very specialized mandibles, that are associated with sponges in the North American Pacific coastal marine region.

Diagnosis. Body small to medium, smooth (rarely mucronate). Urosome 2 dorsally occluded (or nearly so). Rostrum weak. Lateral head lobe rounded. Eyes medium large, subrotund. Antennae short to medium; antenna 1, peduncular segment 3 short. Accessory flagellum minute or lacking.

Upper lip deeply notched, lobes asymmetrical. Lower lip, inner lobes broad, squat; outer lobes small, oblique, rounded. Mandible, molar very reduced, knob-like, apex pilose, non-triturating; spine-row variable in length, blades usually short, stout, pectinate, or highly "molarized" (p. 29), seldom slender, left lacinia multidentate (8+ teeth), right lacinia lacking; palp medium to large, segment 3 often lacking basal "A" seta, segment 2 often with few inner marginal setae. Maxilla 1, outer plate with 9 apical spines; inner plate with single seta; palp usually slender, segment normal. Maxilla 2, inner plate broadened, with single marginal plumose seta. Maxilliped, outer plate smll, narrow, columnar in form, apex rounded, setase, or distal margin convex; inner plate short, apex truncate, with "button" spines; palp segment 2 stout, segment 3 with subtruncate or oblique apex, not exceeding base of pectinate dactyl.

Coxae 1-4 deep, broad, squared below, hind cusps small; coxa 1 broadened distally . Gnathopods variable within genera, from weakly subchelate, subequal, carpus and propod slender, shallow, to powerfully subchelate, subequal or unequal, sexually dimorphic, carpus very short, hind lobe narrow; basis antero-distally setose; merus with posterodistal cusp; propod (when powerful) with median palmar tooth; hind margin setose (rarely bare).

Peraeopods 3-7 ordinary, spinose, segment 4 with strong postero-distal overhang; dactyls short to medium, simple. Peraeopods 5-7 regularly homopodous; coxae medium deep, rounded behind; bases broad, rounded, lobate behind.

Pleon plates broad, hind corners acuminate, quadrate, or mucronate not produced. Uropods 1 and 2 ordinary, rami elongate; uropod 1 with strong disto-lateral peduncular spine. Uropod 3, rami spinose, markedly unequal.

Telson elongate, apex smoothly rounded, keeled proximally. Coxal gills variable, usually large, narrowly sac-like on peraeopods 2-3, plate-like on 4-6. Brood plates normal.

Taxonomic Commentary. This large subfamily (about 35 known species in 7 genera) is somewhat heterogeneous, united mainly by the apomorphic condition of the mandibular molar, maxilliped plates and palp, and relatively low incidence of plesiomorphic character states (Table 1). Some apomorphies are shared with other subfamilies (synapomorphies) but these groups (except for the Neopleustinae) are apomorphic in other directions (e. g. Pleusymtinae) or entrain a high number of plesiomorphies in other character states.

Three main subgroups within Parapleustinae are recognized here: (1) a principal or typical group containing *Parapleustes, Incisocalliope,* and three new genera, that have medium to large, subequal, raptorial gnathopods, and various body color patterns; (2) an *oculatus* group with sexually dimorphic gnathopods, and brilliant, disruptive body coloration; and (3) a *nautilus* group of small body size, relatively weakly subchelate gnathopods, and dull colouration.

Distributional Ecology. Almost all members of the Parapleustinae are endemic to eulittoral shelf habitats of the North Pacific region. A few (including the type genus) penetrate into the North Atlantic region via the Nearctic, but none is exclusively Holarctic. The subfamily Neopleustinae forms a related distributional-ecological counterpart; its six generic groups are restricted to deep shelf (fiord) and abyssal waters and are mainly Holarctic. The parapleustinids and neopleustinids that occur mainly in open coastal and oceanic waters, where light penetration is high, are usually beautifully patterned and maculated; this feature is presumably of significant adaptive value (see Bousfield, 1985). On the other hand, members of *Incisocalliope*, and the *pugettensis* and *nautilus* complexes occur mainly in estuarine and intertidal habitats where waters are usually less transparent; their colour patterns tend to be more subdued (Bousfield and Hendrycks, in prep., Part V.).

Also noted within the *pugettensis* complex is a degree of sexual dimorphism of the gnathopods, setation of the antennae and peraeopods, and modification of other external features, particularly in species exposed to rapidly fluctuating salinities and/or strong tidal currents. In such features. these pleustoideans, appear to have become somewhat gammaroidean in appearance, certainly convergently, but perhaps of significance in revealing mechanisms of evolution within the amphipod body form.

INCERTAE SEDIS AND NON PLEUSTIDS

The following higher taxa have, at one time or another, been assigned to the Pleustidae and/or Calliopiidae-Eusiridae complexes. Because of incomplete or unclear original descriptions, and inability to re-examine type material for this study, their status within the present classification cannot be determined satisfactorily. Further study is needed in these cases.

1. *Dautzenbergia* Chevreux, 1900: 73. The type species is *Amphithopsis grandimana* Chevreux, 1887. Other described species are *D. megacheir* (Walker, 1897), and *D. dentata* (Chevreux, 1920).

The genus was placed in family Eusiridae (*sens. lat.*) by Barnard & Karaman (1991: 316) based on characters that allied it variously with *Eusiroides, Pontogeneoides, Stenopleura,* and *Atylopsis.* The genus does possess some pleustid-like characteristics, especially of the primitive subgroup (p.45), as follows: accessory flagellum minute, vestigial; upper lip moderately notched, lobes slightly asymmetrical; lower lip, inner lobes large, not closely approximated; peraeopod 7 lacking coxal gill; maxilla 1, inner plate with 1-2 apical setae; maxilla 2, inner plate the shorter, with one large marginal plumose seta; gnathopods large, raptorial, unlike; uropod 3, rami lacking marginal setae; coxal gills sac-like. None of these features is exclusively pleustid, however; several advanced eusiroideans variously encompass these character states (Barnard, 1969a).

The genus *Dautzenbergia* is excluded from family Pleustidae, as here defined, on the basis of the following atypical or non-pleustid character states: mandibular left lacinia 5-dentate, mandibular palp segment 3 with numerous facial "A" setae, not basally clustered; maxilla 2, inner plate with strong facial row of setae; coxa 6, anterior lobe subquadrate (not rounded) below; urosome 2 not shortened dorsally; uropods 1 and 2, rami closely subequal, broadly lanceolate, apices not spinose; telson narrowly cleft at apex, not keeled ventrally. These traits are typical of family Eusiridae (within superfamily Eusiroidea) in which (following Barnard & Karaman, *loc cit*) *Dautzenbergia* is best left for the present.

2. *Parepimeriella* Schellenberg, 1931:165. The type species is *P. irregularis* Schellenberg, 1931.

According to Barnard (1969a) the genus is defined as "mandibular molar large, ridged; article 3 of maxillipedal palp not distally produced; gnathopods simple, slender". Schellenberg's original description and figure (1931: 165-66 & fig. 86) indicate some pleustid affinities, especially in the dorsal armature, coxal plates, and upper and lower lips. That author compared his species most closely to *Parepimeria crenulata* (Chevreux, 1913: 160). On the presumption that Schellenberg's thesis (of its similarity to *Parepimeria)* is legitimate, *Parepimeriella* is included in the analysis of subfamilies (p. 51) where it clusters out close to the Atylopsinae. Unfortunately, the very limited original illustration and verbal description of the mouth-parts, peraeopods, uropods, coxal gills, and unpleustid-like form of the gnathopods and telson, prevent credible allocation of the genus to family Pleustidae, as here defined. The genus may yet merit separate subfamily or even distinct full family status. For the present, it seems best left in the category of uncertain classification.

3. *Harpinioides drepanocheir* Stebbing, 1888: 936. A second species, *H. fissicauda* (Schellenberg, 1926), is assigned to this genus by Barnard & Karaman, 1991:324. This austral, deep-water genus was described initially under family Atylidae and later placed within the Calliopiidae by Stebbing who also keyed it within family Pleustidae. Bellan-Santini and Ledoyer (1973, 1986) assigned their material from the

Kerguelen Islands to family Calliopiidae, but that from Marion and Prince Edward Islands was placed within family Eusiridae, near genus *Eusiroides*. *Harpinioides* does exhibit a few superficially pleustid-like characteristics of maxillae 1 & 2, maxillipeds, and rami of uropods 1-3 . However, lack of three features (a significant rostrum, notched upper lip, and keeled telson) and presence of two others (a distinct one-segmented accessory flagellum (Fig. 4(O)), and strong disto-medial peduncular spine of uropod 1, are some features that rule out its natural placement within family Pleustidae. The balance of its character states (e.g. form of the gnathopods (Fig. 6N) and telson (Fig. 3R) more reasonably establishes the genus *Harpinioides* as a member of family Eusiridae, within superfamily Eusiroidea, where it had been recently correctly placed by Bellan-Santini and Ledoyer (1986).

4. "Pleustidae indetermines" Ledoyer, 1977: 404, Fig 27A. The single incomplete specimen partly figured (but not described) by Ledoyer, was later separated from *Pleustoides mediterraneus* (Ledoyer, 1986) (see above, p. 33). Ledoyer's original figures, especially of the antennae, mouthparts, and gnathopods, are unlike those of pleustids, as here defined. They are more similar to those of corophioideans (e.g. Podocerinae), but other character states (e.g. of uropod 3 and telson) appear to be eusiroidean (e.g. family Iciliidae - Laubitz, 1982). Consequently, until a more complete description can be made, this unnamed taxon is best left in uncertain higher taxonomic status.

5. Family Pleustidae Stock, 1986. J. H. Stock (1986) has assigned to family Pleustidae three hypogean species of amphipods from Japan belonging to the genera *Awacaris* Ueno, 1971, and *Relictomoera* Barnard & Karaman, 1982. These taxa were placed within the Calliopiidae-Pontogeneiidae complex of superfamily Eusiroidea by Barnard and Barnard (1983). On overall character states of the mouthparts, gnathopods, uropods. and telson, we concur with Barnards' placement. Stock' s decision was apparently based on a very limited concept of eusiroidean and pleustoidean differences (e.g. upper lip smooth vs notched) and on a possible misinterpretation of original illustrations. Thus, neither of these two genera has a bilobate upper lip. Ueno' s original drawing of the upper lip of *Awacaris* clearly shows a smooth, entire, apical margin although the figure is upside-down from the normal position of taxonomic illustration.

This instance re-affirms the need in revisionary studies, expressed elsewhere by the senior author (Bousfield, 1983), for examination (where possible) of specimens, rather than relying on text and illustrations in the literature, and for multiple-character, rather than few or single-character, assessment of proper phyletic relationships.

DIAGNOSIS OF NEW TAXA AT GENUS AND SPECIES LEVELS

The diagnosis of new subfamilies of pleustid amphipods has been facilitated by previously published descriptions of pertinent type or nominate genera and species. We are grateful to our colleagues and to previous generations of amphipodologists for the extensive taxonomic framework they have provided on which this study depends greatly. In the case of the new taxon Eosymtinae, however, all species and genera of this subfamily known to the authors are previously undescribed. Thus, in supporting and validating the new subfamily name Eosymtinae, the following brief diagnoses of the nominate genus and species are presented.

Eosymtes, new genus

Type species. *Eosymtes minutus,* new species

Species: *Eosymtes,* new species (to be described in Bousfield & Hendrycks, Part IV, in prep.).

Diagnosis. Body small, smooth. Urosome 2 not occluded dorsally. Rostrum short. Lateral head lobe rounded to subacute. Eyes rounded or reniform. Antenna 1, antero-distal peduncular process weak to medium strong. Antenna 2, peduncular segments 4 and 5 setose at distal margins.

Mandible, spine-row short, with 4-7 pectinate blades; left lacinia 6-7 dentate; right lacinia blade-like. Maxilla 1, inner plate with 2 stout apical setae. Maxilliped, outer plate tall, with 3 curved apical spines and straight inner cutting edge; inner plate with 2-3 small inner spines, and 3 slender outer, apical setae; palp segment 3 not produced distally; dactyl slender, curved, micro-pectinate.

Coxae 1-4 medium, little deeper than peraeon, increasing posteriorly; hind corners of 1-3 each with 1-2 small cusps, anterior larger. Gnathopods medium, subequal; carpus longer than one-half length of propod, hind lobe shallow; propod, palmar margin smoothly continuous with weakly setose, elongate hind margin.

Peraeopods 3-7 slender, medium long, dactyls elongate. Peraeopods 5-7, coxae shallow, lobes rounded; bases broadly rounded behind, increasing in size posteriorly, hind margin weakly serrate.

Pleon plates 1-3, hind corners acuminate, not produced, hind margins slightly sinuous. Pleopods normal, not sexually dimorphic. Uropod 3 slender, outer ramus not more than two-thirds the length of the inner ramus.

Telson linguiform, apex subtruncate or slightly incised, paired notch and spinule prominent; telson keeled proximally.

Eosymtes minutus, new species
(Fig. 7)

Material Examined. Northeast of St. Lawrence Island, Bering Sea, Station 2, Dive 2, outside #3, July 9, 1980, P. Slattery coll. - Male HOLOTYPE (and slide mount) and 1 subadult PARATYPE (sex undet). Northeast of St. Lawrence Island, Bering Sea, Station 23, outside # 1, 33 m depth, July 7, 1980, P. Slattery coll. - 1 subadult specimen (sex undet.). HOLOTYPE aand PARATYPE in collections of the Canadian Museum of Nature, Ottawa.

Diagnosis. Male HOLOTYPE (1.8 mm). Eye nearly round, with a core of 15- 20 large dark facets surrounded by a ring of clear facets. Antenna 1, peduncle 1 not noticeably produced antero-distally; flagellum with about 12 segments. Antenna 2, peduncle short, extending little beyond peduncle of antenna 1; flagellum about 8-segmented.

Coxae 1-3, lower hind corner with single cusp. Gnathopod 2, carpal lobe relatively deep; merus with very small posterodistal cusp. Peraeopods 3-7 weakly spinose; segment 5 subequal in length to segment 4; dactyls about 2/3 length of respective propods.

Pleon plate 3, hind corner subquadrate. Uropod 1, ecdysial spine small. Uropod 3, outer ramus about 2/3 length of inner ramus. Apex of telson tapering distally, with 1 prominent notch.

Distributional Ecology. The species is known only from two localities near St. Lawrence I. in the Bering Sea, at moderate shelf depths (20-33 m). This region is adjacent to North Pacific locality records of other presumed relict groups such as the Pleustoidinae within the Pleustidae, the Caprogammaridae within the Caprellidea, and several other family-level gammaridean groups (Bousfield, in prep.).

TAXONOMIC AND PHYLETIC DISCUSSION

The taxonomic and phyletic relationships of the 12 pleustid subfamily groups may be more clearly established through phenetic and cladistic analyses. Although both methods are useful group-comparative tools, both have weaknesses (see Gosliner & Ghiselin, 1984) and neither may produce the most probably correct natural grouping. In this study, results common to the two are believed most probably correct; the differences can be evaluated by other evidence (e.g. biogeographic) and thereby reduce subjectivity of decisions. Plesiomorphies and apomorphies are determined mainly by outgroup comparison with certain families (e.g, Pontogeneiidae, Calliopiidae, Eusiridae) of superfamily Eusiroidea; these are presumed ancestral to the Pleustidae (also Shaw, pers. communic). The phyletic ordering of major amphipod character states has been established elsewhere (Bousfield, 1979, 1982a, 1983) although some disagreement exists among various workers on certain points (e.g. Barnard and Karaman, 1983).

From a phenetic standpoint we may consider the 34 major characters and corresponding character states for each subfamily, as provided in Table I. Corresponding data for the enigmatic genus *Parepimeriella* and family Lafystiidae are also included. An overall indication of the relative degree of primitiveness or advanced nature of each higher taxon is provided by the marginal index of apomorphy, here termed the Plesio-Apomorphic (P.-A) Index.. The latter is derived by totalling (for each subfamily) the values of all of the 20-34 character states used in both cladistic and phenetic analyses, similar to the numerical taxonomic methodology employed for phyletic and semi-phyletic analysis of amphipod superfamilies by Bousfield (1983). Three main levels of character states are recognized here: pleisomorphic, intermediate, and apomorphic. This three-stage system provides a more realistic basis for recognizing differences of a clinal nature that typify members of the family Pleustidae. Similarity percentages of greater than 75% indicate close, of less than 60% indicate distant, relationships between taxa.

The best phenogram plotted from these values (UPGMA, Sneath & Sokal, 1973) is shown in Fig. 8. Because the character states are not weighted, and because some similarities may be homoplasies, coefficients of similarity result in clusterings that may or may not be natural. In Fig. 8, the pleustid subfamilies cluster into two major groups, the primitive groups on the left (with indices of apomorphy of 11 to 28) and the advanced groups on the right (indices of 34 to 54). Relationships based mainly on plesiomorphies appear to have validity here since, in most instances, the plesiomorphies within family Pleustidae are apomorphies by the standards of the principal outgroup families (within superfamilies Eusiroidea and, to lesser degree, within othe leucothoideans such as Lafystiidae and Acanthonotozomatidae). The regularity of increase in value of the Index of Apomorphy, from left to right, supports our belief that the ordering of character states has been essentially correct, and that undetected errors and/or character state reversals have been minimal.

Within the primitive grouping of subfamilies, all having strongly triturating mandibular molars, the Atylopsinae clusters at the 75% similarity level with the enigmatic genus *Parepimeriella*. The Eosymtinae and Pleustoidinae, despite superficially dissimilar body types, cluster at greater than 80% similarity, both joined by the Mesopleustinae at nearly 70% similarity. The family Lafystiidae, with intermediate mouthparts and intermediate index of apomorphy (28), clusters distantly with them, but less distantly than it does with the main advanced group of pleustids. This result suggests a natural relationship between lafystiids and pleustids at a

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Legend for Figure 7. (SEE P. 45 - OPPOSITE)
AI - antenna 1; AC - accessory flagellum; CX - coxa; FL - flagellum; GN I - gnathopod 1; GN-2 - gnathopod 2; IN - inner; LFT - left; LL - lower lip; MD - mandible; MXI - maxilla 1; MX2-maxilla 2; MXPD-maxilliped; OU - outer; P6 - peraeopod 6; PL - plate; RT - right; T - telson; U3 - uropod 3; UL - upper lip; X - enlarged.

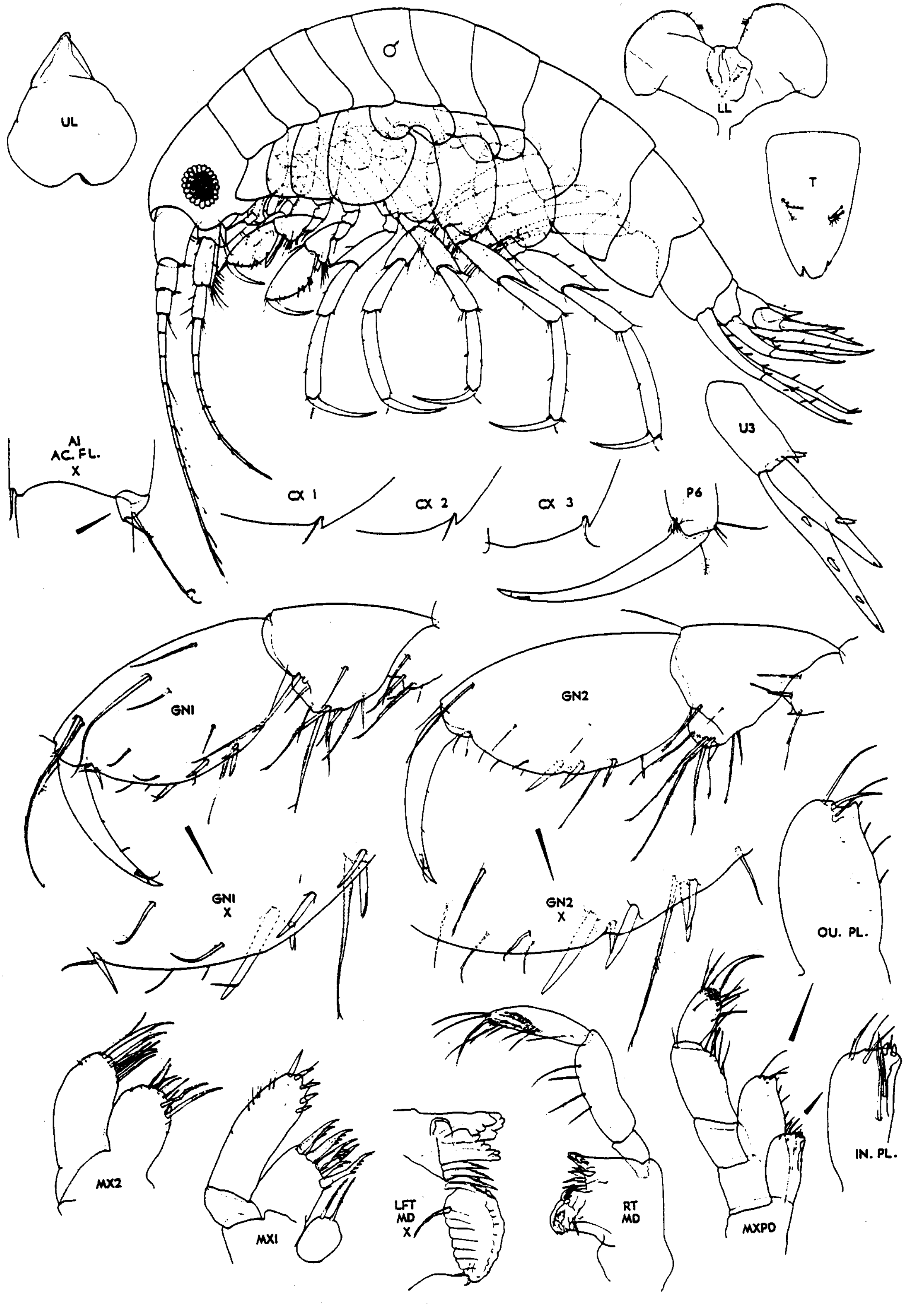

♂
UL
LL
T
U3
A1
AC. FL.
X
CX 1
CX 2
CX 3
P6
GN1
GN2
GN1
X
GN2
X
OU. PL.
MX2
MX1
LFT
MD
X
RT
MD
MXPD
IN. PL.

TABLE I. TAXONOMIC CHARACTERS AND CHARACTER STATES FOR CALCULATION OF SIMILARITY COEFFICIENTS AND INDICES OF APOMORPHY OF SUBFAMILIES WITHIN AMPHIPOD FAMILY PLEUSTIDAE

SUBFAMILY	APOMORPHIC RANKING OF INDIVIDUAL CHARACTER STATES										
	BODY		HEAD				MOUTHPARTS				
					ANTENNA 1				MANDIBLE		
	Carination	Urosome 2 occlusion	Rostrum length	Eye type	Ped. 1 process	Ped. 3 size	Upper lip type	Lower lip type	Molar type	Blade type	Molar flagellum presence
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
1. ATYLOPSINAE	1	0	1	1	0	2	0	0	0	0	0
2. MESOPLEUSTIN	0	0	0	2	0	0	0	0	0	0	0
3. PLEUSTOIDINAE	0	0	1(+)	0	0	1	0 ?	0 ?	0(+)	0	0 ?
4. EOSYMTINAE	2	1(+)	1	0(+)	2(-)	1	0	0	0(+)	0(+)	1
5. STENOPLEUSTIN	1	1	1	1	0(+)	2	2(-)	2	1	1	2
6. AUSTROPLEUST	1	1	1	1	0	2	2	2	1	1	2
7. DACTYLOPLEUST	2	0	1	0(+)	0	2	1	1	2(-)	0	2
8. PLEUSTINAE	0	2(-)	0	2	0	2(-)	1	1	2	1	2
9. PLEUSIRINAE	2	2(-)	1	2(-)	0	2	1	1	2(-)	1	2
10. NEOPLEUSTINAE	0(+)	1	1	1	0(+)	1(+)	2	2	2(-)	1	2
11. PLEUSYMTINAE	2(-)	2(-)	2(-)	1	2	2	2	2	1	1	2
12. PARAPLEUSTIN.	2	2	2	1	0	2(-)	2	2	2	2	2
13. LAFYSTIIDAE	1(+)	1(-)	0	2	1	0	0	0	2	2	2
14. *Parepimeriella*	1	1	2	2 ?	0	1	1(+)	1(+)	0 ?	0 ?	0 ?

(+) character state slightly more apomorphic, or 1-2 genera within the subfamily have more apomorphic condition

(-) character state slightly more plesiomorphic, or 1-2 genera within the subfamily have more plesiomorphic condition

? Guestimate only
Information inadequate

plesiomorphic level. Superficially, *Parepimeriella* appears to be closely pleustoidean. However, its resemblance to Atylopsinae is mainly plesiomorphic, many states of which could not be determined precisely from the original description and figures of Schellenberg (1931). Its pleustid status yet remains uncertain.

Within the advanced group of pleustids, the intermediate level stenopleustinids and austropleustinids cluster closely (above the 80% similarity level). Since many similarities are synapomorphies (Table I), this relationship is here considered natural. The more advanced pleustids form two groups: (1) an intermediate group of Dactylopleustinae, Pleustinae, and Pleusirinae, and (2) an advanced group of Neopleustinae, Pleusymtinae, and Parapleustinae. The advanced group clusters between the 77% and 82% similarity levels, mostly on synapomorphies, and member subfamilies thus appear to be closely related. The intermediate group clusters at 72-75% similarity levels. With fewer synapomorphies, members are more distinctive, and less closely related.

A cladogram of the 12 pleustid subfamilies (Fig. 9) has been plotted on the basis of 20 pairs of character states evaluated in Table II. This smaller number, selected from the 34 characters of Table I, provides greater cladistic manageability, apparently without diminishing the applicability or significance of the results. The method essentially follows that employed in the cladistic analysis of 17 submembers of amphipod family Bogidiellidae by Stock (1981).

The cladistic results (Fig. 9) have a superficial similarity

TABLE I. (cont'd - 2)

PLESIO-APOMORPHIC RANKING OF CHARACTER STATES											
MOUTHPARTS			MOUTHPARTS							PERAEON	
MANDIBLE			MAXILLA 1		MAXILLA 2		MAXILLIPED			COXAE 1 - 4	
Left Lacinia Teeth	Right Lacinia Prsnce	Palp Segment "A" Setae	Outer Plate Spines	Inner Plate Setae	Inner Plate Width	Inner Plate Setae	Outer Plate Type	Inner Plate Ht.	Palp Seg. 3 Prod.	Coxa 1 Type	Coxal Hind Cusps
(12)	(13)	(14)	(15)	(16)	(17)	(18)	(19)	(20)	(21)	(22)	(23)
0	0	0	0	0	0	10 0	0	0	2	0	2
0	0	2	0	0	0	0	0	0	0	2	0
0	0	1(+)	1	1(+)	0	1	0	0	0	1(+	0(+)
0(+)	1	1	1	1(+)	1	1	0	0	0	2	0
2(-)	1	1	2	2(-)	0	2(-)	1(-)	1	2	0	2
2	1	1 ?	1 ?	2(-)	0	2	1	2	2	0	2
0(+)	2	2	2	2	0	2	1	2	0	0	1(+)
1	2	0(+)	1	2	2	2	2	2	0(+)	1(-)	1
2	2	2	1	2	1(+)	2	2	1(+)	1	0	2
2	2	1	1	2	0	2	2	2	1(+)	0	0
2(-)	2	1	1	2	2(-)	2	1	2	0	2	0
2	2	1(+)	1(+)	2	2	2	2	2	1(-)	0	2
1	1	2	0(+)	1	0	0	0	0	0	0	2
0 ?	0	0 ?	0 ?	0 ?	0 ?	0?	0 ?	0 ?	0 ?	1	0

to those of the phenogram (Fig. 8) but differ in some important details. Thus, the subfamilies do divide into two major subgroupings, a primitive group with relatively low apomorphic indices (4-27) on the left, and an advanced group with higher apomorphic indices (7-34) on the right. The two methods also group closely: (I) the Pleustoidinae and Eosymtinae, and more distantly the Mesopleustinae; (2) the Austropleustinae and Stenopleustinae; (3) the Dactylopleustinae, Pleustinae, and Pleusirinae; and (4) the Neopleustinae and Parapleustinae. The major differences are: (1) in the phenogram, the Atylopsinae is remote (< 65% similarity) from all other sub-family groups but in the cladogram it is close to the austropleustinid group; and (2) in the phenogram the Pleusymtinae clusters closely with the two other most advanced subfamilies, but in the cladogram it clusters with the primitive eosymtinid group. The differences are attributable mainly to the basic taxonomic weight given to character states 1 to 4 in the cladogram.

On closer inspection the cladistic results provide more natural groupings than do those of the phenogram. Thus, the the natural assemblage of Atylopsinae, Austropleustinae, and Stenopleustinae is uniquely united by: (1) presence of a coxal gill on pereopod 7 (of some or all members of each subfamily); (2) maxilliped palp, segment 3 variously produced beyond the base of a non-pectinate dactyl; (3) telson centrally keeled; (4) coxal plates 1-4 generally small and weakly or not cuspate below; (5) peraeon and pleon often weakly carinate or toothed above; and (6) pleon plate 3 often rounded and/or quadrate behind. Also, the mandibular molar is often compressed, the apex with a triturating (cobbled) surface that is often small or vestigial in the two advanced subfamilies.

In the second major difference, the cladogram links the highly advanced Pleusymtinae with the relat ively primitive Eosymtinae, Pleustoidinae, and less closely, the Mesopleustinae. The latter has a centrally keeled telson that

TABLE I. (Cont'd - 3) APOMORPHIC RANKING OF CHARACTER STATES

SUB FAMILY NO.	PERAEON				ABDOMEN					COXAL GILLS		TOTALS APOM. INDEX
	GNATHOPOD				Pleon	UROPODS		TELSON				
	GN1 & GN2 Type	Propod Palmar Tooth	Basis Marginal Setation	Peraeopods 3-7 Similar?	Plates 1-3	Urop 1 Ecdys. Spine	Urop 3 Rami Relat.	Notch Type	Keel Type	On P7	Type	
	(24)	(25)	(26)	(27)	(28)	(29)	(30)	(31)	(32)	(33)	(34)	
1	0	0 (+)	1	0	1(+)	0	0(+)	0	0	0	0	11
2	2	2(-)	0	1	0	0	1	2(-)	1	2	2	19
3	1	0	1(-)	0(+)	0	0 ?	2	1(+)	2	2 ?	0 ?	17 ?
4	1	0	2	0	0	1	2	2	2	2	0	26
5	2(-)	2	0	0(+)	1	0	2	2	1(-)	1	0	41
6	0(+)	0	1 (+)	0	2	1	1	1	1	0	0	37?
7	0	0	0	0	0	0	2	2(-)	2	2	1(+)	34
8	2	0	0	2	0	0	2	2(-)	2	2	2	43
9	2	0	2(-)	0	0	1(+)	2	2(-)	2	2	1(+)	48
10	1(+)	2(-)	0	0	0	2	2	2(-)	1(+)	2	1(+)	41
11	1	2	1	0	0	2	2	2(-)	2	2	1(+)	50
12	1(+)	2	1	1	0	2	2	2	2	2	2	54
13	1(+)	0	2	2(-)	1	0	0	2	0	1	1(+)	28
14	0	0	0	0 ?	1	1?	2	2	0 ?	0 ?	0 ?	16 ?

links it to the austral group of subfamilies. The Pleusymtinid-Eosymtinid grouping is united, however, by: (1) mandibular molar with strongly triturating apical surface; coxa 1 narrowing and distally bent forward; (3) coxae 2 and 3 strongly cuspate below; and (4) peduncular segment 1 of antenna 1 often acutely produced distally. On the assumption that the cladogram has given the more probable natural grouping, the fact that the Pleusymtinae shares at least six synapomorphies exclusively with the two major groupings on the right of the cladogram would appear anomalous. However, this result may also indicate that evolution of character states can proceed in parallel, or that character reversals may occur, variously within pleustid subfamilies. We therefore propose the Pleusymtinae-Eosymtinae link as the most probable natural grouping, pending further evidence and further study to the contrary.

On the points of agreement of the two systems, we can be more positive. Thus, the intermediate group of Dactylopleustinae, Pleustinae, and Pleusirinae, is united naturally by: (1) the intermediate form of their upper and lower lips; (2) inward sloping apex of the maxilliped inner plate; (3) short to medium length antennae; (4) lack of median palmar teeth on gnathopod propods; (5) short peraeopod dactyls (especially of peraeopods 3 and 4); and (6) weak (or lacking) ecdysial spine of uropod 1. Some of these characters are additional to those of Table I. This grouping is more cohesive than the pleusymtid grouping but much less close than that of Neopleustinae and Parapleustinae. Modifications entailed in the specialized life styles of the Dactylopleustinae and the Pleustinae tend to mask their phyletic relationships.

Finally, the Neopleustinae and Parapleustinae, with cladistic indices of 29 and 34 respectively, form the most advanced sub grouping. Initially the component genera of Neopleustinae had been grouped within subfamily Parapleustinae based on their many synapomorphies (see Tables I and II). On further analysis, however, it became apparent that members of the *Neopleustes* subgroup were more strikingly carinated, had stronger rostra, less completely occluded urosome 2, and generally less sophisticated

TABLE II. CHARACTER AND CHARACTER STATES UTILIZED IN CLADISTIC ANALYSIS OF SUBFAMILIES

CHARACTER	CHARACTER STATES AND VALUES		
	PLESIOMORPHIC	INTERMEDIATE	APOMORPHIC
	0	1	2
1. Coxal gill peraeopod 7	present on all members	present on some	absent (all members)
2. Lower Lip (form)	Inner lobes weak, narrow; outer lobes large, close	intermediate	Inner lobes wide, flat; outer lobes oblique, wide
3. Upper Lip (form)	Notch shallow; lobes symmetrical	intermediate	Notch deep; Lobes asymmetrical
4. Molar Type	1,2: triturative + whip flagellum	3,4	5, 6: non-triturative
5. molar flagellum	strongly developed	weakly developed	absent
6. MD Right Lacinia	Present	weak vestigial	absent
7. Urosome 2 (occlusion)	wide dorsal margin	narrow	occluded dorsally
8. Telson keel (position)	shallow or lacking	central	proximal
9. Gnathopods, palmar tooth	absent	weak, or on few members	present
10. Maxilla 2: No plumose setae (inner plate)	3+	2	1-0
11. Maxilliped, outer plate	Type 1 (broad)	Type 2 (medium)	Type 3 (columnar)
12. Uropod 1, disto-lateral spine	absent	weak	strong
13. MD Left Lacinia	5-6 dentate	7 dentate	(8+) dentate
14. Rostrum development	strong, elongate	medium, sl exceeding head lobe	short, not exceeding head lobe
15. Mandibular blades	slender, unmodified	tips pectpinate	thick, stout
16. Body carination	strong, on peraeon and pleon	weak toothing	absent
17. MD palp, segment 3, "A"	(3+)	1	0
18. Max 1: outer plate spines	11	9	6-7, or many (>11)
19. Coxa 1 (form)	normal, or widening distally	intermediate	narrowing, bent distally
20. Maxilliped, palp segment 3	Apex truncate, unproduced	slightly produced	Apex oblique, produced beyond dactyl

TABLE III. THE DISTRIBUTION OF SPECIES WITHIN GENERA OF FAMILY PLEUSTIDAE

	NUMBER OF SPECIES WITHIN A GENUS*										TOTALS
	1	2	3	4	5	6	7	9	13	15	
NO. GENERA	**8**	**11**	**8**	**3**	**2**	**2**	**1**	**1**	**2**	**1**	**39!**
TOTAL SPECIES	**8**	**22**	**24**	**12**	**10**	**12**	**7**	**9**	**26**	**15**	**145**

*Average genus:species ratio within family Pleustidae.

! 1 new subgenus (within Pleustinae) included as a separate genus.

mouthparts, especially with respect to the mandibular blades. Some neopleustinids have an obliquely produced segment 3 of the maxilliped palp that is unique (an autapomorphy). Its similarity to that of the stenopleustinid group is convergent since other character states of the maxilliped, especially the dactyl, differ greatly. These differences support our reaffirmation of the Neopleustinae as a subfamily distinct from the Parapleustinae.

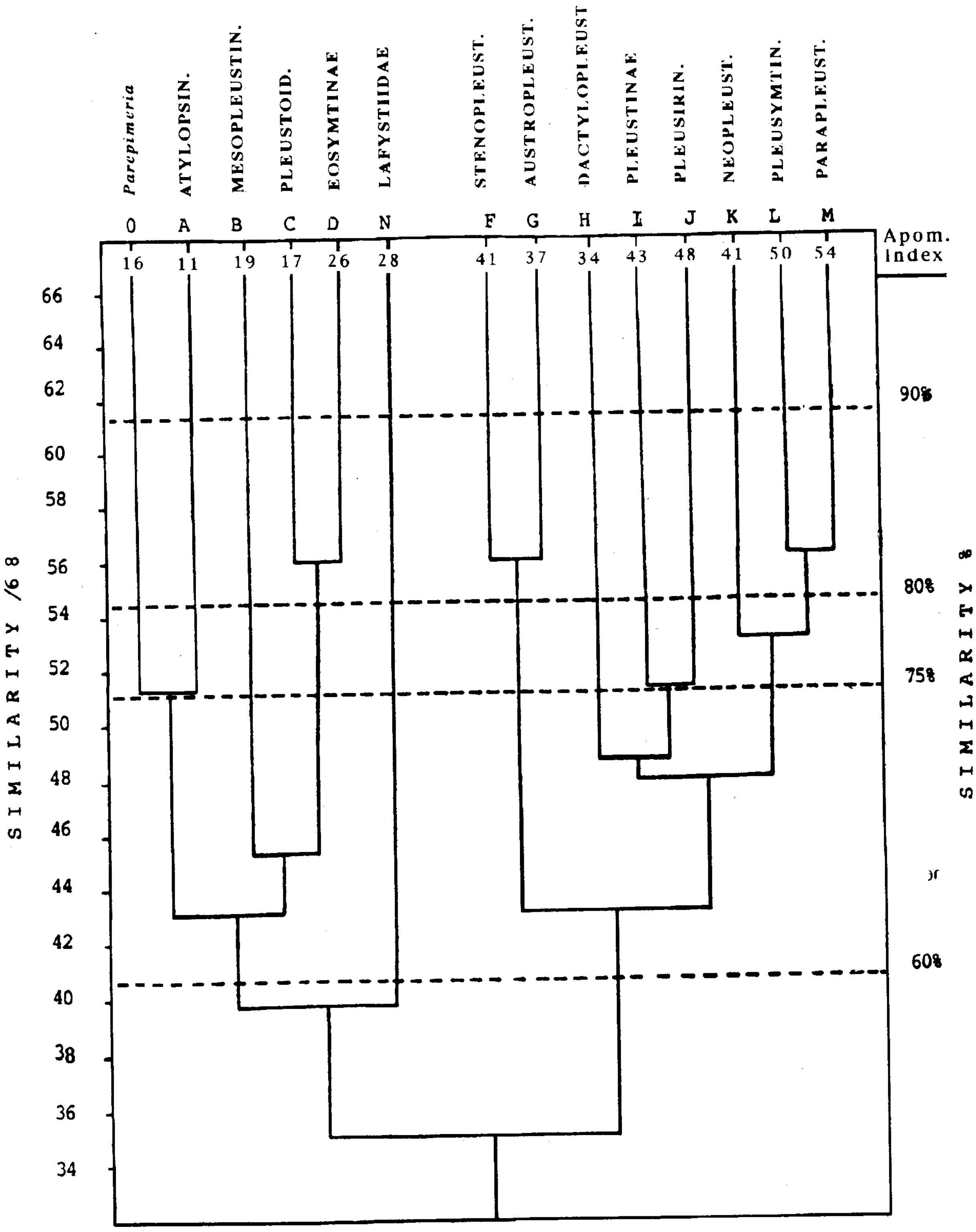
We may conclude,therefore, that the subfamily treatment here proposed validly reflects high-level taxonomic diversity within family Pleustidae. Thus, the subfamilies are internally consistent and distinctive (keyable) on the one hand and, on the other, show intergradations of character states that provide strong indication of the probable course of evolution within the family Pleustidae as a whole.

From the phenetic analysis (above) the family Lafystiidae does have validly close relationships with family Pleustidae, as had been suggested elsewhere (e.g. Bousfield, 1987) Whether these similarities are closer to Pleustidae than to some families of superfamily Stegocephaloidea (wherein the Lafystiidae had been placed by Bousfield, 1982a, 1983) remains to be tested. On the present bases, the lafystiids might be viewed as aberrant pleustids having an ectoparasitic life style. The Laphystiopsidae (especially genus *Prolaphystiopsis* Schellenberg, 1931) also seems taxonomically close to some primitive pleustid subfamilies. However, because of their specialized morphologies and life styles, and pending further study, both ectoparasitic groups might be reclassified as separate families within superfamily Leucothoidea.

In contemplating a revision of family-level magnitude, in which numerous new higher taxa are formulated, concern for "oversplitting" or "over-lumping" is always paramount (e.g. as expressed in Karaman and Barnard, 1979). One measure of stability in higher taxonomic categories is the degree to which the "splits" conform with, or differ from, existing species/genus or genus/family ratios. Data on which these ratios may be calculated for family Pleustidae are summarized in Table III. Thus, for example, 8 genera are monotypic (1 species per genus), three genera contain four species each, and one genus contains 15 species. Most genera are of low diversity (27 of 39 genera contain only 1-13 species each) and many appear to be phyletic relicts. Only seven genera are successful in modern terms (i. e., each containing more than six species) and/or occur over more than one biogeographic province (see p. 10). For the entire family Pleustidae, the average species/genus ratio is 3:7. This value is identical with the species/genus ratio of 3:7 within the Phoxocephalidae, an amphipod family of comparable size and antiquity (data from Barnard & Drummond, 1978). Both figures are below the ratio of 5:2 or 5:4 for gammaridean amphipods world- wide (Barnard, 1959; Bousfield, 1982a). However, in view of the recent trend to refinement of taxonomic criteria (e.g. Bousfield, 1977; Stock, 1981), the overall gammaridean figure may be in the process of reduction.

The genus/subfamily ratio for Pleustidae is only 3:2, rather lower than the comparable ratio of 5:2 for the Phoxocephalidae. The low ratio for Pleustidae undoubtedly reflects the relatively large number of distinctive, monotypic, or nearly monotypic genera within the entire family (e.g. *Atylopsis, Mesopleustes, Dactylopleustes, Pleusirus).* In the interests of classificatory consistency (Tables I & II; Figs. 8 & 9), such genera must be recognized also at the subfamily level. These ratios indicate, therefore, that the taxonomic concepts of subfamilies, genera, and species herewith proposed and recognized within family Pleustidae are basically stable and consistent with those of other workers in other amphipod family groups.

FIGURE 8. PHENOGRAM OF SUBFAMILIES OF PLEUSTIDAE



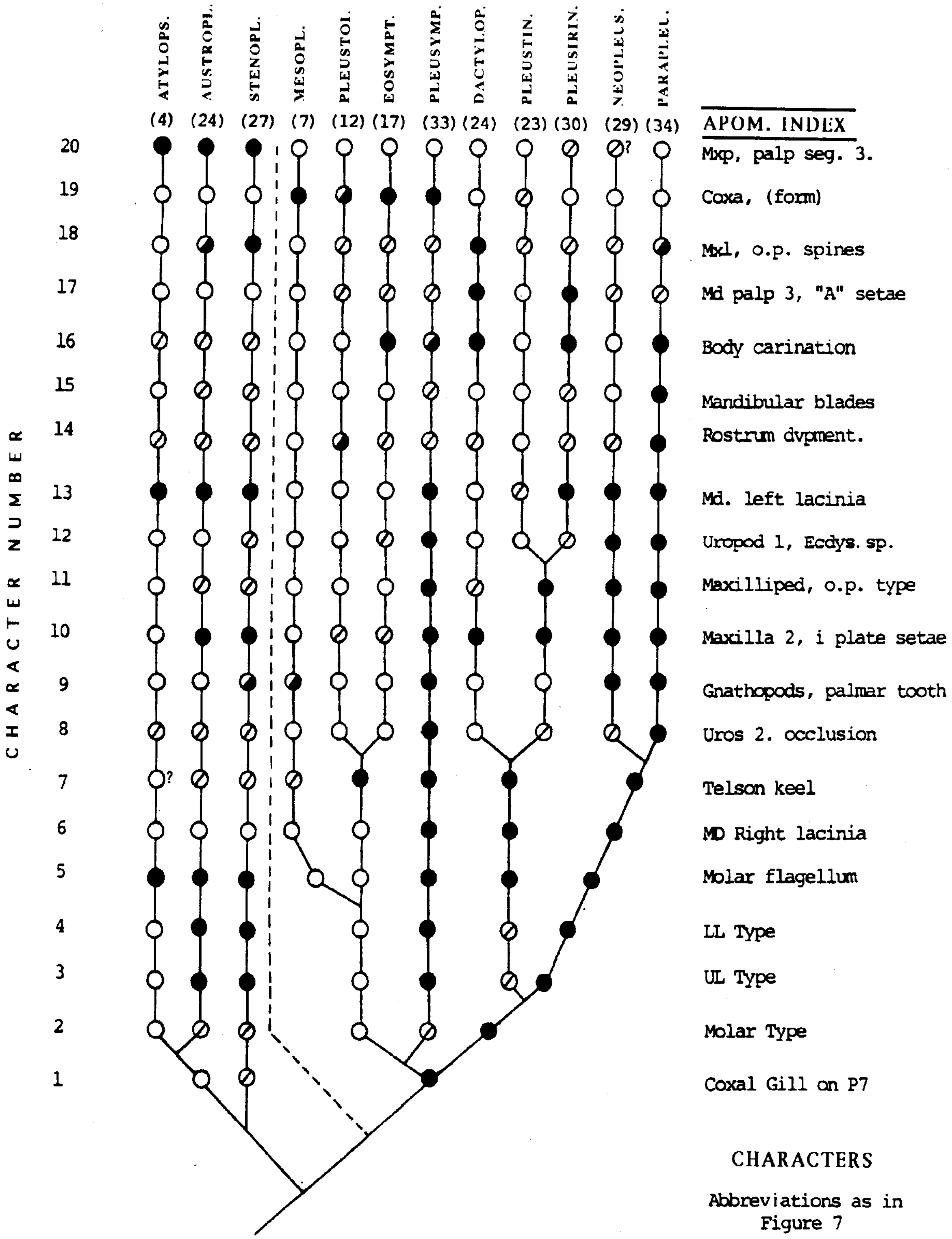


Fig. 9. Cladogram of relationships of 12 subfamilies of Pleustidae

○ - plesiomorphic ⊘ - intermediate ● - apomorphic
◐ - "

TABLE IV. DISTRIBUTIONAL-ECOLOGICAL CHARACTERISTICS OF PLEUSTID SUBFAMILIES

(1) Subfamily	(2) Number Genera: Species	(3) Geographical Distribution	(4) Depth Range	(5) Habitat and Life Style
1. ATYLOPSINAE	2 (7)	AN (M)	S (D)	O (F)
2. AUSTROPLEUSTINAE	2 (4)	AN (IP)	S (I-D)	O (F)
3. STENOPLEUSTINAE	5 (11)	NA (AR;NP)	S (I-D)	O (F)
4. MESOPLEUSTINAE	1 (3)	IPB	AB	O (F)
5. PLEUSTOIDINAE	1 (3)	NP (W)	S (I-D)	O (F)
6. EOSYMTINAE	2 (3)	NP (E)	S (L-D)	O (F)
7. PLEUSYMTINAE	8 (29)	NP (AR;NA)	S (L-I)	O (F)
8. DACTYLOPLEUSTINAE	1 (3)	NP	S (L-I)	O (C)
9. PLEUSTINAE	3 (33)	NP (AR;NA)	S (L-I)	O (F-C)
10. PLEUSIRINAE	1 (2)	NP	S (L)	O (F)
11. NEOPLEUSTINAE	5 (12)	AR (NA;NP)	S (I-D; AB)	O (F)
12. PARAPLEUSTINAE	7 (34)	NP (NA)	S (L-I)	O-E (F-C)

LEGEND

Column (3)

AN - Antiboreal
AR - Arctic
IP - Indo-Pacific
M - Mediterranean
NA - North Atlantic
NP - North Pacific

Column (4)

L - Littoral (0 - 30 m)
I - Intermediate (30-250m)
D - Deep-water (250-1000m+)
AB - Abyssal - (>1000 m)
S - Shelf (200 - 800 m)

Column (5)

E - Estuarine or embayed
O - Oceanic or open coastal
F - Free-living
C - Commensal or otherwise associated with other organisms

BIOGEOGRAPHICAL CONSIDERATIONS

Essential elements of the distributional ecology of component subfamilies of Pleustidae are summarized in Table IV (above).

With respect to overall geographical distribution of the twelve subfamilies (column 3), nine sub-families are confined to the northern hemisphere, one (Austropleustinae) occurs only in southern oceans; one (Atylopsinae) occurs in both hemispheres, and one (Mesopleustinae) is abyssal, mainly in the Indo-Pacific region. Of the nine subfamilies endemic to the northem hemisphere, seven (embracing 97 species in 23 genera) are restricted to, or occur mainly in, the North Pacific region; one (Neopleustinae, with 12 species in 5 genera) occurs mainly in the Arctic; and the other (Stenopleustinae, with 11 species in 5 genera) is found almost exclusively in the North Atlantic and adjacent Arctic region.

Of the seven North Pacific groups, four are small, nearly monotypic, mostly intermediate subfamilies (Pleustoidinae, Eosymtinae, Dactylopleustinae, and Pleusirinae) that occur nowhere else; the other three (containing large, diverse, and advanced subfamilies: Pleustinae, Pleusymtinae, and Parapleustinae) penetrate variously throughout the Arctic to the North Atlantic region.

With respect to depth range (column 4), virtually all subfamilies predominate in coastal shelf waters; only Mesopleustinae (and one genus of Neopleustinae) appear to be exclusively abyssal. More than half the subfamilies occur mainly in moderately deep shelf waters. However, the presumably more recently evolved and larger subfamilies (e.g., Pleustinae, Pleusymtinae, and Parapleustinae) are most diverse and abundant in the eulittoral shallows.

