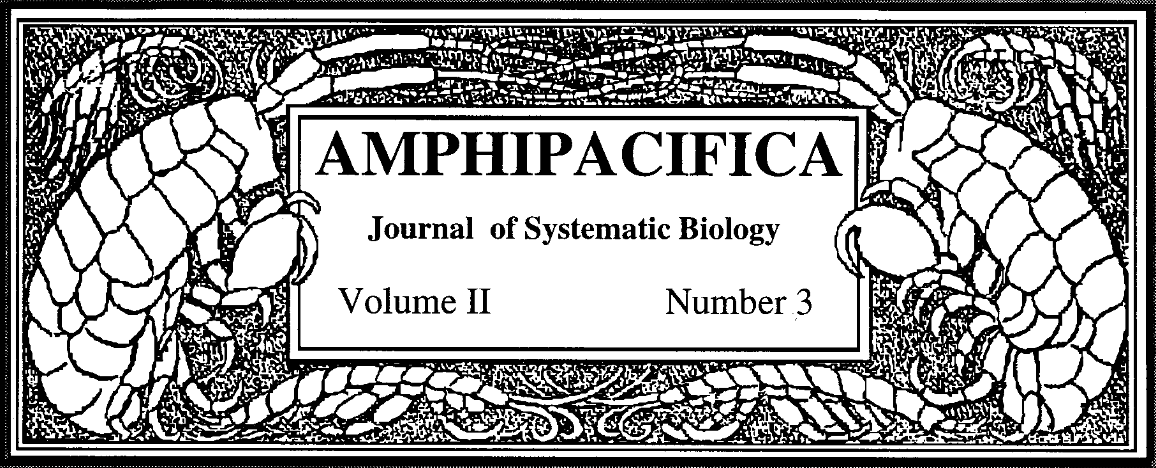
HENDRICKX M.



AMPHIPACIFICA

Journal of Systematic Biology

Volume II Number 3

Contents May 15, 1997.

National library of Canada ISSN No. 1189-9905

MICHEL E. HENDRICKX
LABORATORIO DE INVERTEBRADOS
BENTONICOS
ESTACION MAZATLAN ICML
UNAM
A POSTAL 811 MAZATLAN
82000 SINALOA, MEXICO

AMPHIPACIFICA

JOURNAL OF SYSTEMATIC BIOLOGY

Volume II, Number 3
May 15, 1997.

AMPHIPACIFICA, Journal of Systematic Biology (ISSN No. 1189-9905) contains four numbers per volume, published opportunistically, by Amphipacifica Research Publications, 611-548 Dallas Rd., Victoria, B. C., Canada V8V 1B3. Subscription rates per volume are $40. US or $50. CND

EDITORIAL . . .

The appearance of the third number of Volume II of Amphipacifica follows completion of difficult revisionary studies on calliopiid and corophiin amphipods of the North Pacific region. The studies were complicated by the moving of pertinent collections and curatorial facilities of the Canadian Museum of Nature (CMN) from Ottawa to very recently completed research quarters in Aylmer, Quebec. Regrettably also, this issue marks the termination of the Journal, unless a replacement can be found for the present managing editor, who has undergone prolonged hospitalization during the past year and feels unable to continue the work. He acknowledges with deepest thanks the help of former assistant editors Craig Staude, Phil Lambert, Marianne Wilkinson, Tara Steigenberger, the Advisory Board, and many colleagues and authors who contributed to the success of the Journal to date.

During late spring 1996, Mr. Frank Ling was appointed Chairman of the CMN's Board of Trustees and Director Alan Emery departed. After a lengthy search for his replacement, the position was accepted by Joanne di Cosimo, currently Executive Director of the Manitoba Museum of Man and Nature in Winnipeg, Manitoba. Joanne holds a Master's degree in Public Administration from Harvard University, and has more than 20 years experience with museums. Under her leadership, which takes effect in July 1997, museum priorities might be refocused on the primacy of systematic research, possibly utilizing exciting new cladistic, DNA-DNA hybridization, and serological methodology in developing and confirming natural classifications of the plant and animal resources of Canada. Such a role would dramatically extend the alpha-level systematic and continent-wide exploratory work that formed the basis of the National Museum's distinguished scientific record since 1911, when the Victoria Memorial Museum building opened.

The present issue is commemorative of the lifetime contributions of two outstanding colleagues in crustacean biology. In early January, Leo Margolis died suddenly while leaving his office at the Pacific Biological Station in Nanaimo, British Columbia. Among the tasks left unfinished by Leo's untimely passing was a revison of North Pacific whale parasites (Amphipoda: Cyamidae), his speciality in crustacean systematics.

In mid-February, Jan H. Stock died suddenly of a stroke in Amsterdam, The Netherlands. One of Jan's early scientific contributions (1952) was a description of *Corophium multisetosum,* a tubicolous amphipod species of northwestern European estuaries, that his perceptive eye distinguished from the co-occurring type species, *C. volutator* (Pallas). The corophiin revisionary paper (pp. 67-139) is dedicated in his memory. Tributes to these two outstanding researchers are here provided by colleagues.

Leo Margolis, 1927-1997

The community of systematic biologists lost a very dear friend and colleague with the recent death of Leo Margolis. His lifetime career with the Canadian Fisheries Research Board and Department of Fisheries and Oceans brought international acclaim for his extensive work on the parasites of fishes. Dr. Margolis received numerous honours, including Fellow of the Royal Society of Canada (1975), Officer of the Order of Canada (1990) and the Gold Medal for the Professional Association of Canada (1995). He served as President of the Canadian Society of Zoologists (1976-77), and was one of the founders of the Parasitology Section of the CSZ, and received its prestigious Wardle Award in 1982. He was also a member of the Advisory Board of this journal. Friends will especially miss Leo's delightful sense of humour, his positive outlook, and his never-failing interest in their concerns.

David Welch and Bob Kabata, Nanaimo, B. C.
E. L. Bousfield, Victoria, B. C.

Jan H. Stock, 1931-1997

The recent death of Jan Stock was totally unexpected. His passing is a huge loss, both on a personal level for his many friends and colleagues and for the profession in which he has been a highly regarded scholar and productive researcher for many years. It is difficult to calculate the immense cost of the loss of Jan Stock's vast knowledge of amphipod systematics, biogeography and groundwater ecology. Hopefully, some of the students Jan trained at Amsterdam University will continue his work, but it is doubtful that anyone can immediately fill the large hiatus created by his death. Among those he trained in amphipod systematics were Jos Notenboom, Ronald Vonk, and Dirk Platvoet, who is now the Institute's collections manager. Among collaborators in Copepodology, Shigeko Ooishi feels his loss especially keenly.