With respect to habitat and life style (column 5), most subfamily members are restricted to open coastal or oceanic habitats where summer temperatures are low (c. 10° C.), and salinities high (>30 o/oo). Only a few members (within Parapleustinae) have penetrated embayments and estuaries where summer temperatures are higher, and salinities are lower. Most pleustids are free-swimming and substrate-perching types (*sensu* Steele, 1988), but several (mostly intermediate to advanced) groups live in close association with benthic invertebrates (e.g. Dactylopleustinae with sea urchins; some Parapleustinae with sponges) and large benthic algae (many Pleustinae).

It would appear from their regional diversity and abundance that the origin and evolution of the advanced pleustid subfamilies is centred in cold-temperate and subarctic coastal shelf waters of the North Pacific region. Thus, some of the primitive, presumably ancestral, groups remain there, and some have radiated into the deep sea. The advanced groups have spread through the Arctic into the cold-temperate North Atlantic region. A second, similarly small group of relatively primitive subfamilies (containing only 10 species in 4 genera) is confined almost exclusively to waters of the southern hemisphere and Indo-Pacific and Medi-terranean regions. As noted above (p. 45), its most advanced members (within Austropleustinae) show taxonomic affinities with the Stenopleustinae, the only northern subfamily restricted mainly to the North Atlantic region.

We might speculate, therefore, that the early pleustids were distributionally continuous throughout deeper colder shelf waters of theTethyan Sea in middle to late Mesozoic times. Subsequently the Atlantic widened, and Tethyan connections between it and the modern Indo-Pacific seas were closed off (Howarth, 1981; Adams, 1981). By such a process the stenopleustinid remnant of that early fauna may have become isolated in the North Atlantic, and its primitive austro pleustinid relatives are now confined to the Mediterranean, Indian, and southern oceans. These all remain today as phyleticand biogeographical relict groups.

By contrast, early pleustid members that presumably occurred in the western North Pacific portion of the ancient Tethys Sea apparently expanded around the Pacific rim where their remnants still exist (e. g. Pleustoidinae, Eosymtinae). Although the stimulus for such expansion is unknown, they penetrated the littoral and sublittoral habitats, and presumably gave rise to the richly diverse modern groups such as the Pleustinae, Pleusymtinae, and Parapleustinae that dominate the North Pacific and adjacent Arctic marine shallows today. However, these "modern", narrowly cold-stenothermal, littoral marine subfamilies are totally unrepresented in southern oceans. Their southward dispersal pathways are barred presumably by a combination of high near-surface temperatures in the intervening tropical regions, and lack of innate isothermic submergence capability due to their specialized life styles in the eulittoral zone (Ekman, 1953; Briggs, 1974).

In attempting to assess the age of origin and evolution of the Pleustidae, indirect evidence would suggest a probable early to middle Mesozoic time frame. From a morphological standpoint, the twelve subfamilies here designated embrace a range of mouthpart types that transcend those of nearly all other amphipod families. Only within the primitive superfamilies Lysianassoidea and Phoxocephaloidea, both richly diverse at family and subfamily levels, do other family-level concepts compare in this respect (see Barnard, 1969a; Bousfield, 1982a, 1983). Such diversity of mouthparts implies a corresponding diversity of feeding types, the evolution of which took place very probably over a very long period of time. Also, members of this group (even the most advanced) are among the most primitive members of superfamily Leucothoidea, most families of which may have evolved by the early Tertiary (Bousfield, 1982b). In turn, the most primitive pleustids differ relatively little from presumed ancestral eusiroidean family types. Thus, several eusiroidean genera such as *Epimeriella, Dautzenbergia, Atyloides,* and *Regalia,* exhibit one or more pleustid character states such as the loss of antennal calceoli, callynophore, accessory flagellum, loss of marginal setation of the rami of uropod 3, and loss of the coxal gill from peraeopod 7.

However, few eusiroideans possess any features that may be considered typically pleustoidean. These include an asymmetrically notched upper lip, and widely separated outer lobes of the lower lip; a multi-dentate left lacinia and lack of a right lacinia; vestigial, non-triturative molar; and linear mandibular palp segments. Additional pleustoidean and non-eusiroidean features include: columnar maxillipedal outer plate; gnathopod propods with median palmar tooth; rami of uropods with apical spines; telson ventrally keeled; and coxal gills sac-like (not pleated or lobate). Since these pleustid character states are considered to be apomorphic, pleustids are presumably more recent palaeohistorically than are eusiroideans. Conversely, eusiroideans are almost certainly of greater antiquity and, by inference from comparative morphology, possibly ancestral to the pleustids. The eusiroideans have been classified among the most primitive of extant gammaridean amphipods, the ancestral types of which have been variously dated to the early Mesozoic or even late Palaeozoic, despite lack of a pertinent fossil record (Bousfield, 1982b; Barnard & Barnard, 1983).

We may therefore summarize by describing the Pleustidae as a very old, distinctive, and remarkably diverse family group. Its ancestral types may have been widely distributed in temperate to cold marine regions of middle to early Mesozoic times. The ancestral types are represented today by a few relatively small and/or relict subfamily groups in deep shelf waters around old ocean basins and in the deep sea. Modern family representatives are restricted to Holarctic marine regions, mainly in eulittoral shelf habitats, with a centre ot origin and dispersal in the cold-temperate North Pacific. These modern forms are excluded from southern oceans presumably by their obligate cold-temperate eulittoral life styles and by high shelf water temperates of the intervening tropical oceans.

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THE AMPHIPOD SUPERFAMILY PHOXOCEPHALOIDEA ON THE PACIFIC COAST OF NORTH AMERICA . FAMILY PHOXOCEPHALIDAE. PART I. METHARPINIINAE, NEW SUBFAMILY.

Norma E. Jarrett* and E. L. Bousfield**

ABSTRACT

The amphipod family Phoxocephalidae is represented on the Pacific coast of North America by about 80 species in 35 genera and 7 subfamilies. Metharpiniinae, new subfamily, contains about 45 species in 7 genera, of which 30 species in 5 genera occur in the study region, from Oregon to the Bering Sea, Alaska. In this study, all regional species are described or redescribed, figured, and keyed, and the genera and subfamily are redefined on the basis of new and previously significant character states. The following taxa are new: Metharpiniinae, new subfamily (type genus *Metharpinia* Schellenberg, 1931); *Grandifoxus constantinus,* new species; *G. dixonensis,* new species, *G. pseudonasutus,* new species; *Beringiaphoxus beringianus,* new genus, new species; *Majoxiphalus maximus,* new genus, new species; *Foxiphalus falciformis,* new species; *F. fucaximeus,* new species, *F. slatteryi* new species; ; *Rhepoxynius boreovariatus,* new species; and *R. barnardi,* new species. *Rhepoxynius pallidus* has been elevated to full species status from *R. tridentatus pallidus* (Barnard, 1960).

The subfamily Metharpiniinae is close to, but clearly separable from the primitive Australian subfamily Birubiinae in which its component genera had previously been placed. Phyletic relationships of genera within the subfamily, and of species within genera, are tested by numerical taxonomic methodology. Biogeographically, most species of the Metharpiniinae are North American Pacific, and centred mainly from SE Alaska to southern California. A few primitive species of *Grandifoxus* are isolated along western Pacific shores, and the other species of the subfamily along the North American Atlantic coast, and the Pacific coasts of Central and South America, to the Cape Horn region.

INTRODUCTION

Members of the gammaridean amphipod family Phoxocephalidae are free-living sediment burrowers and micropredators that occur mainly along continental marine coastal shelf regions of the world. Individual species can be extremely abundant, often numbering several hundred or more per square metre of substratum (Slattery, 1985). They serve as important food items for larger invertebrates and fishes, and otherwise as "secondary producers" in marine food energy cycles. Some of the more lab-hardy and easily accessible species are becoming increasingly useful in bioassay assessment of toxic wastes in bottom sediments (e.g. Swartz et al, 1984; Bousfield 1990).

As in most members of the superfamily Phoxocephaloidea and other subfamilies of "Amphipoda Natantia" (Bousfield, in prep), species of family Phoxocephalidae show a primitive reproductive life style whereby mating takes place freely in the water column (Slattery, 1985). There, by means of well-developed eyes, sensory organelles of the antennae, copulatory spines of the hind-most thoracic legs, and powerful pleopods and tail fan, the mature male stage is well adapted for detecting, approaching, and mating with the briefly swimming and newly moulted female (Bousfield, 1979; Barnard & Karaman, 1991). Following copulation, a process yet little understood in this group of amphipods (Conlan, 1992), the presumably non-feeding male soon dies. The female returns to the bottom where she continues to burrow and feed. There during the next several weeks or months, she incubates the fertilized eggs (to hatching stage) in her ventral thoracic brood pouch. As we may note in the following descriptive accounts, character states of such reproductive morphology, especially of the male, are proving to be of fundamental value in the higher classification of these animals.

During the first hundred years of work on amphipod crustaceans of the North American Pacific coast (e.g. Stimpson, 1856; Holmes, 1908; Alderman, 1936; Thorsteinson, 1941, and others) surprisingly little information on free-burrowing species had been developed. The post-WW II arrival on the coasts of Oregon and California of the dynamic J. L. Barnard soon led to the discovery of a rich, almost entirely endemic fauna of phoxocephaloidean burrowers (1954, 1960, etc.). With co-author Margaret Drummond (1978), his extensive revision of the Australian Phoxocephalidae was soon followed by similarly refined and more suitable generic groupings of the N. American Pacific fauna (e.g. Barnard, 1979, 1980; Barnard and Barnard, 1982a, b). These revisions were soon accepted by other N. American workers (e.g. Coyle, 1982). However, Soviet, and to some extent Japanese systematists, working on a less rich northwestern Pacific fauna, partly accepted these changes but continued to coin their own new units (e.g, Gurjanova, 1977, 1980a,b) for some of the same higher taxa. Despite the recent comprehensive descriptive updating of world families and genera of gammaridean amphipods provided by Barnard and Karaman (1991), and the sound taxonomic

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* **83 Havelock St., Ottawa, Ontario, Canada. K1S 0A4.**
** **Natural History Division, Royal British Columbia Museum, Victoria, B. C., Canada. V8V 1X4**

basis on which these generic concepts rest, phyletically correct answers to some of these classificatory problems especially at subfamily level, have remained unresolved.

Among the most primitive members of regional phoxocephalids recognized by Barnard (loc. cit.) were members of his new genera *Grandifoxus, Rhepoxynius, Foxiphalus, Metharpinia* Shellenberg, 1931, and extralimitally, *Microphoxus.* The last two genera were relegated to subfamily Birubiinae directly by Barnard and Drummond (1978), and the first three by their inclusion in keys to subfamily Birubiinae of subsequent studies (e. g. in Barnard, 1979; Barnard and Barnard, 1980a,b; Barnard and Karaman, 1991). As is demonstrated elsewhere in this paper (Table I, p. 60), these five genera, plus two other North American endemic genera newly proposed herein, form a new subfamily, Metharpiniinae, of which *Metharpinia* Schellenberg is the type genus.

The present phoxocephalid material, comprising some 30 species in five genera, was accumulated as part of an extensive series of field expeditions conducted during 1955-1980 by one of us (ELB) and colleagues in the coastal marine waters of British Columbia, and the United States of Washington, Oregon, and Alaska. Complete lists of stations and pertinent station data are provided elsewhere (Bousfield, 1958, 1963, 1968; Bousfield and McAllister, 1962; and Bousfield and Jarrett, 1981), and have been summarized also by Jarrett, Hendrycks, and Bousfield, 1989. The present material of Metharpiniinae, and other phoxocephalid subfamilies, amounts to about 3500 specimens in more than 200 station lots. It helps fill the previous distributional hiatus between Alaska and California that, as mentioned by both Barnard (1980a) and Coyle (1982), had handicapped earlier taxonomic and biogeographical conclusions.

The purpose of this study is to describe, illustrate, and classify this remarkably diverse and interesting phoxocephalid amphipod fauna. It also attempts to establish more closely its phyletic and biogeographical relationships with adjacent, previously studied faunas, on both regional and world-wide bases.

SYSTEMATIC SECTION

PHOXOCEPHALIDAE Sars, 1895

Phoxocephalidae Gurjanova, 1951: 361.—Barnard & Drummond, 1978: 39.—Bousfield, 1982: 256.—Barnard and Karaman, 1991: 588.

Type Subfamily. Phoxocephalinae Sars, 1895: 142.

Subfamilies: Joubinellinae Barnard & Drummond, 1978: 152; Tipimeginae Barnard & Drummond, 1978: 46; Parharpiniinae Barnard & Drummond, 1978: 174; Pontharpiniinae Barnard & Drummond, 1978: 40; Birubiinae Barnard & Drummond, 1978: 190; Metharpiinae, new subfamily (Jarrett & Bousfield, 1994, this paper); Harpiniinae Barnard & Drummond, 1978: 528; Leongathinae Barnard & Drummond, 1978: 146; Brolginae Barnard & Drummond, 1978: 87; Phoxocephalinae Barnard & Drummond, 1978: 416; Coxophoxinae Gurjanova, 1977: 68 (new status).

Taxonomic Commentary: The family has been taxonomically diagnosed by Barnard and Drummond (1978) and Barnard & Karaman (1991) and its phyletic classification updated by Bousfield (1982), and Schram (1986). Within superfamily Phoxocephaloidea, the family Phoxocephalidae is very closely allied with the family Urothoidae Bousfield, 1979, especially in morphological features of male reproductive appendages, and burrowing appendages (Bousfield, 1990). As their name implies, phoxocephalids differ mainly in the hooded form of the rostrum, but also in the non-geniculate antennae, the carnivorous mouthparts (reduced molar, strong raker spines, raptorial maxillipedal palp), the specialized form of peraeopod 7, and the distinct down-flexed resting position of the urosome.

The subfamilies of Phoxocephalidae proposed by Barnard and Drummond (1978) established a welcome new precedent in the higher classification of gammaridean amphipods. These subfamilies were well conceptualized and remain essentially valid. However, many new genera discovered since that time (see especially Gurjanova, 1977) entrain numerous character states whose taxonomic and phyletic significance was not initially realized. Thus, the family Coxophoxidae proposed by Gurjanova (1977) is based on the unique genus *Coxophoxus.* In all major taxonomic features, this genus is unquestionably a member of the family Phoxocephalidae, whereas its taxonomic differences are more logically recognized at the subfamily level of distinction (above). Similarly, justifiable cases might be made for further subfamily designations within the Joubinellinae (*Matong*) and the Phoxocephalinae (*Limnoporeia*) where basic morphologies are enormously varied. Also, as noted previously, the significance of reproductive and natatory morphology in the male, and burrowing morphology of both sexes, has necessitated extensive subfamily realignment of North American genera and the creation of a new subfamily, the Metharpiniinae, for their more correct phyletic classification.

With respect to subfamily identification within the Phoxocephalidae, comprehensive, multiple-character keys have been provided by Barnard and Karaman (1991), thus obviating any need for such treatment here. However, their allocation of the North Pacific genera of Metharpiniinae, treated therein to the subfamily Birubiinae, requires an updating of that particular key, as follows:

1. Antenna 1, segment 1 variously ensiform (with antero-ventral process); uropod ramal apical spines fused or partly embedded; peraeopod 7 (male), copulating spines paired, elongate .... Metharpiniinae (p. 60)
—Antenna 1, segment 1 never ensiform (lacking antero-ventral process);uropod apical spines distinct, large; peraeopod 7 (male) copulating spine single, short,or lacking .. .. Birubiinae

SUBFAMILY SUMMARY

Analysis of nine subfamilies of Phoxocephalidae proposed by Barnard & Drummond (1978) was undertaken in support of comparable subfamily breakout of family Pleustidae (see Bousfield and Hendrycks, 1994). These two groups appear to be morphological-ecological counterparts —two micro-predator groups, one of which lives in sediments, mainly sand (Phoxocephalidae) and the other mainly on hard substrates (Pleustidae). Evolution has proceeded markedly in the mouthparts of the two, in closely comparable ways. Thus, changes in the form of the mandibular molar, utilized by Barnard and Drummond as the basis of subfamily designation in the Phoxocephalidae, are remarkably closely paralleled in the Pleustidae (see Bousfield and Hendrycks, 1994). Therein, the primitive condition is the fully triturative form, but proceeds via a series of reductions of grinding surface, to a small setulose stub, often paralleled by proliferation of molar rim-teeth as cutting tools (Phoxocephalidae), or by modified raker blades, lacinia, and/or incisor (Pleustidae). A 13-character comparison of member genera of subfamilies of Phoxocephalidae is given in Table I. The character states are detailed and ordered in Table II. A summary of subfamily phylogeny, derived by converting the character states into an index of phylogeny, and totalled for each group, gives the ranking in Table I.

TABLE I.

Comparative plesio-apomorphic condition of subfamilies of Phoxocephalidae

Subfamily	Phyletic Index
TIPIMEGINAE Barnard & Drummond	.40
METHARPINIINAE, new subfamily	.45
BIRUBIINAE Barnard & Drummond	.47
JOUBINELLINAE Barnard & Drummond	.51
PONTHARPINIINAE Barnard & Drummond	.53
LEONGATHINAE Barnard & Drummond	.56
PARHARPINIINAE Barnard & Drummond	.58
BROLGINAE Barnard & Drummond	.61
PHOXOCEPHALINAE Sars	.67+
HARPINIINAE Barnard & Drummond	.67

This phyletic order differs in detail from that of Barnard and Drummond (1978). They placed the Pontharpiniinae at the most primitive end and the Joubinellinae in the advanced position, apparently because their concepts of plesiomorphy-apomorphy with respect to gnathopod condition and some other character states were reverse-polarized. The above system tends to agree with phylogenies derived through anlysis of other series of characters and character states and is consistent with analyses in other family groups and with the superfamily analysis developed by ELB (1983). It is especially significant in agreeing with the presence or absence (and location) of calceoli on the antennae of the male, probably the most conservative and fundamental of all characters treated.

METHARPINIINAE, new subfamily

Birubiinae: Barnard & Drummond, 1978: 190 (partim).—Barnard & Barnard, 1982a: 1.— Barnard & Barnard, 1982b: 2.—Barnard & Karaman, 1991: 597 (partim).

Type Genus. *Metharpinia* Schellenberg, 1931: 65.—J. L. Barnard, 1980a: 115.—Barnard & Karaman, 1991: 622.

Genera. *Grandiphoxus* J. L. Barnard, 1979: 374.—Coyle, 1982: 432 (key).—Barnard & Karaman, 1991: 611; *Beringiaphoxus* , new genus (p. 84); *Majoxiphalus,* new genus (p. 86); *Foxiphalus* J L. Barnard, 1979: 372; *Rhepoxinius* J L. Barnard, 1979: 371; *Microphoxus* J L. Barnard, 1960: 291.

Diagnosis: Rostrum laterally incised or fully hooded. Pigmented eyes usually strongly sexually dimorphic. Antennae, peduncular segments heavy, spinose, fossorial. Antenna 1, peduncular segment 2 about equal in length to segment l; accessory flagellum long. Antenna 2, segment 1 variously ensiform. Calceoli (in male) on flagellum of Al, and on peduncle 5 and elongate flagellum of antenna 2.

Upper lip, epistome often produced anteriorly. Lower lip broad, shoulders usually with cones. Mandibular molar, apical surface non-triturative, margins with blade-spines; molar flake lacking; spine row well developed; left lacinia flabellate or irregularly 4-5 dentate; right lacinia bifid, occ. simple or lacking; incisor with weak tendency to 'molarization'; palp, molar hump small or lacking; segment 3 with 1-2 clusters of 'A' setae. Maxilla 1, palp 2-segmented; outer plate ll-spined, outermost often enlarged. Maxilla 2, inner plate the narrower. Maxilliped, inner plate with 1-2 apical spines. Outer plate with inner marginal masticatory spines; palp stout.

Coxae 1-4 relatively short and narrow. Gnathopods 1 & 2, carpus slender, elongate, longer than weakly subchelate propod.

Peraeopods 3 & 4, segment 6 much longer than 5, postero-distal spine elongate, slender; dactyls short. Peraeopods 5 & 6 short, bases and segments 4 & 5 more or less widened; dactyls short. Peraeopod 7, basis small, harpinioid in form; segment 5 (in male) with paired postero-distal copulatory spines; segment 6 often with slight postero-proximal notch.

Pleon 3 plate, hind corner of usually 'rounded' form, face sub-marginally bare of setae. Uropods 1 & 2, rami falcate, weakly spinose behind, apical spines fused or partly fused in ramal tip; peduncle often with stout medial displaced spine. Uropod 3 usually strongly 'parviramus' in female, aequiramous, narrowly lanceolate in male; terminal segment distinct.

Telson lobes long, broad, each usually with two or more apical and one or more (rarely none) dorso-lateral spines.

Coxal gills large, simple, smaller but distinct on peraeopod 7. Brood lamellae narrow, occasionally lacking on peraeopod 5.

TABLE II. COMPARISON OF METHARPINIINAE AND BIRUBIINAE

CHARACTER	CHARACTER STATE	
	Metharpiniinae	**Birubiinae**
1. Al, segment 1	ensiform	simple
2. Uropod apical spines	fused or sunken	free, articulate
3. Peraeopod 7 (male) copulating spines	large, paired	single or absent
4. Mandible, molar	non-triturative no molar flake	weakly triturative molar flake
5. Maxilliped, inner plate	outer plate large	outer plate small
6. Gnathopod propods	slender type, palm vertical	stout type, palm oblique
7. Peraeopods 5 & 6 segments 4 & 5	short, powerful broadened	long, slender often narrow
8. Peraeopod 7, basis	harpinioid, produced behind	narrow, produced downwards
9. Pleon plates 3	rounded, face bare	truncate, face often setose
10. Peraeopod dactyls	short, weak	long, strong
11. U 1 & 2, ramal spines	few, short	many, various
12. Uropod 3 rami	narrow-lanceolate	broad lanceolate
13. Telson spines	dorso-lateral & apical	single, apical only or multiple-apical

Taxonomic commentary. Metharpiniinae is a subfamily name based on the type genus and species *Metharpinia longirostris* Schellenberg, 1931, from the Cape Horn Falklands Island region of South America. The authors agree with the decision of Barnard & Drummond (1978) to exclude *Metharpinia* from their newly erected subfamily Birubiinae, of which the type genus and species is *Birubius panamunus* from SE Australian coastal marine waters. *Metharpinia* as the subfamily type genus, is unfortunately somewhat atypical of most northern hemisphere members of subfamily Metharpiniinae, of which most species are endemic to cool-temperate waters of the Pacific coast of North and South America. Members of the Metharpiniinae are grossly (occ. closely) similar to those of the Birubiinae but are distinguishable by the combination of basic character states in Table II.

Grandifoxus Barnard, 1980

Grandifoxus Barnard, 1980b: 374.—Coyle, 1982: 43.—Barnard & Karaman, 1991: 611.

Type species: *Phoxus grandis* Stimpson, 1856, original designation.

Species. *Grandifoxus acanthinus* Coyle, 1982; *G. aciculahus* Coyle, 1982; *G. lindbergi* (Gurjanova, 1953); *G.longirostris* (Gurjanova, 1938); *G. constantinus*, new species; *G. dixonensis*, new species; *G. nasutus* (Gurjanova, 1936); *G. pseudonasutus*, new species; *G. robustus* (Guranova, 1938, 1951); *G. vulpinus* Coyle, 1982; *G. westi* (Gurjanova, 1980a).

ARTIFICIAL KEY TO GENERA OF METHARPINIINAE

1. Rostrum distinctly incised, emarginate, or concave in front of eyes (dorsal view) .... 2.

---Rostrum, outer margin entire, convex, not incised (in dorsal view) .... 5.

2. Antenna 2, peduncular segment 4 with 3+ anterior marginal clusters of setae; antenna 2, peduncular segment 5 (male) with 4-8 anterior marginal calceoli;uropod 1, peduncular displaced spine lacking (except in the *longirostris* group); maxilliped, inner plate with 2 stout apical spines........... ***Grandifoxus*** (p. 61)

---Antenna 2, peduncle 4 with 1-2 anterior marginal clusters of setae; antenna 2, peduncular segment 5 (male) with 1-2 anterior marginal calceoli; uropod l, peduncular displaced spine usually present, but may be weak; maxilliped, inner plate with single (rarely 2) apical spines ....3.

3. Rostrum very short, base narrow (dorsal view); urosome segment 3 with stout dorsal forward-curving hook .... ***Microphoxus***

----Rostrum normally developed, base broad; urosome 3 smooth above .... 4.

4. Uropod 1, outer ramus with subapical spines or nails; uropods 1 & 2, one or more rami spinose to apex; telson with dorso-lateral spines or setae ....***.Metharpinia***

---Uropod 1, outer ramus with apical and dorso-lateral spines only; uropods 1 &2, rami with only a few (1-2) mid-posterior spines; telson lacking dorsal lateral spines........................ ***Rhepoxynius*** (p. 107)

5. Peraeopod 5, segments 4 & 5 distinctly wider than deep; uropod 2, outer ramus strongly spinose (4-10+) posteriorly; peraeopod 7, segment 5 distinctly wider than segment 4; maxilliped, inner plate with 2 apical spines; animals large (> 8 mm) .... 6.

---Peraeopod 5, segments 4 & 5 not wider than deep; uropod 2, peduncle and rami with few (0-3) posterior marginal spines; peraeopod 7, segment 5 little or not wider than segment 4; maxilliped inner plate l-spinose; animals small.. ***Foxiphalus*** (p. 92)

6. Antenna 1 peduncular segment 2 longer than 1; eyes (female) very small; peraeopod 6, segment 4 much longer than wide; telson lobes lacking dorso-lateral spines. .... ***Majoxiphalus*** (p. 86)

---Antenna 1 peduncular segment 2 shorter than 1; eyes (female) large, conspicuous; peraeopod 6, segment 4 wider than deep; telson lobes with dorso-lateral spines .... ***.Beringiaphoxus*** (p. 84)

Diagnosis: As defined by Barnard (1980b), (1982a), and Barnard & Karaman (1991)(above). with the following notations: Rostrum constricted. Pigmented eyes present, sexually dimorphic. Antenna 1, peduncle 2 elongate, = > ped. 1; junction of peduncle 3 and flagellum oblique. Antenna 2, peduncular segment 1 weakly ensiform; segment 4, facial spines usually in 2 rows, spines thick, anterior marginal setae in 3-5 clusters; segment 5, facial row of 4-12 spines; in male (known species), with 6-8 calceoli. Mandible, left lacinia 4-5 dentate; right lacinia bifid; molar with 4+ splayed spines; palp segment 3, 'A' setae in 1-2 groups, apex short, oblique. Maxilla 1, inner plate 4-setose. Maxilliped, inner plate with 2-3 apical spines; palp, dactyl elongate, nail small or lacking.

Gnathopods 1 & 2, propod and carpus slender, length 2-3 X depth, palms medium, nearly vertical. Peraeopods 3 & 4, dactyls medium, length 2X width; segment 6 heavily spinose distally. Peraeopod 5, basis medium broad, occasionally narrowest proximally, smaller than basis of peraeopod 6; segment 4 broader than 5; segment 6 not longer than 5. Peraeopod 6 normal, segment 6 not elongate (as in *Majoxiphalus).* Peraeopod 7, basis harpinioid; in male, copulating spines of segment 5 subequal, elongate, curving forwards, denticulate proximally; segment 6 with postero-proximal notch.

Epimeron 3, hind margin distally long-setose.Urosome 3 smooth above, without tooth. Uropod 1, peduncle with baso-facial setal cluster, displaced spine weakor lacking (except in *longirostris* and *vulpinus* groups) not continuously spinose to apex; inner ramus of uropod with 1 row of marginal spines. Uropod 2, peduncular outer margin strongly spinose. Uropod 3, rami strong, subequal or somewhat unequal, margins setose in female, more strongly so in male. Telson lobes spinose apically and usually dorso-laterally.

TABLE III. METHARPINIINAE: List of described taxa (* Species of present study range)

GENUS AND SPECIES	ECOLOGY	RANGE
Genus *GRANDIFOXUS* J. L. Barnard, 1979		
* *Grandifoxus acanthinus* Coyle, 1982	coastal	Alaska - SE. Alaska
* *Grandifoxus aciculata* Coyle, 1982	coastal	Alaska - BC
* *Grandifoxus constantinus* Coyle, 1982		Bering Sea
* *Grandifoxus grandis* (Stimpson, 1856)	coastal	BC - Central Cal.
* *Grandifoxus lindbergi* (Gurjanova, 1953)	coastal	Aleut - BC
* *Grandifoxus longirostris* (Gurjanova, 1938)	coastal	USSR - Cemtral BC
* *Grandifoxus dixonensis,* new species		Southern BC
* *Grandifoxus nasutus* (Gurjanova, 1936)	coastal	USSR - Aleutians
* *Grandifoxus pseudonasutus,* new species		Aleutians
Grandifoxus robustus (Gurjanova, 1938)		Japan Sea
* *Grandifoxus vulpinus* Coyle, 1982	coastal	Alaska - BC
Grandifoxus westi (Gurjanova, 1980a)		Japan Sea
Genus *BERINGIAPHOXUS,* new genus		
* *Beringiaphoxus beringianus,* new species	coastal	Aleutians
Genus *MAJOXIPHALUS,* new genus		
* *Majoxiphalus major* (Barnard, 1960)	coastal	S. Cal - SE Alaska
* *Majoxiphalus maximus,* new species	coastal	Aleutians - BC
Genus *FOXIPHALUS* J. L. Barnard, 1979		
* *Foxiphalus aleuti* Barnard & Barnard, 1982a	coastal	Alaska
Foxiphalus apache Barnard & Barnard, 1982a		California
Foxiphalus cognatus (Barnard, 1960)		California
* *Foxiphalus falciformis,* new species		BC - Oregon
* *Foxiphalus fucaximeus,* new species		Washington
Foxiphalus golfensis Barnard & Barnard, 1982a		S. California
* *Foxiphalus obtusidens* (Alderman, 1936)		Central. Cal - Oregon
Foxiphalus secasius Barnard & Barnard, 1982a		S. Californ. - Panama
* *Foxiphalus similis* (Barnard, 1960)		California - BC
* *Foxiphalus slatteryi,* new species		Bering
* *Foxiphalus xiximeus* B. & B., 1982		California - BC
Genus *RHEPOXYNIUS* J. L. Barnard, 1979		
* *Rhepoxynius abronius* (Barnard, 1960)	coastal	California - BC
* *Rhepoxynius barnardi,* new species		BC
* *Rhepoxynius bicuspidatus* (Barnard, 1960)		California - S. BC
* *Rhepoxynius boreovariatus,* new species		BC
* *Rhepoxynius daboius* (Barnard, 1960)	coastal	Calif. - Central. BC
Rhepoxynius epistomus (Shoemaker, 1938)		Atl. N. America.
* *Rhepoxynius fatigans* (Barnard, 1960)		California - BC
Rhepoxynius gemmatus (Barnard, 1969)		S. California
Rhepoxynius heterocuspidatus (Barnard, 1960)		S. California
Rhepoxynius homocuspidatus Barnard & Barnard, 1982b		S. California
Rhepoxynius hudsoni Barnard & Barnard, 1982		Atlantic. N. Amer.
Rhepoxynius lucubrans (Barnard, 1960)		Calif. - Central. BC
Rhepoxynius menziesi Barnard & Barnard, 1982a		S. California
* *Rhepoxynius pallidus* (Barnard, 1960)		California - BC
Rhepoxynius stenodes (Barnard, 1960)		S. California
* *Rhepoxynius tridentatus* (Barnard, 1954)		Ore - Cal
* *Rhepoxynius variatus* (Barnard, 1960)		California - BC
**Rhepoxynius vigitegus* (Barnard, 1971)	subtidal	Oregon - BC
Rhepoxynius species 'C, 'D, 'L, B. & B., 1982		S. California

TABLE III. (cont'd)

Genus *MICROPHOXUS* Barnard, 1960		
Microphoxus minimus (Barnard, 1960)		Costa Rica
Microphoxus comutus (Schellenberg, 1931)		Megellanic
Genus *METHARPINIA* Schellenberg, 1931		
Metharpinia coronadoi Barnard, 1980a		Central America
Metharpinia floridana Shoemaker, 1933)		Florida
Metharpinia jonesi Barnard, 1963		California
Metharpinia longirostris Schellenberg, 1931		S. America; Magellanic
Metharpinia oripacifica Barnard, 1980		Central America

The list contains 51 formally described species names, in 7 genera, of which 30 species, in 5 genera, occur in the present study region (Alaska - N. California), distributed as follows: *Grandifoxus (12)* (10*); *Beringiaphoxus* (1) (1*); *Majoxiphalus (2) (2*); Foxiphalus* (11) *(7*); Rhepoxynius (18)* (10*); *Microphoxus (2) (O); Metharpinia (S) (0*).*

Taxonomic commentary. The twelve component species are fairly diverse in body form and size. Four species are large (10 mm+) e.g. *G. grandis, G. lindbergi, G.longirostris, G. robustus,* and the other eight are medium-sized (6-10mm). Cluster analysis reveals five main subgroupings as outlined in the following key to species, viz: *grandis (*unique), *longirostris* gp. *(3); lindbergi* gp.*(*3, including *robustus* and *westi); acanthinus* gp. (including*vulpinus & aciculus);* and the *nasutus* group.

Grandifoxus grandis (Stimpson, 1856)
(Fig. 1)

Phoxus grandis Stimpson, 1856: 90.—1857: 81-82.
Pontharpinia grandis Stebbing, 1906: 147.
Pontharpinia milleri Thorsteinson, 1941: 82, pl. 5.
Paraphoxus milleri Barnard, 1958: 147.— 1960: 266, pl. 40.
Grandifoxus grandis Barnard, 1979: 374.—1980: 495.—Coyle, 1982: 449, fig. 10 g, h

Material examined.
BRITISH COLUMBIA: Queen Charlotte Islands: ELB & ELM Stns., 1957: H8a (15, including male (8.5 mm), with slide mount; H13 (30); El (5); EI4b (1); E21 (1); WI (5); W2 (5); Wll, Gudal Bay (17, including male (10.0 mm), with slide mount, fig.'d, and 1 male subadult (10.0 mm) CMN Cat. No. NMCC1992-0610. Central Coast: ELB Stns., 1964: HI (10); H7 (4); H13 (30).
Vancouver Island: Northern region, ELB Stns., 1959: N4 (4); N6 (25, including 1 female ov. (lOmm), with slide mount; 017 (1).
Southern region and Strait of Georgia: ELB stns. 1955: P4 (10); P8 (1); P6a (25); Ml (12); Mla (25); M3 (40); M8 (15). ELB Stns, 1964: H40 (2); H41 (1); H45 (25). ELB Stns. 1970: P707 (1 male, subadult (6.0 mm), with slide mount); P708 (2). ELB Stn., 1975: P4a (1 male).
WASHINGTON & OREGON
ELB Stns., 1966: W2 (6); W4 (1); WS (20); W6 (20); W14 (5); W16 (5); W17 (15): Wl9 (3); W24 (25); W39 (1); W40 (2); W41 (10); W45 (20); W46 (16); WSO (3); WSl (l); W52B, Clatsop Spit, Oregon, Aug. 7 (39, including 1 female ov. (10.5 mm) with slide mount, fig.'d) CMN Cat. No. NMCC1992-0611; W53 (1); W59 (1); W61 (10); W62 (8); W63 (30); W64 (10); W66 (2).

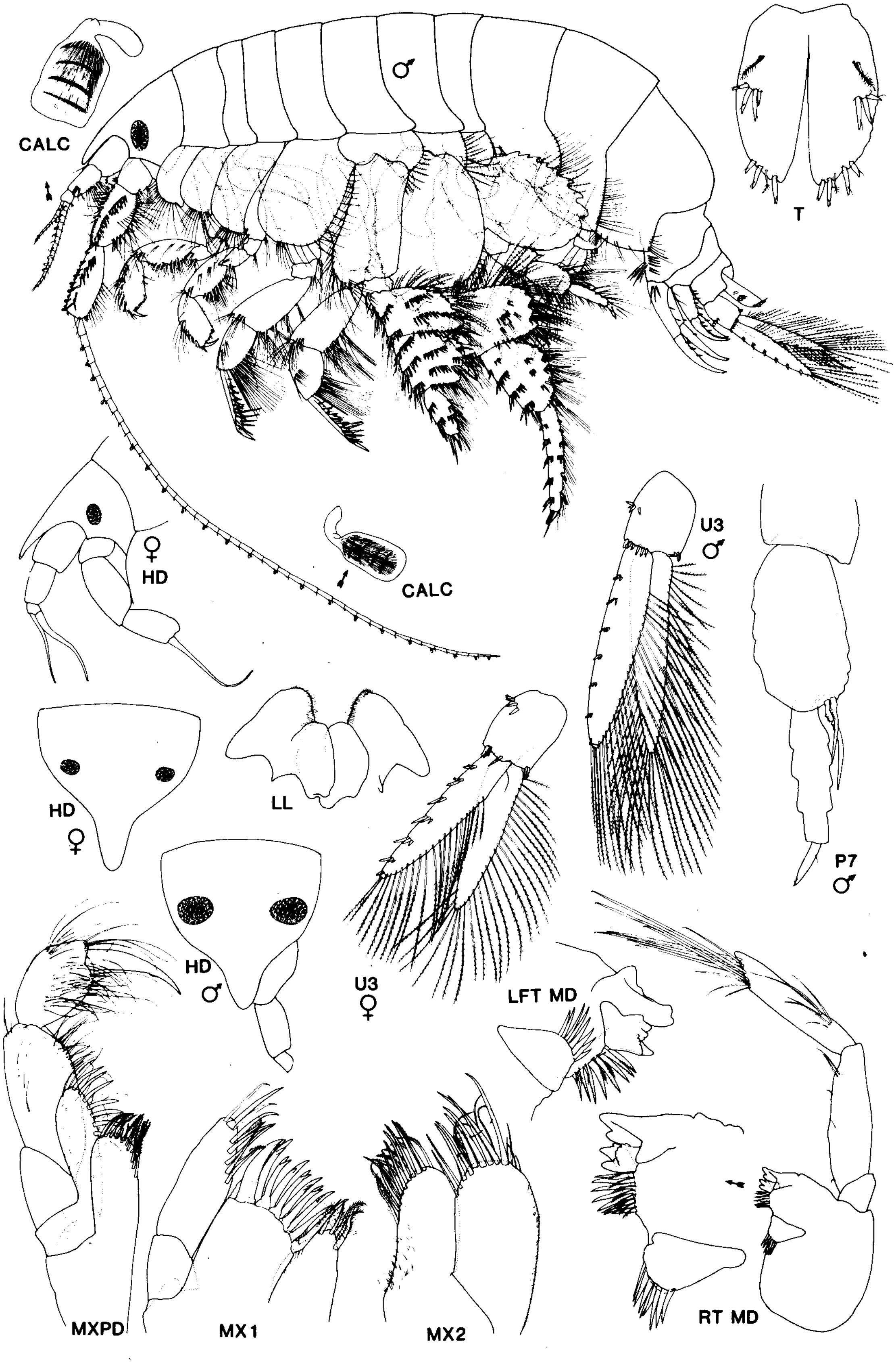
Diagnosis. (Female, 14 mm): Eyes small, oval, weakly pigmented. Rostrum small, basally narrow, tip subacute, barely exceeding peduncular segment 1 of antenna 1. Antenna 1, accessory flagellum long, 12-segmented, nearly equal to 15-segmented flagellum. Antenna 2, peduncular segments 4 and 5 large, broad; segment 4 with nearly continuous facial row of 20+ spines; anterior margin with 6 + groups of spines and/or setae; segment 5 with continuous facial row of about 12 spines.

Mandibular molar prominent, grinding surface weakly

Fig. 1. ***Grandifoxus grandis*** (Stimpson).
MALE (9.5 mm); FEMALE (11.5 mm).
(SEE PAGE 65 - OPPOSITE)

LEGEND FOR FIGURES

Al	- antenna 1	MXPD	- maxilliped
A2	- antenna 2	P3-7	- paraeopods 3-7
CALC	- calceolus (i)	RT	- right
EP1-3	- pleon plates 1-3	U1-3	- uropods 1-3
GNl	- gnathopod 1	UROS	- urosome
GN2	- gnathopod 2	T	- telson
HD	- head	o	- male
LFT	- left	o	- female
LL	- lower lip	MD	- mandible
MXl	- maxilla 1	MX2	- maxilla 2


CALC
♂
T
♀
HD
CALC
U3
♂
HD
♀
LL
P7
♂
HD
♂
U3
♀
LFT MD
MXPD
MX1
MX2
RT MD

KEY TO SPECIES OF *GRANDIFOXUS*

1. Antenna 2, peduncular segment 4, facial spines numerous (usually 15+) in 2 nearly continous rows, anterior marginal setae in 4+ clusters; peraeopod 6, segment 4 wider than long, wider (but not longer) than segment 5 .... 2.

----Antenna 2, peduncular segment 4, facial spines less numerous (usually 8-15), in 2-3 distinct subgroup ings; anterior marginal setae in 2-3 median clusters; peraeopod 6, segment 4 distinctly longer than wide, and longer but not wider) than segment 5 ....5.

2. Uropod 3, both rami elongate and subequal in females and immatures; gnathopods 1 & 2, carpus and propod slender, length (of each) > twice width; peraeopod 5, segment 6 with 1-3 groups of posterior marginalspines .... **G. *grandis*** (p. 64)

---Uropod 3, inner ramus distinctly shorter (2/3) than outer in females and immatures; gnathopods 1 & 2, carpus and propod slightly more robust, shorter, length (of each) twice width; peraeopod 5, segment 6 with poster ior marginal setae only .... 3.

3. Peraeopod 5, segment 4 much wider than long, distinctly wider than segment 5; peraeopods 3 & 4, segment 5, postero-distal spine slender, little wider than adjacent setae; urosome 1 and uropod 1 peduncle, with2-3 clusters of lateral setae; uropod 2, inner ramus marginally bare ....**G. *lindbergi*** (p.68)

---Peraeopod 5, segment 4 little wider than long, or width of segment 5; peraeopods 3 & 4, segment 5, postero-distal spine stout, 45 times wider than adjacent setae; urosome 1 & uropod 1 peduncle with 1- 2 lateral setal clusters; uropod 2, inner ramus with posterior marginal spines ....4.

4. Rostrum short, not extending beyond antenna 1, peduncular segment 1; peraeopod 5, segment 4, 4 - 7 spines in each posterior facial row; peraeopod 7, basis, posterior margin with 5-6 weak serrations . . . .
.... ***G. westi***

---Rostrum long, extending beyond mid-point of antenna 1, peduncular segment 2; peraeopod 5, segment 4, 8-9+ spines in each posterior facial row; peraeopod 7, basis, posterior margin with 7-8 sharp serrations.
....**G. *robustus***

5. Uropod 3, rami subequal in females and immatures; telson lacking dorso-lateral spines; peraeopods 3 & 4, segment 5, postero-distal spine long, about 3/4 length of segment 6 .... 6.

---Uropod 3, inner ramus much shorter (<2/3) than outer in females and immatures; telson with 1(2) dorso-lateral spines; peraeopods 3 & 4, segment 5, posterodistal spine normal, 1/2 - 2/3 length of segment ....7.

6. Peraeopod 6, segment 6 not longer than segment 5; uropod 1, rami with 1-2 posterio-marginal spines . . . .
.... ***G. nasutus*** (p. 80)

---Peraeopod 6, segment 6 distinctly longer than 5; uropod 1, rami with 5-6 posterior marginal spines ......
.... **G. *pseudonasutus*** (p. 82)

7. .Antenna 2, peduncular segment 4, facial spines in 3 distinct groups; peraeopod 5, segment 6 slender, length =segment 5, never with posterior marginal spines; uropod 1, peduncle, outer marginal spines short, stout, posterior marginal displaced spine always stout, much stronger than adjacent spines .... 8.

---Antenna 2, peduncular segment 4, facial spines in 2 distinct groups; peraeopod 5, segment 6 broadest medially, shorter than segment 5; uropod 1, peduncle, outer marginal spines long, slender, posterior marginal displaced spine weak to medium .... 10.

8. Uropod 2, peduncle with numerous (12+) outer marginal spines; telson lobes each with 2 small dorso-lateral spines . . . . *G. dizonensis* (p. 70)

---Uropod 2, peduncle with few (1-4) outer marginal spines; telson lobes each with single dorso-lateral spine . . . . 9.

9. Uropod 1, peduncle with 1 outer marginal spine; uropod 2, rami with 1-2 marginal spines; telson lobes, apical spines short, subequal . . . . *G. longirostris* (p. 68)

---Uropod 1, peduncle with 3-4 outer marginal spines; uropod 2, rami with 3- 4 posterior marginal spines; telson lobes, apical spines unequal, one long . . . . *G. constantinus* (p. 72)

10. Antenna 2, peduncle 5, spines in facial row numerous (10 +); peraeopod 5, segment 6 subovate,posterior margin lacking spine cluster; telson lobes each with 3+ apical spines . . . . *G. acanthinus* (p. 78)

---Antenna 2, peduncle 5 with 5-6 facial spines; peraeopod 5, segment 6 less broad, hind margin with 1 spine group; telson lobes each with 2 apical spines . . . . 11.

11. Peraeopods 5 & 6, dactyls short, length > width of segment 6; uropod 1, displaced spine lacking; uropod 2, inner ramus with 0-1 posterior marginal spines . . . . *G. vulpinus* (p. 76)

---Peraeopods 5 & 6, dactyl medium, length = width of segment 6; uropod 1, peduncular displaced spine medium stout; uropod 2, inner ramus with 2-3 marginal spines. . . . . *G. aciculatus* (p. 78)

triturating, proximal margin with about 8 blade spines; left lacinia 4-5 dentate, right lacinia flabellate; palp segment 3 with single cluster of outer marginal setae ('A' setae of Cole, 1980); apex obliquely truncate. Maxilliped, outer plate slender; dactyl of palp basally stout.

Coxae 1-2 distinctly smaller than 3, narrow, curved, each with poster-distal marginal tooth, lower margins with widely spread setae; coxa 4 front and hind margins subparallel, lower margin broad. Gnathopods 1-2, carpus and propod slender, shallow, propods not broadened distally, palms small, slightly oblique. Peraeopod 3 & 4 large, segment 4 strongly expanding distally; segment 5 shorter than 6, postero-distal spine slender, long (2/3 strongly spinose segment 6); dactyls medium.

Peraeopod 5, basis broadest distally, hind margin slightly concave; segment 4 much broader than long (deep), with two posterior facial rows of spines (10+ spines in each); segment 5 deeper than 4, broad, with 3-4 posterior facial rows of spines; segment 6 sub-linear, with 2-3 hind marginal groups of spines; dactyl small, thin. Peraeopod 6, basis broadly rounding behind; segment 4 subrectangular, broader than deep; segment 5 narrowing distally, deeper than 4, with 2-3 small medio-facial groups of spines; segment 6 slender, longer than 5, hind margin with 5-6 groups of spines; dactyl small. Peraeopod 7, posterior margin of basis with 8-10 strong teeth or serrations, segment 5 slightly longer than 4.

Pleon plates 2 & 3, hind corners about right-angled. Urosome 1 with postero-ventral and lateral clusters of setae Uropod 1, peduncle with small proximo-lateral cluster of setae, weak outer marginal spines, and no postero-distal displaced spine; rami strongly curved distally, weakly marginally spinose. Uropod 2, outer margin of peduncle with 5-6 medium stout spines; rami strongly curved, weakly posteriorly spinose. Uropod 3, rami long, sub-equal, inner margins strongly plumose-setose, outer margin of outer ramus with 5-6 spine clusters, terminal segment minute.

Telson, lobes broad, each with dorso-lateral cluster of 3-4 medium spines; apices with 3-4 medium spines and single setule. Coxal gills on peraeopods 2 and 3 slender, broader on peraeopods 5-6, short-reniform on peraeopod 7.

Male (12 mm): Eyes medium, oval widely separated. Rostrum shorter and blunter than in female. Antenna 1, flagellum 15-segmented, proximal 10-11 with calceoli; accessory flagellum half its length. Antenna 2, segments 4 & 5 sub-equal in length, anterior margin of 4 with brush setae, of 5 with 7-8 calceoli.

Peraeopod 7, copulatory spines slightly unequal, distally curved forwards, inner proximal margin crenulate.

Uropod 3, slightly larger and more heavily plumose-setose than in female, rami closely sub-equal, terminal segment vestigial.

Telson lobes broad, each with single cluster of 3-4 strong dorso-lateral spines; oblique apices each with 3-4 sub-equal spines.

Distribution and Ecology. Along semi-protected sand beaches, from Dixon Entrance (Queen Charlotte Islands) through British Columbia, south through Washington and Oregon to Pacific Grove, California, often in reduced or brackish salinities, and temperatures reaching more than 20°C. Not yet found in Alaska.

Taxonomic commentary. The species is unique, perhaps justifiably subgenerically distinctive in its many plesiomorphic character states. Its closest congener is the distributionally non-overlapping north Pacific species, *G. lindbergi.*

Grandifoxus lindbergi (Gurjanova, 1953)
(Fig. 2)

Pontharpinia robusta lindbergi Gurjanova, 1953: 224-225, f. 7,8.—1980: 95.
Grandifoxus sp. R. Barnard, 1980B: 509-513, fig. 2.
Grandifoxus lindbergi Coyle, 1982: 441, figs. 1, 2.

Material examined.
ALASKA: Aleutian Islands: Unimak Island, P. Slattery stns., June-October, 1982, 50 specimens in 9 lots: Cl; C18; C62, C66 (including 1 female ov. (12 mm), with slide mount, fig.'d.) CMN Cat. No.NMCC1992-0612; C71, C72, C94 (12, including 1 male, penult. (15.0 mm), with slide mount, fig.'d) CMN Cat. no. NMCC1992-0613; Stn. Jl.
St. Paul I., 10 ft. scoop, P. Slattery coll., June 25, 1983: 16 specimens.
Bering Sea, 30 miles W. of Cape Rodney, 80 ft. grab, P. Slattery coll., May 23,1981: 5 specimens.
St. Matthew I., Walrus Cove, 35 ft., P. Slattery collector: 19 specimens.
SE Alaska, Orca Inlet, ELB & DEM Stn. A81, June 19, 1961: 3 specimens.

Diagnosis. (Female ov. to 19 mm). Eyes small, widely separated, weakly pigmented. Rostrum very long, tip subacute, reaching end of peduncular segment 2 of antenna 1. Antenna 1, flagellum about 20-segmented, longer than accessory flagellum. Antenna 2, peduncular segment 4 with about 20 facial spines in nearly continuous row, anterior margin with 6-7 clusters of setae, and a few spines; segment 1 with distinct ensiform process; segment 5 with single facial row of 14-15 spines.

Mandible, molar surface weakly triturative, with 8 distal marginal spines. Left lacinia 4 1/2-dentate; right lacinia unevenly bifid; blade row of about 15 stout blades and accessory plumose setae. Palp segment 3 with 2 clusters of outer marginal 'A' setae; segment 2 with a few outer marginal setae. Maxilliped, inner plate short; dactyl of palp slender, curved.

Coxae 1-3 large, deep, each with small posterior cusp; setae confined to postero-distal corner; coxa 4, margins subparallel. Gnathopods 1 & 2, carpus and propod relatively short and deep; propod distinctly shorter than carpus, length about twice depth.

Peraeopods 3-7, dactyls short. Peraeopods 3 & 4, segment 4 broadening distally; segment 5 short and deep, postero-distal spine slender, short, about half length of strongly spinose segment 6. Peraeopod 5, basis broadest distally, hind margin straight; segment 5 as wide as deep, narrower than 4, with strong anterior and posterior facial spine rows; segment 6 shorter than 5, its slightly bowed posterior margin with clusters of setae only; dactyl short. Peraeopod 6, basis broadly ovate, hind margin nearly straight; segment 4 much broader than deep, with 4-5 posterior facial spine clusters, 2-7 spines per cluster; segment 5 slightly deeper, but less broad, upper posterior facial row with few spines; segment 6 slightly longer than 5, with 4 anterior and 3 posterior marginal spine clusters. Peraeopod 7, basis broad and shallow, hind margin with 5-6 weak teeth; segments 4 & 5 sub-equal in size.

Pleon plates 2 and 3, hind corner slightly obtuse, lower margins convex, heavily setose. Urosome 1 with 2-3 ventrolateral setal groups. Uropod 1, peduncle with strong basofacial setal groups, and 3-4 outer marginal spines; rami curved, with 3- 6 marginal spines. Uropod 2, peduncle with 7-8 outer marginal spines, inner ramus smooth. Uropod 3, inner ramus only 2/3 length of outer, both with a few simple inner marginal and apical setae; terminal segment very small.

Telson lobes broad, each with dorso-lateral cluster of 3 short spines, and 2-4 small spines on obliquely truncate apex.

Coxal gills medium, subrectangular, on peraeopods 2-7, medium small and subovate on peraeopod 7.

Male, penultimate stage (14 mm): Pigmented eyes medium, subovate. Antennal calceoli lacking. Antenna 2, flagellum 35-40 segmented. Peraeopod 7, segment 5, copulatory spines not developed. Uropod 3, rami subequal, inner margins plumose-setose, outer margin with 5-6 clusters of spines.

Distribution and Ecology: From Bering Sea and Aleutian Island south through SE Alaska and Central B.C. coast to southern Vancouver Island, in sub-tidal sands to depths of 2.5 metres.

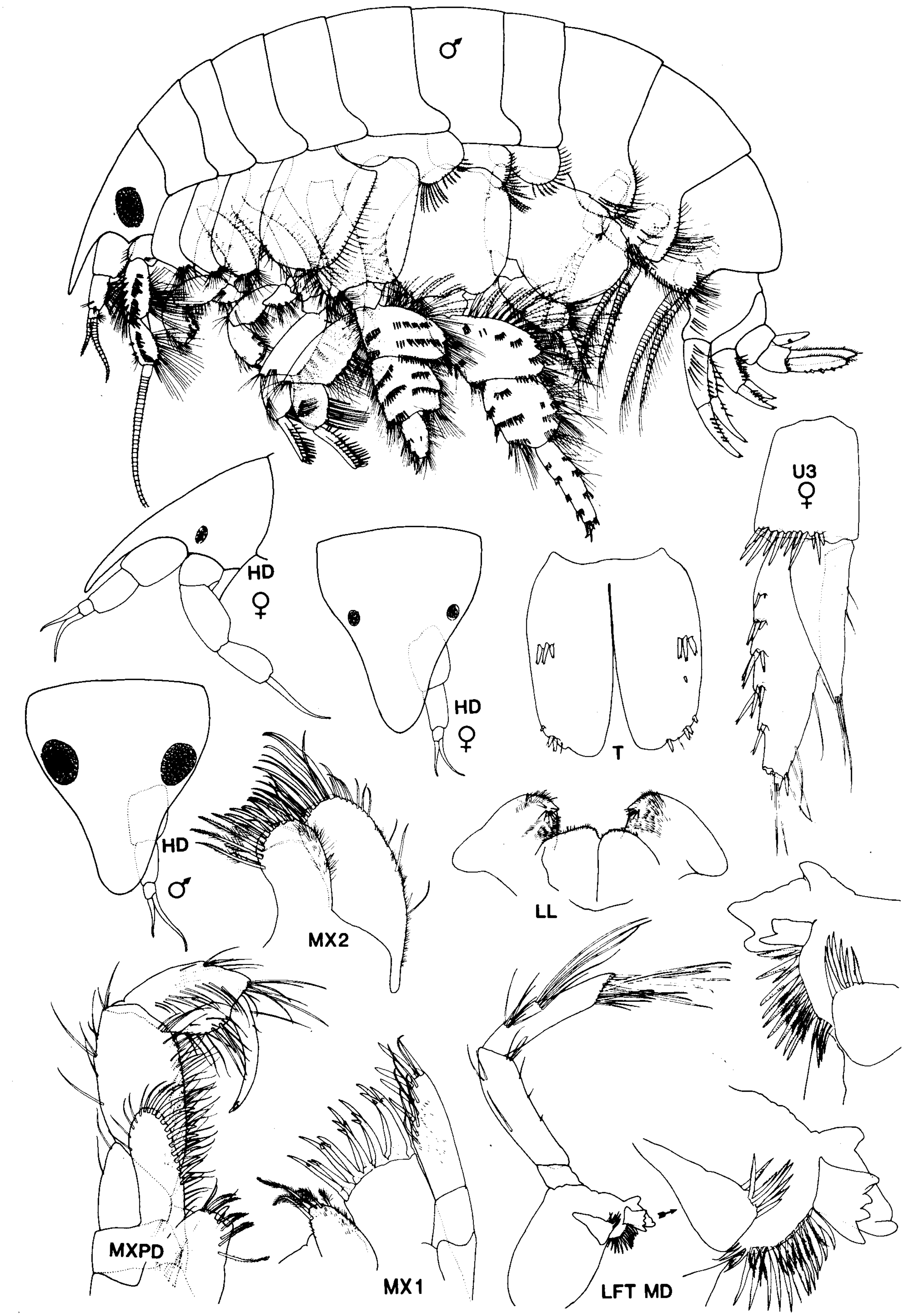
Taxonomic commentary: This largest known species of the genus is usually 12-14 mm., but attains 19 mm in length. Character states are generally less plesiomorphic than in *G. grandis* but less apomorphic than those of the Asiatic Pacific species, *G. robustus* and G. *westi* to which it appears least morphologically remote.

Grandifoxus longirostris (Gurjanova, 1938)
(Fig. 3, male & female; Fig. 4, juvenile?)

Pontharpinia longirostris Gurjanova, 1938: 263, fig. 7.—1951: 385, fig. 235.
Grandifoxus longirostris: Barnard, 1980b: 503, fig. 2.—Coyle, 1982: 447, figs. 8, 9a, b.

Material examined.
ALASKA: Aleutian Islands, Unimak I., P. Slattery coll., June October, 1982: C27 (2 penult males, 3 females); C28 (4

Fig. 2. ***Grandifoxus lindbergi*** (Gurjanova). FEMALE (12.0 mm); MALE penult (15.0 mm).
(SEE PAGE 69 - OPPOSITE)


♂
U3
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MX2
LL
MXPD
MX1
LFT MD

penult males, 1 female ov.); C40 (1 broken specimen); C62 (2 females); C68 (3 imm); C76 (1 female br. II, (8.0 mm) with slide mount, head fig'd.) CMN Cat. No. NMCC 1992-0614; C78 (2 inm. females); C79 (2 females, 13 juv.); C80a (1 female, 4 juv.); C80b (2 females, juvs., 1 penult. male); C93 (2 imm. females, 1 penult. male (8.0 mm) with slide mount, fig'd.) CMN Cat. No. NMCC 1992-0615; Clo-ose (2 females; C121 (2 females).
BRITISH COLUMBIA: Central Coast, ELB Stns., 1964: H13, Lelu I. (1 male); H7, McCauley I. - 1 immature (3.5 mm) with slide mount, CMN Cat. No. NMCC1992-0616. Vancouver I., Bonilla I., J. W. Scoggan coll., August 1, 1965 - 1 female.

Diagnosis. (Penult. Male, 8.0 mm): Pigmented eyes large, sub-ovate. Rostrum short, moderately constricted, little longer than basal breadth, apex rounded, barely exceeding peduncle segment of antenna 1. Antenna 1, flagellum short, 10-segmented. Antenna 2, peduncular segment 4, 3 linear facial groups, 6, 5 and 3 spines per group proceeding distally, anterior margin with 2-3 clusters of setae and 2 spines; segment 5 with single facial row of 5 spines.

Mandible, molar process not triturative, distal margin with 8-9 blades; blade row with 2 raker spines; left lacinia irregularly 4-dentate; right lacinia bifid; palp segment 3 with 1 outer marginal cluster of 'A' setae, apex obliquely truncate. Lower lips broad, shoulders of outer lobes cuspate. Maxilliped, inner plate tall; dactyl of palp slender, curved.

Coxae 1-3 large, setae confined to postero-distal angle; coxa 4 distally narrowing, lower margin rounded. Gnathopods 1 & 2, carpus shallow, posterior lobe medium; propod shorter, broadening distally.

Peraeopods 3 & 4, segment 4 moderately expanding distally; segment 5 about as long as segment 6, posterodistal spine about equal to half length of segment 6; dactyls medium. Peraeopod 5, basis margins sub-parallel, nearly straight; segment 4 wider than deep, posterior facial rows with 3 & 6 spines; segment 5 sub-quadrate, deeper than 4, with 1 posterior facial row of 6-7 spines; segment 6 sublinear, shorter than 5, with posterior marginal setae only; dactyl medium, slender. Peraeopod 6, basis medium broad, hind margin almost straight; segment 4 much deeper than broad, with 1 small group of posterior facial spines and a few setae; segment 5 little broadened, shorter than 5; segment 6 longer than 5, with 3 anterior and posterior marginal clusters of spines and a few setae. Peraeopod 7, basis with 6-7 low, weak posterior marginal teeth; segment 5 longer than 4; dactyl slender.

Pleon plate 2, hind margin slightly concave, hind margin sharply rounded; plate 3, hind corner slightly obtuse, lower margin weakly setose. Urosome 1 apparently lacking ventro-lateral setal clusters. Uropod 1, peduncle with 1-2 outer marginal spines, and stout distal displaced spine; rami shallowly curved, each with 2-3 short marginal spines. Uropod 2, peduncle with 5-6 stout outer marginal spines; rami with 1-2 short marginal spines. Uropod 3, rami subequal, margins plumose-setose.

Telson, lobes broad, each with single dorso-lateral spines; apex obliquely truncate with 2-3 short spines.

Coxal gills broad; gill on P7 much smaller than on P6.

Female (br. II, 8.0 mm): Pigmented eyes small. Tip of rostrum blunter than in male. Accessory flagellum about 12-segmented, 3/4 length of main flagellum. Uropod 3, inner ramus 2/3 length of outer ramus; outer ramus, inner margin distally with 4-5 weakly plumose setae; terminal segment distinct.

Distribution and Ecology. From the Bering Sea (Unimak, I.), south to central B. C. and Vancouver I.; in sand, mostly subtidally, from 40-90 m. in depth.

Taxonomic commentary. This material agrees closely with that of Coyle (1982) from the lower Cook Inlet, Gulf of Alaska, but not with that illustrated by Gurjanova (1951) from the Japan Sea. In the latter, the peduncular facial spines are fewer, the inner ramus of uropod 3 (female) is less than half the outer ramus which bears a rather long terminal segment, and each telson lobe apparently bears only a single apical spine. However, as type material was not examined, formal taxonomic separation of the present material was not attempted.

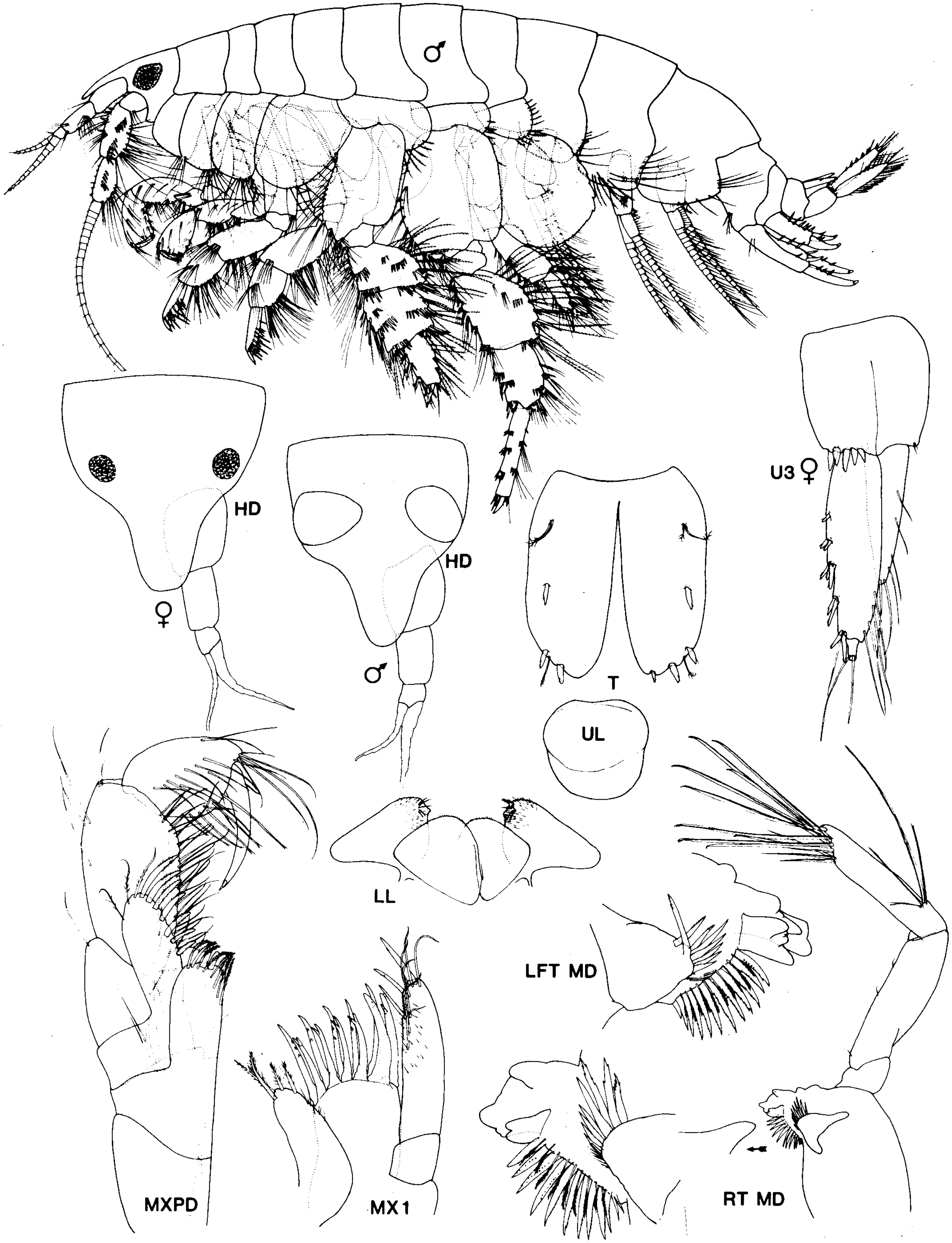
Grandifoxus dixonensis, new species
(Fig. 5)

Material examined.
BRITISH COLUMBIA: Dixon Entrance, inner end, trawl haul, 110 m., fine sand, J. W. Scoggan coll., August 23, 1965: 1 male penult. (8.0 mm) HOLOTYPE, with slide mount, CMN cat. No. NMCC1992-0617; 1 female br. II (6.5 mm) ALLOTYPE, with slide mount, CMN Cat. No. NMCC1992-0618; 2 females, 1 male PARATYPES, CMN Cat. No. NMCC1992-0619.

Diagnosis. (Male, penult. 8.0 mm): Pigmented eyes medium large, sub-rotund. Rostrum large, apex sub-acute, extending well beyond peduncular segment 1, antenna 1. Antenna 1, flagellum short, 10-11-segmented; accessory flagellum 8-segmented. Antenna 2, peduncular segment 4, facial spines in 3 clusters of 6, 6 and 3 proceeding distally, anterior margin with 2-3 setal groups and 1-2 spines; segment 5 with facial cluster of 4 spines. Flagellum 20-segmented, proximal segment apparently conjoint.

Mandible, molar small, with 6 serrated marginal blades; spine row with 10-11 raker blades and accessory setae; left lacinia obscurely 4-dentate; right lacinia weakly bifid (tips

Fig. 3. ***Grandifoxus longirostris*** (Gurjanova).
FEM. br II (8.0 mm); MALE penult (8.0 mm)
(SEE PAGE 71 - OPPOSITE)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appear worn in the type specimen). Lower lip, shoulders cuspate. Maxilliped ordinary, inner plate medium-tall.

Coxal plates 1-3 large, deep, hind corners rounded, richly setose. Coxa 4 relatively small, distally narrowing, lower margin broadly rounded. Gnathopods 1 & 2 medium slender; carpus of 2 with slightly shortened lower margin; propods slightly broadening distally.

Peraeopods 3 & 4 normally expanded, segments 5 & 6 sub-equal in length, postero-distal spines of segment 5 slender, not exceeding adjacent setae, about 2/3 length of segment 6; dactyls medium. Peraeopod 5, basis medium broad, hind margin straight; segment 4 little broader than deep, with 2 postero-facial groups of spines; segment 5 as broad as, but deeper than, segment 4, with 1 posterior facial group of 8-9 spines; segment 6 sub-linear, hind margin with setae only; dactyl medium strong. Peraeopod 6, basis, hind margin nearly straight; segments 4 & 5 little expanded, segment 4 much deeper than 5, with 5 small postero-facial clusters of spines; segment 6 slightly longer than 5, anterior and posterior margins each with 3 spine clusters; dactyl medium strong. Peraeopod 7, hind margin of basis with 7-8 moderately distinct teeth or serrations; segment 5 longer than 4, slightly shorter than linear segment 6; dactyl medium.

Pleon plates 2 & 3, hind corners sharply rounding, lower margins strongly setose. Urosome 1 lacking ventro-lateral setal clusters. Uropod 1, peduncle with 4 marginal spines and stout distal displaced spine; rami with 3-6 posterior marginal small spines. Uropod 2, peduncle with 7-8 strong outer marginal spines; rami with 3-4 posterior marginal spines. Uropod 3, ramal margins plumose setose, terminal segment distinct.

Telson lobes broad, each with single dorso-lateral spine and 2 unequal spines on obliquely truncate apex.

Coxal gills largest on peraeopods 4 & 5, smallest on P6 and 7.

Female (Br. II., 7.5 mm): Pigmented eyes small, oval. Rostrum slightly broader and longer than in male. Antenna 1, flagellum 1-8 segmented. Uropod 3, inner ramus about half length of outer ramus that is weakly plumose-setose distally on inner margin; terminal segment distinct.

Etymology. Named after the type locality in Dixon Entrance, north of the Queen Charlotte Islands, British Columbia.

Distribution and Ecology. Known only from the type locality; in fine sand, at 110 metres in depth.

Taxonomic commentary. The species is closely allied to *G. longirostris,* but differs in the longer rostrum, more heavily spinose and more strongly dactylate peraeopods, more strongly serrated posterior margin of the basis of peraeopod 7, more heavily setose margins of the pleon side plates, more numerous marginal spines on the uropods, and the unequal apical spines of the telson lobes.

Grandifoxus constantinus, new species
(Fig. 6, male)

Material examined.
ALASKA: Amchitka I., dock at Constantine Harbor, C. E. O'Clair coll., Oct. 5, 1968: 1 mature male (9.0 mm) HOLOTYPE, with slide mount, CMN CAT. No. NMCC1992-0620. Constantine Hbr., P. Slattery coll., Sept. 21,1969: 1 male (7.5 mm) broken PARATYPE, with slide mount, CMN CAT. No. NMCC1992-0621.

Diagnosis. (Male, 9.0 mm): Pigmented eyes very large, subquadrate, nearly meeting mid-dorsally. Rostrum medium, apex rounded, extending beyond peduncular segment 1 of antenna 1. Flagellum short, proximal 7 segments bearing calceoli. Antenna 2, peduncular segment 4 with facial spines in 3 groups, each with 3-5 spines; anterior margin with brush setae but no spines; segment 5 with 2 small facial groups of spines, anterior margin with 8 calceoli; flagellum about 40-segmented, calceolate on alternate segments.

Mandible, molar small, margin with 6 blades; spine row with 12 blades; left lacinia evenly 4-dentate; right lacinia bifid; palp segment 3 with one outer marginal cluster of "A" setae, apex obliquely truncate. Lower lip, shoulders with cones. Maxilla 1 inner plate small, with 2-3 apical setae. Maxilliped, inner plate medium tall; palp, dactyl slender, curved.

Coxal plates 1-3 large, hind corners strongly setose but not cuspate; coxa 4 strongly narrowing distally, lower margin rounded. Gnathopods 1 & 2 medium, propods slightly broadening distally.

Peraeopods 3 & 4, segment 5 about equal in length to 6, postero-distal spine slender, about 2/3 length of segment 6; dactyls medium. Peraeopod 5, basis regular, hind margin slightly convex; segment 4 slightly wider than deep, with 3 short postero-facial groups of spines; segment 5 deeper than wide, and deeper than segment 4, with 1 short postero-facial row of spines; segment 6 linear, about equal in length to 5, hind margin with setae only; dactyl relatively long, strong. Peraeopod 6, basis little broadened, hind margin gently convex; segment 4 much longer than wide, with 3-4 small groups of postero-facial spines; segment 5 slightly shorter than 4, little expanded, with 1 postero-facial spine group; segment 6 slightly longer than 5, with 3 clusters of anterior and posterior marginal spines and a few setae; dactyl rela-

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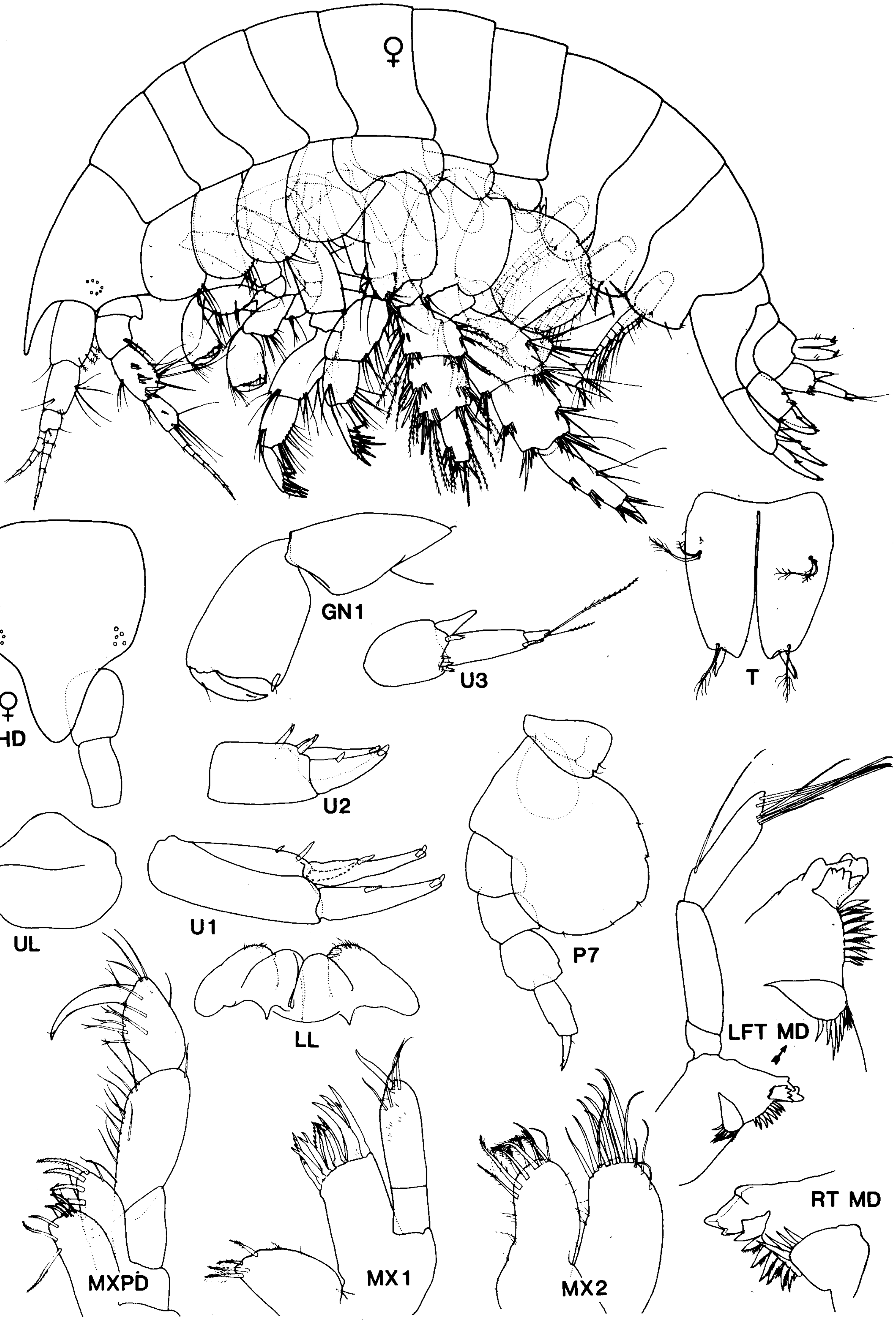
Fig. 4. ***Grandifoxus longirostris*** Gurjanova imm. (3.5 mm). (SEE PAGE. 73 - OPPOSITE)

Fig. 5. ***Grandifoxus dixonensis*** new species. MALE penult (7.5 mm) HOLOTYPE; FEM.br. II (6.5 mm) ALLOTYPE. (SEE PAGE 74)

Fig. 6. ***Grandifoxus constantinus***, new species. MALE (9.0 mm) HOLOTYPE. (SEE PAGE 75)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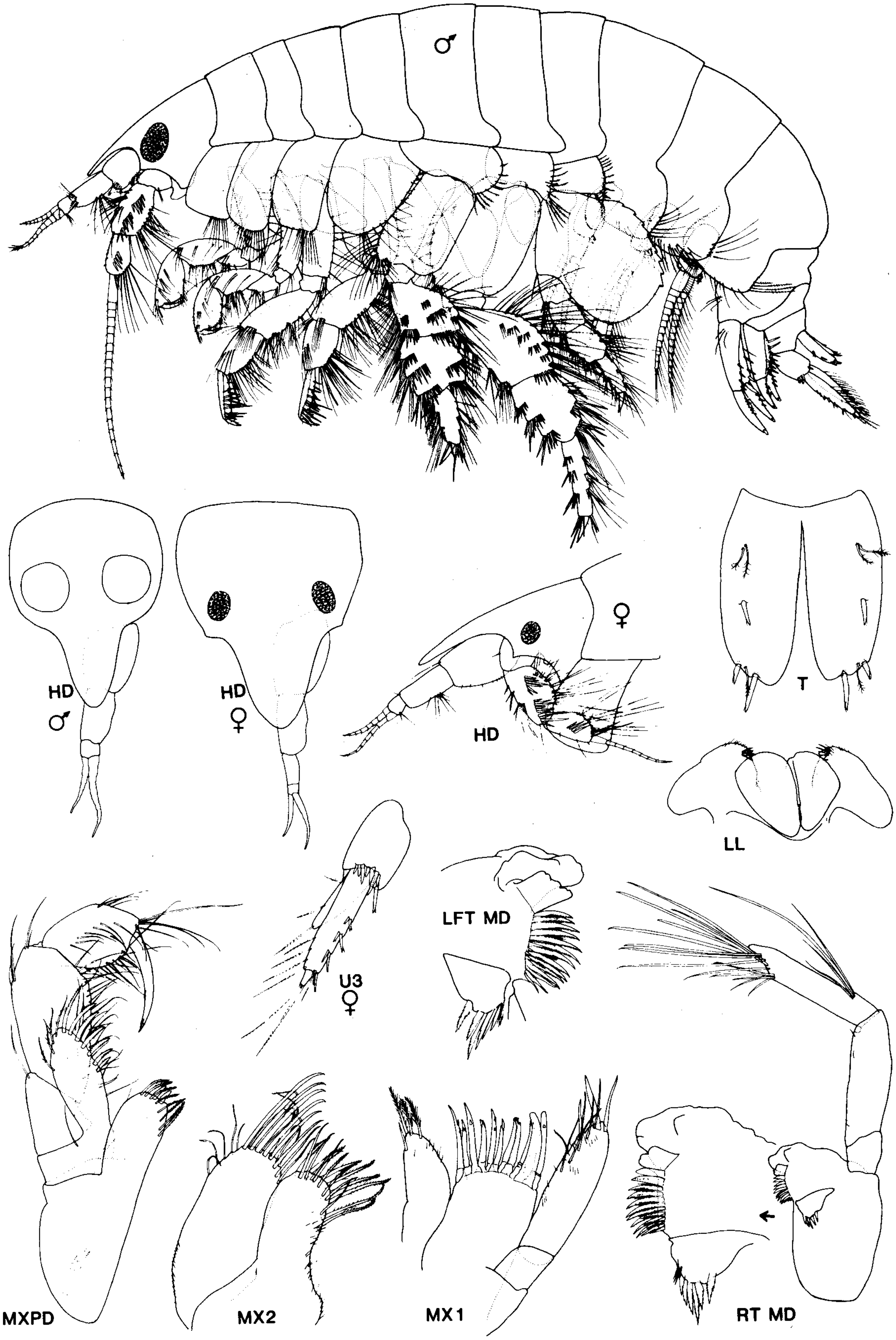
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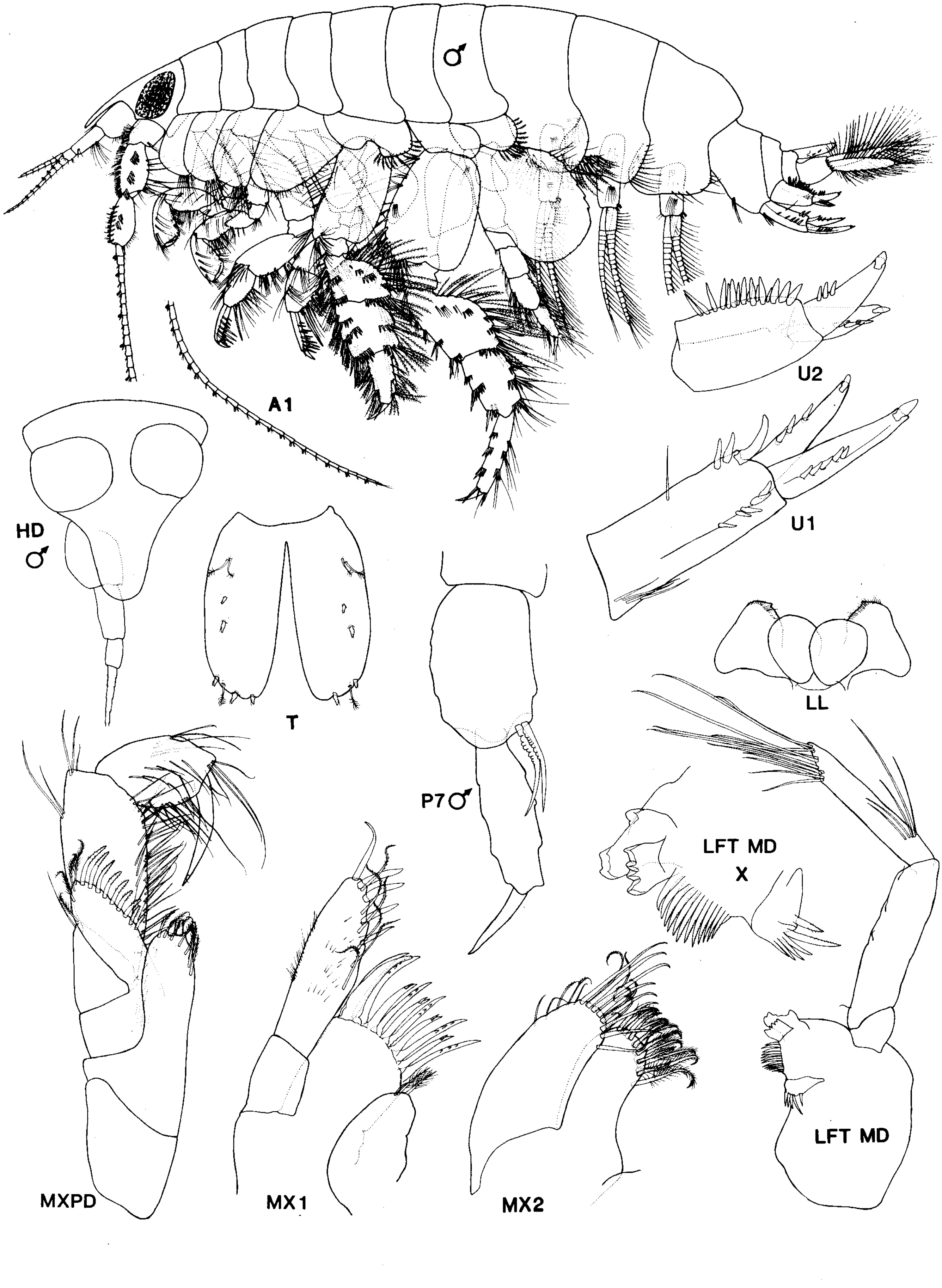
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MXPD
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LFT MD

tively long. Peraeopod 7, basis with 6-8 low posterior marginal teeth; segment 5 distinctly longer than 4, and about equal to 6; paired copulating spines about half the length of segment 6, denticulate proximally.

Urosome 1 lacking ventro-lateral setae. Uropod 1, peduncular outer margin with 4-5 stout spines, displaced spine very large and prominent. Uropod 2, peduncular outer margin with numerous (14+) stout spines; rami 3-4 spinose marginally. Uropod 3, rami strongly plumose setose; terminal segment of outer ramus distinct.

Telson lobes broad, each with 2 small isolated dorsolateral spines, and 2-3 short spines at oblique apices.

Female unknown.

Etymology. Named after the type locality of the species, Constantine Harbour, Aleutian Islands, Alaska.

Distribution and Ecology. Known only from the Constantine Harbour region of Amchitka, Aleutian Islands, Alaska, in sub-tidal sands near shore.

Taxonomic commentary. Even though known only from a mature male specimen, this species is clearly a member of the *longirostris* group. It differs from the nominate species in the less robust gnathopods, less strongly spinose antennal peduncles, but more strongly spinose uropods.

Grandifoxus vulpinus Coyle, 1982
(Fig. 7)

Grandifoxus vulpinus Coyle, 1982: 444, figs. 5, 6.

Material examined.
ALASKA: Unimak I., P. Slattery coll., June-October, 1982: 64 specimens in 10 lots: C5; C22; C40; C42; C43 (5 specimens, including 1 female ov. (6.0 mm), with slide mount, fig.'d, and 1 male penult (5.5 mm), with slide mount, fig.'d.) CMN Cat. No. NMCC1992-0622; C45; C46; C64; C68; unnumbered station.
St. Matthew I., P. Slattery coll., June 27,1983: 4 specimens.
Bering Sea, 30 miles west of Cape Rodney, 80 ft., P. Slattery coll., May 23,1981: 8 specimens.
Pribiloff Is., St. Paul I., P. Slattery coll., June 25,1983: 7 specimens.

Diagnosis. (Female ov., 6.0 mm): Pigmented eyes small, round. Rostrum short, rounded apex barely exceeding peduncular segment 1 of antenna 1. Antenna 1, flagellum short, 7-segmented, little longer than accessory flagellum. Antenna 2, peduncular segment 4 with two facial groups of 6-8 spines each; anterior margin with 3-4 clusters of setae but no spines; segment 5 with single facial group of 6 spines.

Mandible, molar medium, with 4-9 marginal blades; left lacinia 4-dentate, right bifid; palp segment 3 with single weak cluster of "A" setae. Maxilliped ordinary; outer plate slender.

Coxal plates 1-3 medium broad, hind corners with trace of cusp. Coxa 4 slightly narrowing distally, lower margin rounded. Gnathopods 1 & 2, carpus, slender, shallow, propods deeper, shorter, broadening distally.

Peraeopods 3 & 4, segments 4 & 5 stout, postero-distal spine of segment 5 medium strong, short (much shorter than adjacent setae) tips barely reaching mid-point of segment 6; dactyls medium. Peraeopod 5, basis slightly broadening distally, hind margin gently convex; segment 4 wider than deep, with 3-4 small groups of postero-facial spines; segment 5 as wide as,and slightly deeper than, segment 4; segment 6 short, narrowly ovate, posterior margin with I spine cluster and some setae; dactyl short, slender. Peraeopod 6, basis medium broad, hind margin nearly straight; segments 4, 5, and 6 sub-equal in length; segments 4 & 5 little expanded, 4 with a few small postero-facial spine groups, 5 with 2 postero-facial spines groups; segment 6, margins each with 2-3 spine clusters; dactyl short. Peraeopod 7, basis, hind margin with 6-8 weak marginal teeth; segment 5 slightly broadened, segment 6 slightly longer than 5, dactyl medium.

Pleon plate 2, hind corner rounded, lower margin strongly setose; pleon plate 3, hind corner obtuse, with strong cluster of posterior setae. Urosome 1, lacking ventro-lateral setae. Uropod 1, peduncle with baso-facial cluster of setae, 1-2 distal outer marginal spines, lacking distal displaced spine; rami each with 1-2 posterior marginal spines. Uropod 2, peduncle with 3-4 widely separated outer marginal spines; rami each with 1-2 short posterior marginal spines. Uropod 3, inner ramus slender and very short, less than half the length of the slender, distally plumose setose outer ramus; terminal segment distinct.

Telson lobes, slightly narrowing distally, each with 1-2 medium dorso-lateral spines; oblique apices each with 2 medium spines.

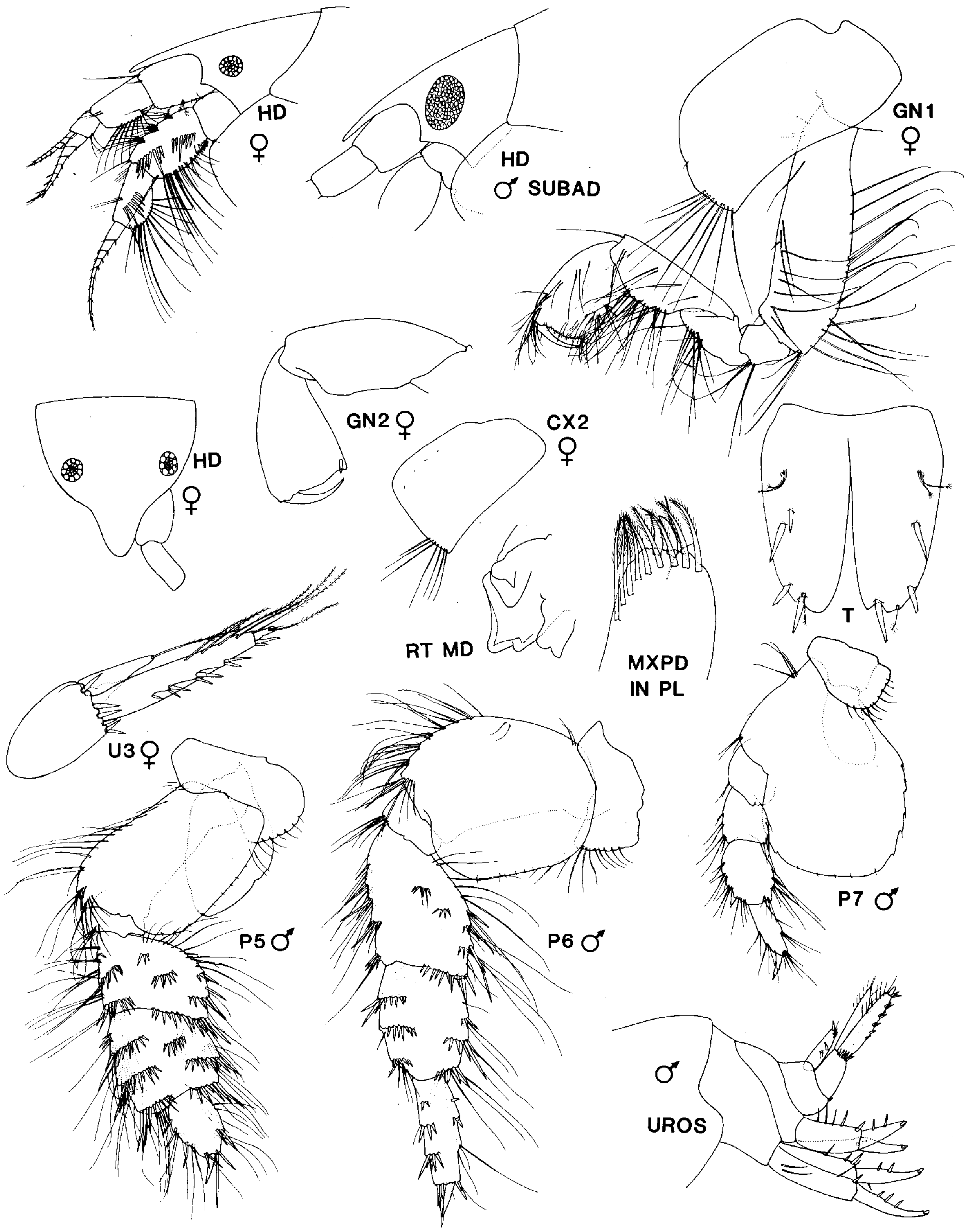
Coxal gills not described.

Male (4.0 mm. penult.): Pigmented eyes medium large, ovate. Antenna 2, flagellum with 18-20 short segments, proximally conjoint. Uropod 3, inner ramus smooth, about 80% length of outer ramus.

Distribution and Ecology. Known only from the central islands, and southeastern part of the Bering Sea to Orca Inlet, subtidally to depths of 87 metres.

Taxonomic commentary. This species is morphologically closest to *G. aciculatus,* and somewhat less so to *G. acanthinus.* In addition to the key characters, it is distinguished by the short rostrum, rounded pleon 2 plate, and sparsely spinose uropods 1 & 2. However, when compared to the Coyle illustrations (1982, fig. 3), the present specimens have slightly more spines on the uropod rami.

Fig. 7. ***Grandifoxus vulpinus*** Coyle.
MALE subadult (5.5 mm)
(SEE PAGE 77 - OPPOSITE)


HD ♀
HD ♂ SUBAD
GN1 ♀
GN2 ♀
CX2 ♀
HD ♀
T
RT MD
MXPD IN PL
U3 ♀
P5 ♂
P6 ♂
P7 ♂
♂ UROS

Grandifoxus aciculatus Coyle, 1982
(Fig. 8)

Grandifoxus aciculata Coyle, 1982: 448, figs. 9c-g, 10

Material examined.
ALASKA: Aleutian Islands, Unimak Island, P. Slattery coll., June October, 1982: C17 (1 male subad. (6.5 mm), with slide mount, fig'd) CMN Cat. No. NMCC1992-0623; unnumbered station (1 female ov. (7.0 mm), with slide mount); C64 (1 female br. II *(5.5* mm), with slide mount, fig.'d., 9 females, 5 imm. males) CMN Cat. No. NMCC1992-0624. St. Paul I., P. Slattery coll., June 25, 1983; 26 specimens in 2 lots. St. Matthew I., Walrus Cove, P. Slattery coll., June 27,1983: 17 specimens.

Diagnosis. (Female ov., 7.0 mm): Pigmented eyes small, round. Rostrum large, basally broad, sharply rounded apex extending well beyond peduncular segment 1 of antenna 1. Antenna 1, flagellum 8-segmented, little longer than accessory flagellum. Antenna 2, peduncular segment 4, facial spines in two groups of 6 and 9-10 spines; anterior margin with 3-4 clusters of setae but no spines; peduncular segment 5 with single group of 4-5 facial spines; flagellum medium, 11-12 segmented.

Mandible, molar small, with a few small marginal blades; left lacinia 4-dentate; right lacinia bifid; palp segment 3 with single cluster of short "A" setae. Lower lip, shoulders with small cones. Maxilliped ordinary.

Coxal plates 1-3 medium large, increasing posteriorly, hind corners square, cusps very small; setae few (6-8). Coxa 4 narrowing distally, lower margin rounded. Gnathopods 1 & 2, carpus medium deep; propod shortened, broadening distally.

Peraeopods 3 & 4, segment 5, postero-distal spine slender, not longer than adjacent setae, tip reaching nearly 2/3 along segment 6; dactyl medium. Peraeopod 5, basis regular, not widening distally, hind margin very slightly sinuous; segment 4 distinctly broader than deep, with 3-4 medium groups of postero-facial spines; segment 5 slightly less broad but deeper than 4, with two unequal groups of postero-facial spines; segment 6 shorter than 5, medially broadest, posterior margin with setae and one spine group; dactyl long, slender. Peraeopod 6, basis medium, hind margin nearly straight; segments 4 & 5 little broadened; segment 4 slightly longer than 5, with 3-4 small groups of postero-facial spines; segment 6 linear, slightly longer than 5, with 1 group of posterior marginal spines and several setae; dactyl slender, medium. Peraeopod 7, posterior margin of basis with 6-10 weak teeth; segments 3-6 increasingly long; dactyl medium, length less than half that of segment 6.

Pleon plates 2 & 3, hind corners sharply rounding, margins richly setose. Urosome 1 apparently lacking ventrolateral setal clusters. Uropod 1, peduncle with proximoventral seta, 3-4 slender outer marginal spines, and medium strong distal displaced spine; rami long, each with 4-5 strong posterior marginal spines. Uropod 2, peduncle with 1 outer marginal spine; rami with 3 slender posterior marginal spines. Uropod 3, rami virtually devoid of setae, except distally, outer ramus about twice length of inner; terminal segment distinct.

Telson lobes broad, outer margins bowed, each lobe with single dorso-lateral spine, and two medium-length apical spines. Coxal gills not described.

Male (antepenult, 6.5 mm): Pigmented eyes only slightly large than in female. Antenna 2, flagellum with about 20 short segments proximally conjoint. Uropod 3, inner ramus distinctly the shorter inner margin of outer ramus plumose-setose. Urosome 3 with small ventro-distal cluster of spines, at base of uropod 3.

Distribution and Ecology. Unimak, St. Paul, St. Mathew Islands and southeastern Bering Sea, Orca Inlet, south to Saanich Inlet, B. C., sub-tidally to depths of nearly 100 metres.

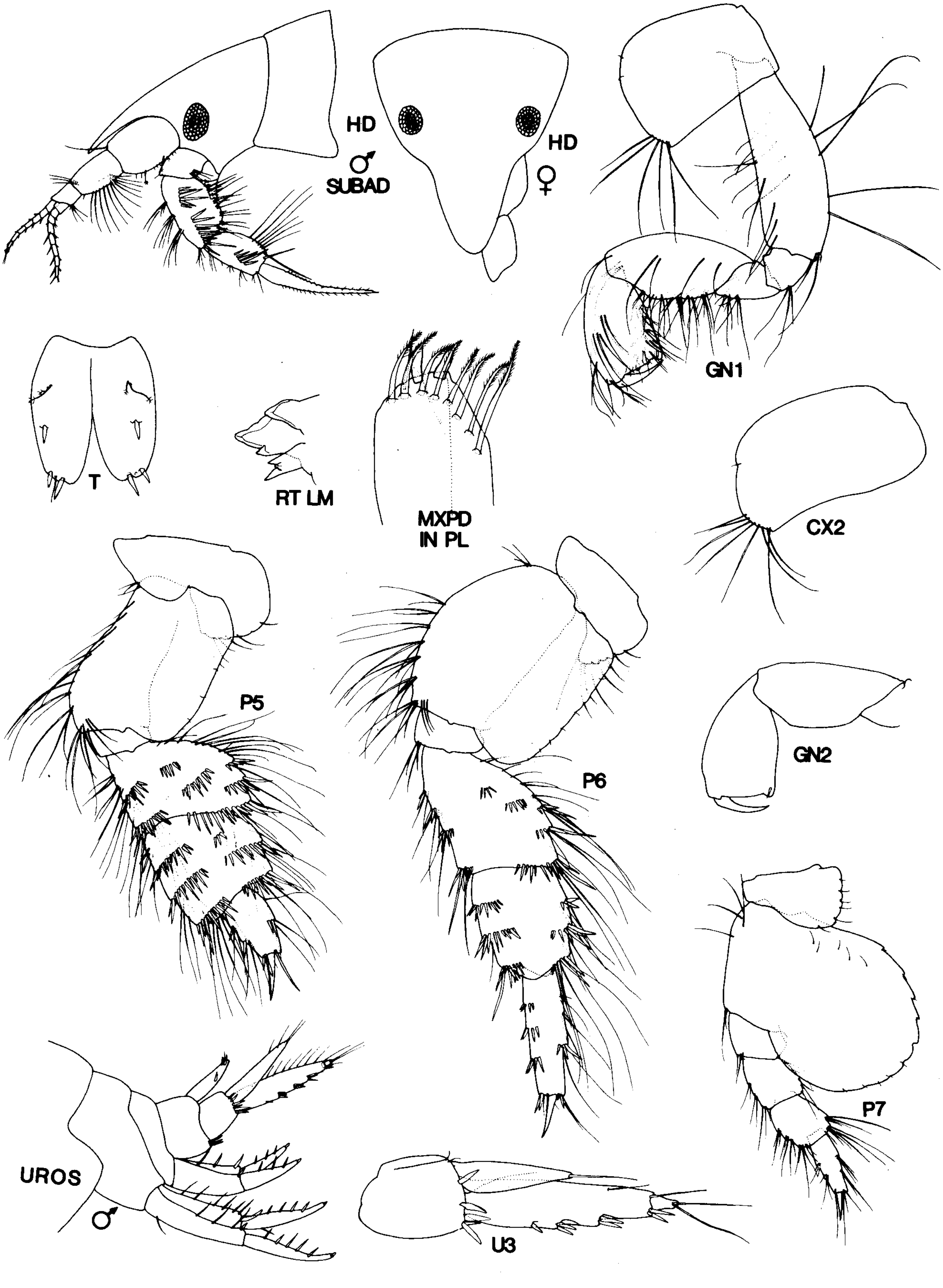
Taxonomic commentary. This species shows many similarities to *G. vulpinus* but is slightly more distant to *G. acanthinus. G. aciculatus* differs not only in the characters of the key (p.) but in its larger, broader rostrum; broader more rounded anterior coxal plates; stronger dactyl of peraeopod 5; but weaker group of postero-distal (pre-peduncular) spines on urosome 3.