It is also extremely sad that Jan Stock is the fourth great crustacean systematist to have died since 1991. His death follows that of Jerry Barnard in 1991, Horton Hobbs, Jr. in 1994, and Tom Bowman in 1995. I seriously doubt that Carcinology will soon recover from these great losses, especially since so few crustacean systematists have been trained to follow in their footsteps.

On a happier note, my acquaintance with Jan Stock goes back to the early 1970s, when we began correspondence over mutual interests in groundwater amphipod systematics. We have shared many good times together -- at meetings, in the field and through numerous exchanges. I first met Jan in person at the international amphipod-groundwater ecology meeting in Schlitz, Germany in 1975. Immediately following that meeting, a group of us, including Jerry and Charline Barnard, Ed and Barbara Bousfield, and Gordan Karaman, visited with Jan and his colleagues at Amsterdam University. After that, we got together twice in 1979, first at the vicariance biogeography symposium at the American Museum of Natural History in May, then for field work in Haiti in November. We enjoyed very productive visits at international amphipod meetings in Ambleteuse, France in June, 1984, at an international symposium on the biology of marine caves in Bermuda in October, 1984, and at the amphipod symposium at the Darling Marine Center, Maine, in September, 1989. We had two more excellent visits in the USA in 1992: at the J. L. Barnard Memorial Symposium at the Smithsonian Institution in April, 1992, and during the meeting of the Crustacean Society in Charleston, South Carolina, later that summer.

I feel very fortunate to have known Jan Stock both as a good friend and a professional colleague. His death is a great personal loss. He was truly a fine gentleman and a great scholar.

John R. Holsinger, Norfolk, Virginia.

Readers continue to submit suggestions for improvement of the journal. Wim Vader and Francis Cook expressed appreciation for the continuity of Amphipacifica at a time when support for systematic biology, particularly in research agencies such as the Smithsonian Institution in Washington, D. C., appears to be declining. With respect to the revisionary studies, Craig Staude feels that subgenera, rather than full genera, might adequately express the necessary level of taxonomic recognition in some instances; however this is an author's "judgement call" that can only be tested by subsequent revisors. Don Cadien, among others, noted editorial and printing oversights, the most serious of which was a printing *lapsus* concerning the name of the type species of *Americhelidium.* Corrections to the papers of Vol II(2) are provided on the final page of this issue.

Readers are reminded that publication of the journal has been changed from a quarterly to an opportunistic basis, depending on the submission date of publishable papers, but the number of issues per volume remains the same (4). The journal now has an e-mail address, as listed in publication information on the inside front and back covers.

With respect to "spin-off" from earlier research papers, the study on Cambrian fossil arthropod classification [Vol. II (1)] has led to further revelations on the Cambrian fossil ancestry of the Chelicerata. The topic was programmed for the 2nd British Columbia Paleontological Symposium, University of British Columbia, Vancouver, May 9-11, 1997.

The Canadian Field-Naturalist

A continuation of 118 years of publication on northern North American biodiversity — 1880-1997.

The Canadian Field-Naturalist is the official publication of The Ottawa Field-Naturalists' Club and features both articles and notes on original research and observations on the natural history of northern North America (including distribution, faunal analyses, taxonomy, ecology, and behaviour). Issues include news and comment (Club annual meetings and awards, tributes and review papers) and book review and new title sections. Since 1984, it has presented edited Status Reports for individual species designated by the Convention on Species of Endangered Wildlife in Canada (COSEWIC). It is entirely supported through club membership and subscriptions, page and reprint charges. The Ottawa Field-Naturalists' Club has 1054 members and *The Canadian Field-Naturalist* an additional 239 individual and 518 institutional subscribers, for a total distribution of 1811 copies.

The Ottawa Field-Naturalists' Club was formed in 1879 by scientists from embryonic federal departments, including the Geological Survey and the Dominion Experimental Farm, and leading amateurs; this type of mix remains its strength to this day. The Club quickly emphasized publication, and for seven years, beginning in 1880, it annually issued the *Transactions of the Ottawa Field-Naturalists' Club.* With volume 3 in 1887, the *Transactions* became a subtitle of Volume 1 of *The Ottawa Naturalist,* a monthly publication. With Volume 3 of *The Ottawa Naturalist* in 1889, the emphasis changed from local members' reports to national ones, and in 1919 the journal was renamed *The Canadian Field-Naturalist* (starting with Volume 33 which was Volume 35 of the *Transactions* but this subtitle was subsequently dropped). The issues per year were gradually reduced from 12 to 9 to 6 and eventually to 4, the last beginning with Volume 67 in 1953. However, the annual number of pages increased, reaching a record of 798 in 1988 (volume 102), although the largest single item was the Percy A. Taverner biographical issue [vol. 102(1), 1996] with 254 pages. Since 1967, the Club has separately published a local (Ottawa area) natural history journal, *Trail & Landscape,* now also issued four times per year.

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

Francis R. Cook

THE AMPHIPOD SUPERFAMILY EUSIROIDEA IN THE NORTH AMERICAN PACIFIC REGION. II. FAMILY CALLIOPIIDAE. SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

by E. L. Bousfield[1] & E. A. Hendrycks[2]

Abstract

The essentially bipolar eusiroidean family Calliopiidae is extensively revised, based mainly on material obtained in the eastern North Pacific coastal region since 1955. In this study, northern hemisphere genera of Calliopiidae, and species within the genera *Calliopius* and *Paracalliopiella* are keyed and illustrated.