Grandifoxus acanthinus Coyle, 1982
(Fig. 9)

Grandifoxus acanthinus Coyle, 1982: 444, figs. 5, 6.

Material examined.
ALASKA: Aleutian Islands, Unimak Island. P. slattery colln., June-October, 1982: 50 specimens in 11 lots, including female imm. (4.5 mm), with slide mount.
Bering Sea, NE of St. Lawrence I., P. Slattery colln., July 10,1980: 13 immature specimens, including 1 male subad. (5.0 mm) with slide mount, fig'd. CMN Cat. No. NMCC1992-0625.
Along shore 25, 26, and 40 miles S. of Nome, P. Slattery colln., May and June, 1981: 20 specimens in 3 lots.
SE Alaska, ELB & DEM stns., 1961: A32, Holkam Fay (35 subadult males and females); Al 40, MacLeod Bay (13 specimens, mostly immature, including 1 female ov. (6.0 mm), with slide mount, fig'd.). CMN Cat. No. NMCC1992-0626.

Fig. 8. ***Grandifoxus aciculatus*** Coyle.
FEM. br. I (5.5 mm); MALE subad. (6.5 mm).
(SEE PAGE. 79 - OPPOSITE)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GN2
P7
UROS
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U3

Diagnosis. (Female 6.0 mm): Pigmented eyes medium, oval. Rostrum medium strong, basis medium broad, subacute apex extending to middle of segment 2 of antenna 1. Antenna 1, flagellum short, with 9-10 segments, longer than 7-segmented accessory flagellum. Antenna 2, peduncular segment 4, facial spines in 2 linear clusters of 6-8 spines each, anterior margin with 3-4 clusters of seta but no spines; segment 5 with weakly divided row of 5-6 facial spines; flagellum 11-segmented.

Mandible, molar small, with 4-6 short blades; spine row with 8-10 short blades; left lacinia 4-dentate; right lacinia bifid; palp segment 3, outer margin with cluster of short "A" setae. Lower lip with weak shoulder cusps. Maxilliped, inner plate short; outer plate straight, with 10 inner marginal blade spines; palp segment 2 strong, broad.

Coxa 1-3 large, rectangular, hind corners squarish, lacking cusps. Coxa 4 slightly broader than 3, slightly narrowing distally, lower margin slightly indented. Gnathopods 1 & 2, carpus relatively short and deep, propod slightly shorter, distally broadest, palms vertical.

Peraeopods 3 & 4, segment 5, distal spine medium strong, not exceeding adjacent setae. Peraeopod 5, basis broad, margins sub-parallel, hind margin nearly straight; segment 4 much broader than deep, with 5 variably sized postero-facial groups (rows) of spines; segment 5 less wide but deeper than 4, with single postero-facial row of spines; segment 6 very short and relatively broad, hind margin setose but lacking spines; dactyl slender, medium. Peraeopod 6, basis broad, hind margin nearly straight; segments 4 & 5 little expanded; segment 4 longer than 5, with 4-5 small groups of poster-facial spines; segment 5 deeper than wide, with 2 weak postero-facial spine clusters; segment 6 little longer than 5, margins each with 3 spine clusters; dactyl short. Peraeopod 7, basis, hind margin with 8-10 weak serrations; segment 5 larger than 4; segment 6 longest; dactyl short.

Pleon plates 2 & 3, hind corner rounded, posterior and lower margins strongly setose. Urosome 1 lacking ventro-lateral setal clusters. Urosome 3 with strong postero-ventral fan of spines at base of peduncle of uropod 3. Uropod 1, peduncle with baso-facial fan of setae, with 6-8 tall, slender outer marginal spines, but lacking distal displaced spine; outer ramus with 6-7 slender posterior marginal spines, inner ramus with a single proximal medial spine and 2 posterior marginal spines. Uropod 2, peduncle with 5-8 slender outer marginal spines; rami each with 3-5 posterior marginal spines. Uropod 3, inner ramus more than half length of outer, inner margin weakly setose; outer ramus, inner margin strongly plumose-setose, outer margin with numerous spine clusters; terminal segment small.

Telson lobes slightly narrowing distally, each with single dorso-lateral spine and 3-5 slender apical spines. Gills undescribed.

Male (subadult, 5.5 mm): Pigmented eyes medium, lateral. Rostrum strong, similar to that of female. Uropod 3, rami sub-equal, inner margins plumose-setose.

Male (mature, 8.0 mm, from Coyle, 1982): Calceoli on proximal 6-8 flagellar segments of antenna 1; 7 calceoli on anterior margin of peduncular segment 2 of antenna 2, and on alternate segments of 40-segmented flagellum. Copulatory spines of segment 5 of peraeopod 7 strongly denticulate proximally.

Distribution and Ecology. Eastern Bering Sea, and Unimak I., also coastal regions from south of Nome to Prince William Sound and Holkam Bay. In varying types of sand, subtidally to 87 m. in depth.

Taxonomic commentary. The present specimens differ slightly from those described and figured by Coyle (1982) in having spines (as well as setae) on the anterior margin of segment 6 of peraeopod 5, but having less spinose peduncular segments of antenna 2, and uropods 1 & 2, and in their generally slightly smaller size.

Grandifoxus nasutus (Gurjanova, 1936)

(Fig. 10)

Pontharpinia nasuta Gurjanova, 1936: 249, fig. 3.—1951: 382, fig. 3.—1951, p. 383, fig. 232.
Pontharpinia nasuta: Gurjanova, 1980a: 95.
Grandifoxus nasuta Coyle, 1982: 446, fig. 7.

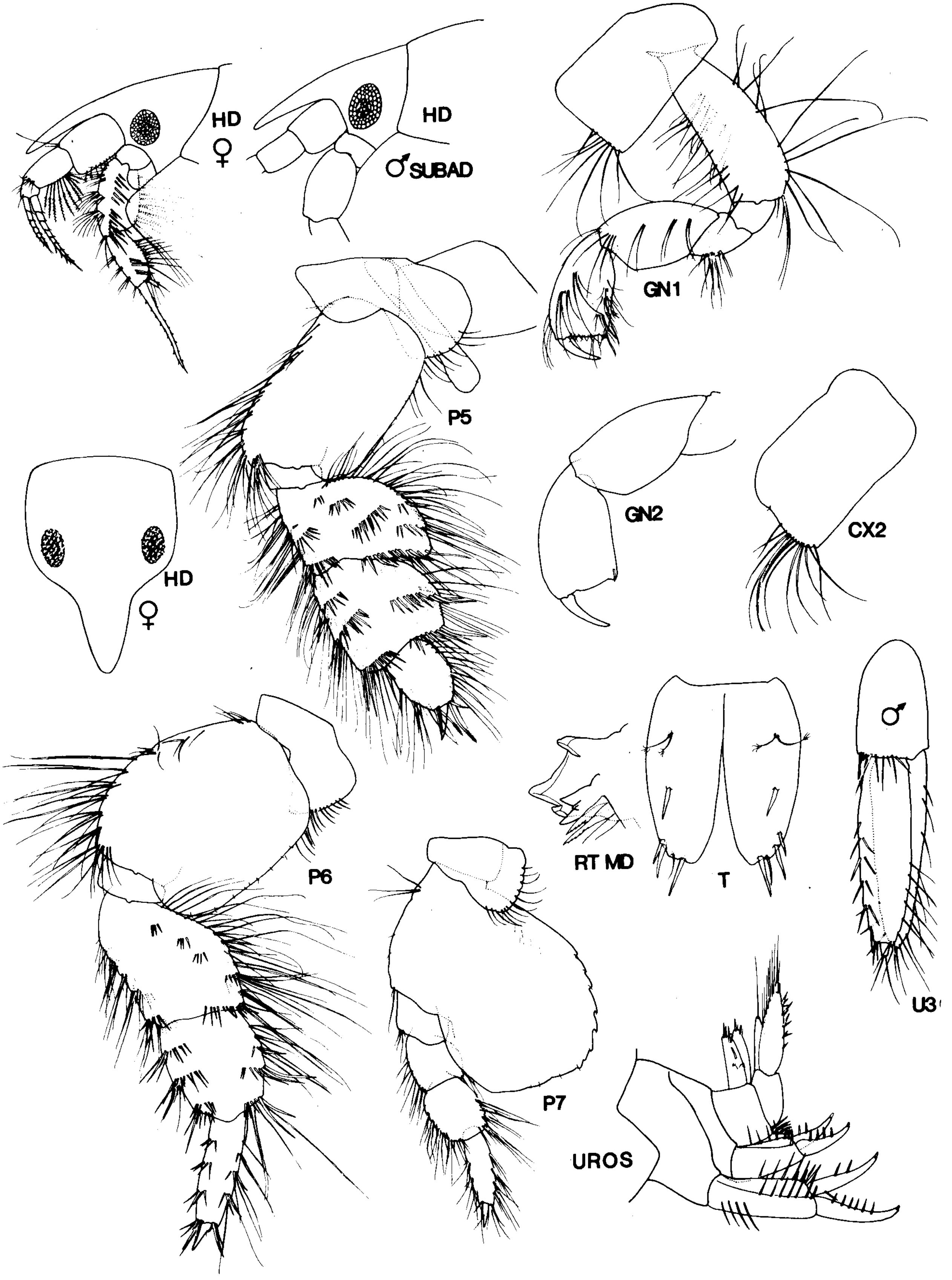
Material examined.
ALASKA: Bering Sea, St. Lawrence I., P. Slattery coll., July 10, 1980: 2 interbrood females (6.5 mm fig'd., 6.75 mm), with slide mounts, 7 females, 1 subadult male (5.5 mm) with slide mount, fig.'d. CMN Cat. No. NMCC1992-0627. Amchitka I., dock at Constantine Harbor, C. E. O'Clair donor, October 5,1968: 1 male.

Diagnosis. Female, br. II (6.75 mm): Pigmented eyes very small, oval. Rostrum medium, broad at base, apex acute, extending well beyond peduncular segment 1 of antenna 1. Antenna 1, flagellum short, 7-8 segmented. Antenna 2, peduncular segment 4 with 3 groups of facial spines, 4-5 spines per cluster; anterior margin with 3-4 clusters of setae, but no spines; segment 5 with single facial cluster of 6 spines; flagellum 7-8 segmented.

Mandible, molar weak, with 8 margin blades; spine row short, with 10-11 blades; left lacinia unevenly 4-dentate; right lacinia bifid; palp segment 3 with weak outer marginal cluster of "A" setae, apex sharply and obliquely truncate. Maxilla 1, apex of palp with 4-5 spines. Maxilliped ordinary.

Coxal plates 1-3 large, deep, hind corners rounded, long-setose. Coxa 1 plate 4 very broad, narrowing distally, rounded below. Gnathopods 1 & 2, carpus relatively short and deep, propods relatively short, broadening distally.

Fig. 9. ***Grandifoxus acanthinus*** Coyle.
FEMALE ov. 6.0 mm); MALE (5.0. mm).
(SEE PAGE 81 - OPPOSITE)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UROS

Peraeopods 3 & 4, segments 5 & 6 subequal; postero-distal spine of segment 5 long, slender, exceeding adjacent setae, and extending about 3/4 length of segment 6; dactyls short. Peraeopod 5, basis large, hind margin gently convex; segment 4 slightly wider than deep; with 2 small postero-facial groups of spines; segment 5 slightly narrower, but deeper than 4, with one postero-facial row of spines; segment 6 sublinear, hind margin with setae only; dactyl slender, but stouter than in P6 & 7. Peraeopod 6, basis medium broad, hind margin straight; segments 4 & 5 little expanded; segment 4 much deeper than 5, with 3-4 small facial clusters of spines near posterior margin; segments 5 & 6 subequal in length, 6 short, with 2 anterior and 1 posterior clusters of spines; dactyl spender. Peraeopod 7, basis broadly rounding, hind margin with 10-12 low teeth or serrations, distally indistinct; segments increasing slightly in length distally.

Pleon plate 2 broadly rounded behind, lower margin strongly setose; pleon plate 3, hind corner obtuse, lower margin with 5-6 setae. Urosome 1 with small cluster of postero-ventral setae. Uropod 1, peduncular outer margin almost bare, displaced spine small or lacking, not larger than adjacent spine; rami with 1-2 posterior marginal spines. Uropod 2, peduncular outer margin distally with 2-3 stout spines, and proximally with 3 slender spines; rami with 1-2 postero-marginal spines. Uropod 3, inner ramus slightly the shorter, inner margins of both with 5-7 plumose setae; terminal segment small but distinct.

Telson lobes broad, lacking dorso-lateral spines, their obliquely rounding apices each with 3 unequal spines.

Coxal gills not described.

Male (antipenult. 5.25 mm): Pigmented eyes relatively small, lateral, ovate. Rostrum slightly broader and more rounded apically than in female. Antenna 2, flagellum with about 15 short segments. Uropod 3, rami subequal; relative to the female the rami are broader, and spines of the outer ramus are shorter.

Distribution and Ecology. Bering Sea, island and coastal continental regions; subtidal sands, to more than 50 m. depth.

Taxonomic commentary. This material is very close to that described from this general region as G. *nasuta* by Coyle (1982). In the mature male specimen (7.5 mm) from the Bering and Chukchi Seas, figured by Gurjanova (1951), antenna 2 is short, with only 19 flagellar segments, alternately calceolate; peduncular segment 5 bears 5 anterior marginal calceoli. Noteworthy in her peraeopod 7 is the pair of very long slender forward-curving copulating spines that extend beyond the distal margin of segment 6.

In balance of apomorphic character states, this species appears to be the most advanced of all species of *Grandifoxus* known to date.

Grandifoxus pseudonasutus, new species
(Fig. 11)

Material examined.
ALASKA: Amchitka I., Constantine Harbor, P. Slattery coll., Sept. 21, 1969: 1 male (6.5 mm) HOLOTYPE with slide mount, CMN Cat. No. NMCC1992-0628.

Diagnosis. (Male 6.5 mm): Eyes large nearly meeting mid-dorsally. Rostrum large, rounded apex reaching mid-point of peduncular segment 1 of antenna 1. Antenna 1, flagellum 10-segmented, proximately calceolate. Antenna 2, peduncular segment 1 with ensiform process; segment 4 relatively short, with 3 groups of facial spines, 3-5 per group, anterior margin with strong brush setae; segment 5 with 5 relatively large calceoli, anterior margin with 7-8 clusters of brush setae; flagellum about 26-segmented, alternately calceolate.

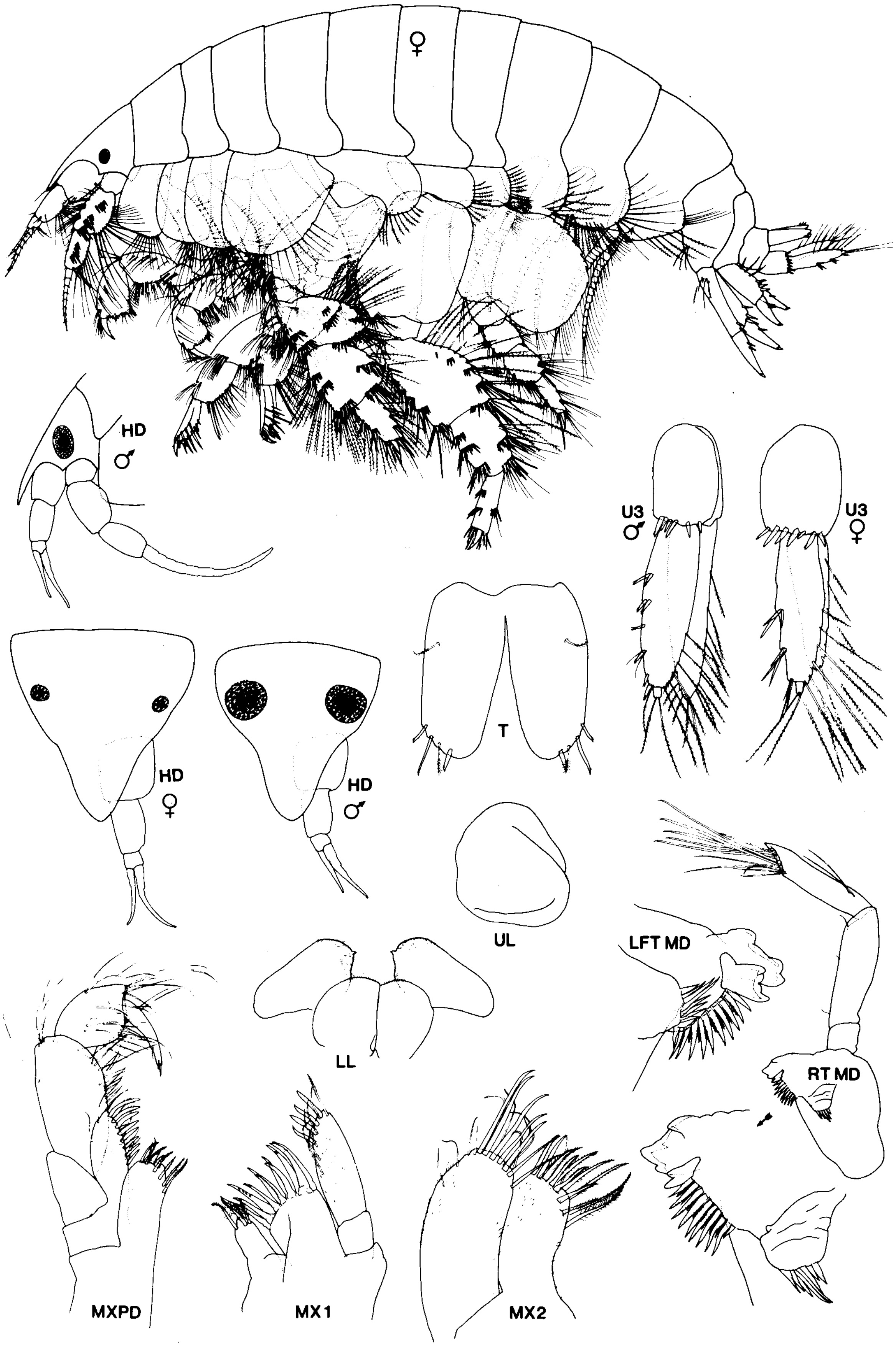
Mandible, molar small, right molar with 6-8 blades, left molar with 4 blades; spines row with 10-11 blades; left lacinia 4-dentate, right lacinia bifid; palp with weak cluster of "A" setae apex obliquely truncate. Maxilla 1, palp with 3 apical spines. Maxilliped ordinary, outer plate relatively narrow and short. Lower lip, shoulders with prominent cones.

Coxae 1-3 large, deep, hind corners rounded, without cusps. Coxa 4 very large, hind process extending considerably under coxa 5, front and rear margins converging distally, rounded below. Gnathopods 1 & 2, carpus relatively short and deep; propods relatively short, broadening distally.

Peraeopod 5, basis medium large, hind margin convex; segment 4 slightly broader than deep, with 2-3 small postero-facial spine groups; segment 5 as wide as, but deeper than, segment 4; segment 6 slightly broadened, not longer than 5, hind margin with setae only; dactyl long, about 1/2 length of segment 6. Peraeopod 6, basis large, broadening distally, hind margin nearly straight; segments 4 & 5 little expanded, segment 4 distinctly the longer, with a few small postero-facial spine groups; segment 6 elongate, anterior and posterior margins with 3 small spine clusters; dactyl medium strong. Peraeopod 7, hind margin of basis with 6-7 weak serrations; segments 4 & 5 subequal; paired copulatory spines subequal, extending slightly more than half way along segment 6; dactyl slender.

Pleon plate 2 broadly rounding behind and below; pleon plate 3, hind corner slightly indented, with strong tuft of setae. Uropod 1, peduncle with 2-3 small outer marginal spines, but no distinct displaced spine; rami strong, with 5-

Fig. 10. ***Grandifoxus nasutus*** (Gurjanova). FEMALE (6.5 mm); MALE (5.5 mm).
(SEE PAGE 93 - OPPOSITE)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6 small posterior marginal spines. Uropod 2, peduncle with about 10 stout outer marginal spines; rami with 5-6 marginal spines. Uropod 3, rami strong, subequal, margins strongly plumose-setose, terminal segment distinct.

Telson lobes lacking dorso-lateral spines, each apex with 2-3 short spines.

Coxal gill very large on P2-6, small, drop-shaped on P7

Female: Unknown

Etymology. Prefix from the Greek root 'pseudes' meaning false, alluding to the similarity of this species to *G. nasutus.*

Distribution and Ecology. Known only from the type locality, Constantine Harbor, Amchitka, Alaska, in sand near shore.

Taxonomic commentary. Non-sex-linked character states of this form are generally similar to those of *G. nasutus,* as figured by both Gurjanova (1951) and Coyle (1982). However, the present male specimen differs in having shorter copulatory spines, more strongly spinose uropods 1 & 2, broader pleonal plates, and smaller telson spines.

Beringiaphoxus , new genus

Type species. *Beringiaphoxus beringianus,* new species.

Diagnosis. Pigmented eyes large, lateral, in both males and files. Rostrum large, hooded, not incised in front of eyes. Antenna 2 (female), peduncular segment 1 weakly or not ensiform; segment 3 with 3-4 lateral setae; segment 4 with single row of facial spines, anterior margin with setal clumps, but no spines; segment 5 with 2 rows of facial spines.

Mandible, molar weak, with slender marginal blades; spine row strong; left lacinia 4-dentate, right lacinia bifid; palp segment 2 not expanded. Lower lip broad, shallow. Maxilla 1 & 2 ordinary. Maxilliped, inner plate with 2 apical spines; palp, dactyl strong basally stout.

Coxae 1-3 large, increasing posteriorly, lower margins rounded, hind corners lacking cusps. Coxa 4 large, narrowing distally, lower margin rounded. Gnathopods 2, carpus stronger and deeper than in 1, propods broadening distally.

Peraeopods 3 & 4 very strong; 4 expanding distally, 5 short, deep. Peraeopod 5, segment 4 broader than deep, facial rows of spines strong. Peraeopod 5, basis very broad; segment 4 broader than deep; segment 5 longer than 4 but shorter than 6. Peraeopod 7, hind margin of basis with numerous (10+) teeth or serrations; segment 5 expanded, as broad as deep (copulatory spines of mature male unknown). All peraeopod dactyls medium.

Uropod 1, peduncle with baso-facial cluster of 5-6 setae, numerous (8+) outer marginal spines, but lacking displaced spine; rami long, spinose posteriorly. Uropod 2, peduncle and outer ramus marginally spinose; inner ramus bare. Uropod 3, rami markedly unequal (female), broad throughout, slightly tapering distally, terminal segment minute; in penultimate male rami broad, nearly subequal, inner margins plumose-setose.

Telson lobes broad, with dorso-lateral and apical spines. Coxal gills large, drop-shaped on peraeopods 2-6, slender on peraeopod 7.

Mature male unknown.

Taxonomic commentary. *Beringiaphoxus* exhibits many of the plesiomorphic character states of the *grandis - lindbergi* subgroup within the genus *Grandifoxus.* It differs from that genus mainly in its unconstricted, elongate rostrum; large eyes in both sexes; and broadened segment 5 of peraeopod 7. From the genera *Foxiphalus* and *Majoxiphalus* the present genus is separated (in combination) by the simple facial spination of the antennal peduncular segments; elongate carpus of the gnathopods; powerful form of peraeopods 3 & 4; short, broad segment 4 of peraeopod 6; broad rami of uropod 3 (both sexes), and to lesser extent the bispinose maxilliped inner plate and lack of displaced spine on uropod 1.

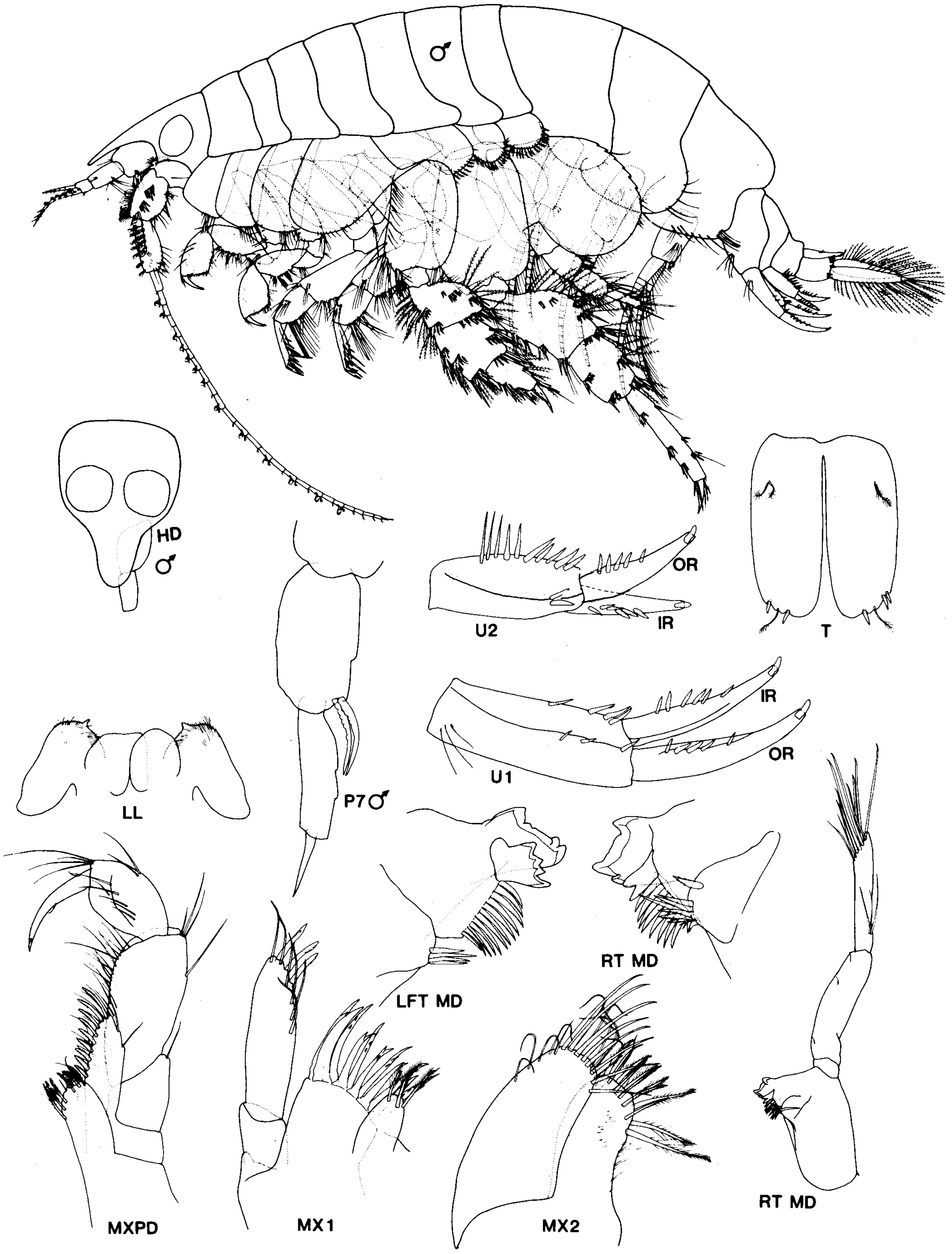
Beringiaphoxus beringianus, new species
(Fig. 12)

Material examined.
ALASKA: Bering Sea: Amchitka Island, Constantine Harbor, inter-tidal sand, P. Slattery coll., Sept. 15, 1971: 1 female br. II (9.5 mm) HOLOTYPE with slide mount, CMN Cat. No. NMCC1992-0629; 1 male penult (8.5 mm) ALLOTYPE with slide mount, CMN Cat. No. NMCC1992-0630; 7 female PARATYPES. CMN Cat. No. NMCC 1992-0715; Ibid; MLW sand, October 30, 1971 - 1 female Br. II (6.0 mm) with slide mount, 7 females, Br. I & II, PARATYPES, CMN Cat. No. NMCC 1992-0716.

Diagnosis. (Female br. II, 9.5 mm): Pigmented eyes large, subovate. Rostrum, apex long, extending to peduncular segment 3 of antenna 1. Flagellum of antenna 11-12 segmented, nearly twice the length of the accessory flagellum. Antenna 2, peduncular segment 4, facial spines in two linear groups of 7-8 spines each; segment 5 with 10-12 facial spines; flagellum 12-segmented.

Mandible, molar with 7-8 blades; spine row with 10-13 rakers and accessory setae; right lacinia bifid, separated from raker spines; left lacinia 4-dentate; incisors tricuspate; palp segment 3 with single cluster of long "A" setae. Upper lip,

Fig. 11. ***Grandifoxus pseudonasutus,*** new species. MALE (6.5 mm) HOLOTYPE.
(SEE PAGE 85 - OPPOSITE)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epistome not produced. Lower lip, shoulder cusps distinct. Maxilla 1, palp segment 2 apex subacute, slope with several slender spines. Maxilliped, outer plate with 13 inner marginal serrate masticatory spines.

Coxal plates 1-3, lower hind margins strongly long-setose. Gnathopods slightly unequal, carpus of gnathopod 2 distinctly shorter and deeper than 1; propod palms vertical.

Peraeopods 3 & 4, segment 5 much shorter than 4, postero-distal spine longer than adjacent setase, about 2/3 length of slender spinose segment 6. Peraeopod 5, basis broad, margins subparallel segment 4 broader than wide; segment 5 less wide, but deeper than 4, with single postero-facial row of spines; segment 6 about equal in length to 5, hind margin setose. Peraeopod 6, basis very broad, hind margin slightly convex; segment 4 as broad as deep, with 1 distinct postero-facial spine group; segment 5 less broad but longer than 4, with one postero-facial spine group; segment 6 with 3 groups of anterior and posterior marginal spines. Peraeopod 7, segment 5 very broad, hind marginal teeth numerous weak; expanded segment 6 with numerous long posterior marginal setae; segment 6 distinctly longer than 5, margins setose.

Pleon plate 2, hind corner rounded; pleon plate 3, hind corner notched, with strong tuft of posterior setae. Urosome 3 with cluster of postero-ventral setae. Uropod 1, with baso-facial group of setae and 8-10 outer marginal spines; rami long, curved, outer ramus with about 10 posterior spines. Uropod 2, outer ramus with 5 posterior spines, inner ramus bare. Uropod 3, inner ramus about half length of outer, plumose setose at apex; outer ramus, terminal segment minute.

Telson lobes broad, each with 2-3 dorso-lateral spines in tandem, oblique apices each with 1-2 short spines.

Male, penultimate (8.5 mm): Pigmented eyes horizontally subovate, lateral. Antenna 2, flagellum of more than 20 segments, proximally conjoint. Uropod 3, inner ramus short-plumose setose on both margins; outer ramus, terminal segment with 2 apical plumose setae.

Etymology. Named after its type locality in the Bering Sea.

Distribution and Ecology. Intertidal and shallow-water sands; to date known only from Amchitka Island, southern Bering Sea, the type locality.

Taxonomic commentary. The species differs from some species of *Grandifoxus* (esp. the *longirostris* group and *G. lindbergi)* in lacking a displaced spine on uropod 1, in lacking spines on the inner ramus of uropod 2, but possessing large pigmented eyes in both sexes. Because of the fully hooded rostrum, the species may bear a certain superficial resemblance to primitive species of *Foxiphalus,* especially *F. aleuti,* which also has a bifid right lacinia, and apically bi-spinose maxilliped inner plate. However, *Beringiaphoxus* is distinguished from *F. aleuti* by its large eyes, dissimilar carpi of the gnathopods, more powerful peraeopods 3 & 4, broadly expanded segment 4 of peraeopod 6, spinose uropods 1 & 2 (lacking displaced spine), and broad uropod rami. The form and calceolation of peduncular segment 5 of antenna 2, and form of the copulatory spines of P7, are unknown, but are needed to establish more precise phyletic relationships of *Beringiaphoxus*.

Majoxiphalus, new genus

Foxiphalus Barnard, 1979: 372 (partim).---Barnard & Karaman, 1991: 609 (partim).

Type species. *Foxiphalus major* Barnard, 1960: 259.

Species. *Majoxiphalus maximus,* new species.

Diagnosis. Pigmented eyes very small (female). Rostrum elongate, not incised in front of eyes, apex acute. Antenna 1, segment 2 slightly longer than segment 1. Antenna 2, segment 1 weakly ensiform, segment 3 lacking lateral setae; segment 4, facial spines in 3 linear clusters; anterior margin with clusters of setae, not spines; segment 5, facial spines in single long submarginal row (female), with 7 anterior marginal calceoli (male); flagellum (of male) short, segments alternately calceolate.

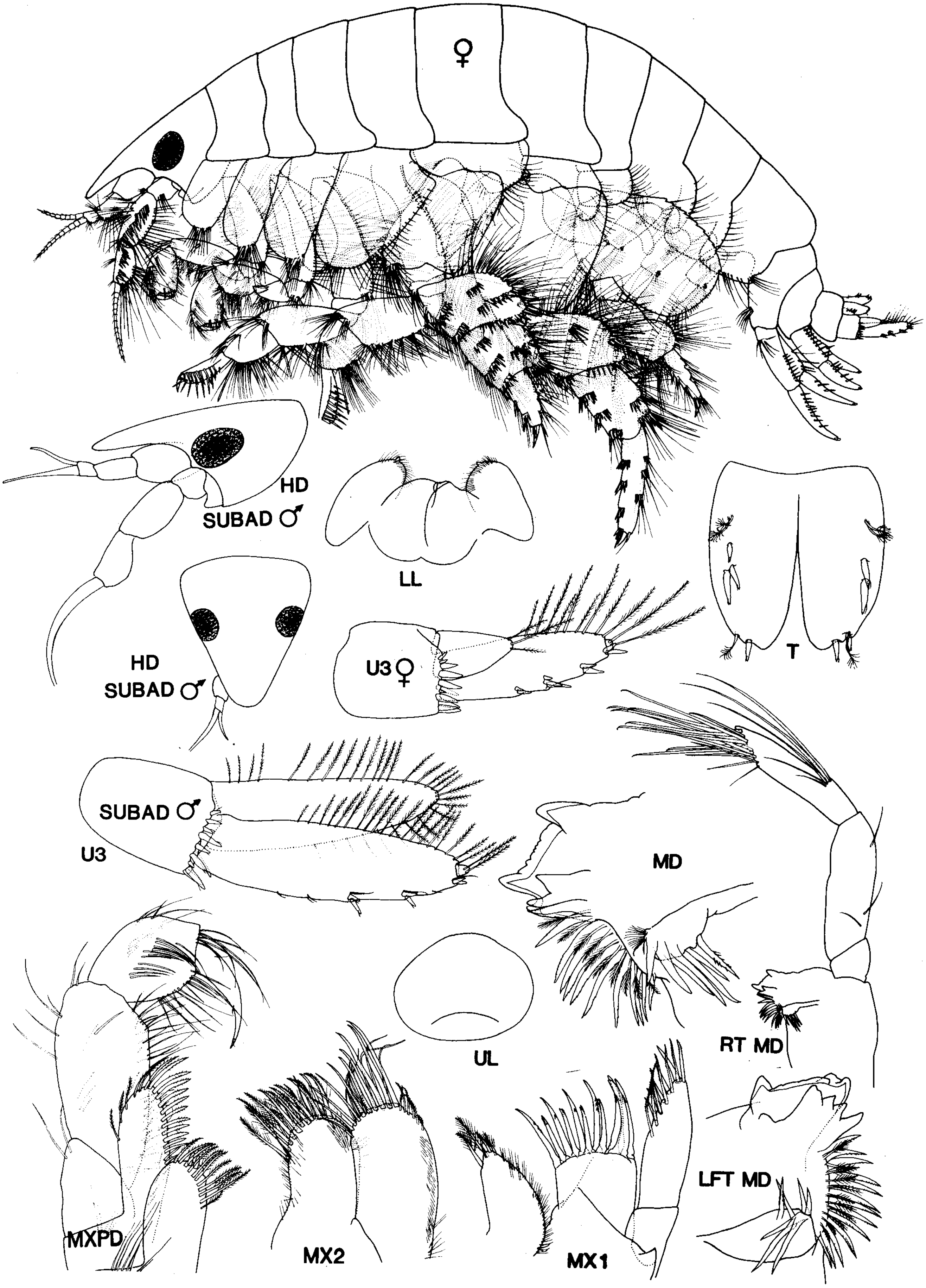
Mandible, molar small with 8-10 marginal blades; spine row strong; left lacinia 4-dentate, right lacinia irregularly bifid; palp segment 2 broadened, setose; segment 3, with two clusters of "A" setae, apex strongly oblique. Lower lip tall, shoulder cones weak. Maxilla 2, inner and outer plates subequal in width. Maxilliped inner plate with 2 (1-3) apical spines, outer plate slender, palp medium strong, dactyl slender.

Coxal plates 1-3 large, deep, lower margins strongly setose. Coxa 4 very large, hind margin arcuate. Gnathopods 1 & 2 differing in strength of carpus: gnathopod 2, carpus with medium-short posterior lobe; propod subovate, palm oblique.

Peraeopods 3 & 4 very powerful, segment 5 short and deep, postero-distal spine strong, long, accompanied by 1-3 slender accessory spines; segment 6 elongate, marginal spines slender, very numerous; dactyls very small. Peraeopod 5, segment 4 broader than deep; segment 5 narrower and deeper than 4, segment 6 longer than 5, hind margin strongly setose. Peraeopod 6, basis large, subovate; segments 4 & 5 little broadened, elongate; segment 6 elongate, margins spinose; dactyl strong. Peraeopod 7, segments 4 & 5 broadened, 5 longer than 6, copulatory spines elongate, slender, setulose distally; dactyl long.

Pleon plates 2 & 3, hind corners subacute, hind margin richly setose. Urosome 1 with ventral cluster of setae. Uropod 1 peduncle baso-facially richly setose; inner margin

Fig. 12. ***Beringiaphoxus beringianus*** new genus, new species. FEMALE br. II (9.5 mm) HOLOTYPE. MALE subadult (8.5 mm) PARATYPE. (SEE PAGE - OPPOSITE)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spinose, distal displaced spine strong; rami long, finely spinose. Uropod 2, rami long, outer ramus spinose, inner ramus weakly spinose or unarmed. Uropod 3, rami subequal, lanceolate (both sexes), margins weakly (female) setose; terminal segment distinct, with 1-2 short apical setae.

Telson lobes narrowing distally, with 1-4 spical spines, dorso-lateral spines lacking.

Coxal gills large, broad, on peraeopods 2-7.

Etymology. Anagrammic combination of "major", the type species, with parts of 'phoxus' (hooded), and 'cephalus' (head).

Taxonomic commentary. This genus has been separated from *Foxiphalus* based on the distinctive morphology of its type species, *M. major* (Barnard). In its several plesiomorphies of ambulatory appendages and mouthparts, *Majoxiphalus* is more closely related to *Beringiaphoxus* and *Grandifoxus* than to *Foxiphalus* (see Discussion, p. 126)

Key to species of *Majoxiphalus*

1. Uropods 1 & 2, outer rami marginally spinose to apex; gnathopod 2, carpus posterior lobe long, about half length of anterior lobe, setae in 2+ clusters; telson, apices each with 3+ spines; .... *Majoxiphalus maximus* (p. 90).

----Uropods 1 & 2, outer rami spinose proximally, distal 1/3 bare; gnathopod 2, carpus posterior lobe short, less than half length of anterior lobe, setae in one big cluster; telson lobes each with 1-2 apical spine. *Majoxiphalus major* (p. 88)

Taxonomic commentary. Members of this genus combine a number of plesiomorphic character states, with specialized features that remove it from the genus *Foxiphalus*, as here defined. The principal differences are: very elongate rostrum; strongly calceolate peduncle 5 of antenna 2 (male); very powerful peraeopods 3 & 4 with several postero-distal spines on segment 5; the unique mandibular palp; elongate rami of uropods 1 & 2; sub-equal rami of uropod 3 (both sexes), and the slender telson lobes that lack dorso-lateral spines.

Distribution and Ecology. The two known species (and variants) are North American Pacific endemic. The records indicate that the component species may be associated with fine, often silty, or partly anaerobic 'black' sands, in semiprotected deposition zones.

Majoxiphalus major (Barnard, 1960)
(Fig. 13)

Paraphoxus major Barnard, 1960: 259, pl. 32.
Foxiphalus major Barnard & Barnard, 1982a: 12, fig. 1.—Barnard & Barnard, 1991: 610.

Material examined.

SE ALASKA: Kruzof I., Kamenoi Pt., dredge 9m, stones and (black) sand, ELB Stn. S18F3, Aug. 2,1980. - 1 male (subadult), 6 imm.; Chichagof I., Column Pt., Lisianski Strait, LW and subtidal fine black organic sand, ELB Stn. S11B3, July 30, 1980: 1 male; Ibid, dredge, 3-6 m, 511 Fl: 1 female ov., 5 subadult females, 1 mature male.

BRITISH COLUMBIA: Queen Charlotte Islands: Parry Passage, Kiusta, LW sand, ELB Stn. H2a, August 24,1957:1 female imm. (6.0 mm) with slide mount.

Hecate Strait, PRG 5-1-16, Stn. 36, from fish stomach, Mar. 21, 1965, (C. Low donor): 1 female br. II (14.0 mm) with slide mount.

Central Coast: Bolivar Island, grab, 15 m., ELB Stn H59, Aug. 9, 1964: 1 female ov. (15.0 mm.) with slide mount, fig'd, 1 mature male (10.5 mm) with slide mount, fig'd., 8 immatures. CMN Cat. No. NMCC1992-0631. Oval Bay, ELB Stn. H10, in sand at LW level, July 12, 1964: 1 female br. II (12.5 mm) with slide mount, 60 immatures.

Vancouver Island: Barkley Sound, Trevor Channel off Long Reach, coarse sand at 30 m., ELB Stn. P10, July 29,1975: 1 imm. female; off Bordelais Islets, fine sand, 44 m., ELB Stn. P21a, August 9, 1975: 3 subadult females (1 photographed), 6 juveniles. Pachena Bay, from gray whale pits in sand, 15-25 m., P. Slattery Stns.: Pit 1, September 16,1982: 1 female br. II, 3 juv., with slide mount of imm. female (5.5 mm); Pit 3, July 25, 1982, 1 female br II (slide mount); April 17, 1983 - 1 subadult female.

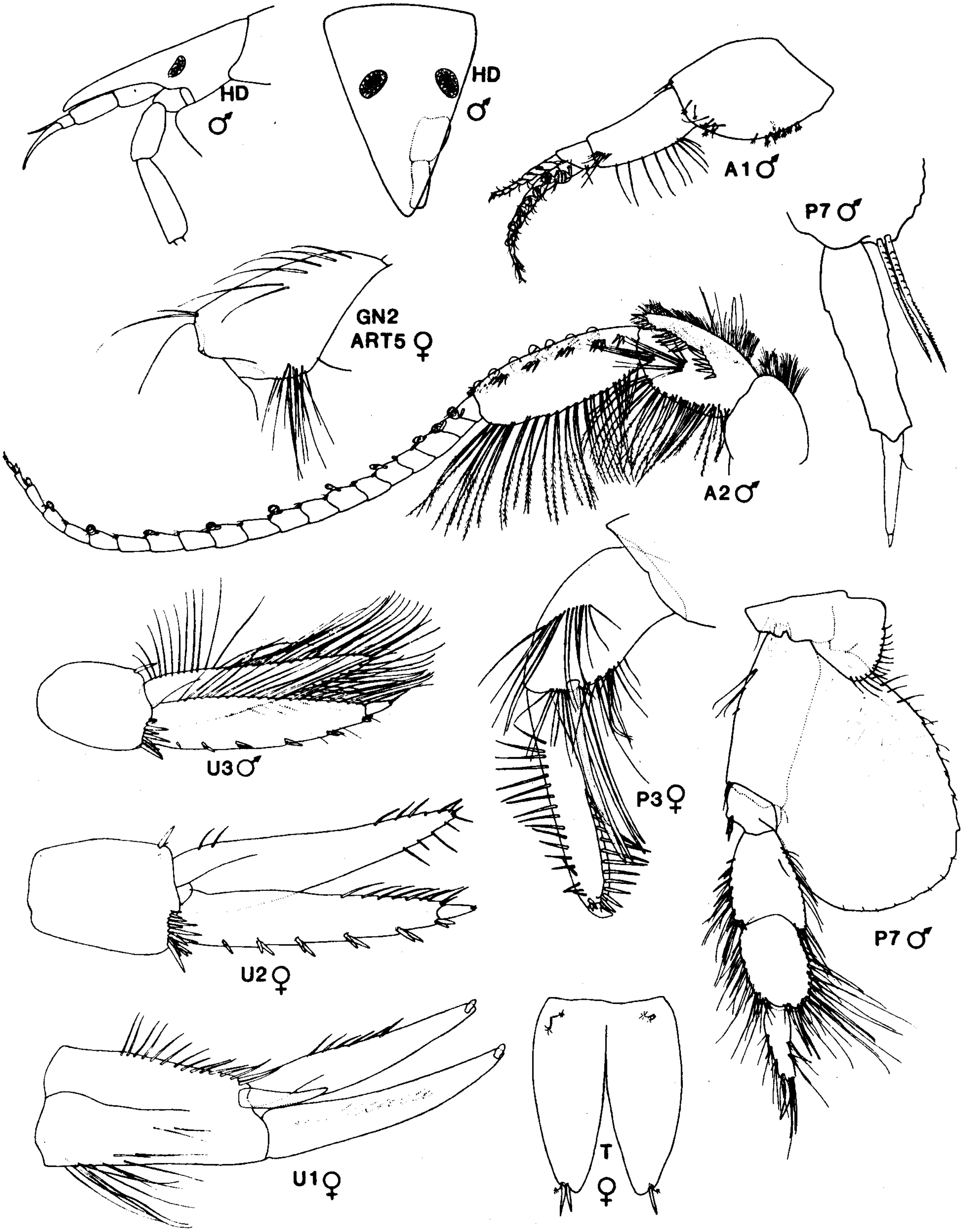
WASHINGTON: Crescent Beach, LW, clean sand above black sand, ELB Stn. W34, July 27, 1966: 1 subadult female, 4 juveniles. Juan de Fuca Strait, Off San Juan Island, Strait of Juan de Fuca, C. P. Staude Stn. KBG-10, June 3, 1976: 10 specimens with slide mount of 1 female ov. (12.0 mm).

Diagnosis. (Female ov., 15.0 mm) (supplementing Barnard (1960), and Barnard & Barnard (1982a)): Pigmented eyes small, ovate. Maxilla 1, inner plate with 4 apical setae. Maxilliped, inner plate with 2 (1-3 occasionally) apical spines; outer plate short, usually extending less than half segment 2 of palp.

Coxa 4, hind margin smoothly rounded. Gnathopod 1, carpus, posterior lobe medium, length about half anterior margin; gnathopod 2 carpus, hind lobe short, rounded, setae in one main cluster.

Peraeopod 5, segment 4, width about 25% greater than depth, proximal margin strongly rounded, postero-facial row of about 8-10 spines; segment 6 little expanded, nearly twice as long as wide; dactyl short. Peraeopod 6, segments 4, 5, & 6 moderate, combined length about 50% great than length of basis. Peraeopod 7, basal lobe rounded not produced posteriorly.

Fig. 13. ***Majoxiphalus major*** (Barnard).
FEMALE. (15.0 mm); MALE (10.5 mm)
(SEE PAGE 89 - OPPOSITE)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HD ♂
A1 ♂
P7 ♂
GN2 ART5 ♀
A2 ♂
U3 ♂
P3 ♀
P7 ♂
U2 ♀
U1 ♀
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Uropod 1, displaced spine very strong, length nearly 1/3 length of inner ramus; distal one-third of rami lack posterior slender spines. Uropod 2, distal third of outer ramus, and all of inner ramus, lack posterior slender spines. Uropod 3, inner margin of rami with short simple setae near apex only. Telson lobes usually each with 2 apical spines and single setule.

Coxal gills not described.

Male (mature, 10.5 mm). Rostrum slightly shorter and broader than in female, apex less acute. Eyes medium small, ovate (in northern material), large, rounded, nearly meeting mid-dorsally (in Californian material). Antenna 1, flagellum, proximal 7 segments calceolate. Antenna 2, peduncular segment 5 with 7 anterior marginal calceoli and 5-6 submarginal facial spine groups, posterior margin heavily plumose-setose; flagellum 20-segmented, distal segments alternately calceolate.

Peraeopod 7, segment 5, copulatory spines elongate (about 3/4 length of segment 6), nearly straight, distally setulose.

Uropod 3, inner margins of rami very heavily armed throughout with long plumose setae.

Distribution and ecology. Southeastern Alaska (Sitka region) and British Columbia, south to central, and Baja California, in fine sand (just above reducing layer) from LW levels (in north) and sub-tidally to depths of 91 m. at Californian stations.

Taxonomic commentary. Considerable variation has been noted in character states of the mouthparts, gnathopods, uropods and telson throughout the range of materials at hand and those described by Barnard (1960) and Barnard and Barnard (1982). The possibility that still other species (than *M. maximus,* new species) are masked by such variation awaits the study of more extensive material.

Majoxiphalus maximus, new species
(Fig. 14)

Material examined.

ALASKA: Bering Sea, St. Lawrence Island, subtidal sand, P. Slattery coll., June, 1983:1 female ov. (15 mm).

BRITISH COLUMBIA: Vancouver Island: Ahous Bay, LW sand, ELB Stn. 012, Aug. 8,1959: female ov. (18.0 mm) HOLOTYPE with slide mount, CMN Cat. No. NMCC1992-0632, 1 female ov. (15 mm), PARATYPE, CMN Cat. No. NMCC 1992-0633. McKenzie Beach, LW sand, ELB Stn. P703, July 7, 1970: 1 female subad. (13.0 mm) with slide mount, 23 juveniles.

Diagnosis. (Female ov., 18.0 mm): Eyes very small weakly pigmented. Rostrum sharply elongate, apex extending almost to base of 12-segmented flagellum of antenna 1. Accessory flagellum 10-segmented. Antenna 2, segment 4, facial spines in 3 clusters of 5, 4 and 5-6; segment 6 not longer than 5, with submarginal facial row of 12-14 spines; flagellum 14-segmented.

Mandible, molar with 9-11 marginal blades; spine row with 10-12 rakers and accessory setae; left lacinia irregularly 4-dentate; right lacinia bifid, closely approximated to raker spines; incisor broad, with 3 cusps; palp segment 2 stout, with numerous setae on both margins; segment 2 with 2 tightly approximated clusters of medium-long "A" setae. Maxilla 1, inner plate with 3 apical setae. Maxilliped, inner plate with 2 strong apical spines; outer plate slender, extending more than half length of palp segment 2, inner margin with 10-11 slender masticatory spines.

Coxa 4 very broad, broader than deep, posterior margin divided into vertical and oblique portions. Gnathopod 1, carpus long and slender; gnathopod 2, carpus shorter, hind lobe nearly half length of anterior lobe, setae in 2+ clusters; propods slender, subovate, longer than respective carpus.

Peraeopods 3 & 4, segment 5, postero-distal spines slender, tips reaching 3/4 length of segment 6; segment 6, marginal spines long, slender, 14-18 on each side, more numerous on outer margin. Peraeopod 5, basis medium broad, hind margin nearly straight; segment 4, width more than 50% greater than depth; disto-facial spine row with 12 + spines; segment 5 expanded, slightly deeper than wide, with no postero-facial spines; segment 6 as long as 5, hind margin setose; dactyl slender. Peraeopod 6, basis expanding distally, rounded below; segments 4 & 5 elongate, little expanded segment 6 elongate, nearly equal to 4 & 5 combined, margins with 5-6 clusters of spines; dactyl, strong, curved. Peraeopod 7, basis subcircular, wider than deep, postero-proximal margin with 5-6 low serrations; segment 5 & 6 stout, width about equal to length; segment 6 slender, not longer than 5; dactyl slender.

Pleon side plates typical of genus, lower margins strongly setose. Uropod 1, peduncle with 4-5 baso-facial clusters of long setae, displaced spine medium strong, about 1/4 length of inner ramus; posterior marginal spines of rami numerous, reaching tips. Uropod 2, outer ramus with about 20 slender posterior marginal spines, nearly reaching apex, inner ramus bare. Uropod 3, rami strongly plumose-setose along inner margins.

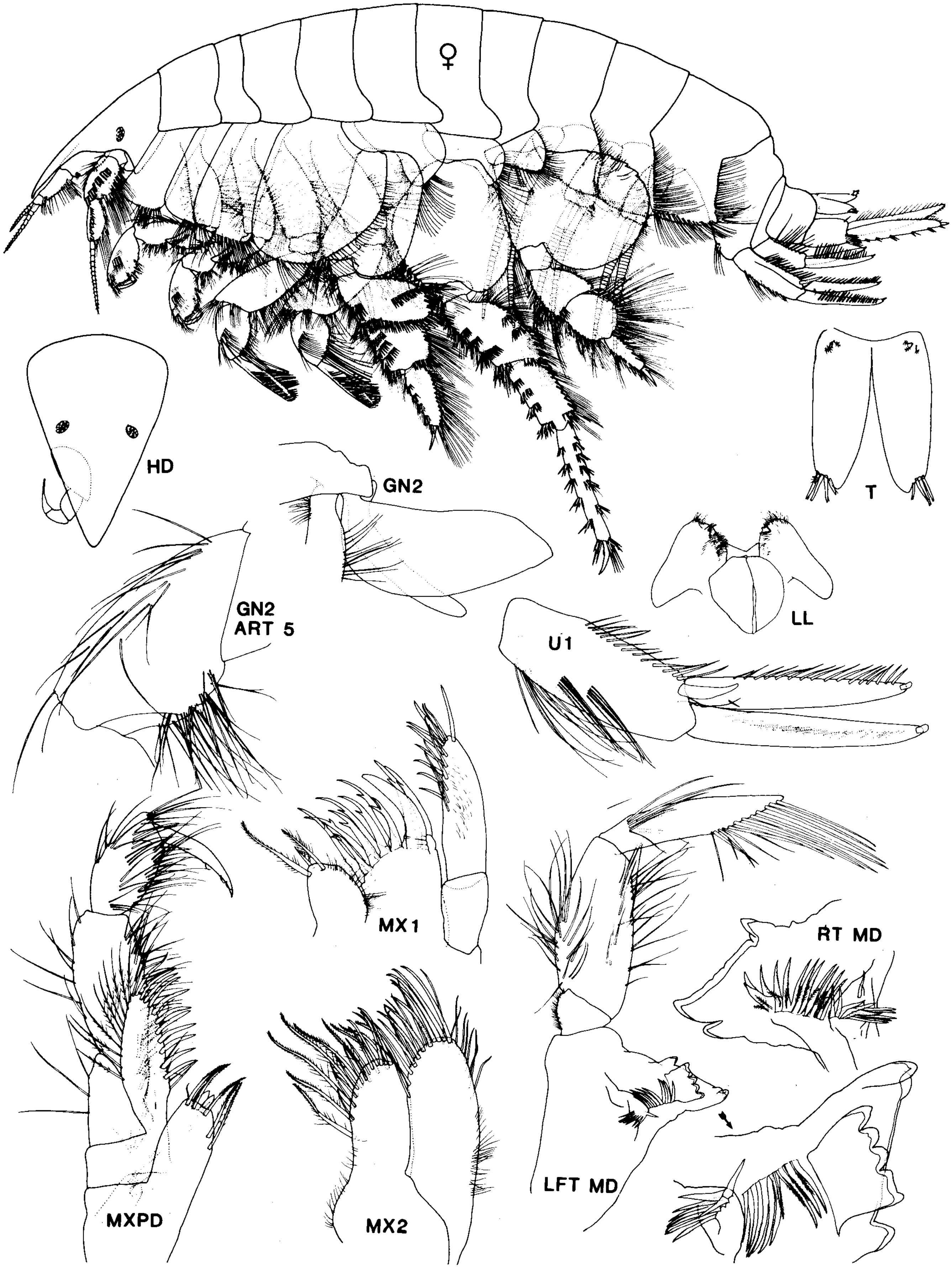
Telson lobes, apices each with 3-4 slender spines and a setule. Coxal gill on peraeopod 2 large, broad, tip subacute.

Mature male unknown.

Etymology. From the Latin 'maximus', referring to the large size of the animal, the largest species known to date.

Distribution and Ecology. Known only from three records, Bering Sea to northern Vancouver Island, in fine sand, LW and sub-tidally. The rarity of this species in collections from sandy beaches may indicate a very special-

Fig. 14. ***Majoxiphalus maximus*** , new species.
FEMALE ov. (18.0 mm) HOLOTYPE.
(SEE PAGE 91 - OPPOSITE)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ized habitat, perhaps associated with fine silty, or anaerobic conditions, not frequently sampled.

Taxonomic commentary. This species is easily distinguished from the type species, *M. major,* by the characters given in the key and in other descriptive details. In the region of distributional overlap, the two species did not occur in the same lots, although ecological requirements appear similar.

Foxiphalus Barnard, 1979

Foxiphalus Barnard, 1979: 372.—Barnard & Barnard, 1982a: 4 (key).—Barnard & Karaman, 1991: 609.

Type species. *Foxiphalus obtusidens* (Alderman, 1936).

Species. *Foxiphalus falciformis,* new species (p. 94); *Foxiphalus xiximeus* Barnard & Barnard, 1982a; *Foxiphalus fucaximeus,* new species (p. 100);*Foxiphalus aleuti* Barnard & Barnard, 1982; *Foxiphalus similis* Barnard, 1960; *Foxiphalus slatteryi,* new species (p. 106); *Foxiphalus cognatus* Barnard, 1960.

Diagnosis. Pigmented eyes very small to medium in female, medium to large in male. Rostrum fully hooded, not incised in front of eyes. Antenna 1, peduncle 2 distinctly shorter than 1. Antenna 2, peduncular segment 1 variously ensiform, segment 3 with 1 lateral seta; segment 4, facial spines in three distinct groups, anterior margin with a few setae but no spines; segment 5 with 1- 2 clusters of facial spines, and 1-2 distal anterior marginal calceoli in male. Flagellum medium in female (length about equal to peduncle 5 & 6), elongate (20 + alternately calceolate segments) in the male.

Mandible, molar with few (5-10) marginal blades; spine row (rakers) medium strong; left lacinia irregularly 4-dentate or modified; right lacinia simple, (occ. bifid or lacking) often adjacent to spine row; incisors broad, bicuspate; palp slender, segment 2 weakly setose; segment 3 with one cluster of "A" setae, apex obliquely truncate. Upper lip, epistome occasionally with sharp anterior process. Lower lip broad, with distinct shoulder cusps. Maxilla 1 outer plate, one outer apical spine enlarged; inner plate with 2-4 apical setae. Maxilla 2, outer plate usually broader than inner. Maxilliped, inner plate with 1 (occ. 2) apical spine(s); outer plate slender, short (not reaching half of palp segment 2); dactyl slender.

Coxae 1-3 medium deep, increasing posteriorly. Coxa 4 large, margins sub-parallel or converging distally. Gnathopods 1 & 2, propods medium strongly sub-chelate, longer than respective carpus palms oblique; carpal lobe of gnathopod 2 very short.

Peraeopods 3 & 4 medium strong, segment 5 with single postero-distal spine; segment 6 spinose distally; dactyl relatively long. Peraeopod 5, basis medium, broad, regular; segment 4 moderately to broadly expanded, occasionally not wider than deep, facial clusters of spines lacking; segment 5 usually deeper than broad, lacking postero-facial spine clusters; segment 6 longer than 5, hind margin setose; dactyl slender, long. Peraeopod 6, basis typically expanding distally; segment 4 not broadened, length often twice its width, lacking facial spines; segment 6 not broadened, not longer than 4 or 6, hind margin with a few long plumose setae and occasionally short spines; segment 6 slender hind margin with 3A weak cluster of spines and single setae; dactyl slender, long. Peraeopod 7, basis with weak posterior marginal serrations; segments 4, 5, and 6 increasing in length distally, 4 & 5 little broadened; copulating spines (in male) slender sub-equal, straight or slightly decurved, proximally weakly denticulate, distally finely setulose.

Urosomite 1 variably with ventral brush of setae. Uropod 1, peduncle usually with single cluster of baso-facial setae, with strong inner marginal, but few or no, outer marginal spines; displaced spine present, usually strong; rami medium, with few posterior marginal spines, apical spines fixed or articulating. Uropod 2, outer margin strongly spinose; rami short, outer few spinose, inner bare. Uropod 3, inner ramus usually distinctly shorter, and marginally smooth in female; sub-equal and strongly plumose-setose in male.

Telson lobes slightly narrowing distally, usually with 1 dorso lateral spines; apices each with 1-3 (4) variable spines and a single plumose setule.

Coxal gills large, ovate or elongate on P2-6, small on P7.

Taxonomic commentary. Members of the genus *Foxiphalus* exhibit the most extensive combination of apomorphic character states of the seven genera formally assigned to subfamily Metharpiniinae. These include mainly reductions in, or modifications of, the mandibular molar, right lacinia, maxilla 1 spines and setae, maxilliped inner plate spines; more powerfully developed gnathopod carpus and propod; more slenderized and less spinose peraeopods, with longer dactyls; reduced size and armature of the uropods, and reduction in telson spination. Especially apomorphic is the reduction in numbers of calceoli on peduncular segment 5 and flagellar segments of antenna 2 in the male.

The genus contains 10 described species, but the illustrations and descriptive remarks of Barnard (1960) and Barnard & Barnard (1982) suggest that additional taxa from the region of Central and southern California await formal recognition. *'Pararpinia' simplex* Gurjanova 1938, from the Sea of Japan, is superficially similar to the *similis* group of *Foxiphalus,* but the balance of generic character states places it more naturally with the Paraphoxinae (Eobrolginae).

Distributional Commentary. The 10 described species of the genus *Foxiphalus* are North American Pacific endemic. However, only five of these *(F. xiximeus, F. fucaximeus, F. similis, F. slatteryi,* and *F. aleuti)* have yet beee been recorded here. The five others (of Table XII) occur from Central California south to Panama, mostly in coldwater areas or regions of upwelling at southern locations, in depths of 50-100 m, and occasionaluy to 300 m.

Key to regional species of *Foxiphalus*

1. Peraeopod 5, segment 4 very broad, width usually more than 1.5 X depth (length); uropod 3 (female), inner ramus longer than 1/2 the outer ramus, inner margin plumose-setose; telson lobes each with dorso-lateral spine(s) .... 2.

—Peraeopod 5, segment 4 little expanded, width little greater than depth; uropod 3 (female), inner ramus short, margins bare, less than half length of outer ramus; telson lobes lacking dorso-lateral spine(s).. 5.

2. Peraeopod 5, segment 5 wider than deep; peraeopod 6, segment 4 moderately expanded, length not greater than 1.5 X width; uropod 1, outer ramus with 0-1 posterior marginal spines; pleon plate 2, lower margin densely setose .... 3.

—Peraeopod 5, segment 5 deeper than wide; peraeopod 6, segment 4 little broadened, length at least 2 X width; uropod 1, outer ramus with 2-4 small posterior marginal spines; pleon plate 2, lower margin with a few (3-6) scattered setae .... 4.

3. Uropods 1 & 2, outer ramus with 1 (2) posterior marginal spines; gnathopod propods medium, distally broadening, longer than carpus; telson lobes each with medium dorso-lateral spine and single apical spine ....***F. xiximeus*** (p. 98)

—Uropods 1 & 2, outer ramus with O (occ. l) posterior marginal spines; gnathopod propods small, little longer than carpus, margins subparallel; telson lobes each with stout dorso-lateral spine and two unequal apical spine ....***F. fucaximeus*** (p. 100)

4. Uropod 1, outer ramus with 3-4 short posterior marginal spine peduncular displaced spine stout; telson lobes, dorso-lateral spine small; mandible, left lacinia 4-5 dentate .. ***F. obtusidens*** (p. 94)

—Uropod 1, outer ramus with 2 short posterior marginal spines; peduncular displaced spine lacking; telson lobe, dorso-lateral spine long, slender; mandible, left lacinia sickle-shaped .... ***F. falciformis*** (p. 94)

5. Peraeopods 3 & 4, segment 5, postero-distal spine massive, 5-6 times width of adjacent setae; upper lip, epistome not produced; peraeopod 7, segment 5 expanded, ovate, hind margin densely setose; uropod 1, outer ramus with 4 posterior marginal spines .... ***F. aleuti*** (p. 98)

—Peraeopods 3 & 4, segment 5, postero-distal spine normal, slender, about 2-3 X width of adjacent setae; upper lip, epistome moderately to strongly produced to a sharp apex; peraeopod 7, segment 5 not broader than 4, hind margin sparsely setose; uropod 1, outer ramus with 3 (occ. 4) medium posterior marginal spines .... 6.

6. Peraeopod 5, segment 5 narrowing distally; epistome moderately produced, length not exceeding basal width; pleon plate 3, hind margin with 3 setae closely bunched near hind corner .... ***F. cognatus***

—Peraeopod 5, front and hind margins subparallel; epistome strongly produced, length exceeding basal width; pleon plate 3, setaespread widely along hind margin .... 7.

7. Coxa 1, lower margin setose almost throughout; coxa 4, margins slightly converging distally, lower margin broad, flat; telson lobes each with 3 small apical spines .... ***F. similis*** (p. 102)

—Coxa 1, lower margin setose along posterior half only; coxa 4, margins strongly converging distally, lower margin rounded; telson lobes each with 2 normal but unequal apical spines .... ***F. slatteryi*** (p. 106)

Foxiphalus obtusidens (Alderman, 1936)

Pontharpinia obtusidens Alderman, 1936: 54, figs. 1-13. —Barnard, 1954: 4.
Paraphoxus obtusidens Barnard, 1960: 249.---Barnard, 1975: plate 72 (22).
Foxiphalus obtusidens Barnard & Barnard, 1982a: 4, fig..l.

Material examined. The species has apparently not yet been taken in the study region, but might be expected in southern Oregon.

Diagnosis. Although reasonably well described by previous authors (loc. cit. above), at least three species may be included in the figures of Barnard (1960). One of these (his Plate 37) has already been removed to the synonomy of *F. golfensis* by Barnard and Barnard (1982). Two other probably distinct species are represented in Barnard's 1960 Plate 35 and Plate 36 (figs, A-F). Moreover, despite limitations of Alderman's 1936 original description and figures, they do differ in a number of important details even from those of Barnard's plate 34 (1960) on which the latter author bases his redescription of *F. obtusidens.* However, failing careful reexamination of Barnard's material, and since his material is fully outside the present study region, these forms are not described, named, keyed, or otherwise included here.

The following summary of diagnostic character states of *F. obtusidens,* as treated by authors above (loc. cit.), is included for direct comparison with *F. falciformis,* new species (below).

Female (8.5 mm): Pigmented eyes separated dorsally by their length. Rostrum relatively long, apex subacute. Antenna 1, flagellum 9-10 and accessory flagellum 7-8 segmented. Antenna 2, segment 4 wilh 9-14 facial spines and 1 postero-distal long spine, anterior margin with cluster of 3 setae and 1 spine; segment 5 with 3-5 facial spines; flagellum of 9-10 segments.

Mouthparts described but incompletely figured by Alderman (loc. cit). Barnard and Barnard (1982a) described the mandibular molar as small; right molar with 7 primary marginal blades and 1 disjunct (displaced) blade, left molar with 5 blades and a disjunct blade; spine row with 10 short curved rakers; right lacinia unequally bifid, adjacent to spine row; left lacinia 5-dentate (not falciform). Upper lip, epistome not produced, ridge-like. Lower lip with shoulder cones. Maxilla 1, outer plate with enlarged outer apical spine. Maxilliped inner plate with 1 apical spine; inner plate with 10 setulose masticatory spines on inner margin.

Coxae 1-3, lower marginal setae confined to postero-distal corner. Coxa 4, lower margin strongly rounded and continuous with anterior and posterior margins. Gnathopods 1 & 2 medium strong. Gnathopod 2, carpus short, with 1-2 posterior clusters of setae. Peraeopods 3 & 4 moderately strong, segment 5, postero-distal spine stout, length about 2/3 segment 6, having fossorial spines confined to distal end only; dactyl strong. Peraeopod 5, segment 4 little expanded, width about 1.3 X depth (length), lacking postero-facial spines; segment 5 about as wide as deep, longer than 4. Peraeopod 6, segments 4, 5, and 6 relatively short, 4 little expanded, 5 shortest, dactyl medium. Peraeopod 7 unremarkable.

Uropod 1, peduncle with 4-5 medium strong inner marginal spines; displaced spine strong, reaching nearly to pair of posterior marginal spines of the inner ramus; outer ramus with 4 posterior marginal spines; both rami with single articulated apical spines.

Uropod 2 peduncle, outer margin with 8 strong spines; outer ramus with 4 posterior marginal spines; inner ramus marginally bare. Uropod 3, inner ramus nearly equal to proximal segment of outer ramus, both margins plumose-setose distally; outer ramus weakly plumose on inner margin; terminal segment distinct.

Telson lobes broadest medially, each with single short dorsolateral spine; apices rounded, each with 2 sub-equal slender spine and single setule.

Male (5.0 mm): Not described or illustrated by Alderman (1936). Antenna 1 primary flagellum of 11 segments, calceolate on the proximal 2. Copulatory spines of peraeopod 7 not described.

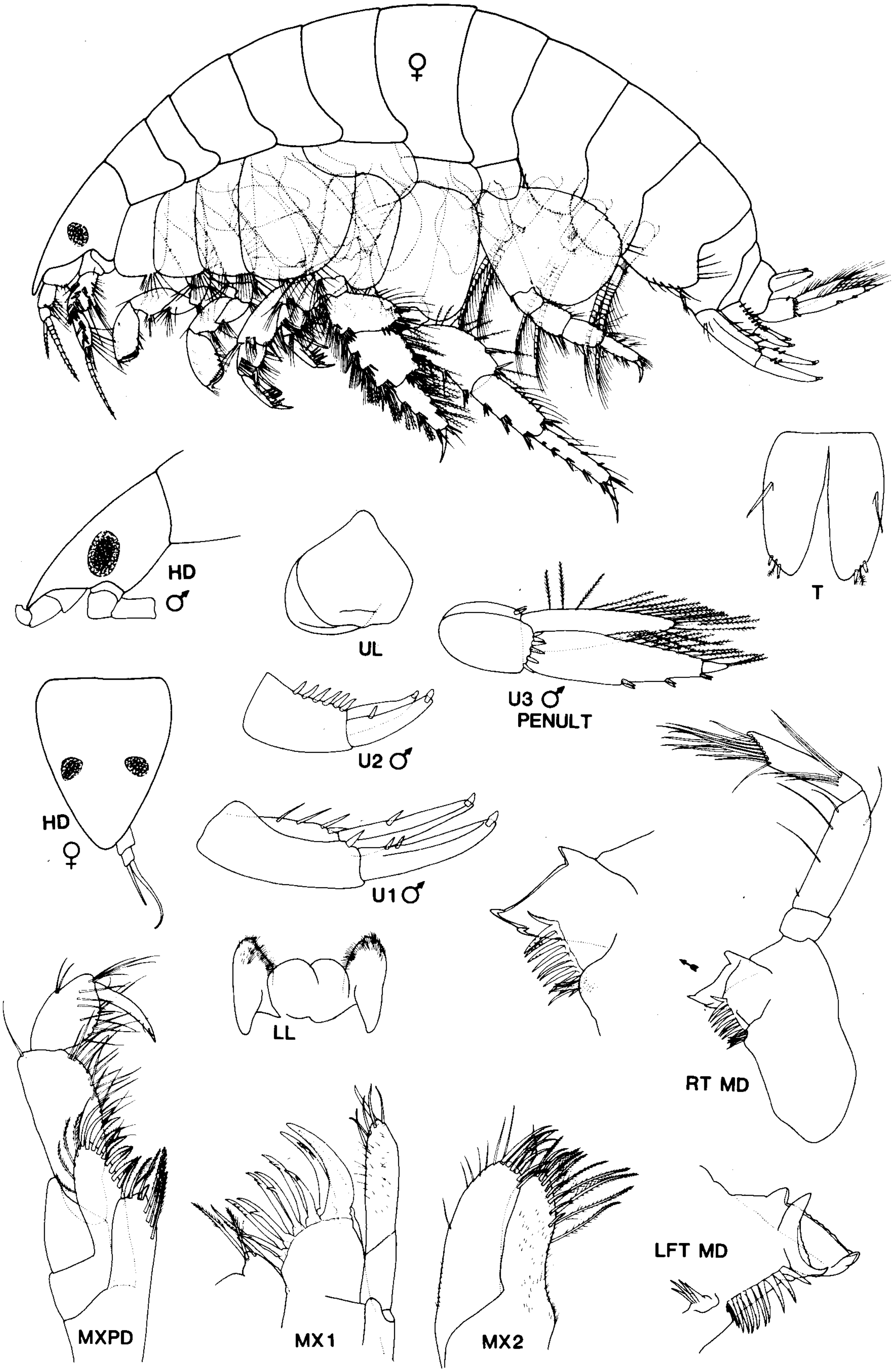
Distribution and Ecology. Off the central California coast, taken from among kelp hold-fasts (presumably close to sandy substrata). Barnard and Barnard (1982a) extend the range from Monterey Bay, central California, southwards to Isla Cedros, Baja California, in subtidal depths, shoreline to 210 m.

Taxonomic commentary. The *obtusidens* group is distinguished by a combination of: epistome unproduced, gnathopod propods relatively strongly developed, mandibular molar small, right lacinia unevenly bifid, left lacinia 5-dentate, peraeopods 5 & 6, segments 4 & 5 little broadened, uropod 1 peduncle with strong displaced spine, and uropod 3 (female) both rami nearly fully developed and marginally setose. The group includes some of the undescribed forms originally figured by Barnard (1960), including *G. golfensis,* and (despite the unusual form of the left lacinia, and lack of a pronounced displaced spine on uropod 1) also *F. falciformis,* new species.

Foxiphalus falciformis, new species
(Fig. 15)

Material examined:
BRITISH COLUMBIA: Queen Charlotte Islands: Parry Passage, ELB & ELM Stn. H2, August 24, 1957: 1 female ov. (8.0 mm) HOLOTYPE with slide mount, CMN Cat. No. NMCC 1992-0634;1 subadult female (6.0 mm) with slide

Fig. 15. ***Foxiphalus falciformis*****,** new species. FEMALE ov. (8.0 mm) HOLOTYPE; MALE penult (6.5 mm) ALLOTYPE. (SEE PAGE 95 - OPPOSITE)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HD
♂
UL
U3 ♂
PENULT
T
HD
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U2 ♂
U1 ♂
LL
RT MD
MXPD
MX1
MX2
LFT MD

mount, 13 subadult females, 16 immatures, PARATYPES CMN Cat. No. NMCC 1992-0635; Graham I., Masset Harbour, Stn. H14, Aug. 23-27, 1957: 5 specimens, including female br. II (7.0 mm) with slide mount; Yakan Pt., Stn. H14, August 25, 1057; 1 male penult. (6.5 mm) ALLOTYPE, with slide mount, CMN Cat. No. NMCC1992-0636; Ibid: 5 females, 3 males, 2 juveniles, PARATYPES, CNN Cat. No. NMCC1992-0717.
WASHINGTON: Pacific coast, Juan de Fuca Strait, ELB Stns. W22, W24, W34, LW sand, July - August, 1966: 8 females (1 br. III 3 males, penult. San Juan Islands region: off Jamestown, C. P. Staude coll, June 2, 1976: 1 female br II, 1 male subadult (5.5 mm) with slide mount, 1 subadult male, broken.
OREGON: LW sand, ELB Stns. W58, W60, W61, W63 Aug. 13-16, 1966: 52 females, 15 penult. males, 9 imm., including: W63, Cape Kiwanda, Aug. 16, 1966: 1 female, br. II (8.0 mm) with slide mount, male penult. (6.0 mm) with slide mount.

Diagnosis. (Female br. II, 8.0 mm): Pigmented eyes small, subovate. Rostrum medium, broad, subacute apex reaching about mid-point of segment 2 of antenna 1. Antenna 1, flagellum 10-11 segmented, accessory flagellum 6-7 segmented. Antenna 2, peduncular segment 4 with 10-11 strong spines in 3 facial clusters; segment 5 with 6-7 spines in 2 facial clusters.

Mandible, molar very small with 4-6 short marginal blades; raker spines 7-10, short; left lacinia bidentate, outer teeth falciform, centre teeth apparently suppressed; right lacinia deeply bifid, at distal end of raker row; incisor bi- or tri-cuspate; palp segment 3 with cluster of 4-6 medium-long "A" setae. Maxilla 1, outer plate, one lateral apical spine much enlarged, heavy; palp slender, segmental line indistinct. Maxilla 2, inner marginal setae of inner plate long, finely plumulose. Maxilliped outer plate with 1 apical spine, outer plate short, with 8-9 inner marginal masticatory spines.

Coxal plate 1-3 broad, deep, setal clusters confined to hind corner. Coxa 4 broad, deep, rounding posteriorly, upper margins sub-parallel. Gnathopods 1 & 2, carpus, posterior lobe short, with 1 main cluster of setae; propod, length about twice its depth, palms slightly oblique.

Peraeopods 3 & 4, segment 5, postero-distal spine long, tip nearly reaching distal end of segment 6; dactyls medium. Peraeopod 5, basis medium, margins sub-parallel, nearly straight segment 4 expanded, width about 50% greater than length, postero-facial spines lacking; segment 5 deeper than wide, about as long as linear segment 6. Peraeopod 6, basis slightly broadening distally; segment 4 little expanded, length about twice width; segments 5 and 6 linear, hind margins with 4 clusters of single spine and single long, plumulose setae. Peraeopod 7, basis with about 6 indistinct posterior serrations; distal segments sub-linear.

Abdominal side plates 2 & 3, hind margins weakly long-setose; hind corners obtuse, lower margins convex.
Uropod 1, peduncle with 3 baso-facial setae, inner margin with 3-4 slender spines, displaced spine lacking (or very small); rami proximally with 1-2 short posterior spines, apical spines articulating. Uropod 2, peduncle with 5 stout outer marginal spines; outer ramus with 1-2 posterior spines inner ramus bare. Uropod 3, inner ramus more than 2/3 length of outer, both margins distally plumose setose; terminal segment of outer ramus medium-large, with 2 apical plumose setae.

Telson lobes narrowing distally, each with longish dorso-lateral spine, oblique apex with 2 short spines and single setule. Coxal gills large, elongate on peraeopods 2-5, shorter on 6, and short, drop-shaped on peraeopod 7.

Male (penult., 6.0 mm): Rostrum slightly longer than in female, apex reaching nearly to distal end of segment 2, antenna 1. Eye medium-large, ovate. Uropod 3, rami nearly equal, fully plumose-setose.

Mature male: unknown.

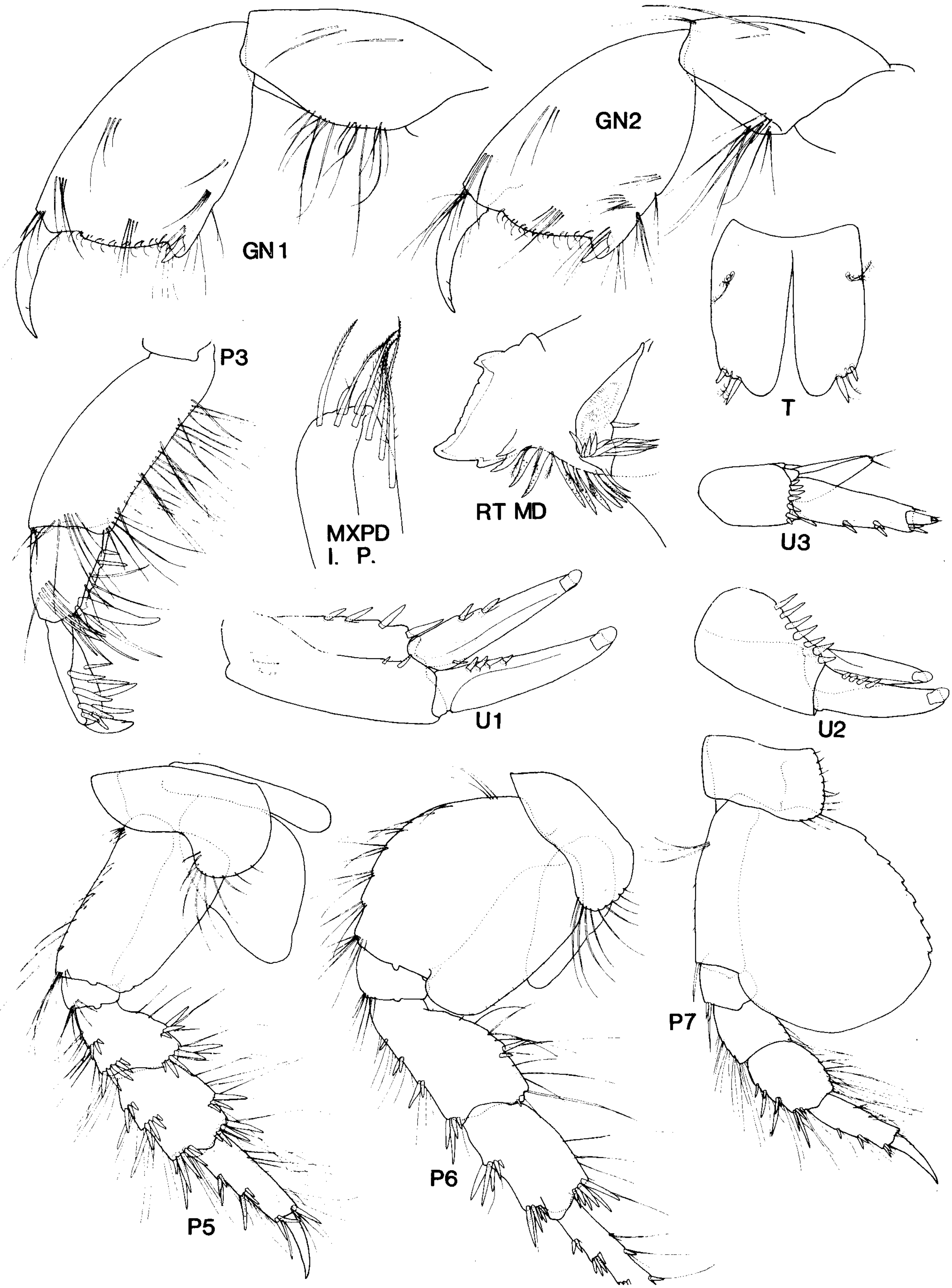
Etymology. From the Latin 'falx' (sickle) + 'forma', referring to the sickle-shaped form of the teeth of the left mandibular lacinia mobilis.

Distribution and Ecology. From the Queen Charlotte Islands south to Central Oregon, in medium fine surf-exposed sands at LW level. The absence of specimens from the Vancouver Island region is an apparent collecting anomaly, not easily comprehended in view of the large number of sandy habitats investigated in that region.

Taxonomic commentary. This species is very close to the generic type species, *F. obtusidens* Alderman, in the fully setose and elongate rami of uropod 3 of the female. *F. falciformis* differs markedly from the type species, however, mainly in the lack of a pronounced displaced spine on uropod 1, the more strongly expanded segments 4 & 5 of peraeopod 3, the less spinose uropods 1 & 2, the shorter, broader rostrum, the more slender dorso-lateral spines of the telson lobes, and the peculiar sickle-shaped form of the outer teeth of the left lacinia mobilis.

Although no mature males were found in the present material, its morphology is presumed similar to that of the mature male of *F. obtusidens* figured by Barnard (1960, pl. 35, S-X) from San Quintin, California, and described in more detail by Barnard and Barnard (1982a, p. 9). In their material, the eyes are very large, nearly meeting mid-dorsally, and the rami of uropod 3 are about equal in length, and fully marginally setose. The 11-segmented flagellum of antenna 1 is calceolate on segments 2-6, and on alternate segments of the elongate flagellum of antenna 2; a single calceolus is located antero-distally on peduncular segment 5 of antenna 2. The copulating spines of peraeopod 7 have apparently not been described.

Fig. 16. ***Foxiphalus aleuti*** Barnard.
FEMALE br. II (9.0 mm)
(SEE PAGE 97 - OPPOSITE)


GN1
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RT MD
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U2
P5
P6
P7

Foxiphalus aleuti Barnard and Barnard, 1982
(Fig. 16)

Foxiphalus aleuti Barnard & Barnard, 1982: 14, Fig. 1.

Material examined.
ALASKA: Aleutian Islands, Unimak I., subtidal sands, P. Slattery coll., June - October, 1982: 1 female br. II (9.0 mm) with slide mount, fig'd., CMN Cat. No. NMCC1992-0637.

Diagnosis. (Female br. II., 9.0 mm): Rostrum broad, elongate, reaching end of peduncular segment 2 of antenna 1. Accessory flagellum 10-12 segmented, about 60% length of primary flagellum. Antenna 2 weakly ensiform; peduncular segment 5 with a single facial cluster of 3-5 spines.

Epistome unproduced. Mandible, molar with 9-10 marginal blades, and a single displaced blade; spine row with 9-10 rakers and associated setae; right lacinia unequally bifid, offset from the spine row.

Gnathopods 1, carpus slender, hind margin with several clusters of setae; propod little longer than carpus, broadening distally, palmar margin slightly oblique. Gnathopod 2, carpus relatively short, hind lobe sub-acute, with only 2-3 clusters of setae; propod longer than carpus, slightly wider than propod of gnathopod 1.

Peraeopods 3 & 4, segment 5 short, postero-distal spine massive, tip extending 3/4 length of short segment 6; distal marginal spines of segment 6, 4 on each side; dactyl short, stout. Peraeopod 5, basis slightly narrowing distally; segment 4 moderately broadened, width about equal to length; segment 5 distinctly longer than 4 but sub-equal to segment 6; dactyl strong. Peraeopod 6, segments 4 & 5 little expanded, sub-equal in length, in each, width 70-75% of length; segment 6, hind margin with 3 small clusters of single spine and seta; dactyl medium. Peraeopod 7, segment 5 expanded, nearly as wide as long, hind margin strongly setose; dactyl strong.

Uropod 1, peduncular inner margin with 3-4 stout spines, displaced spine stout, length about 1/3 inner ramus, tip reaching beyond single proximal marginal spine of inner ramus; outer ramus with 4 posterior marginal spines. Uropod 2, peduncle with about 7 stout outer marginal spines; outer ramus with 4 closely set posterior spines; both rami with stout embedded apical spines. Uropod 3, both rami short, devoid of lateral marginal setae, inner ramus narrowing, with 2 apical setae; terminal segment distinct, apex minutely setulose.

Telson lobes broad, margins sub-parallel, lacking dorsolateral spines; apices each with 2 unequal spines and single setule.

Coxal gills on peraeopods 5 & 6 medium, narrowing distally. Mature male unknown.

Distribution and Ecology. From Unalaska, south to Santa Catalina Island, California, in subtidal sands to 110 m. depth.

Taxonomic commentary. This species was only partially figured by Barnard & Barnard (1982a), based on a subadult female from California and a subadult male from Unalaska. The species differs from most other species of *Foxiphalus* in a few plesiomorphic character states (e. g. maxilliped inner plate with 2 apical spines; mandibular right lacinia bifid, offset from spine row). Until more extensive study material becomes available, the species seems best retained as a relatively primitive member of the genus *Foxiphalus.*

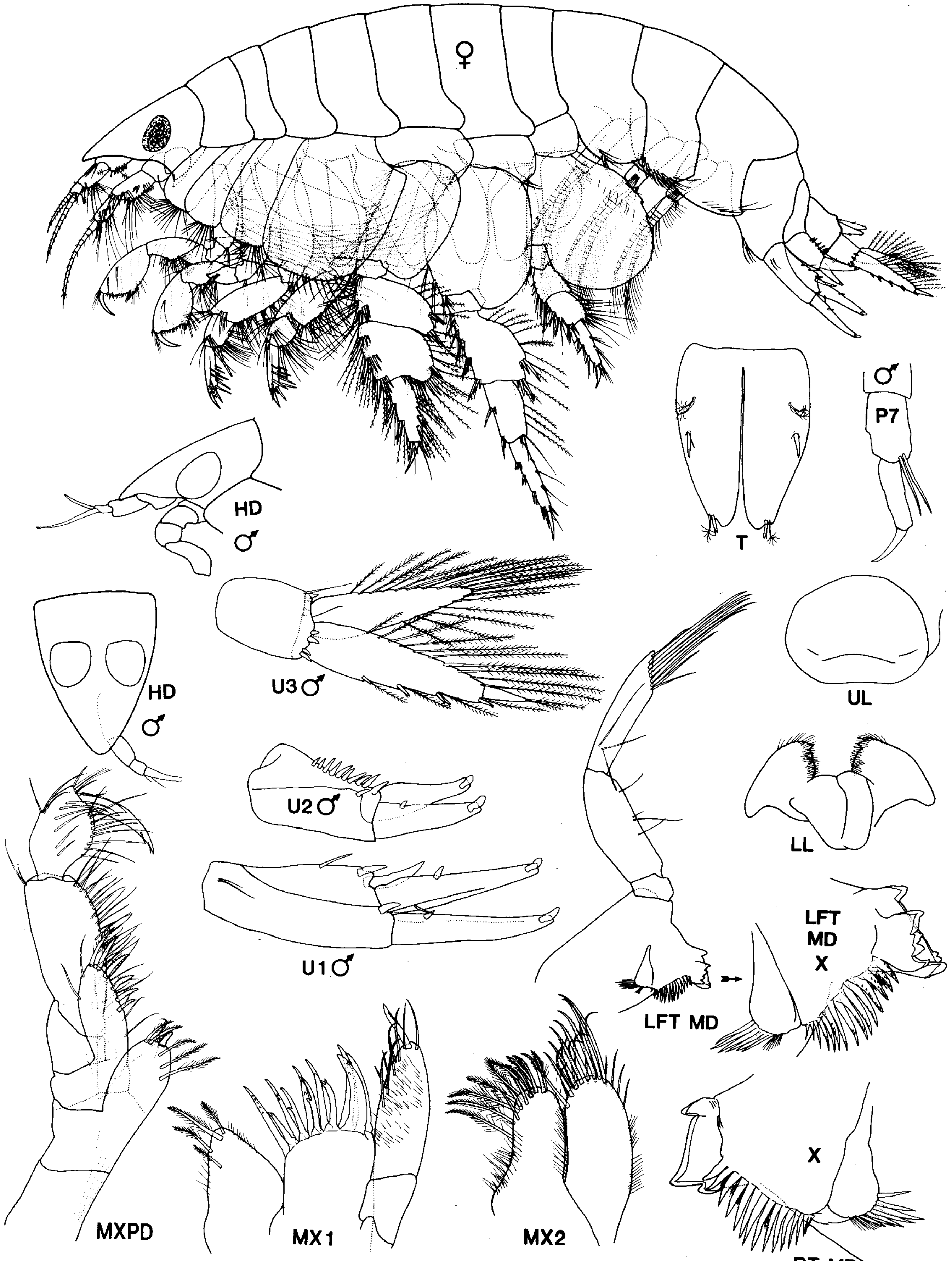
Foxiphalus xiximeus Barnard and Barnard, 1982a
(Fig. 17)

Foxiphalus xiximeus Barnard & Barnard, 1982a: 17, fig. 2.—Bousfield, 1990, fig. 2.—Bousfield, 1991, fig. 3.

Material examined.
ALASKA: Aleutian Islands, Unimak I., P. Slattery coll., (12).
SE Alaska: ELB Stns., 1961: A175 (4) A140 (1); A139 (10); A81(1); A48 (1); A33 (11); A27 (2); A25 (3); A18 (1), A8 (1). ELB stns, 1980 - S1F2 (10); S4B3 (2); S4B5 (1); S8B1 (3); S8B2 (10); S8B1 (3); S8B2 (10); S11B4 (1); S13B3 (1); S18F1 (1000); S18F3 (20); S18F2 (40); S19B2 (1); S19 (B3 (2); S20B4 (3); S22F1 (2).

BRITISH COLUMBIA: Queen Charlotte Islands, ELB Stns., 1957: H2 (96, with slide mounts of 3 females (4.5 - 6.0 mm) and 2 males (5.0 - 5.5 mm); H2b (1); H3 (30); H11 (2); H14 (2).
Central coast: ELB Stns., 1964: HS (1); H8 (25); H26 (8); H30 (1); H35 (8); H43 (50); H44 (10); H50 (30); H57 (4); H59 (10).Swanson Bay, C. Levings coll. (8).
Vancouver Island: ELB Stns, 1955: F1 (5); F3 (250); F4a (25); F5 (1); F6 (50); F9 (53). ELB Stns., 1959: N11 (30); N15 (6); N16 (2); ELB Stns. 1970: P711(1); P716 (100); P717 (80). ELB Stn., 1976: B3: 1 male (3.0 mm) with slide mount); B11: 1 female ov. (7.0 mm) with slide mount); B27 (1). ELB Stns 1964: B5a Metchosin Lagoon: ca. 100 specimens, with slide mounts of 1 female ov. (7.0 mm), fig'd., 1 male (5.0 mm) with slide mount, fig'd., 7 females ov. (4.5 - 6.0 mm), 5 males (3.5 - 5.0 mm) CMN Cat. No. NMCC1992-0638. ELB Stns., 1977 - B5b (6); B5 d. (1); B6 b (1); B8 (2). Pachena Bay, gray whale feeding pits, P. Slattery coll. Pit 1, September 16, 1982: 30 specimens, with slide mount of female ov. (5.0 mm), CMN Cat. No. NMCC1992-0639; April 17,1983: 83 specimens with slide mounts of 1 female ov. (3.8 mm), and 1 male (3.25 mm), CMN Cat. No. NMCC1992-0639. Near Victoria, B. Carl, 1929: (23).

FIG. 17. ***Foxiphalus xiximeus*** Barnard & Barnard
FEMALE. ov. (7.0 mm); MALE (5.0 mm).
(SEE PAGE 99 - OPPOSITE)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X
LFT MD
X
RT MD
MXPD
MX1
MX2

WASHINGTON & OREGON: ELB Stns., 1966: W22 (22); W24 (6); W26 (1); W33 (2); W34 (20); W44 (1); W45 (4); W50 (25); W53 (1); W57 (1); W58 (500); W60 (25); W61 (3); W63 (40); W64 (25); W66 (20). Juan de Fuca Strait, C. P. Staude, coll., June, 1976: 140 specimens in 41 lots, slide mounts 2 females ov. (4.25, 7.0 mm) and 1 male (4.25 mm).

Diagnosis. (Female ov., 7.0 mm): Pigmented eyes medium, ovate. Rostrum medium, subacute apex reaching midpoint of segment 2, antenna 1. Antenna 1, flagellum 8-9 segmented; accessory flagellum 6-8 segmented. Antenna 2, peduncular segment 4 with 10-11 strong spines in 3 facial clusters; anterior margin usually with 1 cluster of setae and a single spine; segment 5 with about 6 spines in 2 facial clusters, and 1 disto-ventral long spine; flagellum relatively long, 9-11 segmented.

Mandible, molar small with 6-7 marginal blades; spine row long, with about 15 mainly short rakers; left lacinia irregular 4-dentate; right lacinia simple (or lacking?); incisor tricuspate; palp segment 2 weakly setose, inner margin only; segment 3 with small cluster of 3 slender "A" setae. Maxilla 1, outer plate, strong outer spine not exceeding adjacent spines. Maxilliped, inner plate with 1 apical spine; outer plate medium tall, inner margin with 6 masticatory spines.

Coxal plates 1-3 deep, not broad, setal cluster extending more than half way along lower margin. Coxa 4 very large, fore and hind margins sub-parallel. Gnathopods 1 & 2, carpus medium, slender, hind lobe with 2-3 setal groups: propods medium large, broadening distally (length about 1.7 X maximum width), palms oblique.

Peraeopods 3 & 4, segment 5 not very powerful, postero-distal spine medium, tip reaching about 3/4 length of segment 6; postero-distal spines of segment 6 relatively long, slender; dactyl medium. Peraeopod 5, basis broad, hind margin convex; segment 4 very broad, width nearly twice length (depth), lacking postero-facial spines; segment 5 narrower, width about equal to length, lacking postero-facial spines; linear segment 6 longer than 5, posterior margin plumose-setose; dactyl medium long, slender. Peraeopod 6, basis regular, hind margin early straight; segment 5 moderately expanded, lacking postero-facial spines, length about 50% greater than depth; segment 5 slightly shorter, little expanded, hind margin with a few long plumose setae; segment 6 linear, longer than 5, hind margin with a few clusters of single spine and seta. Peraeopod 7, basis ordinary, hind margin with 4-5 indistinct serrations; segments 4 & 5 little expanded, 5 densely setose behind; segment 6 linear, longer than 5; dactyl slender.

Pleon plate 2, hind corner obtuse, lower margin convex, strongly setose; pleon plate 3, hind corner acuminate, with small cluster of postero-distal long setae. Uropod 1, peduncle with weak baso-facial setal cluster, inner margin with 1-2 slender spines, displaced spine medium-strong, about 1/3 length of inner ramus; rami each with 1 posterior marginal spine, and articulate apical spine; inner ramus with single proximo-medial spine. Uropod 2, peduncle with variable numbers (usually 9-10) of stout inner marginal spines; outer ramus with 1 small proximo-posterior spine. Uropod 3 inner ramus more than 2/3 length of outer, margins distally fully plumose-setose; terminal segment of outer ramus large, with 2 apical plumose setae.

Telson lobes narrowing distally, each with medium dorso-lateral spine; apex with single spine and setule.

Coxal gills large, elongate on peraeopods 2-6, somewhat smaller on peraeopod 7.

Mature male (4.25 mm): Pigmented eyes very large, unevenly subovate, nearly meeting mid-dorsally. Rostrum slightly longer than in female. Antenna 1, proximal 7 segments calceolate. Antenna 2, peduncle segment 5 with single antero-distal calceolus; flagellum elongate, alternate segments calceolate.

Peraeopod 7, copulatory spines slender, nearly straight, distally setulose, subequal, about 80% of length of segment 6.

Uropod 3, rami sub-equal, fully plumose-setose.

Distribution and Ecology. Alaska and SE Alaska to S. California: LW and sub-tidal sands, to depths of about 20 m., along medium surf-exposed and protected beaches. Perhaps the most common and frequently encountered shallow-water metharpiniid species of the North American Pacific region.

Taxonomic commentary. The species is morphologically variable throughout its range, within the same population, and even between left and right sides of the same animal, especially in the spination of the peduncle and rami of uropods 1 & 2. Northern specimens tend to differ from southern types in character states that vary according to size and instar.