Broadly within the genus *Calliopius* the following subunits are recognized: (1) a boreal North Pacific subgroup of ***C. carinatus,*** n. sp., ***C. pacificus,*** n. sp., and ***C. columbianus,*** n. sp.; (2) a primitive subarctic North Pacific species, *C. behringi* Gurjanova; and (3) a relatively advanced subarctic-boreal North Atlantic subgroup comprising *C. laeviusculus* (Kr.), *C. crenulatus* Chevreux & Fage, *C. rathkii* (Zaddach) and ***C. sablensis,*** n. sp. The North Pacific endemic genus *Paracalliopiella* comprises: (1) a primitive subgroup of large carinated species containing *P. bungei* (Gurjanova), ***P. shoemakeri,*** n. sp., and ***P. haliragoides,*** n. sp.; (2) a further primitive subgroup of smaller and less strongly carinated species, including ***P. beringiensis,*** n. sp. and ***P. tzvetkovae,*** n. sp.; (3) a more advanced subgroup of *P. pacifica* Tzvetkova & Kudrjaschov, ***P. slatteryi,*** n. sp., and a more distantly related ***P. kudrj-aschovi,*** n. sp.; and (4) a most advanced subgroup of *P.litoralis* (Gurjanova) and *P. pratti* (J. L. Barnard).

Other North Pacific calliopiid taxa treated here include *Oligochinus lighti* Barnard, endemic to North American coastal marine shallows; *Bouvierella carcinophila* (Chevreux) and *Oradarea longimana* (Boeck) from deep fiords of British Columbia; and the genus *Laothoes (L. polylovi* Gurjanova, and *L. pacifica* Gurjanova) of subarctic Asiatic Pacific waters. Peripheral to the Bering Sea region are *Halirages fulvocincta* M. Sars and *H. nilssoni* Ohlin, *Apherusa glacialis* (Hansen) and *A. megalops* (Buchholz); and *Weyprechtia pinguis* (Kroyer), and *W. heugleni* (Buchholz).

In the northern hemisphere, the family Calliopiidae is centred in the High Arctic region from whence it has apparently radiated into the North Pacific (15 spp. in 7 genera), North Atlantic (20 spp. in 7 genera), and the deep sea (3 spp. in 3 genera). Bipolar subgroups include the relatively primitive and morphologically "plastic" genera *Halirages, Haliragoides,* and *Oradarea*; fourteen other genera are exclusively antarctic and antiboreal. Along the subarctic and boreal North American Pacific coast the family Calliopiidae is moderately diverse, with 10 species in 6 genera, whereas only 5 species in 3 genera have been recorded from equivalent waters of the western North Pacific region. None lives wholly within warm-temperate marine regions.

Calliopiids, along with pontogeneiids and perhaps bateids, are relatively unspecialized, mainly littoral and epibenthic, marine eusiroidean carnivores and detritivores. Morphologically advanced members within the genera *Calliopius, Paracalliopiella,* and *Apherusa* exhibit some degree of sexual dimorphism of the gnathopods. Such functional morphology within taxa of selected inshore habitats may reflect an increasingly benthic life style in which pre-amplexing reproductive behaviour is presumed to be advantageous.

INTRODUCTION

The family Calliopiidae was first proposed by G. O. Sars (1895) to encompass a group of medium- to small-bodied, coastal marine eusiroideans having a natatory uropod 3 and entire telson. Initially the group consisted of eight northern hemisphere genera: *Calliopius* Liljeborg, 1865, *Laothoes* Boeck, 1871, *Amphithopsis* Boeck, 1861, *Halirages* Boeck, 1871, *Leptamphopus* G. O. Sars, 1895, *Cleippides* Boeck, 1871, *Apherusa* Walker, 1891, and *Haliragoides* Sars, 1895, and five southern hemisphere genera, *Stenopleura* Stebbing, 1888, *Harpinioides* Stebbing, 1888, *Chosroes* Stebbing, 1888, *Atylopsis* Stebbing, 1888, and *Schraderia* Pfeffer, 1888. In a subsequent expansion and redefinition of the group, Stebbing (1906) added the genera *Sancho* Stebbing, 1897, *Paraleptamphopus* Stebbing, 1899, and *Paracalliope* Stebbing, 1899, all from the region of Australia and New Zealand (ANZAC). J.L. Barnard (1958) included six additional genera from the southern hemisphere and the deep sea, viz., *Bouvierella* Chevreux, 1900, *Calliopiella* Schellenberg, 1925, *Clarencia* K.H. Barnard, 1931, *Metaleptamphopus* Chevreux, 1911, *Regalia* K.H. Barnard, 1930, and *Stenopleuroides* Birstein and Vinogradov, 1964, and one from the Northern Hemisphere, *Oradarea* Walker, 1903, for a combined total of 20 genera. More recent additions include *Oligochinus* Barnard, 1969b, *Rozinante* Stebbing, 1897, and *Paracalliopiella* Tzvetkova & Kudrjaschov, 1975 (=*Callaska* J.L. Barnard, 1978). with *Leptamphopus litoralis* Gurjanova as the type species.

It is not the purpose of this paper to revise the family Calliopiidae in its entirety. However, an important new dimension to its understanding has been added by the present diverse new material from the North Paciific region. Further revision of the group must be based on detailed comparison with members of the type genus *Calliopius* as here re-

---

[1] Research Associate, Royal Ontario Museum, Toronto, Ontario, Canada M5S 2C6.
[2] #2-542 MacLaren St., Ottawa, Ontario, Canada K1R 5K7.

examined and redefined. If we employ as prime character states the type and occurrence of antennal calceoli, the form of the mouthparts (esp. the mandibular palp and maxilliped), and the presence of pleated coxal gills, setose uropod 3, unmodified peraeopod 7, and unkeeled entire telson, at least three subgroupings (subfamilies) within the family can be recognized, as outlined below. Particularly significant would be the transfer of *Atylopsis* to the Pleustidae (see Bousfield & Hendrycks, 1994), and *Paraleptamphopus* (along with *Falklandella* and related groups from continental fresh waters of the Southern Hemisphere) to separate family groupings (Bousfield & Shih, 1994; Bousfield, in prep).

Studies of North Pacific regional calliopiids have been infrequent. A few early records are included in Stebbing (1906). Holmes (1904) listed no calliopiids from the Alaskan coast, and his calliopiids from off the coast of California (1908) later proved to be species of Eusiridae (see Bousfield & Hendrycks, 1995). Neither Stout (1913), nor Alderman (1936) worked up their extensive collections of Calliopiidae. The calliopiid records of Barnard (1954, 1958, 1969a, b) are summarized in the generalized keys and accounts of Barnard (1975), Armstrong et al. (1976), Staude et al. (1977), Staude (1987), and Barnard & Karaman (1991). Studies on species of the Bering Sea region have been summarized mainly by Gurjanova (1951), and Tzvetkova & Kudrjaschov (1975). A very few records of calliopiids from northern Japan (e.g., in Nagata, 1965) have been summarized by Ishimaru (1994).