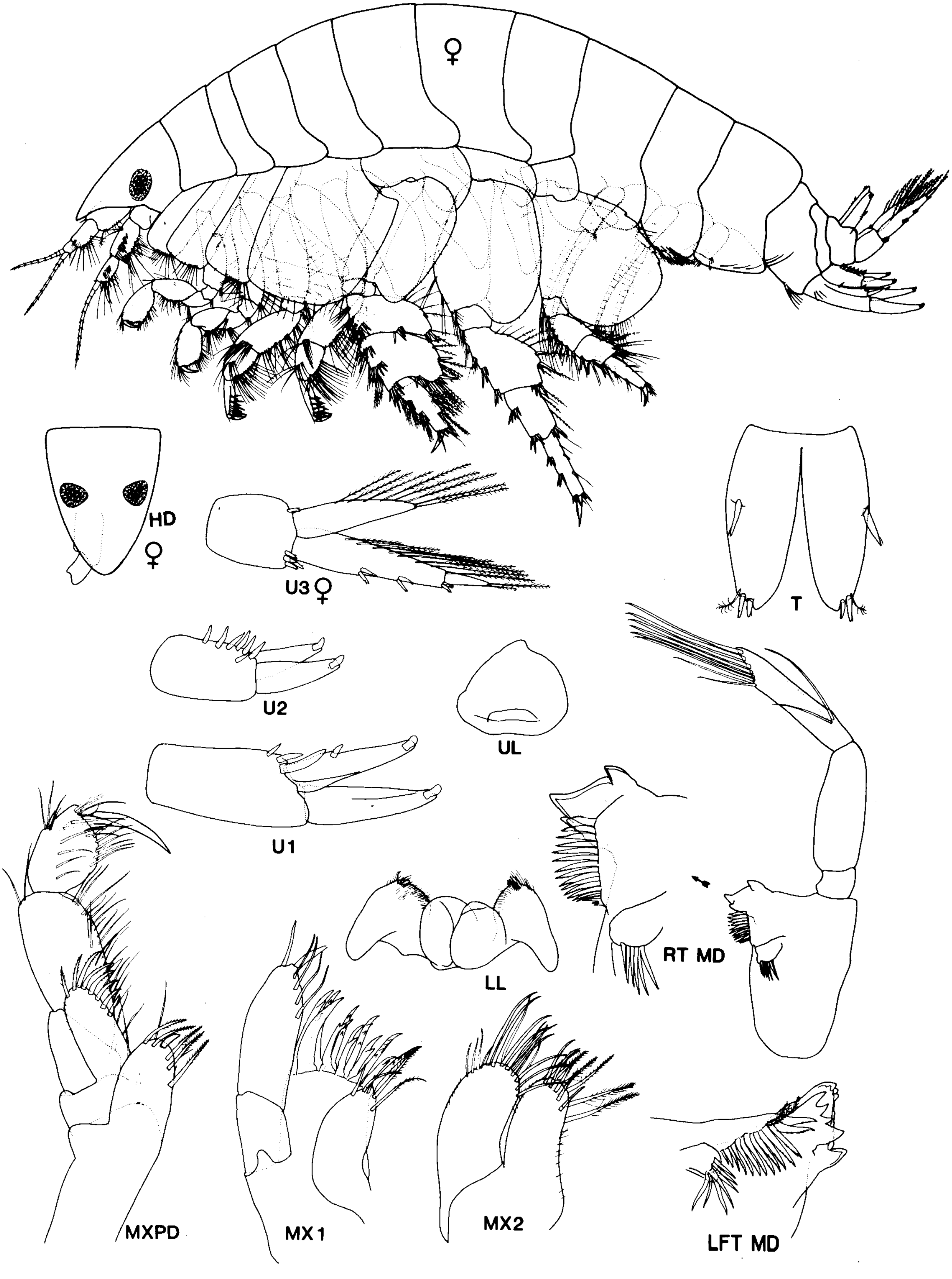
Foxiphalus fucaximeus, new species
(Fig. 18)

Material examined.

WASHINGTON: Neah Bay, LW sand, ELB Stn. W39, July 30, 1966: 1 female ov. (5.5 mm) HOLOTYPE, with slide mount, CMN CAT No. NMCC1922-0641.

Diagnosis. (Female ov. 5.5 mm): Pigmented eyes medium, ovate. Rostrum medium, broad, apex slightly exceeding peduncular segment 1, antenna 1. Antenna 1, flagellum 9-segmented; accessory flagel-lum 9-segmented. Antenna 2, peduncular segment 4 with 6-7 medium strong spines in 3 facial clusters, anterior margin with single cluster of setae and 1 spine; segment 5 with 4-5 spines in single facial cluster; flagellum 10-segmented.

Fig. 18. ***Foxiphalus fucaximeus***, new species
FEMALE ov. (5.5 mm) HOLOTYPE.
(SEE PAGE 101 - OPPOSITE)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HD ♀
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U2
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RT MD
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MX1
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LFT MD

Mouthparts very similar to those of *F. xiximeus*. Upper lip, epistome flat, not produced. Mandibular palp segment 2 lacking marginal setae; segment 3 with slightly stronger cluster of 3 "A" setae. Maxilliped, outer plate, and palp segment 2 slightly more robust and more strongly arched than in *F. xiximeus*.

Coxa 1-3 deep, narrow, corners more angular than in *xiximeus*. Gnathopods 1 & 2, carpus and propod relatively slender and longer than in *F. xiximeus;* propod only slightly longer than carpus, little expanded distally.

Peraeopods 3 & 4, segment 6, postero-distal marginal spines relatively short, 5-6 per side; dactyl short.

Peraeopod 5, basis deep, slightly narrowing distally; segment 4 very broad and shallow, with lower facial cluster of 3 spines; segment 5 nearly as broad, wider than deep; segment 6 linear, posterior margin plumose-setose; dactyl short. Peraeopod 6, basis ordinary; segment 4 moderately expanded, nearly as wide as long (deep), hind margin with 2 spines and several singly inserted setae; segment 5 stout, shorter than 4, hind margin with 1-2 isolated setae; segment 6 linear, not elongate, length about equal to segment 4; dactyl medium. Peraeopod 7, basis with 5-6 weak posterior marginal serrations, segment 5 not longer than 4, hind margin strongly setose; segment 6 linear, dactyl short.

Pleon plate 2, hind corner rounded, lower margin convex, strongly setose; pleon plate 3, hind corner slightly bluntly produced, with weak cluster of posterior setae, lower margin about straight, weakly submarginally setose.

Uropod 1, peduncular margins nearly unarmed, 1 basofacial slender spine; displaced spine stout, length more than 1/3 inner ramus, and nearly reaching single posterior marginal spine; outer ramus marginally bare, both rami with articulating apical spines. Uropod 2, peduncular inner margin with 6 stout spines; rami short lacking marginal spines. Uropod 3, inner ramus short, inner margin distally plumose-setose, outer ramus nearly twice length of inner, inner margin strongly setose, terminal segment large, with 2 apical setae.

Telson lobes narrowing distally, each dorso-laterally with stout spine, apices each with 2 short spines and setule.

Coxal gills on peraeopods 2-6 large, elongate, apices subacute, slightly smaller on peraeopod 7.

Mature male: Unknown, but its antennal calceolation is probably very similar to that of *F. xiximeus* described and figured by Barnard (1960).

Etymology. A combining form of "fuca", from the nearby Strait of Juan de Fuca, and *xiximeus*, its nearest species relative.

Distribution and Ecology. Known only from the type locality, Neah Bay, Washington, in medium sand at LW, along with several specimens of *F. xiximeus* and other phoxids.

Taxonomic commentary. Regrettably only a single specimen of this species was found in the material examined. It is most readily distinguished from its close relative, *F. xiximeus,* by the smaller gnathopods, the broadly expanded segments 4 & 5 of peraeopod 5, the shorter inner ramus of uropod 3, and the nearly unarmed rami of uropods 1 & 2.

Foxiphalus similis (Barnard, 1960)
(Fig. 19)

Paraphoxus similis Barnard, 1960: 230, pls. 22, 23.—Barnard & Barnard, 1982a 19, fig. 3.

Material examined:

ALASKA: SE Alaska and Prince William Sound, mainly on surf-protected sand, from LW intertidal to 10 m, ELB Stns., 1961: A7 (3), A3 (1), A33 (1); A37 (1), A30 (7), A8 (7), A98 (1), A117 (1), A161(1), A147 (1), A165 (1), A163 (34 specimens, with slide mount of 1 male (4.0 mm) fig'd., CMN Cat No. NMCC1992-0642. "Super males" were also taken at Stns. A105 (1 "super male:, 1 "super female"); A110 (several "super males", 1 female); A139 (1).

Sitka Region, mostly sub-tidal to 10 m., ELB Stns., 1980: S1F1 (1); S1F2 (4), S17F1 (10), S18F3 (1).

BRITISH COLUMBIA: Queen Charlotte Islands, mostly in fine and silty sands, LW to 10 m., ELB Stns., July-August, 1957: E5 (1); E9 (20); W4a (1); W4b (8); H8b (1); H9 (1); H11 (20); H2 (1 male (3.75 mm) with slide mount); H9 (1 female (4.5 mm) with slide mount).

North central coast: in surf-protected shallow sand, mainly LW to 25 m., ELB Stns., July 1964: H3 (1); H5 (100); H11 (1); H15 (2); H17 (1); H25 (1, plus 1 "super female"); H29 (1); H30 (30); H39 (1); H47 (30); H50 (10); H53 (70 specimens, with slide mounts of 1 female ov. (3.75 mm), fig'd., 1 subadult male (3.2 mm) and 1 male (2.75 mm) CMN Cat. No. NMCC1992-0643; H64 (4). Vancouver Island, North end, ELB Stns., 1959: V3 (1), V11 (1), N22 (2), 013 (1).

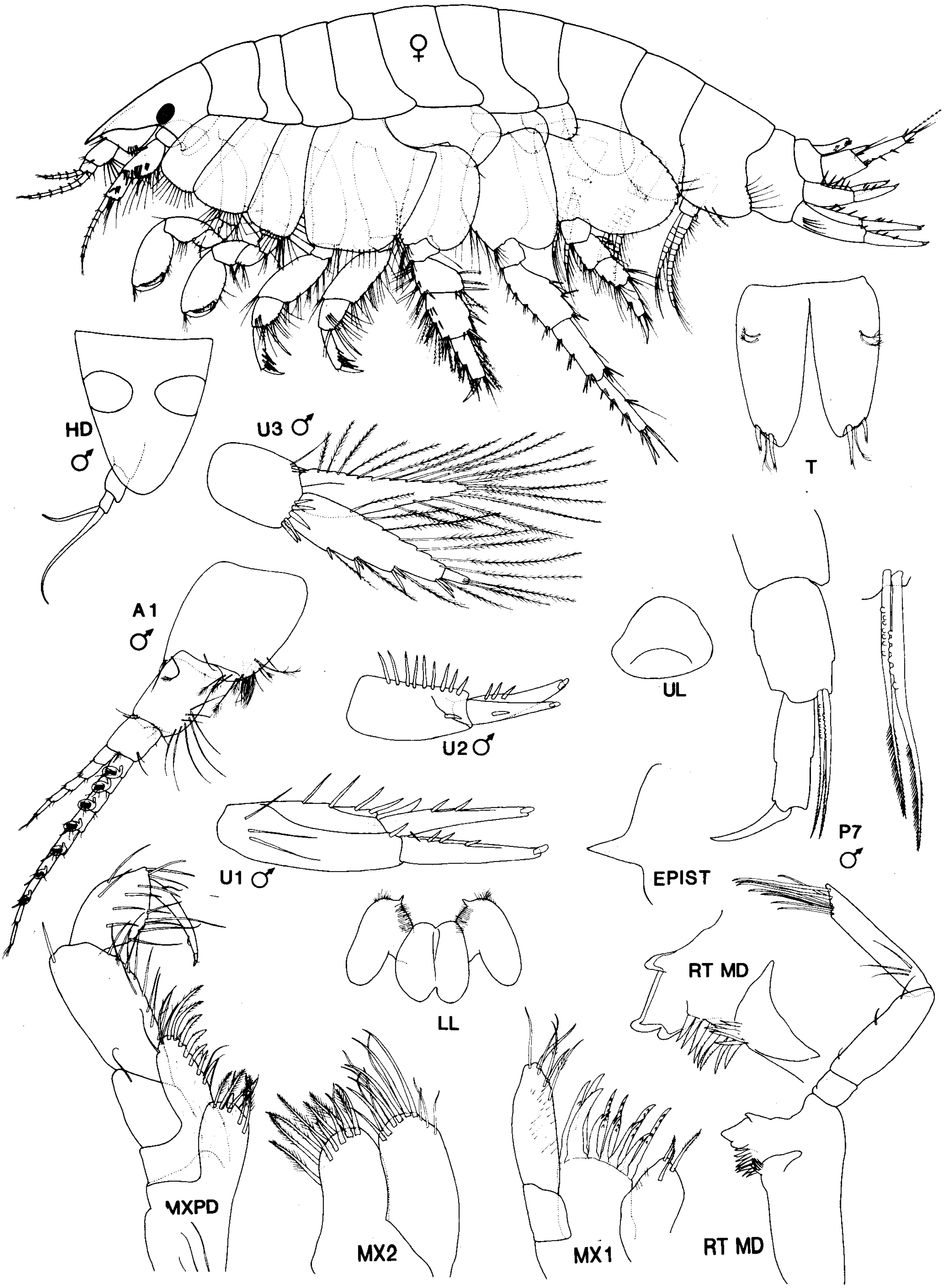
Vancouver Island, South end, LW sand, ELB Stns., 1955: G20 (3), F9 (25); ELB Stns., 1970: P710 (4), P712 (4), P719 (1), P721 (3).

Barkley Sound, LW and sub-tidal sands: Diana I., ELB 2th. P17, August 6,1975: (20); ELB Stns., 1976: B2c (1), B11a (50), B11b (100+), B27 (2).

Burrard Inlet region, sub-tidal to 15 m. ELB Stns., November 4, 1977: E2 (4); E3 (6).

Other material: J.F.L. Hart coll.: Departure Bay, 1938 (1); 1955 (1); Willows Beach 1941(12); Saturna I., 1955 (20); South Pender I. (15). Quinsam I., E. Black coll., 1981(3). Saanich Inlet, H.E. Conlan coll., January, 1976: ca. 250 specimens in 14 lots, with slide mounts of 1 male (4.0 mm), 1 female ov. (3.75 mm).

Fig. 19. ***Foxiphalus similis*** (Barnard)
FEMALE ov. (4.5 mm); MALE (4.0 mm)
(SEE PAGE 103 - OPPOSITE)


♀
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U3 ♂
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U1 ♂
EPIST
P7
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LL
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MXPD
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RT MD

WASHINGTON & OREGON: Juan de Fuca Strait: Friday Harbor, ELB Sta. F7, 1955 (10); ELB Stns, 1966, W34 (2), W39 (2), W13 (12). Off San Juan Island, C. P. Staude coll., June, 1976 (ca. 150 specimens, with slide mount of 1 male (3.0 mm), 1 female ov (3.75 mm), 1 female br. II. (3.25 mm). Otter Rock, LW sand, ELB Stn. W60, August 14, 1966: (12).

Diagnosis. (Female ov., 4.5 mm): Pigmented eyes small, oval, near lateral margins. Rostrum normal, rounded apex nearly reaching end of peduncular segment 2 of antenna 1. Antenna 1, peduncular segment 3 not setose posteriorly; flagellum 6-7 segmented; accessory flagellum 5-6 segmented. Antenna 2, segment ensiforn; segment 4 with 7-6 medium spines in 3 disto-facial groups, and long postero-distal spine, anterior margin with cluster of spines and a few setae; segment 5 with 3 facial spines and 1 apical spine; flagellum 6-7 segmented.

Mandible, molar small, with about 5 marginal blades; spine row weak, with 8 rakers; right lacinia apparently lacking; left lacinia irregularly 4-dentate; incisor tricuspate; palpar hump distinct; palp segment 2 weakly short-setose anteriorly; segment 3 with weak cluster of 3 "A" setae. Upper lip, epistome strongly produced, acute. Lower lip, outer lobes with strong mandibular wings and distinct shoulder cusps. Maxilla 1, inner plate with 3 apical setae; outer plate outer apical stout spine not exceeding adjacent spines; palp apex setose. Maxilla 2, plates subequal in width. Maxilliped, inner plate with 1 apical spine, outer plate short, with 5 slender masticatory spines; dactyl of palp slender.

Coxa 1-3 large, deep, lower margin of coxa 1 almost entirely setose. Coxa 5 very large, margins converging distally, lower margin straight. Gnathopods 1 & 2 moderately strongly subchelate; gnathopod 2 stronger, carpus, hind lobe short, with 1 setal cluster; propod ovate, broadening distally, twice length of carpus.

Peraeopods 3 & 4, segment 5, postero-distal spine long, tip nearly reaching distal end of segment 6 that is spinose distally only; dactyl strong. Peraeopod 5, basis broad, hind margin convex; segment 4 little expanded, short, width and depth sub-equal, postero-facial spines lacking; segment 5 longer than 4, about equal to linear segment 6 that has a setose posterior margin; dactyl slender. Peraeopod 6, basis ordinary; segment 4 very slightly expended, length slightly greater than sub-equal segments 5 & 6; segment 6 with 1 posterior marginal cluster of spine and seta; dactyl medium long, slender. Peraeopod 7, basis extended posteriorly, hind margin with 7-8 weak serrations; segments 4 & 5 short, weakly setose behind; segment 6 longer, dactyl strong.

Pleon plate 2, hind margin with 2 distal setae; corner obtuse, lower margin convex, setose anteriorly; pleon plate 3 broad, hind margin distally with 6-7 long setae, hind corner obtuse, lower margin with 2 setae.

Urosome 1 lacking ventral setal brush. Uropod 1, peduncle with 3-4 long baso-facial setae, inner margin with 3-4 slender spines, displaced spine stout, extending beyond single spine of inner margin of the inner ramus; outer ramus with 3 posterior marginal spines, both rami with single articulated apical spine. Uropod 2, peduncle with 5-6 outer marginal spines; outer ramus with 2, inner ramus occasionally with 1, posterior marginal spines. Uropod 3, inner ramus very short, about 1/3 length of outer ramus that has plumose setae apically and on prominent terminal segment.

Telson lobes slightly narrowing distally, lacking dorsolateral spines, each oblique apex with 2 slender unequal spines and single setule.

Coxal gills large, sac-like on peraeopods 2-6, moderately large on peraeopod 7 (length = 2/3 length of basis).

Mature male (3.75 mm): Pigmented eyes very large, oval, extending from lower margin nearly to mid-dorsal line. Antenna 1, flagellum 9-segmented, calceolate on proximal segments. Antenna 2, peduncular segment 5 with single antero-distal calceolus; flagellum about 20-segmented, alternate segments calceolate.

Peraeopod 7, copulatory spines very long, straight, nearly equal, proximally denticulate, distally finely setulose, tips extending beyond end of segment 6.

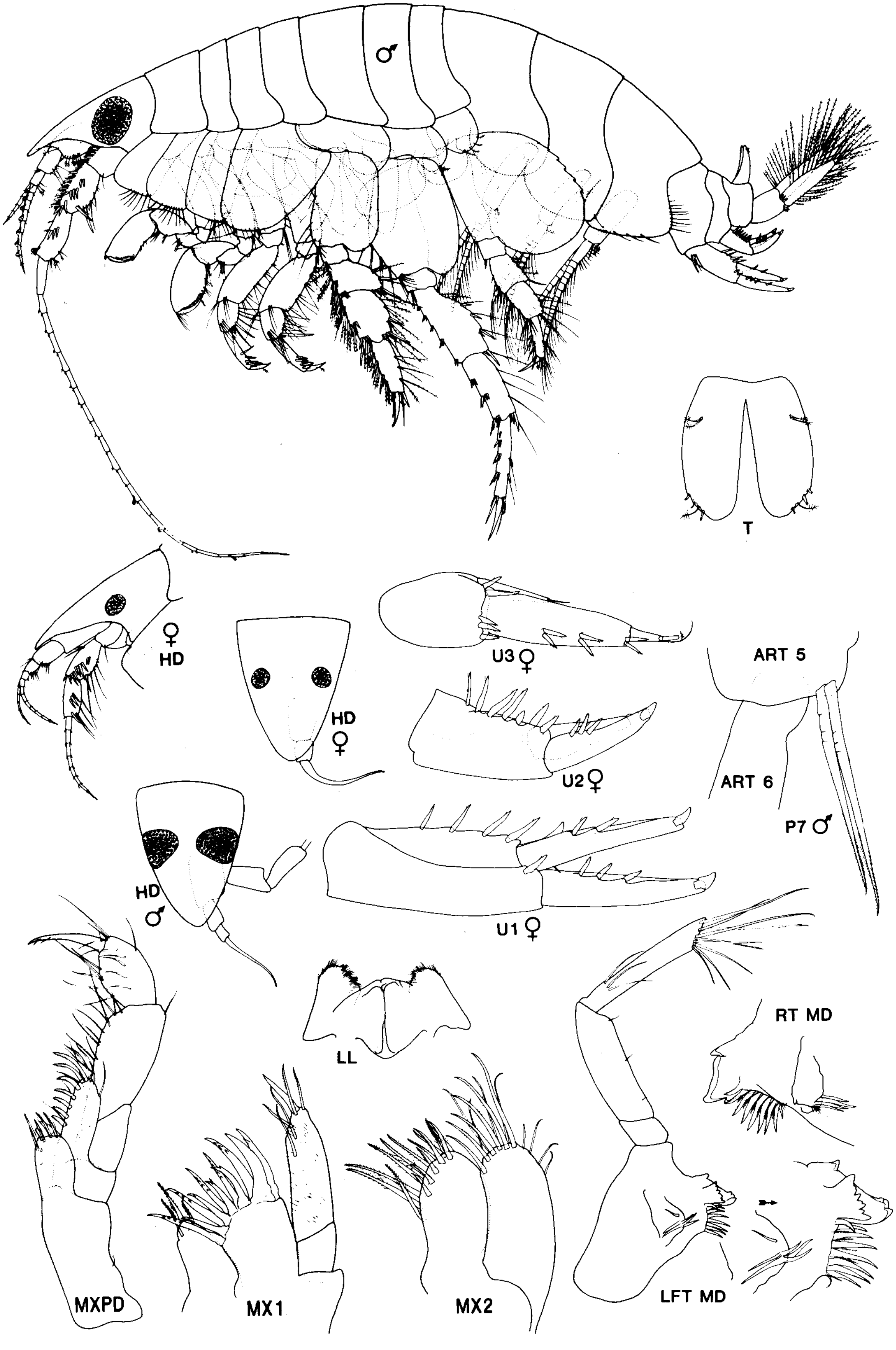
Uropod 2, peduncle with 5-7 marginal spines. Uropod 3, rami lanceolate, inner slightly the shorter, inner margins moderately plumose setose, outer margin with spines and a few setae.

"Super male" (4.0 mm): Several larger males (so-called "super males" of Barnard and Barnard, 1982a) are listed above. They differ only slightly from regular males in having generally more strongly spinose appendages, and 3-4 apical spines on the telson lobes.

Distribution and Ecology. Occurring widely in present collections from Prince William Sound and SE Alaska, southward through British Columbia, Washington State and Oregon, and (in other records) to southern California. It is recorded mainly on surf-protected and finer grained sands, in the north mainly from the lower intertidal level to shallow sub-tidal depths (10-20 m), but at southern localities in depths mainly of 60-100 m, occasionally to more than 300 m.

Taxonomic commentary. This species is the type of the *similis* group, having strongly developed epistomal process, ensiform antennal segment 1, strong uropod 1 displaced spine, inaequiramous uropod 3 (female); and generally weakly spinose peraeopods and uropods. Some of the specimens listed from Unalaska by Barnard and Barnard (1982a) may be referable to *F. slatteryi* or perhaps a third species. The *similis* group appears superficially similar to some members of the Eobrolginae, especially the genus *Eobrolgus* Barnard, in the overall form of the male peraeopods and copulatory spines of peraeopod 7.

Fig. 20. ***Foxiphalus slatteryi*,** new species.
MALE (4.0 mm) HOLOTYPE; FEM. (5.0 mm) ALLOTYPE. (SEE PAGE 105 - OPPOSITE)


♂
T
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ART 5
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U2 ♀
ART 6
P7 ♂
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LL
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MX1
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LFT MD

Foxiphalus slatteryi, new species
(Fig. 20)

Material examined.
ALASKA: Amchitka I., Constantine Harbor, shallow net haul over sand, C. E. O'Clair coll., October 5, 1968: 1 mature male (5.0 mm) HOLOTYPE, with slide mount, CMN Cat. No. NMCC1992-0644; 19 male PARATYPES, CMN Cat. No. NMCC1992-0645. Constantine Harbor LW sand, P. Slattery coll., Sept. 21,1969:1 female ov.(4.0 mm) ALLOTYPE, with slide mount, CMN Cat. No. NMCC1992-0646; 1 mature male (4.5 mm) with slide mount, 4 mature males, 2 adult females PARATYPES, CMN Cat. No. NMCC1992-0647.

Diagnosis. (Mature male, 5.0 mm): Pigmented eyes very large, broadly ovate, nearly meeting mid-dorsally. Rostrum medium large, subacute apex reaching end of segment 2 of antenna 1. Antenna 1, flagellum 9-segmented, proximal 7 calceolate; accessory flagellum 5-6 segmented. Antenna 2, peduncular segment 4 with 7-8 medium spines in 3 facial clusters, hind margin with strong distal spine; segment 5 with single cluster of 3 facial spines, and single antero-marginal calceolus; flagellum elongate, with about 20 long segments, last 14 alternately calceolate.

Mandible, molar small, with 4-6 marginal blades, and 1 displaced blade; spine row weak, 8-9 short rakers; left lacinia irregularly toothed or flabellate; right lacinia simple (near spine row) or lacking; incisor weakly bicuspate; palp, molar hump distinct; segment 2 lacking marginal setae; segment 3 slender, with cluster of 3 weak "A" setae; apex short, obliquely truncate. Upper lip, epistome with acute process. Lower lip, outer lobes with strong shoulder cusps. Maxilla 1, inner plate with 3 apical setae; outer plate short, outer apical spine little enlarged. Maxilla 2, plates subequal in width. Maxilliped, inner plate with apical spine; outer plate short, inner margin with 7 slender masticatory spines; palp, dactyl very slender.

Coxal plates 1-3 large, deep, distal setae extending along 2/3 of lower margin. Coxa 4, margins strongly converging distally. Gnathopods 1 & 2, carpus relatively short, deep, hind lobe with 1-2 setal clusters; propods subovate, longer than carpus, palms oblique; propod 2 larger than 1.

Peraeopods 3 & 4 not powerfully developed, segment 5 relatively small, postero-distal spine slender, tip reaching 3/4 of segment 6; segment 6 linear, with few (2-3) slender spines on each side; dactyl strong.

Peraeopod 5, basis broad, hind margin very slightly concave; segment 4 little expanded, short; segment 5 nearly twice as long as wide; segment 6 linear, equal in length to segment 5, hind margin with 3 pairs of long plumose setae; dactyl medium long. Peraeopod 6, basis not very broadly expanded, hind margin slightly convex; segments 4 & 5 scarcely at all expanded; segment 4 more than twice as long as wide, hind margin with 4 clusters of spines and plumose seta; segment 5 linear, with 3 posterior marginal setae; segment 6 narrowly linear, equal in length to 5, hind margin with a few clusters of single spine and seta; dactyl long, slender. Peraeopod 7, basis, hind margin with 5-6 weak serrations; segment 4 little expanded, weakly setose behind, pair of copulatory spines nearly straight, setulose tips reach more than halfway along segment 6 that is emarginate proximo-posteriorly; dactyl slender.

Pleon plate 2 broad, margins weakly setose, hind corner obtuse; pleon plate 3 broad, hind margin setose, hind corner rounded, lower margin with 1-2 slender spines. Uropod 1, peduncle with single cluster of baso-facial setae; inner margin with 4 spines, displaced spine strong, tip extending beyond small proximo-medial spine to first of two posterior marginal spines of inner ramus; outer ramus with 3 posterior spines, rami each with articulated apical spine. Uropod 2, peduncle, outer margin with 7-8 stout spines; outer ramus shorter than peduncle, with 3 posterior marginal spines. Uropod 3, rami sharply lanceolate, inner ramus a bit shorter, margins plumose-setose; outer ramus with outer as well as inner marginal setae; terminal segment distinct.

Telson lobes slightly widest medially, lacking dorsolateral spines, each oblique apex with 3 short spines and a single setule.

Coxal gills large, subovate on peraeopods 2-6, about half the size on peraeopod 7.

Female ov. (4.0 mm): Pigmented eyes medium small, nearly round. Rostrum similar to that of male. Antenna 1, peduncular segment 3 with small cluster of posterior marginal setae; accessory flagellum 5-6 segmented, main flagellum 8-segmented. Antenna 2, peduncle 5 with cluster of 3 facial spines and single long postero-distal spine; flagellum 8-segmented.

Uropod 3, inner ramus short, less than half the length of the outer, margins bare; outer ramus short, little longer than peduncle, margins lacking plumose setae; terminal segment distinct.

Etymology. Named after Dr. Peter Slattery, collector of the species, who has contributed greatly to knowledge of marine invertebrate animals, especially those associated with whale pits, and especially in the Bering Sea region.

Distribution and Ecology. Known only from the type locality at Constantine Harbor, Amchitka I., Alaska, in and above shallow sub-tidal sands.

Taxonomic commentary. *Foxiphalus slatteryi is* a member of the *similis* group having slender, weakly spinose peraeopods, broad pleon plates 2 & 3, parviramous uropod 3 (female), and lacking dorso-lateral telson spines. It differs from *F. similis* mainly in the less extensive setae of the lower margin of coxal plates 1 & 2, the smaller more distally narrowing coxa 4, and shorter apical telson spines.

Rhepoxynius Barnard, 1979

Rhepoxynius Barnard, 1979: 371.—Barnard & Barnard, 1982a: 2 (key).—Barnard & Karaman, 1991: 629.

Type species. *Pontharpinia epistoma Shoemaker*, 1938a, original designation.

N. American-Pacific regional species. *R. fatigans* (Barnard, 1960): 209, pl. 9; *R. daboius* (Barnard, 1960): 210, pls. 10,11; *R. variatus* (Barnard, 1960): 198, pls. 3,4; *R. boreovariatus,* new species; *R. vigitegus* (Barnard, 1971): 74, figs 44-46; *R. bicuspidatus* (Barnard, 1960): 218, pls. 15; *R. barnardi,* new species; *R. tridentatus* (Barnard, 1954): 4, pls 4, 5; *R. pallidus* (Barnard, 1960): 261, pls. 38, 39; *R. lucubrans* (Barnard, 1960): 212, pl. 12; *R. abronius* (Barnard, 1960): 203, pl. 5.

Diagnosis. Body generally short, broad, small in size (6 mm). Rostrum strongly incised in front of eyes, typically distally narrow. Pigmented eyes small in female, large, subquadrate, nearly meeting mid-dorsally in male. Antenna 1, peduncular segment 2 shorter than 1. Antenna 2, segment 1 variously ensiform, segment 4 with 2-3 small groups of antero-facial spines; segment 5 with 0-1 facial groups. In male, calceoli on proximal flagellar setae of antenna 1; also on antenna 2: distally on alternate segments of elongate flagellum, and 2 calceoli antero-distally on peduncular segment 5.

Upper lip, epistome variously produced or not. Lower lip broad, shoulders often with weak cones. Mandible: molar small, with few (<10) marginal blades; spine row medium; right lacinia bicuspate rarely simple; left lacinia 4-5 dentate; incisor tricuspate; palp segment 3 shorter than 2, with single cluster of "A" setae, apex obliquely truncate. Maxilla 1, palp short, relatively broad, apically with setae and single spine; inner plate with 3-4 apical setae; outer plate, outer apical spine seldom enlarged. Maxilla 2 inner plate distinctly the smaller. Maxilliped, inner plate, apex rounded, with single apical spine; outer plate short, slender; palp segment 2 variously broadened, dactyl slender, often curved.

Coxal plates 1-4 increasingly deep, 4th broadest, lower margins rounded, setose near hind corner. Gnathopods 1 & 2 slender, carpus longer than weakly subchelate propod, posterior lobes long; propod, little broadening distally, palm vertical, or nearly so.

Peraeopods 3 & 4 medium strong, segment 5 with elongate posters distal spine; segment 6, distal spine(s) slender; dactyl short. Peraeopods 5-7, bases large, broad, dactyls short. Peraeopod 5, basis large, about as deep as in peraeopod 6; segments 4 & 5 expanded, with single postero-facial row of spines; segment 6 stout usually shorter than 5. Peraeopod 6, segment 4 broadened, length greater than width; segment 5 shorter than 6 margins sub-parallel. Peraeopod 7, basis, hind margin often conspicuously toothed; segment 5 variously 'swollen' and setose behind; paired copulatory spines of male (of regional species) sub-equal, slender, straight or slightly curving forwards, denticulate basally, tips often setulose.

Pleon plates 2 & 3, hind corner sub-quadrate or rounded, lower margins strongly setose. Urosome 1, rarely with ventral brush of setae. Uropod 1, peduncle often with baso-facial setal cluster, lacking distal displaced spine (in all regional species except *R. lucubrans),* margins usually sparsely spinose; rami unequal, shorter than peduncle, sparsely spinose posteriorly. Uropod 2, peduncle variously with stout outer marginal spines; rami unequal, posteriorly with few (or no) short spines. Uropod 3 of female short, inaequiramous, inner ramus with few (or no) marginal setae terminal segment conspicuous, apex bisetose; of male large, aequiramous, margins plumose-setose; terminal segment small.

Telson lobes long, straight, lacking dorso-lateral spine(s); each usually with 2 to several long, very slender apical spines and setule.

Coxal gills large, elongate on peraeopods 2-6, small on peraeopod 7.

Taxonomic commentary. Several other species of North American Pacific species of *Rhepoxynius* occur from southern California to Baja California but are not expected to be found in the present northerly study region (Table XII). These southern species are variously described, figured, and keyed in Barnard (1960), and Barnard and Barnard (1982b) and include: *Rhepoxinius menziesi, R. stenodes, R. gemmatus, R. homocuspidatus,* and *R. heterocuspidatus.* The last four species lack a displaced spine on uropod 1, and the last three possess small, stout 'rhombic' or jewel-like spines on the rami and peduncle of uropods 1 & 2.

Species of *Rhepoxynius* of the N. American Atlantic coast *(R. epistomus* Shoemaker 1936, *R. hudsoni* Barnard & Barnard, 1982b, and various figured but unnamed species) tend to exhibit plesiomorphic character states such as heavily spinose uropods, often with displaced spine; ventrally setose urosome 1; 2 apical spines on the inner plate of the maxilliped; and three or more calceoli on peduncle 5 of antenna 2. In the very closely related genus *Microphoxus* (Pacific Costa Rica, and Magellanica), the rostrum is short, the mandibular incisor is 'molarized', segment 4 of peraeopod 6 narrows distally, and urosome 3 bears a stout forward-curving sabre-like process. In the tropical genus *Metharpinia* (e. g. *M. floridana* (Shoemaker, 1933), *M. oripacifica* Barnard, 1980a), the rostrum is constricted and reduced, antennae 2 is not ensiform, and sub-apical spines or nails occur on one ramus of uropods 1 & 2.

Distributional Commentary. The biogeographical affinities of the genus *Rhepoxynius* are apparently southern and warm temperate-tropical. Component species do not occur outside the North American coastal marine region. On the Pacific coast, the genus reaches its northern limit along the north-central coast of British Columbia, including the

Key to North Pacific species of *Rhepoxynius*

1. Pleon plate 3, hind corner sub-quadrate; uropod 3 (female), inner ramus more than half length of outer ramus, margins with a few setae; telson apical spine(s) short, thick. . . . . 2.

---Pleon plate 3 rounded behind and below; uropod 3 (female), inner ramus very short, margins lacking setae; telson, spical spines long, slender . . . . 3.

2. Uropod 1, peduncle lacking displaced spine; peraeopod 7, hind margin of basis with 7-10 low serrations epistome strongly produced; gnathopod 2, carpus elongate; uropod 1, outer ramus with 4-5 marginal spines . . . . **R. abronius** (p. 109)

---Uropod 1, peduncle with stout displaced spine; Peraeopod 7 hind margin with 3-4 stout teeth; epistome not, or weakly produced; gnathopod 2, carpus shortened & deepened; uropod 1, outer ramus with 1-3 posterior marginal spines . . . . **R. lucubrans**

3. Peraeopod 5, basis with proximal post process; urosome 1 with forward-curving mid-dorsal process; uropod 1, rami markedly unequal; epistome with upwardly curving process . . . . . . **R. vigitegus** (p.116)

---Peraeopod 5, basis rounded behind; urosome 1 smooth above; epistomal process straight . . . . 4.

4. Peraeopod 7, hind margin of basis with 3-5 prominent teeth; uropod 2, peduncle with numerous (3+) inner marginal spines . . . . 5.

---Peraeopod 7, hind margin of basis with 2 spikes, or with 3-5 unremarkable serrations; uropod 2, peduncle with few (1-4) marginal spines . . . . 6.

5. Uropod 2, peduncle, outer margin with 4-5 stout rhombic spines, telson with short apical spines . . . . **R. pallidus** (p. 112)
---Uropod 2, peduncle, outer margin with 2-3 unequal spines; telson apices each with pair of long setae . . . .**R. tridentatus** (p. 110)

6. Peraeopod 7, basis with 2 stout posterior margin teeth or processes . . . . 7.

---Peraeopod 7, basis with 3-5 teeth, not prominent . . . . 8.

7. Telson, apical spines slender, long; gnathopod propods, broadened distally, palms oblique; peraoepod 7, basis, upper 'spur' of hind margin not larger than lower spur; segment 5 'swollen', setose behind . . . .**R. barnardi** (p. 120)

---Telson, apical short; gnathopod propods weak, slender, palms vertical; peraeopod 7, basis, upper spur of upper spur of hind margin distinctly larger than lower spur; segment 5 regular .**R. bicuspidatus** (p. 118)

8. Epistome weakly produced, length not greater than basal width; peraeopod 5, segment 4 strongly broadened; pleon plate 3, lower margin short, not overlapped by pleon 2 (in normal position) . . . . 9.

---Epistome strongly produced; peraeopod 5, segment 4 little wider than long (deep); pleon plate with with slightly indented hind margin pleon 3, lower margin long, overlapped by pleon 2 . . . . 10.

9. Rostrum narrow, apex subacute; peraeopod 7, basis regularly rounded behind; telson lobes each with 5-6 long slender spines . . . . **R. fatigans** (p. 122)

---Rostrum medium broad, apex rounded; peraeopod 7, basis, postero-distal margin nearly straight; telson lobes each with 1 long, slender spine (and a few short setae) . . . . **R. daboius** (p. 122)

10. Peraeopod 7, basis, hind margin with 3-4 strong, sub-equal teeth; uropod rami lacking posterior spines; peraeopod 5, segment 4 distinctly broader than deep .... ***R. variatus*** (p. 116)

----Peraeopod 7, basis, hind margin with 4-5 normal teeth, increasing in size distally; peraeopod 5, segment 4 little broader than deep; uropods 1 & 2, one or both rami with single posterior marginal spine .... ***R. boreovariatus*** (p. 114)

Queen Charlotte Islands, and on the Atlantic coast, in the Cape Cod region (Barnard & Barnard, 1982b). No species of *Rhepoxynius* have yet been recorded from the coasts of eastern Asia, or elsewhere in the western Pacific region.

Rhepoxynius abronius (Barnard, 1960)
(Fig. 21)

Paraphoxus abronius Barnard, 1960: 203, Pl. 5.
Rhepoxynius abronius: Barnard & Barnard, 1982a: 26.—Bousfield, 1990: 13.—1991: 84.

Material examined:

BRITISH COLUMBIA: Queen Charlotte Islands, ELB Stns., 1957: E14c (26 specimens with slide mounts of 2 females ov. (4.5, 5.5 mm) and 1 male (4.5 mm); H2 (4 specimens with slide mount of 1 imm. female (4.0 mm) and 1 male (4.0 mm); H3 (2 specimens).
Central Coast: ELB Stns., July-August, 1964: H8 (11); H10 (30 specimens, with slide mounts of 1 female br. II (5.5 mm), fig'd., 1 mature male (5.0 mm), fig'd., and 2 males (4.0, 4.5 mm) CMN Cat. No. NMCC1992-0648; H13 (30); H23 (1); H37 (1); H49 (1).
Vancouver I.: ELB Stns., 1959: V7 (20); 07b (4), 07d (1); 013 (25); ELB Stn., 1964: H4I (l); ELB Stns. 1970: P711 (10); P703 (ca. 100 juv.); ELB Stns. 1975: P29b (2); P22 (9); P21a (7); P21b (2). ELB Sths., 1976: B4 (1); 9c (2); B9e (6). ELB Stns., 1977: B8 (2) ELB Stn., 1955: Fl (1).
French Creek, Penny O'Rourke coll., August 23, 1977: 3 specimens, with slide mount of 1 female ov. (5.0 mm). Pachena Bay, gray whale feeding pits, P. Slattery coll., Pit 1, September 16, 1982: 9 females, 11 subadult males, with slide mounts of 1 imm. male (3.75 mm) and 1 male (4.25 mm).

WASHINGTON: ELB Stns., 1966: W31(2); W33 (40); W39 (2).
Juan de Fuca Strait, C. P. Staude Stns., June 3, 1976, 76 specimens; Twin R., June 14, 1976: mature male (4.25 mm) (slide mount) and a series of slide mounts prepared by C. P. Staude.

Taxonomic commentary. The material from the present northern study region is generally larger in size, and exhibits heavier armature of the appendages, than Barnard's original material from southern California (loc. cit). However, the smaller southern material shows somewhat more strongly developed gnathopod propods. The northern material also exhibits some degree of morphological variability attributable to both meristic growth, and to local population factors, but nothing that merits serious consideration of further species subdivision and recognition. As the species is proving useful in bioassay testing of toxic waste materials in north-eastern Pacific bottom sediments (e. g. Bousfield, 1990, in McLeay Associates, Rpt, 1991, Swartz, 1989-90), a full description is provided below in order to assist in reliable identification of the species in this region.

Diagnosis. (Mature male, 5.0 mm): Pigmented eyes very large, sub-quadrate, nearly meeting mid-dorsally. Rostrum short, narrow, subacute apex reaching little beyond peduncular segment 1 of antenna 1. Antenna 1, flagellum short, 8-segmented, proximal 5 calceolate; accessory flagellum 7-segmented. Antenna 2, segment 1 strongly ensiform; segment 2 gland cone distinct; segment 4 with 2 small clusters of facial spines and single posterior marginal spine; segment 5 with 1 small cluster of facial spines, and 2 antero-distal marginal calcoli; flagellar segments about 40-45 in number, individually short, distally alternately calceolate.

Epistome acutely produced. Lower lip, shoulders with small cones. Mandible: molar small, with 5-7 blades; spine row medium with 9-11 rakers, and associated setae; left lacinia flabellate, right lacinia broadly and unequally bifid; incisor narrow, tricuspate; palp segment 2 arched distally, lacking facial cluster of setae; segment 3 with cluster of 3 unequal "A" setae. Maxilla 1, palp short, broad, obliquely truncate apex not reaching tips of apical spines of outer plate. Maxilla 2, plates tall, inner plate narrow; outer plate, outer margin strongly setulose. Maxilliped, inner plate apically rounded; outer plate with 7-8 slender masticatory spines; palp strong, segment 2 medium strong; dactyl strong, nearly straight.

Coxae 1-3 medium, increasing in depth posteriorly. Coxa 4 nearly as broad as deep, smoothly rounded below, hind process acute. Gnathopods 1 & 2, propods slender, little broadening distally, palms nearly vertical.

Peraeopods 3 & 4 medium strong, segment 5 not narrowed, postero-distal spine not reaching end of segment 6; segment 6, posterior spines longer than dactyl, confined to distal half of segment. Peraeopod 5, basis slightly broadening distally; segment 4 very broad, width 50% greater than depth (length), posterior facial spine row strong; segment 5 deeper, narrowing distally; segment 6 strong, longer than 5; dactyl long. Peraeopod 6, basis broadest distally; segment 4 about twice as long as wide; segment 5 much shorter, margins sub-parallel; segment 6 linear, about as long as segment 4; dactyl slender. Peraeopod 7, basis sub-circular, hind margin with 8-10 weak teeth; segment 6 elongate, not swollen; copulating spines about half length of segment 6, sub-equal, nearly straight, proximal 2/3 denticulate; dactyl slender.

Pleon plate 2, hind corner obtuse, lower margin convex, with vertical sub-marginal fan of plumose setae; pleon plate 3, hind corner acuminate, lower margin convex, strongly setose. Urosome 1 with ventral cluster of setae. Uropods 1 & 2 relatively long and slender; uropod 1, peduncle with 1-2 baso-facial setae; inner margin with 7-8, outer margin with 4 medium spines, lacking displaced spine; outer ramus with 4-5, inner ramus with 2, posterior marginal spines. Uropod 2, peduncle, outer margin with 6-8 tall spines; outer ramus with 3-4, inner ramus with 2, posterior marginal spines. Uropod 3, rami long, lanceolate, sub-equal, margins richly plumose-setose; terminal segment distinct.

Telson, lobes slender, long, apices each with 2 unequal spines.

Coxal gills on peraeopods 2-5 medium broad, apices rounded, slightly smaller on peraeopod 6, short, drop-shaped on peraeopod 7.

Female br II (5.5 mm): Rostrum similar to that of male. Pigmented eyes small, ovate. Antenna 2, peduncular segment 4 with 3, segment 5 with 2, clusters of facial spines. Uropod 3, inner ramus narrow, with a few apical and subapical plumose setae, about equal in length to proximal segment of outer ramus; outer ramus with 3-4 plumose setae along distal margins; terminal segment distinct apex with 2 plumose setae.

Distribution and Ecology. Queen Charlotte Islands and north central coast of British Columbia, southward through Washington and Oregon to California. The species occurs commonly and abundantly inshore and sub-tidally, mostly at surf-protected localities, in sand, variously to depths of 10-15 metres. Records below 50 m. depth may refer to other, yet undescribed, species.

Taxonomic commentary. Considerable morphological variability is evident throughout the geographical range of this species. Specimens from H10 (Oval Bay) are larger (5.0 mm) than those from California described by Barnard & Barnard (c. 3 mm). In specimens from the N. central B. C. coast, the epistomal cusp is less elongate, and the telson lobes each bear 1 (not 2) apical spines. Antenna 2 is strongly ensiform in B. C. specimens. The pattern of spines on peduncle and rami of uropods 1 & 2 also varies in size and number.

R. abronius demonstrates mostly plesiomorphic character states and, as cluster analysis demonstrates (p. 125), it is isolated rather widely from other species of the genus. This situation appears similar to that of the ultra-primitive species, *G. grandis,* within the genus *Grandifoxus.* Remarkably, such primitive species are the most intertidal, the most widespread, and most commonly encountered regional species within their respective genera. However, both species appear to be 'generalists' and tolerate a relatively wide range of substrate types, salinities, and year- round temperatures. These features lend themselves to use as relatively lab-hardy experimental animals, and value as indicator species of marine environmental conditions.

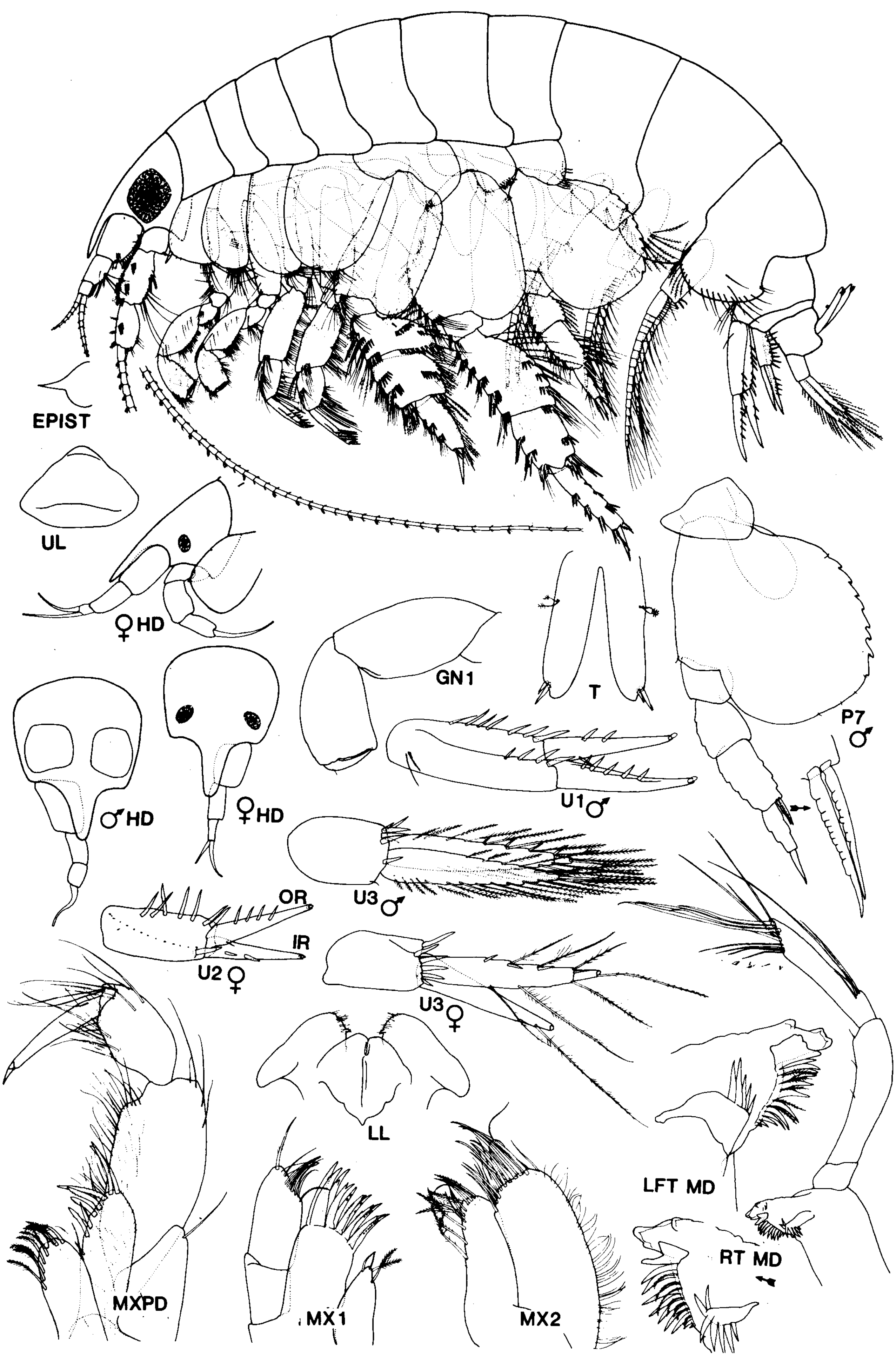
Rhepoxynius tridentatus (Barnard 1954)

Pontharpinia tridentata Barnard, 1954: 4, pls. 4, 5.
Rhepoxynius tridentatus: Barnard & Barnard, 1982a: 42 (part) non Fig. 6b.
non: *Paraphoxus tridentatus pallidus Barnard, 1960:* 261, pls. 38, 39.
non: *Paraphoxus heterocuspidatus Barnard, 1960:* 224, pls. 19, 20.