ACKNOWLEDGEMENTS

Several institutions and interested colleagues contributed to the success of this study. Most material was obtained during the course of regional field expeditions of the National Museum of Natural Sciences (NMNS), now Canadian Museum of Nature (CMN), led by the senior author, during the period 1955 - 1980. Valuable assistance in the field was provided by the Pacific Biological Station, Nanaimo, and the Bamfield Marine Station. Detailed acknowledgements are provided in the published station lists of Bousfield (1958, 1963, 1968), Bousfield & McAllister (1962), and Bousfield & Jarrett (1981). Charles O'Clair (1977) and Peter Slattery (pers. comm.) obtained material from the Bering Sea and Aleutian regions, kindly made available for this study. For the loan of additional study material, the authors are indebted to the Royal British Columbia Museum, Victoria, B. C., the Zoological Institute, St. Petersburg, Russia, and the Smithsonian Institution, Washington, D. C.

Taxonomic research was conducted mainly at the NMNS (now CMN) in Ottawa, and the use of its collections and facilities is gratefully ackknowledged. Valuable commentary on the text was provided by Dr. Craig P. Staude, Friday Harbor Laboratories (FHL), WA, Marjorie Bousfield, Wolfe Island, Ont., and Patrick Shaw, Canadian Wildlife Service (CWS), Vancouver, B. C. The illustrations were prepared with the very capable assistance of Susan Laurie-Bourque, Hull, Quebec. Marjorie Bousfield also provided translations of pertinent Russian literature.

The authors gratefully acknowledge research support from the Natural Sciences and Engineering Research Council of Canada, and from the Royal Ontario Museum, Toronto.

SYSTEMATICS

Family Calliopiidae G. O. Sars, 1895 (revised status)

Calliopiidae G. O. Sars, 1895: 431.—Stebbing 1906: 285 (part).—Gurjanova, 1951: 599.—Barnard, 1969a:167 (part).—Bousfield, 1973: 79.—Lincoln, 1979: 404 (part).—Bousfield, 1982a: 265.

Eusiridae Stebbing, 1888: 953 (part).—Barnard & Karaman, 1991: 284 + key (part).

Type genus: *Calliopius* Liljeborg, 1865 (TYPE - *Amphithoe laeviusculus* Kroyer, 1838).

Northern Hemisphere genera: *Amphithopsis* Boeck, 1861 (TYPE - *A. longicaudata* Boeck, 1861); *Apherusa* Walker, 1891 (TYPE - *Amphithoe jurinei* Milne-Edwards, 1830); *Bouvierella* Chevreux, 1900 (TYPE - *B. carcinophila* (Chevreux, 1889); *Cleippides* Boeck, 1871 (TYPE - *Acanthonotus tricuspis* Kroyer, 1846); *Dolobrotus* Bowman, 1974 (= *Schraderia* Pfeffer, 1888?) (TYPE - *D. mardeni* Bowman, 1974); *Halirages* Boeck, 1871 (TYPE - *Amphithoe fulvocincta* M. Sars, 1858); *Haliragoides* G. O. Sars, 1895 (TYPE - *Halirages inermis* G. O. Sars); *Laothoes* Boeck, 1871 (TYPE - *Laothoes meinerti* Boeck, 1871); *Leptamphopus* G. O. Sars, 1895 (TYPE - *Leptamphopus sarsi* Vanhoffen, 1897); *Oligochinus* J. L. Barnard, 1969b (TYPE - *Oligochinus lighti* Barnard, 1969b); *Oradarea* Walker, 1903 (TYPE - *O. walkeri* Shoemaker, 1930); *Paracalliopiella* Tzvetkova & Kudrjaschov, 1975 (TYPE - *Leptamphopus litoralis* Gurjanova, 1938); *Rozinante* Stebbing, 1894 [TYPE - *R. fragilis* (Goes)]; *Weyprechtia* Stuxberg, 1880 (TYPE - *W. heugleni* Buchholz, 1874).

Diagnosis. Body often dorsally carinated on pleon, occasionally on peraeon. Rostrum short to medium. Eyes large, well pigmented. Head lobe truncated or narrowly incised; inferior antennal sinus sharply incised. Antennae (of males often, and females occasionally) calceolate; peduncular segments short. Antenna 1 usually shorter than antenna 2; accessory flagellum small, often minute, occasionally lacking; callynophore usually lacking, rarely weakly developed.

Mouthparts basic. Upper lip simple, apex rounded or slightly incised. Lower lip, inner lobes lacking or weakly developed. Mandible normally developed; molar strong, triturative, with distal flagellum; palp segment 3 normal or shorter than 2. Maxilla 1 regular, inner plate setose; outer plate with 9-11 apical spines; palp 2-segmented, occasionally reduced. Maxilla 2, inner plate, facial row of setae variously reduced. Maxilliped normal, strong; outer plate often large or modified.

Coxal plates 1-4 medium, increasing posteriorly, lacking hind cusp. Gnathopods subsimilar, subchelate, trending to sexual dimorphism (propod more powerful in male); carpus (especially of gnathopod 2) variable, often elongate.

Peraeopods 3 & 4 regular, dactyls short to medium. Peraeopods 5-7 regular, homopodous; coxae posterolobate; postero-distal angles of segments 4 & 5 weakly produced.

Pleon segments large, uncoalesced. Pleopods strongly developed, especially in male. Pleon plates regular, hind corners variable. Urosome segments separate. Uropods 1 & 2, rami sublanceolate or sublinear, outer ramus the shorter, margins serially spinose, apices unequally spinose. Uropod 3, rami lanceolate, subequal, margins serially spinose, plesiomorphically setose.

Telson plate-like, apex acute, rounded, or variously notched; penicillate setae in two pairs, inner member of distal pair often spine-like.

Coxal gills usually strongly pleated, especially in male. Brood plates very broad and strongly marginally setose; occasionally slender, weakly setose on peraeopod 5.

Males usually slightly smaller than females, and having more slender body form, more strongly calceolate antennae, larger eyes, and stronger gnathopods.