Taxonomic commentary. Material ascribable to Barnard's original type species from Oregon was not found in present collections. Barnard (1960) established the subspecies *R. tridentatus pallidus* on the basis of material from the San Juan Islands and Puget Sound region. He also included, within the *tridentatus* group, his (then) new species *R. heterocuspidatus* from S. California, and postulated that differences in the strength of the gnathopods was probably attributable to ecophenotypic variation. Barnard and Barnard (1982a), in essence, considered *R. tridentatus* to represent a clinal series of forms from *pallidus* in the north to *heterocuspidatus* in the south. Doubtless these three morphotypes are closely similar in several, mainly apomorphic character states such as: short, broad rostrum; large antennal gland cone; unproduced epistome; small mandibular molar and short spine row; stout maxilliped palp with weakly falcate dactyl; small coxal plates 1-4; tridentate P7 basal margin, and generally short uropods with rhombic spine on uropod rami. However, in our view, the differences between these forms are significant in both quantity and quality, and at the same levels that separate other closely related species within the genus (e. g., *R. fatigans and R. daboius; R. bicuspidatus, and R. barnardi;* and *R. variatus* and *R. boreovariatus.* These species level differences are recognized in the key to species (p. 108) and in the detailed descriptive accounts elsewhere (*R. pallidus,* p. 112*)*.

Distribution and Ecology: Authentic material of this species has to date been recorded only from the coast of Oregon, on fine sand, in 40-80 m. depth.

Fig. 21. ***Rhepoxynius abronius*** Barnard.
MALE (5.0 mm); FEMALE br II (5.5 mm).
(SEE PAGE 111 - OPPOSITE)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LL
LFT MD
RT MD
MXPD
MX1
MX2

Rhepoxynius pallidus (Barnard, 1960)
(Fig. 22)

Paraphoxus tridentatus pallidus Barnard, 1960: 261, pls. 38, 39.
Rhepoxynius tridentatus Barnard and Barnard, 1982a: 42 (most), fig. 6.
non *Rhepoxynius heterocuspidatus* (Barnard, 1960): 224, pls. 19, 20.

Material examined.
BRITISH COLUMBIA: North central coast, mostly LW to 7 m., ELB Stns., July, 1964: H2, Kiusta village: 4 specimens, with slide mount of 1 female br. II (4.5 mm); H13, Lelu I.: 1 male penult. (6.0 mm) with slide mount, fig.'d, CMN Cat. No. NMCC1992-0649; H25, Cox Pt.: 5 specimens, with slide mount of 1 female ov. (4.6 mm), fig'd., CMN Cat. No. NMCC1992-0701.
Southern Vancouver Island: Victoria, Trial Island Pt., LW to sub-tidal sand and fine gravel, ELB Stn. B6c, May 18, 1977 (2); Haro Strait, D. V. Ellis Sta. 2403, March 8,1979 (1).
Saanich Inlet, K. E. Conlan Stns., 1975-1976: 22 specimens in 10 lots.

Diagnosis. (Male, penult (6.0 mm): Body broad, dorsoventrally depressed and broadened. Pigmented eyes large, nearly meeting mid-dorsally. Rostrum short, broad, apex sub-acute, reaching middle of peduncular segment 2, antenna 1. Antenna 1, peduncle 1 short, deep, not longer than slender segment 2; flagellum 10-segmented; accessory flagellum 7-segmented. Antenna 2, segment 2, gland cone prominent; segment 4 with 3 facial groups of spines (3-4 per cluster); segment 5 with single facial group of 2 spines; flagellum with about 27 short segments, conjoint proximally.

Epistome not produced. Lower lip with shoulder cones. Mandible: molar small, with 4-5 blades; spine row short, with 7-8 weak rakkers; right lacinia bifid; left lacinia broad, 5-dentate; incisor broad, bi- or tri-cuspate; palp short, segments heavy, segment 3 with cluster of 3 unequal "A" setae. Maxilla 1, palp broadening distally, apex nearly reaching tips of outer plate spines, outermost of which is strongly developed. Maxilla 2, outer plate, outer margin finely setulose. Maxilliped, inner plate not short, apex rounded; outer plate with 6-7 inner marginal masticatory spines; palp large, segment 2 broad, dactyl heavy, little arched.

Coxal plates 1-4 medium, increasing posteriorly. Coxa 4, margins converging slightly distally, lower margin gently convex; hind process rounded. Gnathopods 1 & 2 slender; carpus long, slender, propod narrow proximally, deepening (widening) distally, palm vertical. Peraeopods 3 & 4 medium strong, segment 5 short, postero-distal spine not reaching end of segment 6; posterior spines along distal half of segment 6, spines longer than dactyl. Peraeopod 5, basis broad, margins slightly diverging distally, hind margin nearly straight; segment 4 about 30% broader than deep; segment 5 sub-quadrate, nearly as broad as 4 but slightly deeper, margins convex, postero-facial spines stout, not slender; segment 6 shorter, hind margin with 2-3 setal groups; dactyl medium. Peraeopod 6, basis broadening distally; segment 4, moderately broad, length 50% greater than width; segment 5 much shorter than linear segment 6; dactyl short. Peraeopod 7, basis directed distally rather than posteriorly, hind margin with 3-4, sub-equal prominent teeth, distal margin slightly convex; segment 5 slightly swollen, slightly longer than 4, hind margin with 4-5 setal clusters; dactyl medium, curved, about half length of slender segment 6 (not thick, long and straight as in *R. tridentatus*).

Pleon plate 2 narrow, evenly rounding and heavily setose below. Pleon plate 3, hind corner broadly obtuse, or with slight angle, with 5-6 lower marginal setae. Uropods 1 & 2 short. Uropod 1, peduncle with baso-facial cluster of 3 setae; inner margin with 3 spines, heavier distally; rami each with single posterior marginal short spine. Uropod 2, peduncle with 4-5 outer marginal stout 'rhombic' spines, heavi-est at distal angle; outer ramus lacking, inner ramus with single, short posterior marginal spine. Uropod 3, rami sub-equal, broadly elongate, inner margins distally short setose; terminal segment distinct, apically bisetose.

Telson lobes with single, short, thin, apical spine and setule.

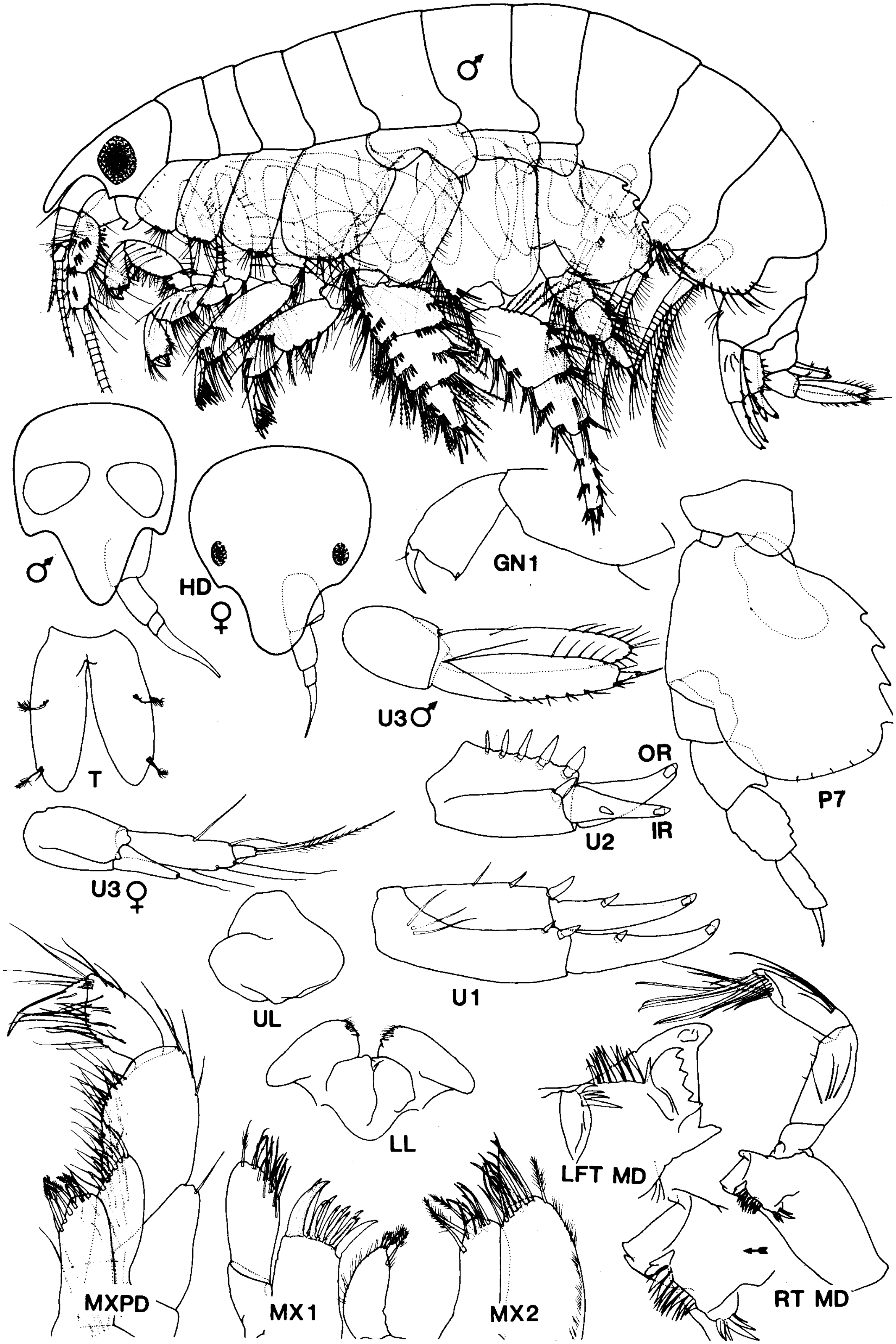
Coxal gills medium broad, elongate, spade-shaped on peraeopods 2-5, slightly smaller, leaf-like on peraeopod 6, small, drop-shaped on peraeopod 7.

Female ov. (4.5 mm): Pigmented eyes small, oval, lateral. Rostrum slightly shorter, apex more broadly rounded than in penultimate male. Uropod 3, inner ramus tall conical, about half length of outer ramus, apex with single long seta; outer ramus sub-linear, margins distally with 2-3 setae and accessory spines (outer); terminal segment stout, with 2 long apical setae.

Taxonomic commentary. *Rhepoxynius pallidus is* unquestionably closely related to *R. tridentatus,* but differs consistently in characters of the key (p.108) and the following: rostrum distinctly broader and longer; antenna 2, segment 5 with 2-3 facial spine (vs. 0); mandibular spine row longer, rakers more numerous (7-8 vs 4-6); gnathopods 1 & 2, propod palms vertical, vs. slightly oblique; peraeopods 3 & 4, segment 6, posterior spines elongate, extending along distal half of segment 6 (vs. sub-apical only); peraeopod 5, segments 4 & 5 broader and shorter, poster-facial spines stronger; peraeopod 7, dactyl slender and curved (vs. thick and straight); uropod 2, outer margin with 4-5 outer marginal (rhombic) spines (vs 2 spines); uropod 3 (female), inner ramus long-conical (vs short-conical); telson lobes with single short spine (vs 2 long setae).

The *R. tridentatus* group displays a number of plesiomorphic traits that places it well below the most

Fig. 22. ***Rhepoxynius pallidus*** (Barnard)
MALE penult (6.0 mm); FEMALE ov. (4.5 mm)
(SEE PAGE 113 - OPPOSITE)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RT MD

advanced species groups within the genus. The group is not very closely related to any other regional species complex, but in balance may be least remote from the *bicuspidatus* group (see phenogram, p. 127).

Distribution and Ecology. Known only from coastal waters of British Columbia, from the North central region to the Strait of Juan de Fuca, and Puget Sound; from LW and immediate sub-tidal sands to muddy sands at more than 40 m. in depth.

Rhepoxynius boreovariatus, new species
(Fig. 23)

? Rhepoxynius variatus Barnard, 1960: 19, fig. 4.

Material examined.
BRITISH COLUMBIA: North Central Coast: ELB Stns. 1964: H13, Lelu I: (2 females); H17, off Kennedy I: 8 specimens, with slide mount of male (3.5 mm).
Vancouver Island: North end: Oyster Bay, ELB Sta., June 21,1959: V22 (1); Barkley Sound: ELB Stns., July 29,1975: P13 (2). ELB Stns., June July, 1976: B9e (9); B10a, b, (5), B12a (1); B14 (2 females ov. (4.0, 4.5 mm) with slide mounts).
Vancouver I., South End: Sidney Spit, ELB Stn., August 19, 1955: F9 (1); ELB Stn., May 17,1977: BSa (1); Quinsam I., E. Black coll., May 5, 1981: (2); Victoria Region, C. Low coll., August 7, 1981: 1 female ov. (4.0 mm) with slide mount. Off Cape Caution, Fisheries Research Board of Canada coll., 1968, 4 males; Haro Strait, D. V. Ellis coll., March 8, 1979: 3 specimens in 2 lots; Near Nanaimo, off French Creek, P. O'Rourke Stns, August 23, 1977: FC6: 1 male (4.0 mm) HOLOTYPE, with slide mount, CMN Cat. No. NMCC1992-0702; 4 females, 1 juvenile PARATYPES, CMN Cat. No. NMCC1992-0703; FC10: 1 female ov. (4.5 mm) ALLOTYPE with slide mount, CMN Cat. No. NMCC1992-0704; 2 males PARATYPES, CMN Cat. No. NMCC1992-0705; FC1 (7); FC4 (6); FCS (2); FC7 (1); FC9 (5); FC13 (2) Mainland Coast: English Bay, ELB Stn. B4, June 16,1976: (5).
Coastal Shelf, Institute of Ocean Sciences, 1979-81: 1D3-BM (8, with slide mount of male (3.5 mm); 1D3-A1 (1 male, 1 female); 1D1-BS (1 female, 1 imm.); 1D1-B4 (1 imm,); 1D3-B2 (1 female); 1AS-BM (2 females); 1D3-A3 (1 female); 1D3-B6 (2); 1D2-AS (1 female (3.5 mm) with slide mount.
WASHINGTON: Juan de Fuca Strait: off San Juan Islands, C. P. Staude coll., 1976-1978: 23 specimens in 4 lots: off Twin Rivers: (2 specimens with slide mount of female ov. (4.0 mm) CMNCat. No. NMCC1992-0706.

Diagnosis. (Male, 4.0 mm): Rostrum short, medium to narrow, apex nearly reaching middle of peduncular segment 2, antenna 1. Pigmented eyes separated dorsally by about their width. Antenna 1, flagellum 6-7 segmented, accessory flagellum 5 segmented. Antenna 2, peduncular segment 4 with 2 small groups of facial spines, and a distal cluster; segment 5 with single facial spine and 2 antero-distal calceoli; flagellum elongate, 45-50 segmented distal segments alternately calceolate except for distal 6 segments.

Epistome strongly and narrowly produced. Lower lip with weak shoulder cones. Mandible: molar small, with 4 marginal blades; spine row moderate, with 9-10 rakers and accessory setae; left lacinia 5-dentate; right lacinia bifid; palp segment 3 with cluster of 2 "A" setae. Maxilla 1, palp slightly exceeding apical spines of outer plate. Maxilliped, outer plate, apex sub-acute, inner margin with 10 masticatory spines; palp segment 2 not broadened, dactyl curved.

Coxa 4 deeper than broad, margin converging distally, lower margin nearly straight. Gnathopods 1 & 2, propods medium, widening distally, palms slightly oblique.

Peraeopods 3 & 4 not powerful, segment 5 not shortened, postero-distal spines as long as segment 6; dactyls short. Peraeopod 5, basis, hind margin convex; segment 4 little wider than deep; segment 5 deeper than wide; segment 6 sub-linear, shorter than 6. Peraeopod 6, segment 4 50% longer than wide; segment 5 much shorter, margins sub-parallel; segment 6 linear, hind margin weakly setose; dactyl medium. Peraeopod 7, basis, distal margin with 4 distinct teeth, size increasing distally, distal margin nearly straight; segment 5 'swollen' strongly setose behind, copulatory spines straight, subequal, distally setulose; dactyl slender.

Pleon plate 2, lower hind angle very broadly obtuse; lower margin setose anteriorly. Pleon plate 3, hind margin rounded, lacking setae. Uropod 1, peduncle with cluster of 2 baso-facial setae; peduncle with 2-3 inner marginal spines, but lacking displaced spine; rami sub-equal, posterior margin of each with 1 spine; Uropod 2, peduncle with 3-4 stout outer marginal spines; rami sub-equal, outer margin with 1 posterior marginal spine. Uropod 3, rami narrowly lanceolate, inner shorter, margins moderately strongly plumosesetose.

Telson, apices of lobes subacute, each with 2 sub-equal, long, slender spines, and setule.

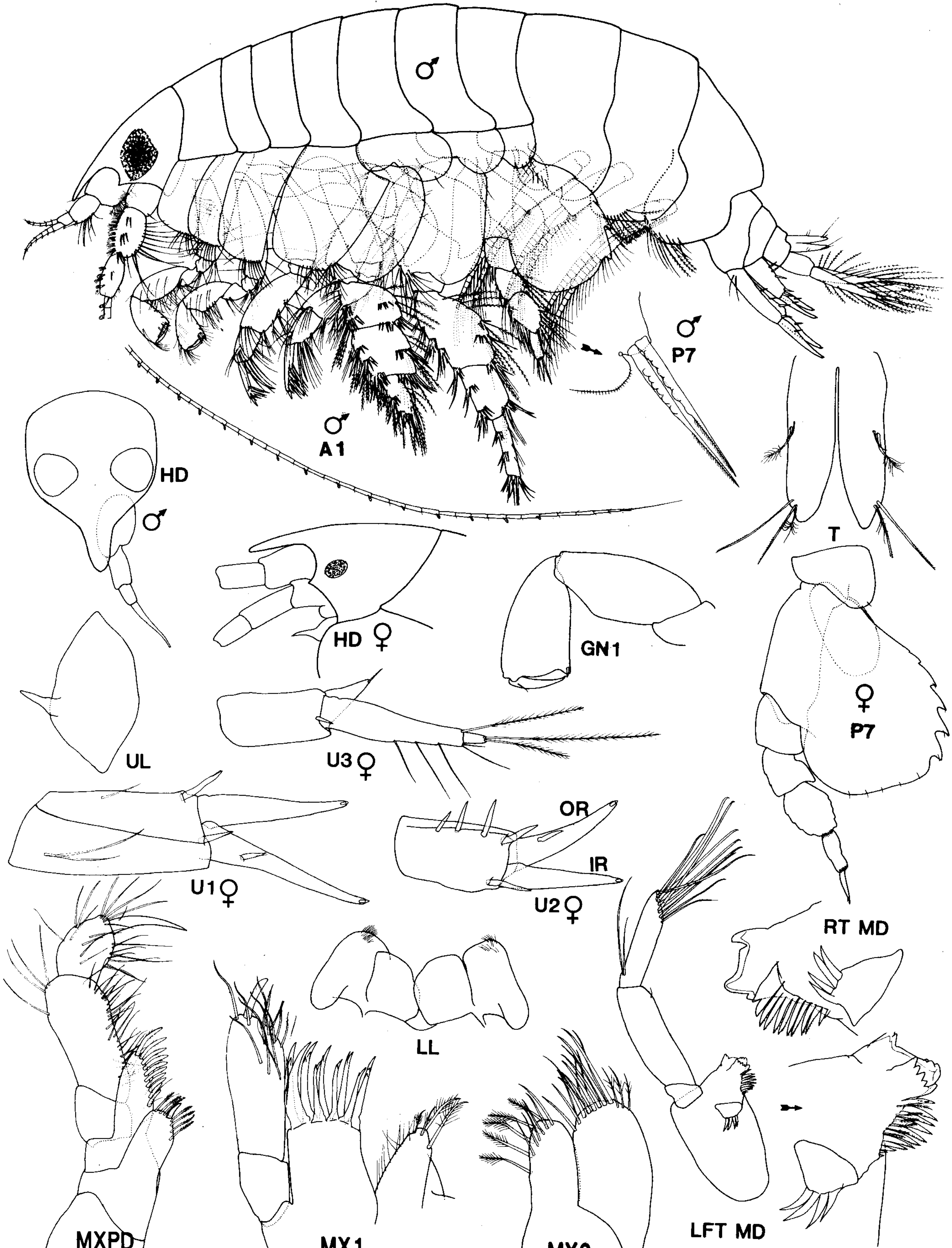
Coxal gills on peraeopods 2-6 large, elongate, distally subacute; on peraeopod 7, small, rounded below.

Female ov. (4.5 mm): Pigmented eyes small, nearly horizontally elliptical. Antenna 2, peduncular segment 4 with 2 distinct facial groups of spines and a distal group; segment 5 with 1-2 facial spines; flagellum 8-9 segmented.

Uropod 3, inner ramus very short, elongate-conical, apex with seta; outer ramus about 40% longer than peduncle, outer margin with a few simple setae; terminal segment distinct, apex with 2 plumose-setae.

Taxonomic commentary: Diagnostic features of this northern material agree fairly closely with those described initially by Barnard (1960, plate 4). Minor differs include the narrower rostrum, slightly stronger gnathopods, and sub-

Fig. 23. ***Rhepoxynius boreovariatus***, new species. MALE (4.0 mm) HOLOTYPE; FEMALE ov. (4.5 mm) ALLOTYPE. (SEE PAGE 115 - OPPOSITE)


♂
A1 ♂
P7 ♂
HD ♂
T
HD ♀
GN1
P7 ♀
UL
U3 ♀
U1 ♀
OR
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RT MD
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MXPD
MX1
MX2
LFT MD

equal apical paired slender spines of the telson lobes, relative to the conditions in the Californian specimens. Major differences with *R. variatus* Barnard are given in the key (p. 108).

Distribution and Ecology. Central British Columbia, Vancouver Island, and Washington State, on sandy mud, sub-tidally to about 40 m. in depth.

Rhepoxynius variatus (Barnard, 1960)

Paraphoxus variatus Barnard, 1960: 198, pl. 3.
non *Paraphoxus variatus* Barnard, 1960, pl. 4.
non? *Rhepoxynius variatus* Barnard & Barnard, 1982a: 24, fig. 4.

Taxonomic commentary. The original description of Barnard (1960) embraced two or more dis- tinct species, as indicated by the 'variation' in major character states of material from different stations in his Table 3. The first species illustrated under this name (a 4.0 mm female from station 2310-53, plate 3) becomes, by priority, and by Barnard's designation of this station as the type locality, the HOLOTYPE of the name 'variatus'. The 4.75 mm. female from Sta. 2618-54, portrayed in his Plate 4, and many of the other materials listed in Table 3, apply to other, apparently distinct, but unnamed species. Barnard and Barnard (1982a) subsequently ascribed to the name '*variatus*' a 3.11 mm female and a 2.77 - male, from AHF VELERO IV Sta. 5973, as well as accessory (smaller) female and male specimens from Sta. 5180, and other (earlier) material from off Corono del Mer, southern California. Unfortunately, as those authors did not clarify the original species type and, as indicated by some of their descriptive detail (almost no figures provided), they may have treated a very closely similar third species in their VELERO material.

In collections from the present study region (north of California) no specimens referable to the designated type of *variatus* (above) have been found to date. However, several lots of specimens closely referable to the apparently unnamed species of Barnard's (1960) Sta. 2618-54 and Plate 4 are described and named elsewhere in the paper (p.114) as *Rhepoxynius boreovariatus,* new species. Critically diagnostic character states from Barnard's original type species, R. *variatus,* are summarized below:

Diagnosis (Female ov., 4.0 mm): Rostrum large, narrow, sharply rounded apex reaching end of peduncular segment 2 of antenna 1. Antenna 2, peduncular segment 5 with a single facial spine.

Upper lip, epistome acutely produced. Mandible, palp segment 2 stouter than 3, the latter with a group of two "A" setae. Lower lip with cones. Maxilla 1, palp segment 2, length about twice width.

Gnathopods 1 & 2 slender, propods thin, palms vertical.

Peraeopod 3 medium strong, segment 6 not shortened, with 2 slender postero-distal spines nearly equal in length to segment 6. Peraeopod 5, basis broad, hind margin nearly straight; segment 4, width 1.5 X depth; segment 5 subequally broad and slightly deeper; segment 5 slightly shorter than 5, widest medially. Peraeopod 6, segment 6 expanded, about 60% deeper than broad; segment 5 shorter than 4, broader than linear segment 6; dactyl short. Peraeopod 7, basis posteriorly with 4 large sub-equal prominent teeth, distal margin 'squared', almost straight; segment 5 slender, hind margin with a few long setae; dactyl medium.

Pleon plate 2, evenly rounded below, lower margin richly plumose-setose; pleon plate 3, hind corner obtuse, with very slight acumination; lower margin posteriorly long-setose. Uropod 1, peduncle apparently lacking inner marginal spines (except apical spine), displace spine lacking; rami sub-equal, without posterior marginal spine(s). Uropod 2, peduncle with 2-3 stout marginal spines; inner ramus only slightly the shorter, both lacking posterior spines. Uropod 3 inner ramus very short, conical, length about equal to terminal segment of outer ramus, outer margin of which bears distally a few long slender setae; apex bi-setose.

Telson lobes, apices subacute, each with an unequal pair of slender spines.

Coxal gills not described.

Mature Male not described nor figured. Sexually diagnostic features are probably similar to those illustrated for *R. boreovariatus,* new species, and varieties (e.g. Barnard, 1960, plate 4).

Distribution and Ecology. Off Southern California coast, on sandy mud bottoms, at depths of 10 m. to more than 100 m., but mostly shallower than 40 m.

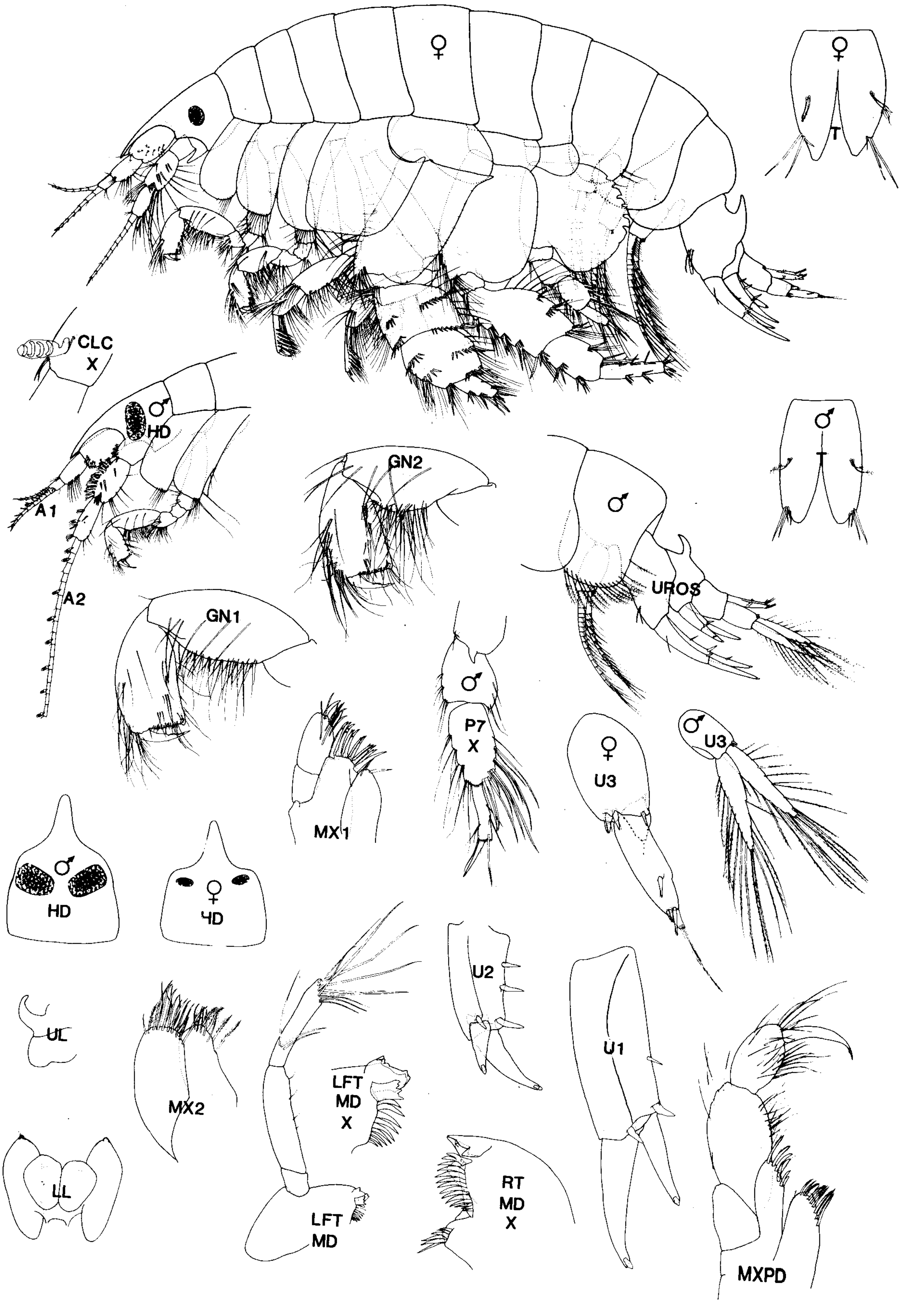
Rhepoxynius vigitegus (Barnard, 1971)

(Fig. 24)

Paraphoxus vigitegus Barnard, 1971; 70, figs. 44-46.—
Barnard & Barnard, 1982b: 47.

Material Examined.
BRITISH COLUMBIA: Vancouver I., McKenzie Beach, sand at LW, ELB Sta. P703, July 7, 1970: 1 male, 1 female ov., 1 sub-adult female CMN Cat. No. NMCC1992-0707. McKenzie Beach, medium fine sand at LW level, D. McLeay coll., November 9,1990:1 female ov (4.5 mm) with slide mount, fig'd., RBCM Collections; 1 male (4.0 mm), with slide mount, fig'd., RBCM Collections.

FIG. 24. ***Rhepoxynius vigitegus*** **(Barnard).**
FEMALE (4.5 mm); MALE (4.0 mm).
(SEE PAGE 117 - OPPOSITE)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UROS
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P7
X
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U3
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U3
♂
HD
♀
HD
UL
MX2
U2
U1
LFT
MD
X
RT
MD
X
LL
LFT
MD
MXPD

Diagnosis. The species has been thoroughly described and figured by Barnard (1971) and Barnard & Barnard (1982b) above. Further diagnostic aspects of this distinctive species are added below:

Female ov. (4.5 mm): Rostrum short, narrowing to acute apex. Antenna 2, peduncle 5 lacking facial spines.

Epistomal process strong, recurved upwards. Mandibular palp segment 3, with single cluster of three "A" setae. Maxilla 1, palp short, little exceeding apical spines of outer plate. Maxilla 2, inner plate distinctly narrower than outer. Maxilliped, segment 2 broad; dactyl curved, falciform.

Coxal 4 very broad, margins little converging distally, lower margin nearly straight, postero-medial process acute. Gnathopods 1 & 2 slender; propods not expanded distally, pale vertical.

Peraeopods 3 & 4 not stout, segment 5 relatively long; distal spines of segment 6 long and slender; dactyl slender. Peraeopod 5, postero-proximal process of basis acute, reaching hind margin of coxa; segment 5 as broad as segment 4, fore and hind margins convex. Peraeopod 7, hind margin of basis with 5-6 deeply separated, evenly "capped", saw-toothed serrations.

Uropods 1 & 2, rami markedly unequal (inner shorter), posterior margins bare. Uropod 3, inner ramus very short, sub-conical, little longer than broad. Coxal gills large, sac-like on peraeopods 2-6, short, small on peraeopod 7.

Male (4.0 mm.): Rostrum slightly broader, less sharply incised than in female. Eyes large, vertically subrectangular, nearly meeting mid-dorsally. Antenna 1, flagellum 8-9 segmented, calceolate on proximal 5 segments. Antenna 2, peduncular segment 5 with single facial spine, 2 antero-distal calceoli; flagellum elongate (25-segmented?), alternate segments calceolate.

Peraeopod 7, copulatory spines of segment 5 slender, subequal, distally smooth, curving forwards, proximally denticulate.

Uropod 3, rami narrowly lanceolate, margins moderately plumose-setose; terminal segment short, with 2 apical setae. Telson lobes, apical slender spines longer than in female.

Distribution and Ecology. From central B.C., LW level, to off Oregon, 30 m in sand. The sexually mature specimens of this medium-depth species that were netted along the B.C. shoreline in November (also taken there during a previous survey in July-August) may be the result of entrapment in wind-driven surface waters during pelagic mating activities at the time.

Taxonomic commentary. The present adult female differs from the original type material from off Oregon in features that are here considered of varietal significance only. Theseinclude the more numerous pigmented eye facets, in a definitive eye region; less strongly spinose uropod 1; shorter inner ramus of uropod 3; and more acutely pointed telson lobes.

Rhepoxynius bicuspidatus (Barnard, 1960)

Paraphoxus bicuspidatus Barnard, 1960: 218, pls. 15, 16.—Barnard, 1964: 243, fig. 12.—Barnard, 1971: 68-70.---Barnard & Barnard, 1982a: 44.

Taxonomic remarks. Barnard (1960, loc. cit) appears to have included at least two distinct species in his original description of *R. bicuspidatus.* Although the designated type specimen is a 3.3 mm. female from Santa Maria Bay, Baja California, he has figured (plate 15) a 4 mm. female from Sta. 2610-54, and parts of a 4.5 mm. female and 3 mm. male from other stations off Huntington Beach, Southern California. The two figured females show striking differences in the form and position of the two strong spurs on the hind margin of the basis of peraeopod 7, and in the relative lengths of the inner ramus of uropod 3. Barnard and Barnard (1982, loc cit) have described in considerable detail yet another 4.57 mm. female, and a 3.86 mm. male from southern California that differ in other details such as armature of the telson lobes, and recorded the total range of all forms as 'Oregon to Baja California, 8-475 m.'. Whatever form may prove to be the type of the species *R. bicuspidatus,* none of these has been detected in material from the present, more northerly study region.

For comparative purposes, the form of *R. bicuspidatus* illustrated by Barnard (1960, plate 15) is briefly diagnosed here, and is included in the key to species (p.).

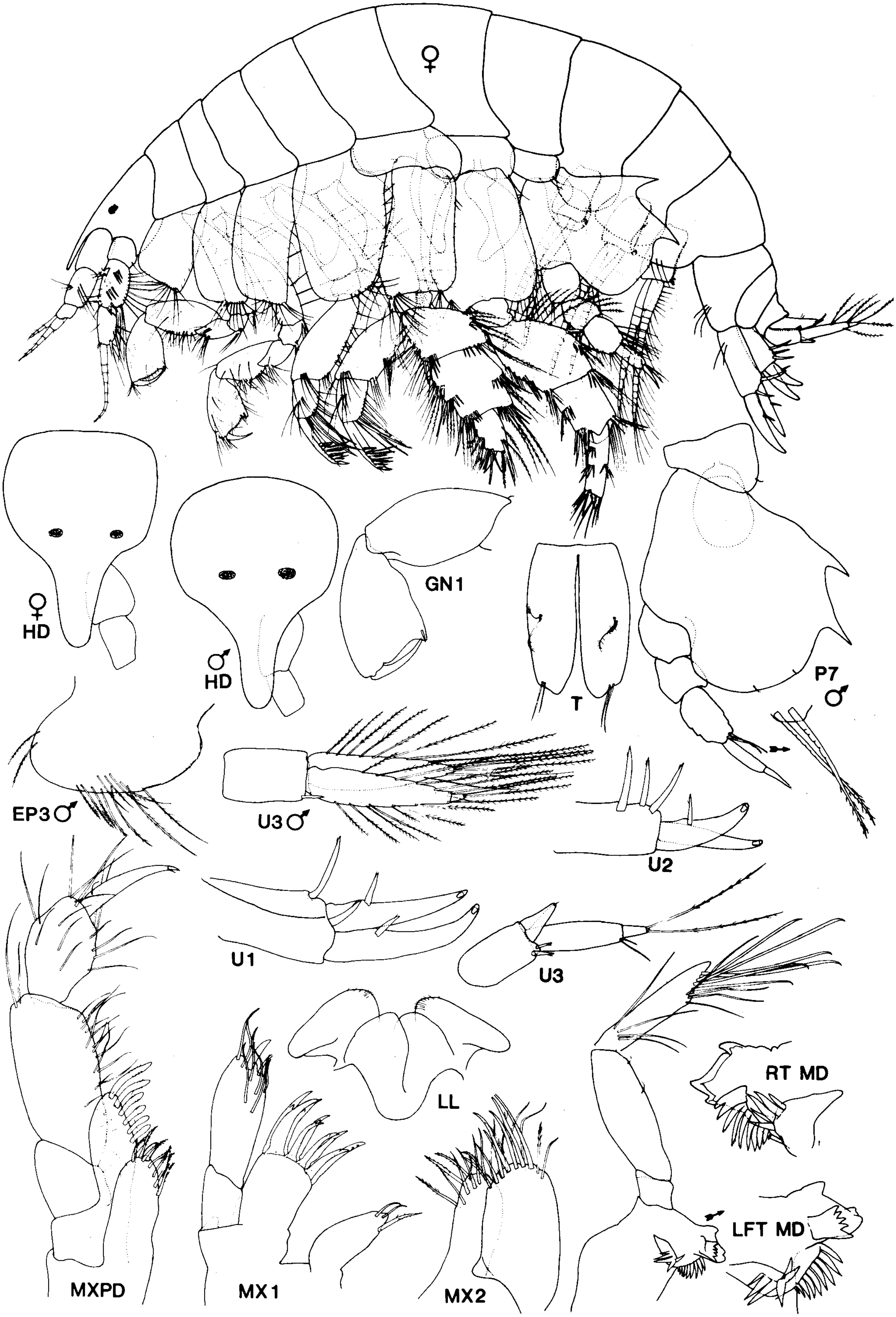
Diagnosis (Female ov., 4.0 mm). Body short, very broad. Rostrum narrow. Antenna 2, segment 1 strongly ensiform; segment 4 with two facial clusters of spines (5) and distal group of 2 spines, hind margin strongly long-setose; segment 5 lacking facial spines

Epistome produced very slightly. Mandible, molar small, with few marginal blades; spine row short; palp segment 3 with cluster of 2 "A" setae. Maxilla 1, palp longer than apical spines of outer plate. Maxilliped, palp segment 2 greatly broadened, dactyl nearly straight.

Gnathopods slender, propods not widening distally, palms nearly vertical. Coxa 4 deeper than broad, margins converging distally, lower margin gently rounded, hind process rounded.

Peraeopod 3 medium-strong, segment 5 somewhat deepened, 2 postero-distal spines exceeding length of segment 6 in which the lateral spines are clustered sub-apically; dactyl short. Peraeopod 5, basis hind margin nearly straight; segment 4 about 25% wider than deep; segment 5 slightly

Fig. 25. ***Rhepoxynius barnardi,*** new species. FEMALE ov. (3.0 mm.) HOLOTYPE; MALE (4.0 mm) ALLOTYPE (SEE PAGE 119 - OPPOSITE)


♀
♀ HD
♂ HD
GN1
T
P7 ♂
EP3 ♂
U3 ♂
U2
U1
U3
LL
RT MD
LFT MD
MXPD
MX1
MX2

deeper, slightly narrowing distally; segment 6 short, 'thick'; dactyl small. Peraeopod 6, segment 5, length about twice width; segment 5 short, slightly narrowing distally; segment 6 linear, with 2 posterior groups of spines. Peraeopod 7, basis, upper posterior spur longer than the lower spur, distal margin nearly straight; segment 6 not swollen or broadened, shorter than segment 6; dactyl medium.

Pleon plate 3, lower margin setose near hind corner. Uropod 1, peduncle with 4 inner marginal spines increasing distally; displaced spine lacking; rami unequal, each with small posterior marginal spine. Uropod 2, peduncle with 4 stout outer marginal spines; outer ramus with 1 posterior marginal spine. Uropod 3, inner ramus very short, tall-conical; outer ramus with 2-3 outer marginal spines; terminal segment distinct, apex short-setose.

Telson lobes apically subacute, each with two short slender spines and setule.

Mature Male: The 3.0 mm specimen from another station figured by Barnard (1960, plate 16) exhibits a medium broad rostrum and very large pigmented eyes, nearly meeting mid-dorsally.

Distribution and Ecology. Oregon to Baja California, 8-475 m. (Barnard & Barnard, 1982a).

Taxonomic commentary. *Rhepoxynius bicuspidatus* (and species complex) is unique and unmistakable in having two prominent spurs on the outer margin of the basis of peraeopod 7. It is a morphologically apomorphic species, with closest relationships to the *R. variatus* complex of species and forms.

Rhepoxynius barnardi, new species
(Fig. 25)

Rhepoxynius bicuspidatus Barnard & Barnard, 1982a: 44 (partim).

Material examined.
BRITISH COLUMBIA: Southern Vancouver Island: Esquimalt, off McCauley Point, fine sand at 59 m., G. W. O'Connell coll., August 26,1976: 1 female ov. (3.0 mm) HOLOTYPE with slide mount, CMN Cat. No. NMCC1992-0708; 1 mature male (4.0 mm) ALLOTYPE, with slide mount, CMN Cat. No. NMCC1992-0709; 5 female PARATYPES, CMN Cat. No. NMCC1992-0710.

Diagnosis. Since the form of the type species has not yet been clarified (see p. 118 above), the present diagnosis will be restricted largely to points of difference with the closest previous morphology, that figured by Barnard (1960, Plate 15).

Female ov. (3.0 mm): Rostrum long (almost = head length), narrow, sharply rounded apex nearly reaching midpoint of peduncular segment 2 of antenna 1. Antenna 2, peduncular segment 4 with 2 facial groups of spines (3 per group) and a distal group of 3 spines peduncular segment 5, lacking facial spines.

Epistome not produced. Mandible, molar weak, with 5-6 marginal blades; spine row weak, with 7-8 rakers; right lacinia bifid, left lacinia 5-dentate; incisor tricuspate; palp segment 3 with cluster of 3-4 medium "A" setae. Maxilliped, outer plate short, with 7 inner marginal masticatory spines; palp segment 2 not noticeably broadened dactyl curved distally.

Coxae 1-3 relatively broad, deepening progressively posteriorly. Coxa 4 distinctly deeper than broad, margins little converging below, hind process subacute. Gnathopod propods distinctly widening distally, palms oblique.

Peraeopods 3 & 4 medium strong, postero-distal spines of segment 5 reaching end of segment 6; postero-distal spines of segment 6 long and slender, occupying distal half of segment 6; dactyl short. Peraeopod 5, basis hind margin very slightly emarginate; segments 4 & 5 moderately broadened, 5 distinctly longer than 4, margins not narrowing distally; segment 6 very short. Peraeopod 6, segment 4 relatively short and broad, depth only 30% greater than width; segment 6 with 1 group of posterior marginal spines; dactyl short. Peraeopod 7, basis subovate, upper spur of hind margin not larger than lower spur, distal margin convex, not straight; segment 5 'swollen', nearly as wide as long; segment 6 not longer than 5; dactyl slender, long.

Pleon plate 3, lower marginal setae not reaching hind corner. Uropod 1, peduncle with 3 baso-facial setae, a single large inner marginal spine, but lacking a displaced spine; rami each with single posterior marginal spine. Uropod 2, outer margin of peduncle with 2 tall postero-distal outer marginal spines; inner ramus with single posterior marginal spine. Uropod 3, inner ramus short, tall-conical; outer ramus lacking outer marginal spines or setae; terminal segment distinct, with 2 apical plumose setae.

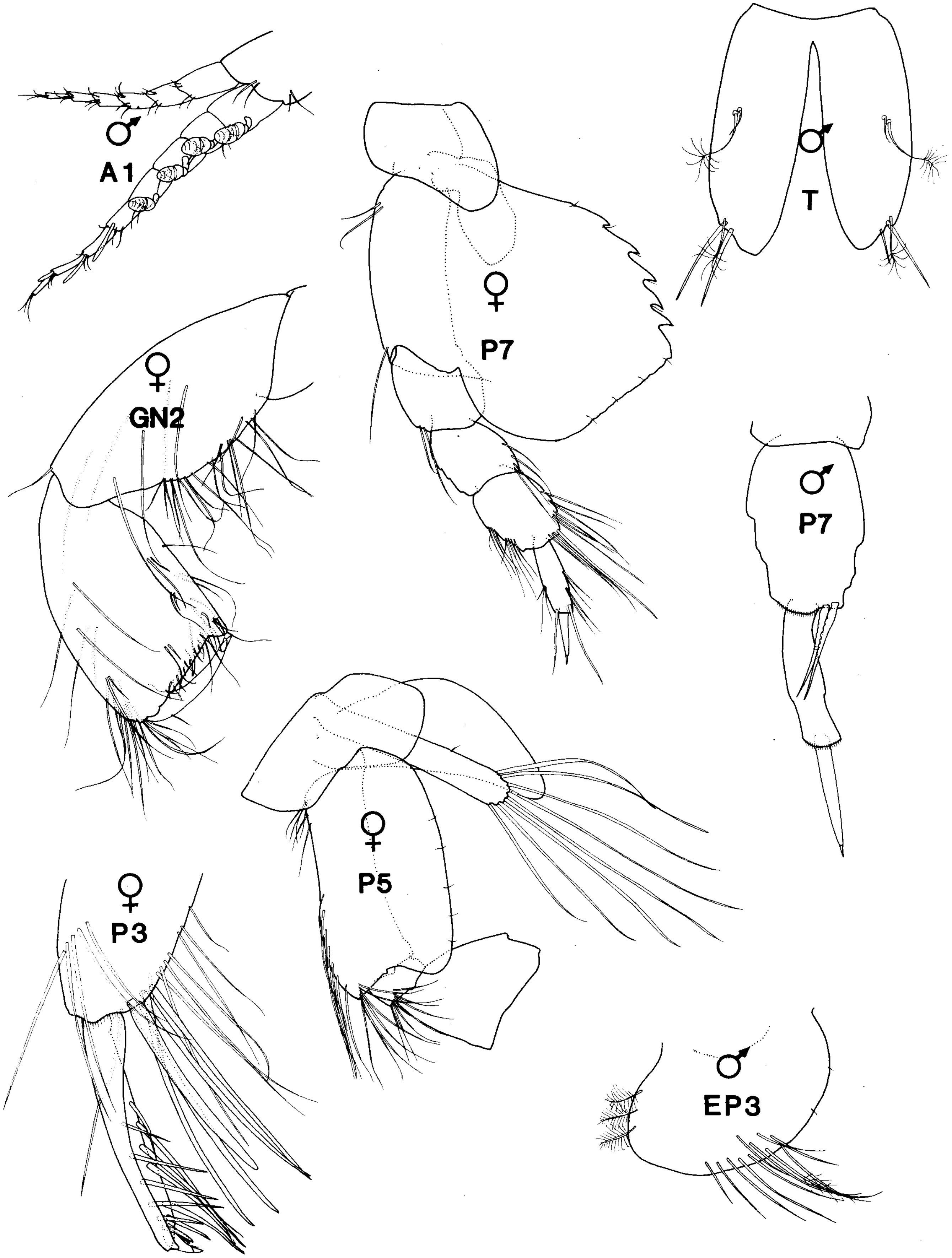
Telson apices each with 2 sub-equal, slender, closely set setae. Coxal gills on peraeopods 2-6 of medium size, slender; gill on peraeopod 7 small, rounded.

Mature male (4.0 mm): Pigmented eyes in specimen at hand are little larger than in female. Rostrum relatively slightly longer. Antenna 1, proximal 5 segments of 7-segmented flagellum of antenna 1, with calceoli. Antenna 2, peduncular segment 5 with 2 antero-distal calceoli; flagellum elongate, with calceoli on alternate segments except last 4-5.

Peraeopod 7, segment 5 not as broadened as in female, copulatory spines very slender, length about half of slender segment 6, slightly curved forwards anteriorly.

Uropod 3, rami sub-equal, margins moderately plumose-setose; terminal segment small.

Fig. 26. ***Rhepoxynius daboius*** Barnard
MALE (3.5 mm); FEMALE (3.75 mm).
(SEE PAGE 121 - OPPOSITE)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EP3

Etymology. Named in honour of the late Dr. J. Laurens Barnard whose impact on the systematics and biogeography of North American-Pacific amphipods, and especially the Phoxocephalidae, has been profound.

Taxonomic commentary. This species of the *bicuspidatus* group exhibits mainly apomorphic character states, and is apparently closest to the *variatus* complex. The small size of the pigmented eyes in the mature male specimen at hand may be anomalous.

Distribution and Ecology. Known only from the type locality, near Victoria, British Columbia, at the southern tip of Vancouver Island, in fine sand at 59 m. that is exposed sporadically to effluent from a major submarine sewage outfall.