Taxonomic Commentary. The family Calliopiidae encompasses a number of morphologically diverse generic forms that share many symplesiomorphies but few synapomorphies. Based on type of calceolus, the family Calliopiidae is closely related to family Pontogeneiidae in the more primitive subgroup of families of superfamily Eusiroidea (Stapleton et al., 1988, Bousfield & Shih, 1994; Bousfield & Hendrycks, 1995). Perhaps paradoxically, eusiroideans have developed the most complex (and presumably most advanced) forms of calceoli (Lincoln & Hurley, 1981; Barnard, 1989), and surface ultrastructure (Halcrow & Bousfield, 1986), yet exhibit many of the most plesiomorphic macromorphological character states within the entire assemblage of gammaridean amphipods (Bousfield, 1982a, 1983). Such a combination of macroplesiomorphies, combined with the dominance of component families along ancient (e.g., ANZAC and North Pacific) coastlines, suggests a relatively early lineage for superfamily Eusiroidea, extrapolated for mid-Mesozoic (Bousfield, 1982b).

The present authors have not followed Barnard & Karaman (1991) in submerging Calliopiidae, Pontogeneiidae and Gammarellidae within family Eusiridae (sens. lat.). Recognized families within superfamily Eusiroidea are treated in Bousfield & Hendrycks (1995). Doubtless the morphological overlap between families, homoplasious or otherwise, is real, and is complemented by the somewhat similar life styles (free-swimming detritivores (Enequist, 1949) and carnivores) and overlapping distributional ecologies of selected member species. On these bases, a reasonable case can be made for merging families Pontogeneiidae and Calliopiidae (p. 61). On the other hand, the imperfectly known antarctic genus *Clarencia* K. H. Barnard, 1931, was given separate family status (Clarenciidae) by Barnard & Karaman (1987). The genus *Calliopiurus* (type species *C. excellens* Bushueva, 1986) from intermediate depths in the antarctic Davis Sea region, is superficially calliopiid in its short rostrum, linear subsimilar gnathopods, and short, plate-like telson. However, in its combination of other character states including a relatively deep, narrow, eyeless head, callynophorate antenna 1, highly modified mouthparts, narrow coxal plates, heteropodous bases of peraeropod 5-7, slender lanceolate uropods, and notched telson apex, the species encompasses features of several other mainly non-calliopiid and even non-eusiroidean families. Its classificatory status is here considered uncertain. With few exceptions, members of family Eusiridae possess a distinct accessory flagellum, specialized calceoli (when present), often well developed callynophore, specialized mouthparts (mandible with large incisor, reduced molar, slender palp), powerfully raptorial gnathopods, elongate peraeopods, serrate pleon plate 3, and large, narrowly separated telson lobes (Bousfield & Hendrycks, 1995).

Compared to eusirids, members of family Calliopiidae tend to be more detritivorous in feeding style, and occupy inshore, shallow-water and benthic habitats (Enequist, 1949). Their adaptive morphology is reflected in a mixture of plesiomorphic and apomorphic character states such as simple calceoli, loss of accessory flagellum, relatively "basic" mouthparts (toothed incisor, large molar), relatively unspecialized gnathopods, short stoutly dactylate peraeopods, simple pleon plates, linear uropod rami, and plate-like telson. Some coxal gills remain pleated in *Calliopius*. As treated by Barnard (1958) and Barnard & Barnard (1983), most calliopiids are marine, and most are (or tend to be) powerful swimmers, even if primarily benthic crawlers and scavengers (e.g., *Bouvierella, Oradarea, Dolobrotus*). Their reproductive style is primarily synchronously free-swarming in the water column (Conlan, 1991; Bousfield & Shih, 1994). However, inshore benthic calliopiids, especially in more southerly ranging species of genera such as *Apherusa* and *Paracalliopiella*, demonstrate a tendency towards both dissimilarity and sexual dimorphism of the gnathopods.

It is not surprising, therefore, that attempts have been made to split up this somewhat unwieldy calliopiid assemblage into more naturally related (phyletic) units. The freshwater paraleptamphopids of New Zealand and Tasmania have been placed in a separate family group, allied to the Falklandellidae of the South Atlantic continental island (Bousfield, 1980, Bousfield & Shih, 1994). Some antipodean marine genera (*Atylopsis, Harpinioides)* have been given subfamily status within the Pleustidae (Bousfield & Hendrycks, 1994). The genera *Gammarellus* and *Weyprechtia* were transferred from Gammaridae and given separate family status (Gammarellidae) within Eusiroidea by Bousfield (1977, 1979), but were subsequently submerged within Calliopiidae (Bousfield, 1983). Barnard (1989) recently resurrected family Gammarellidae to encompass *Gammarellus*, *Austroregia* and *Chosroes*, on the basis of synapomorphies in the microstructure of antennal calceoli. Single-character diagnoses of higher taxonomic groups are inherently risky and unstable, even when based on such fundamentally significant characters as antennal calceoli.

KEY TO NORTHERN HEMISPHERE GENERA OF CALLIOPIIDAE

1. Accessory flagellum prominent, 2+ segmented (Fig. 36); mandibular palp segment 3 distinctly longer than segment 2 (Fig. 38) . . . . *Weyprechtia* (Stuxberg) (p. 54)
—Accessory flagellum minute, 1-segmented or lacking (Fig. 15, 20); mandibular palp segment 3 equal to or shorter than segment 2 (Fig. 25). . . . . 2.

2. Antennae calceolate (Figs. 2, 13); antenna 1, peduncular segment 3 with postero-distal process; uropod 3, rami subequal, margins setose (Fig. 11) . . . . 3.
—Antennae lacking calceoli; antenna 1, peduncular segment 3 unmodified; uropod 3, rami various, margins spinose or with spines and weak inner marginal setae only (Figs. 21, 34). . . . . 4.

3. Gnathopods 1 & 2 sexually dimorphic (Fig. 22); telson entire, linguiform (Fig. 1); pleon plate 3, hind margin smooth (Fig. 1). . . . . *Calliopius* Lilj. (p. 7)
—Gnathopods similar in both sexes; telson apically notched (Fig. 30); pleon plate 3, hind margin toothed (Fig. 30) . . . . *Halirages* Boeck (p. 45)

4. Gnathopod 2, carpus and propod very slender, elongate, much longer than gnathopod 1 (Fig. 34) . . . 5.
—Gnathopod 2 little longer than gnathopod 1, carpus and propod short or not elongate (Figs. 1, 33). . . 8.

5. Pigmented eyes lacking; telson distinctly cleft (Fig. 35) . . . . *Bouvierella Chevreux* (p. 51)
—Pigmented eyes present; telson shallowly notched or entire (Fig. 34). . . . . 6.

6. Uropod 3, rami subequal in length; peraeopods 3-7, dactyls spinose . . . . *Cleippides* Boeck
—Uropod 3, rami markedly unequal; peraeopod dactyls smooth, normal . . . . 7.

7. Accessory flagellum 1-segmented; gnathopod 2, propod elongate, longer than basis. . *Oradarea* (p. 49)
—Accessory flagellum lacking; gnathopod 2, propod shorter than basis . . . . . .*Leptamphopus* G. O. Sars

8. Antenna 1, aesthetascs conspicuous, on alternating flagellar segments (Figs. 17, 18) . . . . 9.
—Antenna 1, aesthetascs inconspicuous and/or present on all flagellar segments (Figs. 11, 30). . . . . . 13.

9. Peraeopods 3-7, dactyls serrated; mandibular palp segment 3 broadened . . . . . *Amphithopsis* Boeck
—Peraeopod dactyls normal, smooth; mandibular palp segment 3 not broadened medially . . . . 10.

10. Telson apically cleft; gnathopods 1 & 2 sexually similar . . . . 11.
—Telson entire, apex rounded or acute; gnathopods sexually dimorphic . . . . 12.

11. Inferior antennal head lobe acutely produced; accessory flagellum lacking . . . . . . *Rozinante* (Goes)
—Inferior antennal head lobe not produced; (Fig. 15); accessory flagellum 1-segmented . . . . *Oligochinus* J. L. Barnard (p. 24)

12. Accessory flagellum lacking; mainly North Atlantic, Arctic . . . .*Apherusa* Walker (p. 47)
—Accessory flagellum 1-segmented; North Pacific endemic . . . *Paracalliopiella* Tzvet. & Kudrj. (p. 26)

13. Maxilliped, outer plate abnormally enlarged (Fig. 31); maxilla 2, inner plate lacking facial setae; pleon plate 3, hind margin smooth . . . .*Laothoes* Boeck (p. 47)
—Maxilliped, outer plate normal; maxilla 2, inner plate with facial setae; pleon plate 3, hind margin with one tooth . . . . *Haliragoides* G. O. Sars.

Thus, presumptions must be made about otherwise closely related groups in which all members lacking calceoli. However, the taxonomic level and phyletic ordering of the nine categories of calceoli described by Lincoln and Hurley (1981) have been reorganized on a more consistent phyletic basis (Bousfield & Shih, 1994). Thus, the simple body and serial elements of the phoxocephalid and crangonyctid types of calceoli (nos. 8 & 9 of Lincoln & Hurley, loc. cit.) appear to be more rationally placed at the plesiomorphic, rather than apomorphic, end of the phyletic scale. Moreover, some convergence of form is apparent in separate lineages; the advanced oedicerotid form, presumably from a paracalliopiid ancestral type, is similar to the complex eusirid type presumably derived from a pontogeneiid ancestral form.

Despite these reservations, however, we are inclined to support Barnard's revival of family Gammarellidae, with the expectation that other antipodean genera will fall into this family concept following more comprehensive analyses of surface microstructure. *Weyprechtia*, however, is tentatively retained within the Calliopiidae, since its calceolus is primitively pontogeneiid in form (viz., Bousfield & Shih, 1994, Fig. 9). Further subdivision of family Calliopiidae may be helpful, perhaps employing subfamily categorizations after the fashion of Barnard and Drummond (1978) or Bousfield & Hendrycks (1994), but is beyond the scope of the present regional study*.

Calliopius Liljeborg

Calliopius Liljeborg, 1865: 11.—Stebbing, 1906: 295.—Gurjanova, 1951: 617.—Barnard, 1969a: 176.—Bousfield, 1973: 80.—Lincoln, 1979: 480.—Barnard & Karaman, 1991: 313.

Type species. *Calliope Leachii* Bate 1857 (=*Amphithoe laeviuscula* Krøyer, 1838).

North Pacific Species: *Calliopius behringi* Gurjanova, 1951; *C. carinatus*, new species (p. 13); *Calliopius pacificus*, new species (p. 16); *Calliopius columbianus*, new species (p. 19).

North Atlantic Species. *Calliopius rathkii* (Zaddach, 1844); *C. crenulatus* Chevreux & Fage, 1925; *C. sablensis*, new species (p. 13) (+ *C. laeviusculus*).

Diagnosis. Body medium, robust, weakly to strongly mid-dorsally carinated or tuberculated, especially on the pleon; cuticle often highly pigmented in mottled or banded patterns. Head, rostrum short but distinct; inferior head lobe not produced. Eyes large, subrectangular, strongly pigmented. Antennae stout, not elongate; antenna 1 shorter than 2; distal peduncular and flagellar segments calceolate (both sexes); calceoli simple (pontogeneiid type). Antenna 1, peduncular segment 3 with variously developed posterodistal process; accessory flagellum minute, variously fused with segment 3; flagellum faintly (or not) basally callynophorate.

Mouthparts regular. Lower lip with weak inner lobes. Mandible, palp segment 3 large, falciform, with 1-3 basofacial groups of "A" setae; segments 1 & 2 with inner marginal setae; left lacinia 5-7 dentate, right lacinia 3-4 cuspate; spine row medium strong. Maxilla 1 normal; right palp broadly 2-segmented; inner plate with 2-6 apical setae; outer plate with 11 apical spines. Maxilla 2, inner plate narrowed, with 1-2 facial seta, one often strong. Maxilliped plates regular, not enlarged; palp strong.

Coxae 1-4 medium deep. Gnathopods 1 & 2 powerfully subchelate, raptorial, subsimilar, slightly sexually dimorphic; propod palms oblique, with 3-5 spines near posterodistal angle; dactyls minutely setulose behind; carpus short, deep; merus small.

Peraeopods 3-4 regular; segment 5 not shortened; dactyls stout, curved. Peraeopods 5-7 homopodous, increasing posteriorly; bases broadly rounding, hind lobes distinct.