Rhepoxynius daboius (Barnard, 1960)
(Fig. 26)

Paraphoxus daboius Barnard, 1960: 210, pls. 10,11.
Rhepoxynius daboius: Barnard & Barnard, 1982a: 30.

Material examined.
BRITISH COLUMBIA: North Central Coast: Open Bight, in fine muddy sand, at 25 m., ELB Stn. H37, July, 1964: 1 female ov. (3.5 mm) with slide mount, fig'd., CMN Cat. No. NMCC1992-0711.
Vancouver Island: Trevor Channel, dredged in muddy sand at 45-50 m., ELB Stn. B14, May 25, 1977: 47 specimens, including 1 male (3.75 mm), with slide mount, fig'd. CMN Cat. No. NMCC1992-0712.

Taxonomic remarks. This species has been fully figured by Barnard (1960, loc. cit). It is closely similar to *R. fatigans* in the weakly produced epistomal cusp, few "A" setae of the mandibular palp, powerful maxilliped palp, strongly rounded coxa 4, form of peraeopod 7 basis, narrow pleon plate 2, and weakly spinose uropods 1 & 2, among other, mainly apomorphic character states.

R. daboius differs from *R. fatigans* chiefly in its more powerfully subchelate gnathopods, less broadly expanded segments 4 & 5 of peraeopod 5, straighter postero-distal margin of the basis of peraeopod 7, and the fewer slender apical spines of the telson lobes.

Distribution and Ecology. A typically deep-water species in fine mud and sandy mud, 77-813 m., shallower in the north, from north central British Columbia south through Oregon to southern California. The present record extends the range north from Oregon.

Rhepoxynius fatigans (Barnard, 1960)
(Fig. 27)

Paraphoxus fatigans Barnard, 1960: 209, pl. 9.—Barnard, 1966: 28, 29, figs. 6, 7.
Rhepoxynius fatigans Barnard & Barnard, 1982a: 28.

Material examined.
BRITISH COLUMBIA: North central coast: Goose Island Anchorage, ELB Stn. H49, August 5,1964: 3 females, 1 penult. male.
Vancouver Island, Barkley Sound region: Trevor Channel, off Brady's Beach, fine sand at 20 m., ELB Stn. B10c, June 28, 1976: 5 females, 1 penult male, 3 immatures. Pachena Bay, gray whale feeding pits, 20 m., P. Slattery coll., April 17, 1983 - 37 females & immatures, with slide mounts of 1 female ov. (3.0 mm), 1 male (2.5 mm), fig'd. CMN Cat. No. NMCC1992-0713. Coastal Shelf, off Vancouver I., Institute of Ocean Sciences, ID3-DM, 1979-81: 3 females.
WASHINGTON: Juan de Fuca Strait: Neah Bay, low intertidal silty sand, ELB Sta. W39, July, 1966: 1 immature. Off San Juan I., C. P. Staude Stn. KGB-10, May, 1978, Lot 1:14 females, 6 penult. males with slide mounts of 1 female ov (3.25 mm), fig'd., and 1 female ov. (3.5 mm) mouth parts fig.'d, CMN Cat. No. NMCC1992-0714; Ibid, Lot 2: 4 females, 9 penult males; Ibid, Lot 3: 12 females.

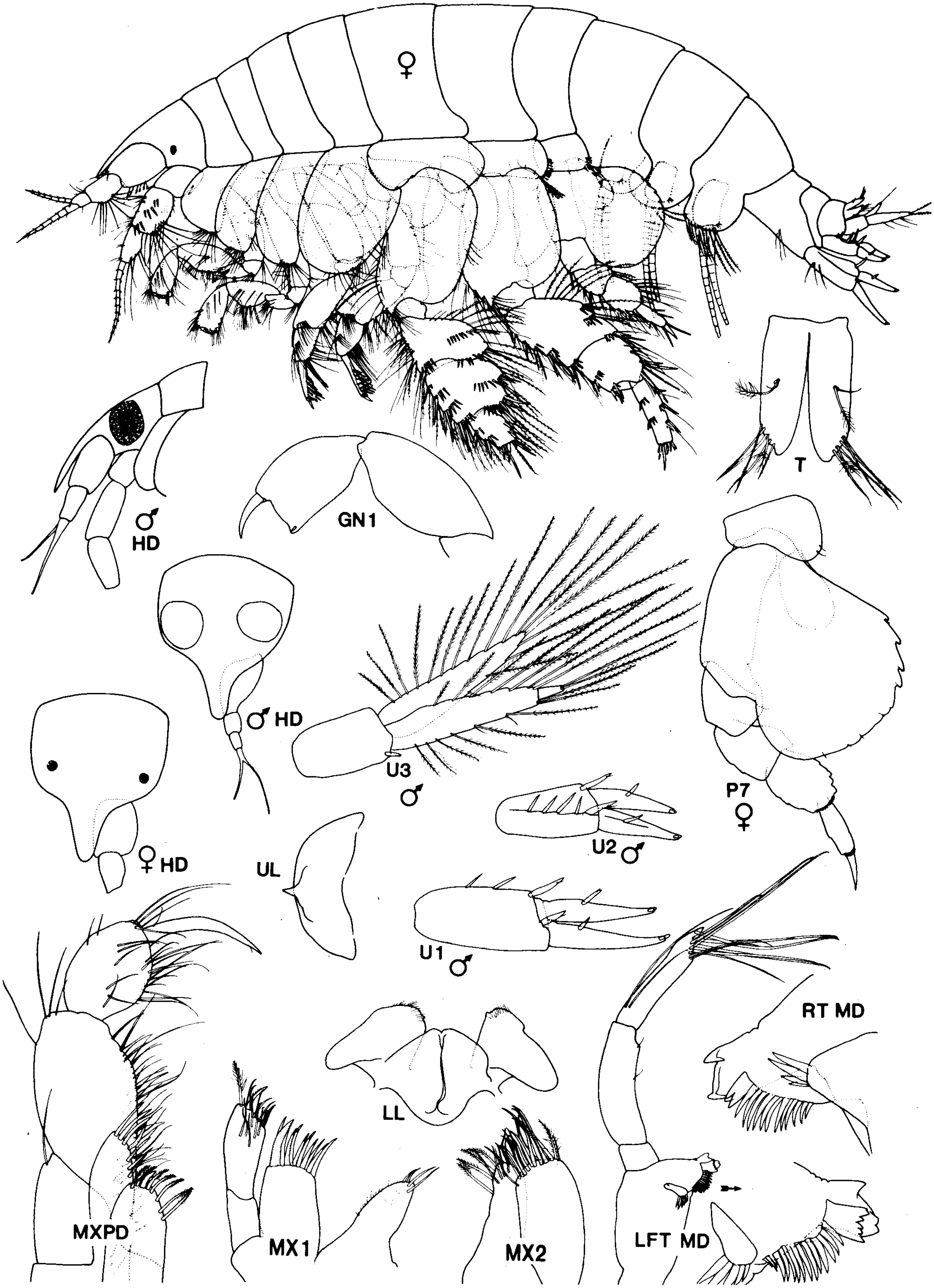
Diagnosis. (Female, 3.25 mm): Pigmented eyes very small, round. Rostrum medium, narrow, subacute apex reaching peduncular segment 2, antenna 1. Antenna 1, peduncular segment 1 large, stout; flagellum and accessory flagellum each 6-segmented. Antenna 2, segment 4 with 3 clusters of facial spines; segment 5 lacking facial spines; flagellum 9-10 segmented.

Epistome slightly produced, process length about equal to width Mandible: molar small, with 4-5 marginal blades; spine row medium with about 12 rakers; left lacinia irregularly 5-dentate, right lacinia subequally bifid; incisor narrow, tricuspate; palp segment 2 bowed; segment 3 with cluster of 2 long "A" setae. Maxilla 1, palp segment 2 broadening to truncate apex, not exceeding outer plate spines. Maxilla 2, inner plate small. Maxilliped, inner plate relatively large; outer plate slender, with 8 slender masticatory spines; palp segment 2 broad; dactyl slender, strongly curved or falcate.

Coxae 1-3 medium, increasing in length posteriorly, lower margins rounded. Coxa 4, lower margin rounded, continuous with anterior and posterior margins, hind process quadrangulate. Gnathopods slender; propods little expanded distally, palms vertical.

Peraeopods 3 & 4 strong, segment 5 short, postero-distal spines not reaching end of segment 6; segment 6, posteriorly spinose along more than half of margins; dactyls medium. Peraeopod 5, basis large, broad, hind margin straight; segment 4 strongly broadened; segment 5 deeper; segment 6 short, 'thick'; dactyl short. Peraeopod 6, segment 4 broad, about 35% deeper than wide; segment 5 almost as broad, margins slightly convex; segment 6 linear, hind margin with 3 groups of spines and slender seta; dactyl slender. Peraeopod

FIG. 27. ***Rhepoxynius fatigans*** (Barnard).
FEMALE ov. (3.5 mm); MALE (2.5 mm).
(SEE PAGE 123 - OPPOSITE)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MX2
LFT MD

7, basis sub-rotund, hind margin with 4-5 small teeth, distal margin nearly straight; segment 5 'swollen', strongly setose behind; segment 6 not longer than 5, hind margin with 2 spines; dactyl medium.

Pleon plate 2 strongly rounded below, little or not overlapping pleon 3, the latter with rounded hind corner, strongly setose ventrally. Uropod 1, peduncle with 1 stout inner distal marginal spine, displaced spine lacking; rami each with one posterior marginal spine. Uropod 2, peduncle, outer margin with 4-5 stout spines; rami each with single posterior marginal spine. Uropod 3, inner ramus short, conical, with single apical seta; outer ramus, outer margin with a few distal setae; terminal segment with 2 apical plumose setae.

Telson lobes each with 4-6 long slender apical spines and single setule. Coxal gills medium broad, curve-tipped, on peraeopods 2-6, short and pear-shaped on peraeopod 7.

Mature Male (2.5 mm): Pigmented eyes ovate, separated mid-dorsally by less than their diameter. Antenna 1, flagellum calceolate on proximal 6 flagellar segments. Antenna 2, segment 5 with single facial spine and 2 anterodistal calceoli; flagellum elongate (40 + segments), calceolate on alternate segments.

Peraeopod 7, copulatory spines not observed. Uropod 3, rami plumose setose on all margins, terminal segment distinct.

Taxonomic commentary. The present material differs very little from that described originally as R. *fatigans* by Barnard (1960, plate 11) from off Santa Catalina Island, Southern California, except that the mandibular palp has two (rather than one) "A" setae, and apical slender telson spines are more numerous.

Distribution and Ecology. From the north-central coast of British Columbia, south through Washington and Oregon to Baja California, on fine sandy mud, in sub-tidal depths, generally 20-100 m, to more than 330 m.

TAXONOMIC ANALYSIS*

The foregoing description of the rich regional metharpiniin fauna of 30 species in 7 genera raises the problem of the natural relationships and phyletic classification of the component taxonomic units. For this purpose, the characters and character states of the genera, and species within genera, have been analyzed 'semi-phyletically', using a modification of the phenetic UPGMA (cluster analysis) system of Sneath and Sokal (1973). The modification, introduced by Bousfield (1981) and adapted by Dickinson (1982), Conlan (1983), and Staude (1986) involves the phyletic ordering of character states, and calculation there from of a 'Plesio-Apomorphic (P-A.) Index' for each species. This modification permits an assessment of (1) the degree of phyletic or natural significance of morphological similarities, and (2) the relative degree of primitive or advanced condition of the sub-clusters or sub-groupings. A carefully selected matrix of 14-18 characters and corresponding 28-36 character states are considered for the analysis of (a) generic relationships (Table IX), and species relationships within (a) *Grandifoxus* (Table X), *Foxiphalus* (Table XI) and *Rhepoxynius* (Table XII). The number of characters therefore ranges between equal to, or twice, the number of corresponding taxa, and is considered adequate for modified phenetic (semi-phyletic) analysis, within the amphipod literature (above). Character states reflect the most discontinuous conditions of each character. Here the plesiomorphic condition is coded as '0' and the apomorphic or derived condition as '2'. Overlap or intergradation of some states is inevitable; such intermediate cases are coded as '1' (Tables IX-XII). Members of the Birubiinae and of the Pontharpiniinae were selected for outgroup comparison (see Bousfield, 1981). In general, character states of species of these two subfamilies are more plesiomorphic, but in some instances more apomorphic, than in species of Metharpiniinae.

With respect to preparation of corresponding phenograms, the characters and character states are provided in Tables V - VIII in the Appendix (pp. 133-136). The phenograms are included as follows: Genera of Metharpiniinae (Fig. 28); *Grandifoxus* species (Fig. 29); *Foxiphalus* species (Fig. 30); and *Rhepoxynius* (Fig. 31). Group average methods were used in the construction of phenograms.

With respect to relationships between genera, the phenogram (Fig. 28) reveals three main subclusters, viz. a *Grandifoxus* sub-grouping (encompassing also *Beringiaphoxus and Majoxiphalus*), a *Metharpinia* subgrouping (including *Microphoxus*) and a *Rhepoxynius* sub-grouping (including *Foxiphalus*). Three observations from this phenogram are especially notable: the subgroups are not closely related, with clustering splits at between 50 and 60%; the genera within subgroups are also not closely related, with 'splits' at the 65 - 75% levels; the *Grandifoxus* subgroup is the most primitive (P-A. Index of about 11), the *Metharpinia* group intermediate (P-A. Index of 18) and the *Rhepoxynius* group the most advanced (P-A. Index of 25).

In pragmatic terms, the *Grandifoxus* group is characterized by several basic plesiomorphies that are reversed or apomorphic in the *Rhepoxynius* group. These plesiomorphies include: large numbers of calceoli (7-8) on peduncle 5 of antenna 2 (male); maxilliped inner plate with 2 apical spines; mandibular spine row very strong; and uropod 2, peduncle and rami strongly spinose. Character states of the rostrum (incised or fully hooded) and uropod 1 (displaced spine, presence or absence) had been considered of major taxonomic significance previously (e. g. in Barnard & Barnard, 1982a, b; Coyle, 1982). These are here observed to vary within closely related groups, or exhibit the converse condition of otherwise primitive or advanced groups, and are thus

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*** Tables V- XIII are given in the APPENDIX (p. 132)**

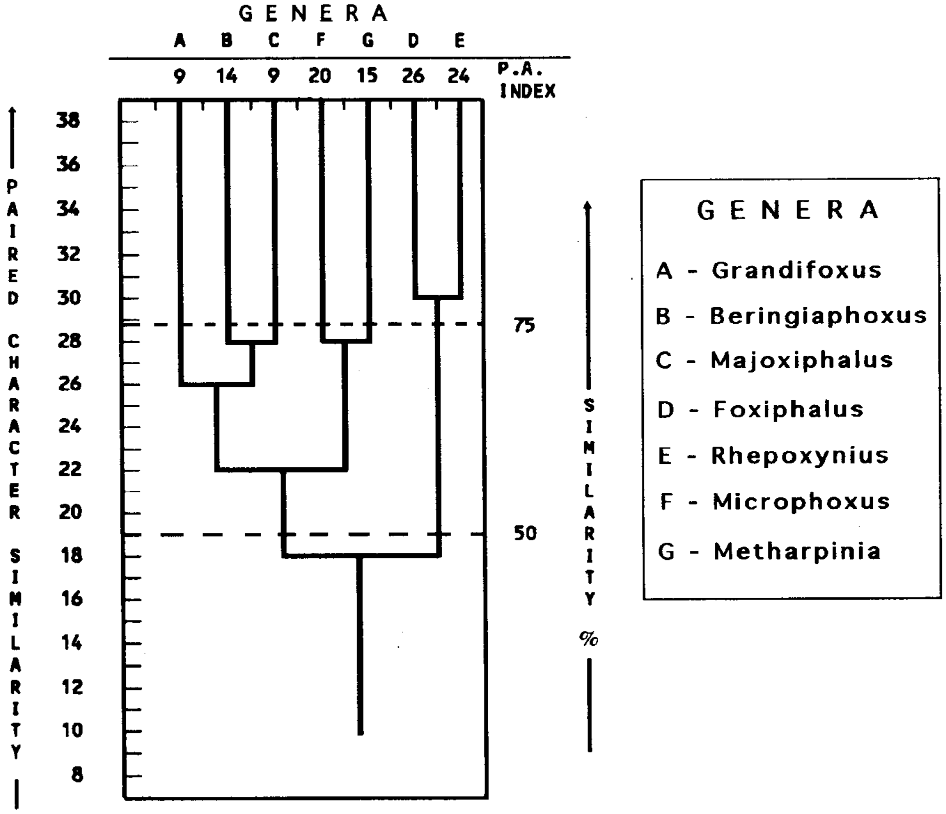

FIG. 28. Phenogram: Genera of Metharpiniinae

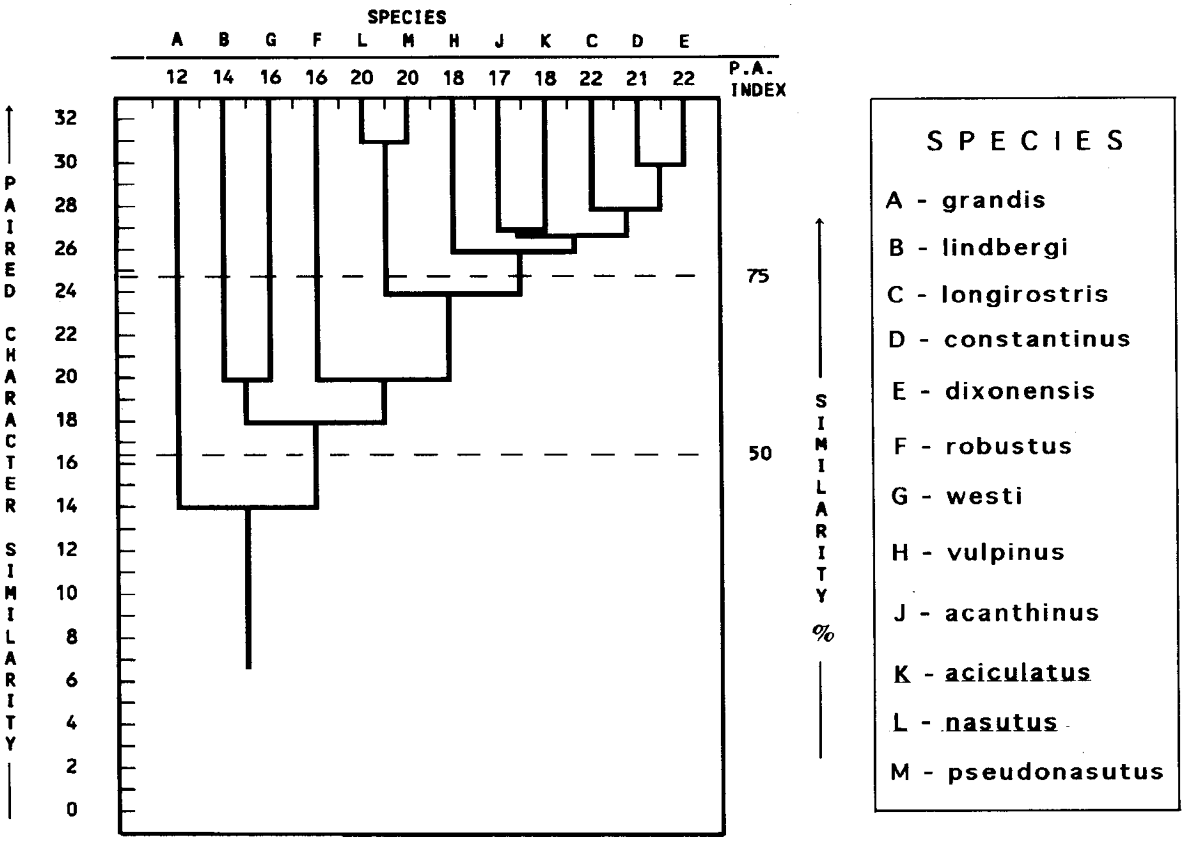

FIG. 29. Phenogram: Species of *Grandifoxus*

concluded to be now of much lesser generic (or higher) phyletic value.

With respect to species within the genus *Grandifoxus*, Fig. 29 reveals five main subclusters: *grandi* (unique); *lindbergi* (including the western Pacific species, *robustus and westi*); *vulpinus* (including *aciculatus and acanthinus*); *nasutus (*including *pseudonasutus*); and *longirostris* (including *constantinus and dixonensis*).

The following observations appear noteworthy:
(l) *G. grandis* is the most primitive species (P-A. index of 12) and phyletically remote from the others (group 'splits' at less than 50% similarity);
(2) the *lindbergi* group (including the western Pacific species) is also primitive (P-A. index of about 15) and least remote from G. *grandis* ('splits' at about 65% similarity);
(3) the *vulpinus* and *longirostris* groups are relatively advanced (P-A. Indices of 17-22) and closely related ('splits' above 80% similarity); and
(4) the *nasutus* group is also relatively advanced (P-A. Index of 20) but is isolated from the others at about 75% similarity.

The *grandis-lindbergi* subgroups share plesiomorphies such as the strongly calceolate and elongate peduncle 5 of antenna 2 in the male, and elongate rami of uropod 3 of the female, character states that are largely reversed in the advanced groups. The degree of morphological isolation of these subgroups, esp. that of *G. grandis* might allow for further generic (and certainly subgeneric) formal categorizations. Coyle (1982) also noted a similarly wide range of character stales within his distinctive Alaskan species, along with the difficulty of applying Barnard's (loc. cit.) generic criteria to its separation from *Rhepoxynius* and some of the Australian forms, but made no attempt at further generic revision. Such should reasonably await the collection of more extensive material, especially of the single-record species, and from poorly sampled areas of overlap or intergradation.

Within the larger *Rhepoxynius* group, four major subclusters can be readily identified: an *abronius* group (including *menziesi* and *lucubrans); a tridentatus* group (including *pallidus* and *stenodes); a gemmatus* group (including *homocuspidatus* and *heterocuspidatus)* and a *fatigans* subgroup (including *daboius, bicuspidatus,* v*ariatus, boreovariatus, barnardi,* and *vigitegus*). The following observations seem significant phyletically:

(l) the *abronius* subgroup is primitive (P-A. Index of 11) and isolated from the others (similarity only about 50%) whereas the others are within 65-75% similarity of each other);
(2) the *gemmatus* and *tricuspidatus* groups (occurring mainly south of the present study region) are phyletically intermediate (P-A. Indices about 20); the *fatigans* group comprises a number of mainly advanced (P-A. Indices of 20-26), but not clearly differentiated internal sub-groupings.

These sub-clustering 'break-outs' are not unlike those of the genus *Grandifoxus*, having one primitive unit isolated morphologically from the other, much more advanced, subgroupings, which, in turn, are not very closely related to each other. Plesiomorphic features shared by the primitive group include: facially spinose peduncular segment 5 of antenna 2; multi-cuspate hind margin of the basis of peraeopod 7; quadrate or acuminate hind corner of pleon plate 3; subaequiramus uropod 3 in the female; and apically short-spinose telson lobes. Here again, the presence or absence of an uropod 1 displaced spine within related species of *Rhepoxynius* appears convergent and, although its presence tends to be plesiomorphic, is of limited classificatory significance. The present species clusterings within genus *Rhepoxynius* are similar to those of Barnard and Barnard (1982b: 4), based on many of the same characters and character states. Those authors were likewise struck by the remarkable morphological diversity within the genus, and suggested that the especially distinctive species, *R. vigitegus*, might be a candidate for separate generic recognition of its own. Again, such revisionary work on a formal basis is perhaps best postponed until further material comes to hand, especially of northern, deeper-water, and single-record species.

With respect to the less speciose genus *Foxiphalus*, again four distinct sub-clusters (Fig. 30) seem clearly recognizable: the unique *aleuti* ; an *obtusidens* group (including *falciformis* and *golfensis*); *xiximeus* group (including *fucaximeus*, and less closely, *cognatus*); and a *similis* group (including *slatteryi*). Here again, we may note that:
(l) the species groups, including even the most advanced *similis* and *xiximeus* subgroups (P-A. indices of 23-25) are not closely similar to each other (less than 75% similarity); and (2) the most primitive species groups, *aleuti and obtusidens*, (PA. Indices of 16-20) are isolated from the others at little better than 50 % similarity.

Again, as noted in the *obtusidens* subgroup, the displaced spine of uropod 2 is variably present, and thus not of major taxonomic significance. The primitive subgroups share rather fewer plesiomorphies (than is the case in counterpart members of *Grandifoxus and Rhepoxynius*); one notable example is the condition of the mandibular right lacinia that is bifid in primitive, and spike-like or lacking in advanced, species. Such wide phyletic separation between the genera, and species groups within genera, indicates strongly that subfamily Metharpiniinae is both ancient and long-established on the North American Pacific coast. From indirect considerations of world distribution and comparative morphology, Bousfield (1982b) has estimated the minimum geological age of the primitive superfamily Phoxocephaloidea as Jurassic (c. 150 m.y.b.p.). In view of the relatively close morphological relationships (e.g. in antennal calceoli) of the Phoxocephaloidea to the primitive superfamily Crangonyctoidea (a continental fresh-water group that may extend back to the Triassic, or even Permian), the origin of the marine phoxo's may be older than Jurassic. The finding of such widely disjunct morphologies within one of the more primitive superfamily sub-groupings on this geologically long-undisturbed, open-oceanic Pacific North American coast is not unexpected, and tends to support the

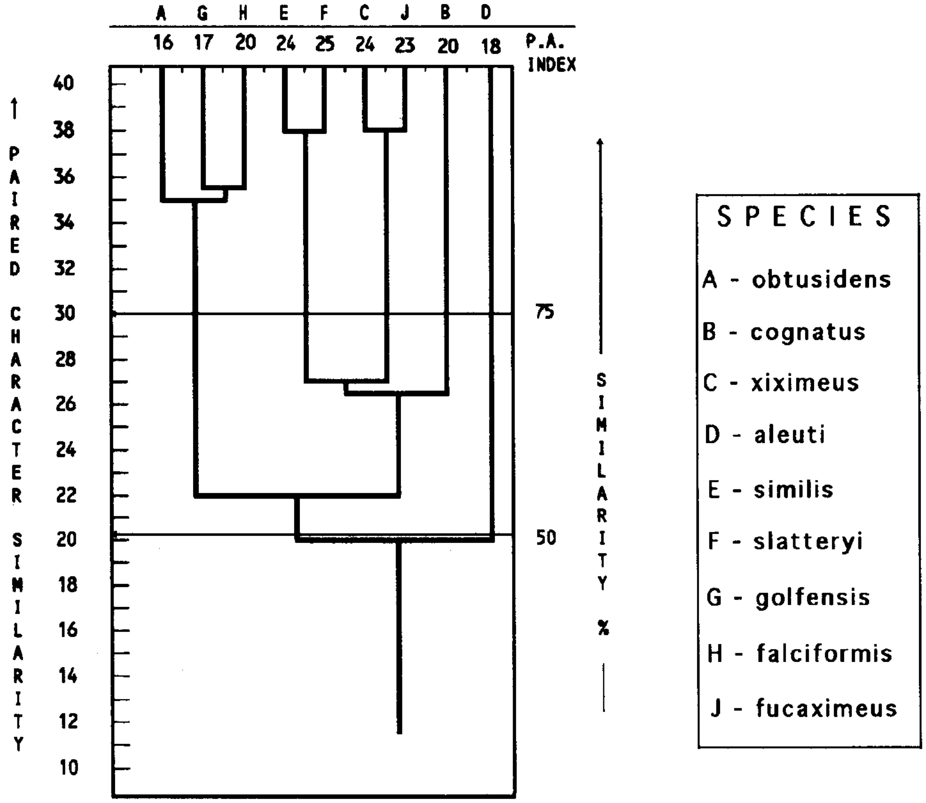

FIG. 30. **Phenogram: Species of *Foxiphalus***

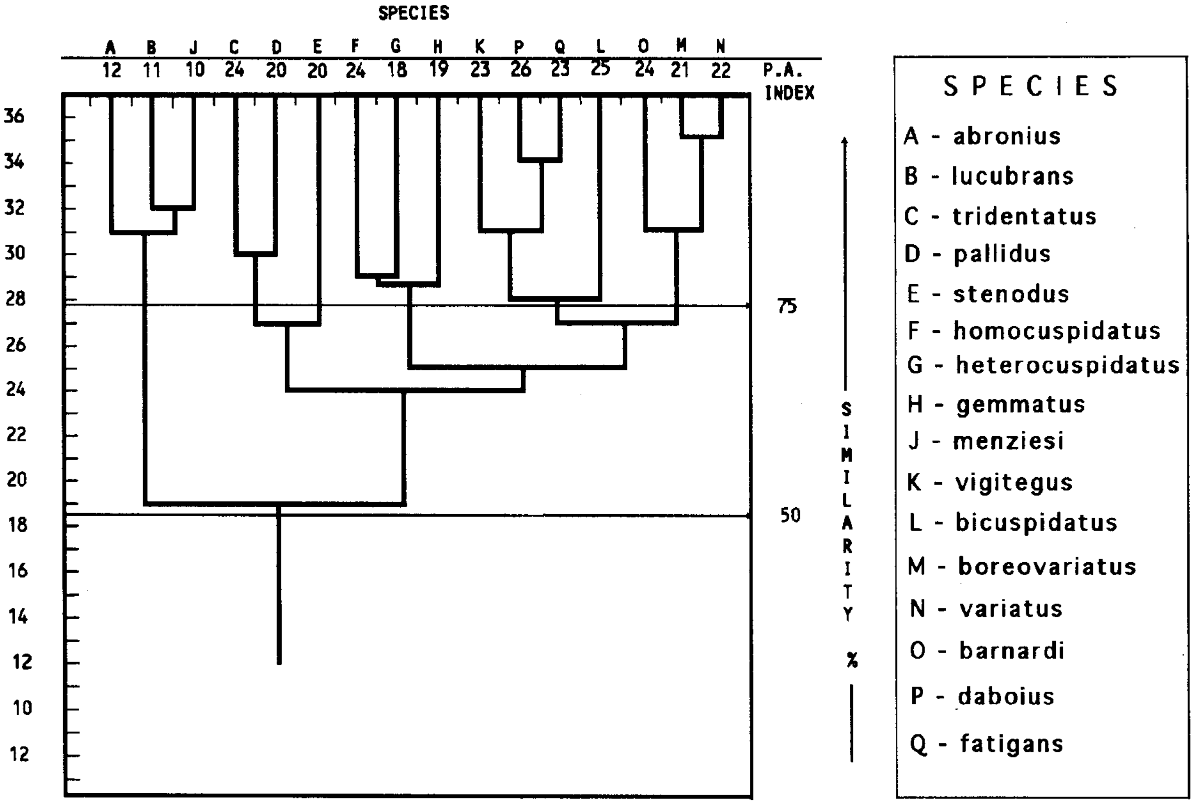

FIG. 31. **Phenogram: Species of *Rhepoxynius***

primitive nature of this subfamily within the family and superfamily.

We may also note that within each generic group, member species that are relatively large and powerfully fossorial dwell in sands and coarser sediments of high energy inshore environments and tend to be the most primitive morphologically (e.g. *grandis* in the genus *Grandifoxus*; *obtusidens* in the genus *Foxiphalus*, and *abronius* within the genus *Rhepoxynius*). Conversely, members that are small, and relatively weakly fossorial (weakly expanded and weakly armed segments of antennae, peraeopods and uropods) and dwell in deeper, off-shore, fine silty sands and mud, tend to be the most advanced morphologically (e.g. *similis* within *Foxiphalus; daboius* within *Rhepoxynius*). We may fairly conclude, therefore, that the evolutionary 'thrust' within genera and species of Metharpiniinae is from large, strongly fossorial, and reproductively primitive species of inshore habitats, to smaller, less fossorial and phyletically more advanced forms that occupy deeper, offshore habitats.

DISTRIBUTIONAL-ECOLOGICAL ANALYSIS

The subfamily Metharpiniinae is largely endemic to the Pacific coast of North America, a region in which about 80% of described species have been recorded to date (Table IV). Certain features of distribution are especially noteworthy. Whereas the *Grandifoxus* group especially is diverse in the Bering Sea region, none is yet known from the Arctic or from the icy waters of the Kamtchatka region of the western Pacific. In general, however, if the essentially tropical and antipodean genera *Metharpinia* and *Microphoxus* are excluded from consideration, members of the most primitive genera are dominant at the most northerly localities, whereas those of the most advanced genera are most diverse in southern regions. Thus, members of the primitive genera *Grandifoxus* and *Beringiaphoxus* occur only from the Bering Sea southward to Central California, and also disjunctly westward in the Sea of Japan. In the advanced genus *Rhepoxynius*, by contrast, the centre of distribution is in central and southern California. Only about half the known Pacific species range northward into Canadian coastal waters, and none has yet been recorded from SE Alaska or northward. The phyletically intermediate genus, *Foxiphalus*, is also distributionally intermediate, with a centre of distribution in northern California and Oregon, and its member species range northwards in progressively diminishing numbers through coastal waters of Canada and SE Alaska to the Bering Sea. The phyletically primitive genus, *Majoxiphalus*, with two known species centred in coastal waters of British Columbia, ranges both northwards to the Bering Sea and southwards to California, thus also basically fitting the above phyleticdistributional phenomenon.

However, when individual species distributions are examined, exceptions to the above general trend may be noted. Thus, within the genus *Grandifoxus* (sens. lat.), the most primitive species, *G. grandis*, is much the most southerly. It ranges considerably south of the relatively advanced *G. longicomis* group, yet has not been recorded from either SE Alaska or the Bering Sea regions, either by Coyle (1982) or in the present extensive material. On the 'flip' side of this analysis, within the southern genus *Rhepoxynius*, one of the most primitive species, *R. abronius*, ranges as far north as even the most advanced species, *R. fatigans* and *R. daboius*. Similarly, within the southerly genus *Foxiphalus*, the most primitive species *F. aleuti* regionally co-occurs in the Bering Sea region with the advanced *R. similis* complex.

A reasonable explanation of this apparent exception may lie partly in the differing life styles and ecological requirements and partly in presumed differences in evolutionary history of the species concerned. Thus, *Grandifoxus grandis is* a relatively large, powerfully fossorial species that inhabits inshore sands and relatively coarse-grained sediments of relatively high-energy habitats. It is also apparently more broadly ecophenotypic, and tolerates a relatively wide range of temperatures (4 - 20C+), and salinities (>15 p.p.t.). Such habitats in Alaska and the Bering Sea region are only now developing during post-Pleistocene deglaciation and marine warming of coastal SE Alaska, that has presumably hitherto formed a biogeograpnic barrier to slowly dispersing inshore fossorial species (see Bousfield, 1970). Similarly, barriers to northward dispersal of more deeply subtidal rhepoxiniids may be represented by the cold coastal waters of SE Alaskan whose inlets and fiords (except for southeastern portions of Prince William Sound) are year-round icy cold, and are dominated mainly by fossorial lysianassids, oedicerotids, pontoporeiids, and other competing groups of phoxocephalids (e. g. harpiniids) having fully arctic thermal requirements (Jarrett & Bousfield, in prep.).

LEGEND FOR TABLE III (PAGE 129 - opposite)

I. Occurrence
X - abundant in region (or presumed so)
x - marginally in region.
xS - essentally south of this region (tropical)
II. Coastal Regions (Progression: North-west to
South- east)
1. Japan Sea and Western Pacific
2. Bering Sea and Aleutian Chain to Kodiak I.
3. Prince William Sound & South-eastern Alaska
(N. of Dixon Entrance.)
4. North central B. C. coast and Queen Charlotte
Ids. 5. Southern B.C. coast and Vancouver Island.
6. Washington and Oregon
7. Northern and Central California
8. Southern and Baja California

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

TABLE IV. Distribution of North American Pacific Species of Metharpiniinae

	NORTH PACIFIC SUBREGION							
	1	2	3	4	5	6	7	8
I. GRANDIFOXUS								
robustus	X							
westi	**X**							
constantinus		X						
pseudonasutus		X						
nasutus		X						
vulpinus		X	x					
aciculatus		X	x	?				
acanthinus		X	X					
lindbergi	X	X	X	**X**	**X**			
longirostris		X	X	X	X			
dixonensis				X				
grandis			X	X	X	X		
II. BERINGIAPHOXUS								
beringianus		**X**						
III. MAJOXIPHALUS								
maximus		X	X	X	x			
major			x	X	X	X	x	
IV. FOXIPHALUS								
aleuti		X						?
slatteryi		X						
similis			x	X	X	X	X	
xiximeus			**X**	X	X	X	X	X
fucaximeus						**X**		
falciformis				X	X	X		
obtusidens						x	**X**	**X**
cognatus							x	X
golfensis								X
apache								X
secasius								xS
V. RHEPOXYNIUS								
pallidus				X	X	x		
vigitegus				X	X	X		
boreovariatus				**X**	X	X		
fatigans				X	X	X	X	x
daboius				x	?	X	X	X
variatus				X	?	?	x	X
abronius				X	X	X	X	X
barnardi					**X**	**?**		
tridentatus					X	?		
bicuspidatus						x	X	x
lucubrans							x	X
stenodes							?	X
homocuspidatus								X
heterocuspidatus								X
menziesi								xS
gemmatus								xS
VI. METHARPINIA								
jonesi								X
VII. MICROPHOXUS								xS

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. Especially helpful in the provision of study material and systematics ecological commentary have been Drs. Craig P. Staude, Friday Harbor, and Peter N. Slattery, Moss Landing, USA. 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. For advisory and curatorial assistance in preparation of this report, we are especially grateful to museum colleagues Kathleen E. Conlan, Ed Hendrycks, and Judith A. Price. Preparation of the line illustrations was most capably assisted by Susan Laurie-Bourque, Hull, Quebec. 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.

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APPENDIX

PAGE NO.

TABLE V. Species of Metharpiniinae: Characters, Character States, and Plesio-Apomorphic (P.-A.) Codings

	CHARACTER STATES	
CHARACTERS	**Plesiomorphic** 0	**Apomorphic** 2
1. Rostrum shape	laterally incised	fully hooded
2. Antenna 1, peduncle 2, length	elongate (> segment 1)	short (< segment 1)
3. Ant. 2, (male), no. peduncle 5 calceoli	4 - 8	1 - 2
4. Ant. 2, segment 5, no. facial spine gps	1 - 2	0
5. Mandible, right lacinia cusps	2 - 3	1
6. Mandible, blade row	long	short
7. Urosome 1, v. setae	present	lacking
8. Mxpd. inner plate no. apical spines	2	1
9. Mxpd. dactyl, form	straight	curved
10. Gnathopods 1 & 2	slender, elongate	stout, deep
11. Coxal plate 4; relative size	small	large
12. Peraeopods 3 & 4	large	small
13. Peraeopod 5, segments 4 & 5, width	narrow (W < D)	broad (W > D)
14. Peraeopod 6, segments 4 & 5, width	narrow (W < D)	broad (W > D)
15. Peraeopod 7, seg. 5	narrow	broad
16. Uropod 1, size of displace spine	large, stout	small, lacking
17. Uropod 2, ram. spines	strong	weak or lacking
18. Urop. 3 (female)	aequiramus	parviramus
19. Telson lobes, dorso-lateral spines	present (1 - 3+)	lacking

TABLE VI. Species of *Grandifoxus*: Characters, Character States, and Plesio-Apomorphic (P.-A.) Codings

	CHARACTER STATES	
CHARACTERS	**Plesiomorphic** (=0)	**Apomorphic** (=2)
1. Peraeopod 7, basis poster, serrations	strong	weak
2. Rostrum, breadth	narrow	broad
3. Peraeopod 5, segment 6, post. mar. spines	present (1 - 3 gps)	lacking
4. Mandible, right lacinia	multi-cusped	bifid
5. Coxa 4, hind margin	straight	convex
6. Gnathopods 1 & 2 propod form	slender (L > 2X D)	deep (L < 2X D)
7. Peraeopods 3 & 4 seg. 5 dist. spines	short	long
8. Peraeopod 5, basis no. apical spines	wide	narrow
9. Peraeopod 5, segment 4	narrow (L > W)	broad (W > L)
10. Peraeopod 6, seg. 4, shape	smoothly sloped	sub-rectangular
11. Peraeopod 7 hind cusps	weak (5)	strong (8)
12. Uropod 1, displaced spine	lacking	present
13. Uropod 2, outer ramus spines	many (6+)	few (1 - 3)
14. Uropod 3 (female) ramal form	aequiramal	inaequiramal
15. Telson lobes, gps. dorso-lat. spines	1 - 2	0
16. Antenna 2, ped. 4 no. spine groups	1	2 - 3

TABLE VII. Species of *Foxiphalus:* Characters, Character States, and Plesio-Apomorphic (P.-A.) Codings

	CHARACTER STATES	
CHARACTERS	**Plesiomorphic** (=0)	**Apomorphic** (=2)
1. Epistomal cusp	lacking	strong
2. Eye size (female)	large	small
3. Antenna 2, ped. 4, no. facial spines	many (10)	few (3 - 8)
4. Coxa 4, hind margin	straight	convex
5. Mandible, right lacinia	bifid	monocuspate
6. Mandible, left lacinia	4-dentate	few-dent
7. Mxpd. i.p. spines	2	1
8. MX1, palp, apci. sps.	2	0 - 1
9. Gnathopods 1 & 2, form of propod	expanding distally	margins sub-parallel
10. Gnathopods 1 & 2, form of carpus	elongate lobe wide	short, lobe narrow
11. Peraeopod 5, segments 4 & 5, width	narrow (L > W)	broad (W > L)
12. Peraeopod 6, segment 4, width	narrow (L > W)	broad (W > L)
13. Uropod 2, number of ramal spines	numerous (3 - 5)	few (0 - 2)
14. Pleon 3, marg. setose	few	many
15. Uropod 1, extent of ramal spines	proximal & distal	proximal only
16. Uropod 1, displ. sp.	absent	present
17. Uropod 3, term seg.	large	small
18. U3 (fem.) ram. marg.	setose	spinose
19. Telson, apic. spines	2 - 3	1
20. Telson, d.-l. spines	present	0 (or setae)

TABLE VIII. Species of *Rhepoxynius*: Characters, character states, and plesio-apomorphic (P.-A.) codings

	CHARACTER STATES	
CHARACTERS	**Plesiomorphic** (=0)	**Apomorphic** (=2)
1. UL, epistome	rounded	produced
2. Rostrum, excavate	deeply	shallowly
3. Antenna 2, ped. 4, no. spine groups	1 - 2	0
4. Mandible, no. of molar spines	many (5+)	few (< 5)
5. Mxpd. no. outer plate spines	many (10+)	few (< 10)
6. Maxilla 1, palp length	long	short
7. Gnathopod 2, shape of propod	linear (shallow)	expanded (deep)
8. Peraeopods 3 & 4, seg. 6. no. distal spines	many (10+)	few (< 10)
9. Peraeopod 5, width of segment 4	narrow (W < L)	broad (W > L)
10. Peraeopod 5, width of segment 5	narrow (W < L)	broad (W > L)
11. Peraeopod 6, seg. 4	narrow	broad
12. Peraeopod 7, basis no. hind serrations	many (6+)	few (2 - 3)
13. Pleon side plate 3	square	rounded
14. Urop. 1, ram. spines	many (5+)	few (0 - 1)
15. Uropod 1, size of displaced spine	large	lacking
16. Uropods 1 & 2, rhombic spines	lacking	present
17. Uropod 2, ped. spines	many	few
18. Urop. 3 (fem), rami	aequiramal	inaequiramal
19. Telson lobes, apices	spinose	setose

TABLE IX. Genera of Metharpiniinae: Character States and Plesio-Apomorphic (P.-A.) Codings

TABLE IX. Genera of Metharpiniinae: Character States and Plesio-Apomorphic (P.-A.) Codings

GENUS		CHARACTER STATES																			
SYM	NAME	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	P.-A. INDEX
A	GRANDIFOXUS	0	1	0	0	0	0	1	0	1	1-	1+	0	0	1	1	1+	0	1	0+	9
B	BERINGIAPHOX	2	2	0+	0	0	0+	1-	0	1	1-	1	0	2	1	2	0	0	1+	0	14
C	MAJOXIPHALUS	2	0	0	0	0	0+	0	0	0+	1	2	0	2	0	2	0	0	0	2	11
D	FOXIPHALUS	2	2	2	1	1	1+	2	2	1	2	2	1	0+	0+	0+	1+	2	2	2	29
E	RHEPOXYNIUS	0	2	2	1+	1	1-	2-	2	2-	0+	1	1	1+	0+	1	1+	2-	2	2	24
F	MICROPHOXUS	0	0	1?	0+	2	2	1-	2	0	1-	1	1	2	2	0	2	2	1+	0	20
G	METHARPINIA	0	0	1?	0+	1+	2-	0	1	1	2	1	1	2	1	0	0	0	1+	0	14

TABLE X. Species of *Grandifoxus*: Character States and Plesio- Apomorphic (P.-A.) Codings

SPECIES		CHARACTER STATES																P.-A. INDEX
SYM	NAME	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
A	grandis	0	0	0	0	0	0	2	2	2	2	2	0	2	0	0	0	12
B	lindbergi	1	2	2	1+	0	1	0	1	2	1+	0	0	1	2	0	0+	14+
C	longirostris	2	2	2	2	1	1	1?	1-	1	0	1-	2	2	1+	1	2-	12+
D	constantinus	2	2	2	1	1	1	1	1-	1	0	1	1	2-	2	1	2	21
E	dixonensis	2	2	2	2	1+	1	1+	1-	1	0	1	1	2-	2?	1	2	22
F	robustus	0+	2	2	?	?	1+	2-	1-	1	1+	1+	?	?	1+	1	0+	16?
G	westi	2	2	2	?	?	?	1	1	0	1+	0	0?	?	2-	1?	0+	16?
H	vulpinus	2-	1	1	1	1	2	1-	0	1	0	0+	1	2	2	1	2-	18
J	acanthinus	2-	1	2	1+	0+	1	1	0+	1	0	1	1+	1	2	1	2	17
K	aciculatus	2-	2	1	?	0	1	1+	0+	1	0	1	2	1+	2	1	2-	18
L	nasutus	2	2	2	2	1+	1	2-	0	0+	0	1	1	2	0+	2	2	20
M	pseudonasutus	2	2	2	2	2	1	2	0	0+	0	1	1	1	0+	2	2	20

TABLE X. Species of Grandifoxus: Character States and
Plesio- Apomorphic (P.-A.) Codings

TABLE XI. Species of *Foxiphalus*: Character States and Plesio- Apomorphic (P.-A.) Codings

SPECIES		CHARACTER STATES																				P.-A.
SYM	NAME	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	INDEX
A	obtusidens	0	1	1	1+	0	0	2	2	1+	2	0+	1	0	0	0	0+	1	0+	0+	0	16+
B	cognatus	1	1	2	2	2	0	2	1	1	1	1	1	0	0	0	1+	1	1	0+	0	20+
C	xiximeus	0	0	2	0	2	0	2	1	1	1	2	2	2	2	2	2	0	1	2	0	24
D	aleuti	0	0	0	0+	0	0	0	2	1	1	0	1+	2	1	2	2	1+	2	1-	2	18
E	similis	2	1	2	1	2	1	2	0	2	2	0	0	1	1	0	2	1	2	0-	2	24
F	slatteryi	2	1	2	2	2	1	2	0	2	2	0	0	1	1	0	2	0+	2	1-	2	25
G	golfensis	0+	2	2	2	0	0	2	1	2	2	0	1	0?	0	0	2+	1-	0+	0	1	17
H	falciformis	0	2	1+	2	0	0?	2	1	2	2	0	1	2	1	0	0+	1+	2	0	2	20
J	fucaximeus	0	0	2	0+	2	0	2	1	1	1	2	2	2	2	2	2	0	1-	1	0	23

TABLE XI. Species of *Foxiphalus* : Character States and Plesio- Apomorphic (P.-A.) Codings

TABLE XII. Species of *Rhepoxynius*: Character States and Plesio- Apomorphic (P.-A) Codings

SPECIES		CHARACTER STATES																			P.-A. INDEX /38
SYM	NAME	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
A	abronius	2	0	0	1	1-	2-	0+	0+	2	1+	1	0	0	0	2	0	0	0	0	12
B	lucubrans	1	1+	0+	0	1?	0	1-	2	2	1+	1	0	0+	1-	0	0	0+	0	0	11
C	tridentatus	0	2-	1+	2	1-	0	1	1	1	2	2-	1+	2-	1	2	1	1	2	1	24
D	pallidus	0	2-	0+	1+	1	1+	1-	0-	2-	2	2-	1+	1-	0+	2	1	1	2	0+	20
E	stenodes	0	1	1+	2	1?	0+	2-	1-	1+	1	1+	1	0+	1	2	2	1-	1	1+	20
F	homocuspidatus	2	2	1+	2-	2-	1+	0+	0+	1+	1+	2	1-	1	2	2	2	2	0+	1+	24
G	heterocuspidatus	0	2	1	2-	1	0+	0	1-	0+	1	1-	0+	0	2	2	2	2	0	1+	18+
H	gemmatus	2	2	1	1	1+	0+	0	1	1	1	1	0+	1+	2	0	2	1	0	1	18+
J	menziesi	2	0+	0	0	1	0+	1-	0	2	1	1	0	0	1	0	0	1-	0	0+	10
K	vigitegus	2	0+	1+	1+	1	2-	0+	0	2	2	1	0+	2	2	2	0	1+	2	1+	23
L	bicuspidatus	2-	2	2	2-	1+	1	0-	1+	1	1	1	2	2	1	2	0	1	2	1	25
M	boreovariatus	2-	1	1+	2	0	1+	0+	0+	0+	1	0+	1	2	2	2	0	2	2	1+	20+
N	variatus	2	2-	1	2	0	1	0+	0+	0+	0+	0	1	2-	2	2	0	1+	2	2-	22
O	barnardi	1+	1	2	2-	1+	1	1+	0	0	0	1	2	2	2	2	0	2	2	2-	24
P	daboius	1	1	2	2	1	1	1-	0	2-	2-	1+	1+	1+	2	2	0	2	2	2-	26
Q	fatigans	1	0+	2	2	1+	1+	0+	0	2-	2-	1+	1+	2	2	2	0	1	2	2	23

TABLE XII. Species of *Rhepoxynius*: Character States and
Plesio-Apomorphic (P.-A) Codings