Pleon plates 2-3 broad, hind margins smooth, lower margins (and often facially) spinose; hind corners acuminate, not produced. Pleopods strong, slightly sexually dimorphic. Uropods 1 & 2, rami sublinear, apices truncate, spinose, outer ramus shorter. Uropod 3, rami subequal, margins variously setose and short-spinose, inner ramus broadly lanceolate.

Telson linguiform, apex rounded; penicillate setae median. Coxal gills on peraeopods 3 & 4 strongly pleated, especially in male. Brood plates large, margins strongly setose.

Taxonomic and distributional commentary. Members of the genus *Calliopius* are markedly distinct from other northern genera of calliopiids. *Calliopius* appears most closely allied with other phyletically advanced genera, namely *Apherusa, Paracalliopiella* and the South African genus *Calliopiella* (Table I, and Fig. 39). Apomorphic character states include stout antennae with posterodistal peduncular process and vestigial accessory flagellum; powerfully developed, slightly sexually dimorphic gnathopods with short deep carpal segments; well developed peraeopod dactyls; sublinear, apically spinose uropods 1 & 2, and plate-like telson. However, *Calliopius* retains several plesiomorphies including strongly calceolate antennae, relatively unmodified mouthparts, fully homopodous peraeopods, and strongly setose and natatory uropod 3 (both sexes).

Distributionally the genus *Calliopius* is subarctic-boreal, and ecologically eulittoral along high salinity rocky coasts of the North Atlantic and North Pacific regions. Members are generally associated with winter conditions of icing or low temperature (5-10^{o}C.), but are absent from both high arctic and warm temperate shores. Their plesiomorphic calceolate antennae and natatory uropod 3, in combination with apomorphically powerfully raptorial and sexually dimorphic gnathopods, well developed peraeopod dactyls, and linear uropod rami presumably facilitate their primarily free-swimming and perching/clinging life style, near shore, along mainly rocky coasts.

Calliopius laeviusculus (Krøyer)
(Fig. 1)

Amphithoe laeviusculus Krøyer, 1838: 281.
Calliopius laeviusculus (Kr.) Sars, 1895: 449, pl. 158.—Stebbing, 1906: 296.—Gurjanova, 1951: 618, fig. 419.—Barnard, 1969a: 176, fig. 71a.—Bousfield, 1973: 80, pl. XIV.1.—Lincoln, 1979: 406, fig. 193 .
non *Calliopius laeviusculus* (Kr.) Wailes, 1931: 40.—Wailes, 1933: 8.—Barnard, 1954: 8, pl. 8.—Bousfield, 1970: 34.

---

* Stapleton et al. (1988) count 18 families of amphipods in which one or more known species bear calceolate antennae. However, the actual number is closer to 30 families, in 8 superfamily (or equivalent) groups, as outlined by Bousfield & Shih (1994, p. 94).

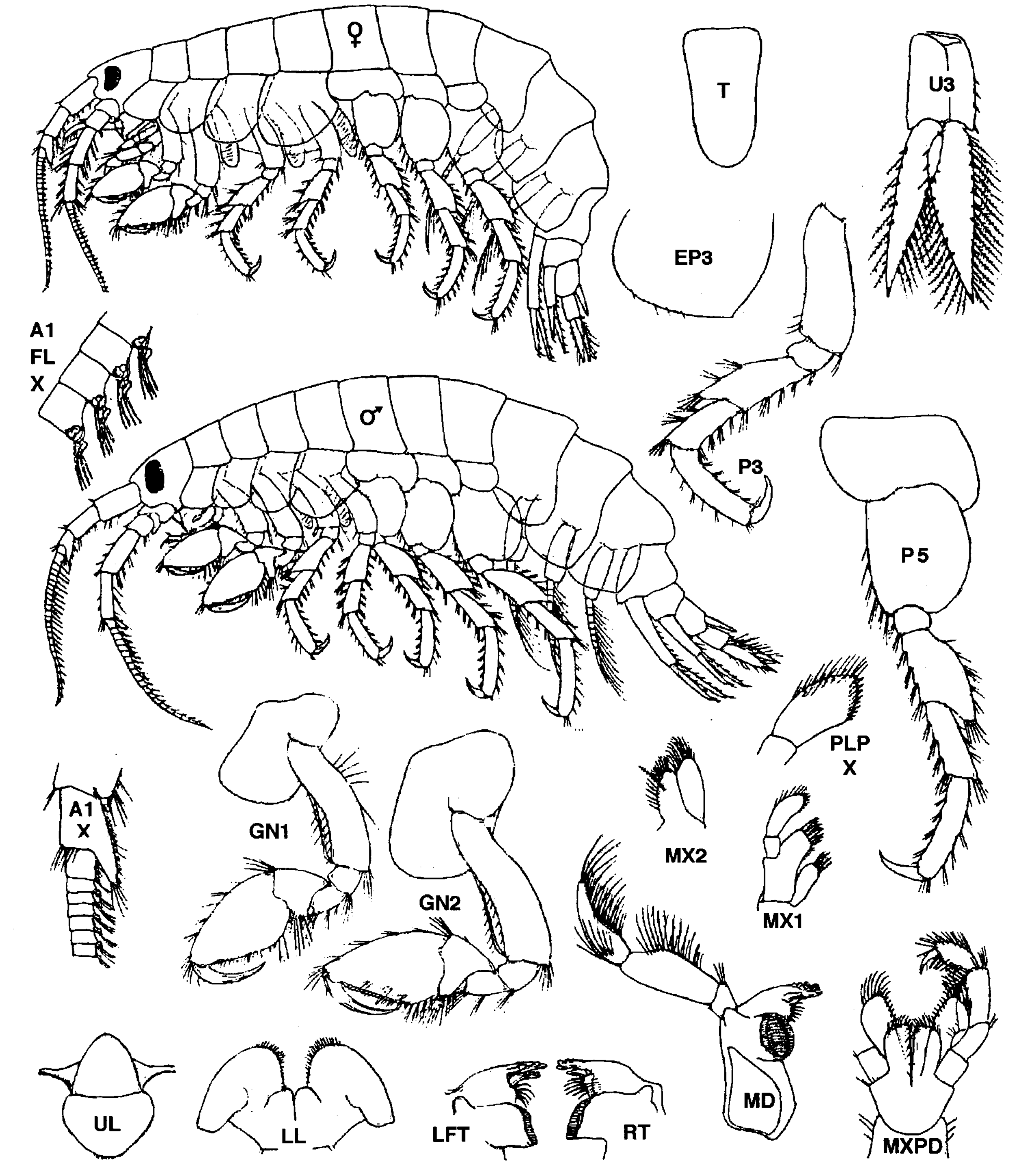


Fig. 1. *Calliopius laeviusculus* (Kroyer). Northeastern Atlantic region. Fem. (12.0 mm); male (13.0 mm). (after Sars, 1895)

Material Examined: None authentically from study region. Previous records from the North Pacific (e.g., Wailes, Barnard, loc. cit.) are possibly attributable to one or more of the regional new species described below. Comparative North Atlantic material (CMN, Ottawa) was utilized here.

Diagnosis. Body nearly smooth, with low carinations mid-dorsally on pleonal, rarely on posterior 1-2 peraeonal, segments. Head, eyes intermediate, broadly reniform. Inferior head margin vertical. Antenna 1 & 2, calceoli relatively large, in single posterior (inner) marginal rows; peduncular segment 3 short, posterodistal process intermediate, little exceeding 1st flagellar segment; accessory flagellum barely discernible, apex with several setae.

Mandibular palp segment 3 large, apex acute, subequal in length to segment 2; basal "A" setae strong (7-11 in main

KEY TO SPECIES OF *CALLIOPIUS*

1\. Antennal calceoli in three to several rows on posterior face of peduncular segments; Pacific species . . 2.
—Antennal calceoli in 1(2) rows along posterior margin of peduncular segments; Atlantic species . . . . 5.

2\. Antenna 1, posterodistal process of peduncular segment 3 extending along 4-6 basal flagellar segments; uropod 2, outer ramus short (length ~1/2 inner ramus); gnathopods 1 & 2 little larger in male than in female . . . . *C. behringi* Gurjanova (p. 21).
—Antenna 1, posterodistal peduncular process short, not extending beyond flagellar segment 1; uropod 2, outer ramus ~2/3 length of inner ramus; gnathopods 1 and 2 distinctly sexually dimorphic . . . . 3.

3\. Peraeon segments 5-7 and pleon segments 1 & 2 distinctly carinate; pleon plate 2, facial setae in 5-7 submarginal rows . . . . *C. carinatus,* n. sp. (p. 13)
—Peraeon and pleon segments not (or weakly) carinate; pleon plate 2, facial setae in 2-3 submarginal rows . . . . 4.

4\. Antennal flagella short (<20 segments); peraeopods 5-7, dactyls large, heavy, ~1/3 length of segment 6; maxilla 1, inner plate with 2 apical setae . . . . *C. pacificus,* n. sp. (p. 16)
—Antennal flagella elongate (>30 segments); peraeopods 5-7, dactyls small, <1/3 length of segment 6; maxilla 1, inner plate with 5 apical setae . . . . *C. columbianus,* n. sp. (p. 19)

5\. Uropod 3, rami conspicuously setose on inner and outer margins . . . . 6.
—Uropod 3, rami conspicuously setose on inner margin only . . . . 7.

6\. Antenna 1, posterodistal process of peduncular segment 3 elongate, exceeding flagellar segment 1; pleon plate 2, facial spines in submarginal row . . . . *C. laeviusculus* (Kr.) (p. 17)
—Antenna 1, peduncular posterodistal process short, length <flagellar segment 1; pleon plate 2, facial spines in 3 submarginal rows . . . . *C. sablensis,* n. sp. (p. 13)

7\. Coxae 1-4 , lower margin distinctly crenulate; peraeopods 5-7, dactyls strong, length > 1/3 segment 6 . . . . *C. crenulatus* Chevreux & Fage (p. 11)
—Coxae 1-4, lower margin nearly smooth; peraeopods 5-7, dactyls short, slender, length <1/3 segment 6 . . . . *C. rathkii* (Zaddach) (p. 10)

---

cluster, left palp). Maxilla 1, inner plate with 4 setae. Maxilla 2, inner plate, facial seta strong. Maxilliped, outer plate intermediate.

Coxal plates 1-4 medium, deeper than broad, rounded below. Gnathopods 1 & 2, palmar margins with 4 medium stout spines near posterior angle. Anterior facial setae strong (up to 6 clusters).

Peraeopods 3 & 4 medium stout, segment 5 slightly shorter than 4. Peraeopods 5-7 closely homopodous, margins spinose only; segment 4 moderately broadened; dactyls medium. Basis of peraeopod 7 regularly rounded behind, posterodistal lobe not broadening distally; segment 6 not as long as basis, with 5-6 anterior margin spine clusters.

Pleon plates 2 & 3, facial spines few, in clusters of 2-3, middle spine slender, hind corner obtuse, very weakly acuminate. Uropod 2, length of outer ramus 2/3 inner ramus; apical spines medium. Uropod 3, inner ramus not strongly broadened; outer ramus, outer margin with 7-8 singly inserted spines and setae.

Telson elongate linguiform, basally broadest; apex evenly rounded.

Coxal gills narrowly sac-like, smallest on peraeopod 7.

Female: body slightly larger and more robust than male; gnathopod propods smaller and less powerful. Brood plates large, broad, margins moderately fully setose

LEGEND FOR FIGURES

A1	**antenna 1**	**MX2**	**maxilla 2**
A2	**antenna 2**	**MXPD**	**maxilliped**
AC FL	**accessory flagellum**	**O. P.**	**outer plate**
		P3-7	**peraeopods 3-7**
BR PL	**brood plate**	**PED**	**peduncle**
CLC	**calceolus**	**PL**	**pleopod**
CX	**coxa**	**PLEON**	**pleon segments**
DCTL	**dactyl**	**PLEOS**	**pleosome**
EP	**epimeral plate**	**PLP**	**palp**
FL.	**flagellum**	**RT**	**right**
GN1	**gnathopod 1**	**SET**	**seta**
GN2	**gnathopod 2**	**SP**	**spine**
HD	**head**	**T**	**telson**
I. P.	**inner plate**	**U1-3**	**uropods 1-3**
LAC	**lacinia**	**UROS**	**urosome**
LFT	**left**	**X**	**magnified**
LL	**lower lip**	**♂**	**male**
MD	**mandible**	**♀**	**female**
MX1	**maxilla 1**		

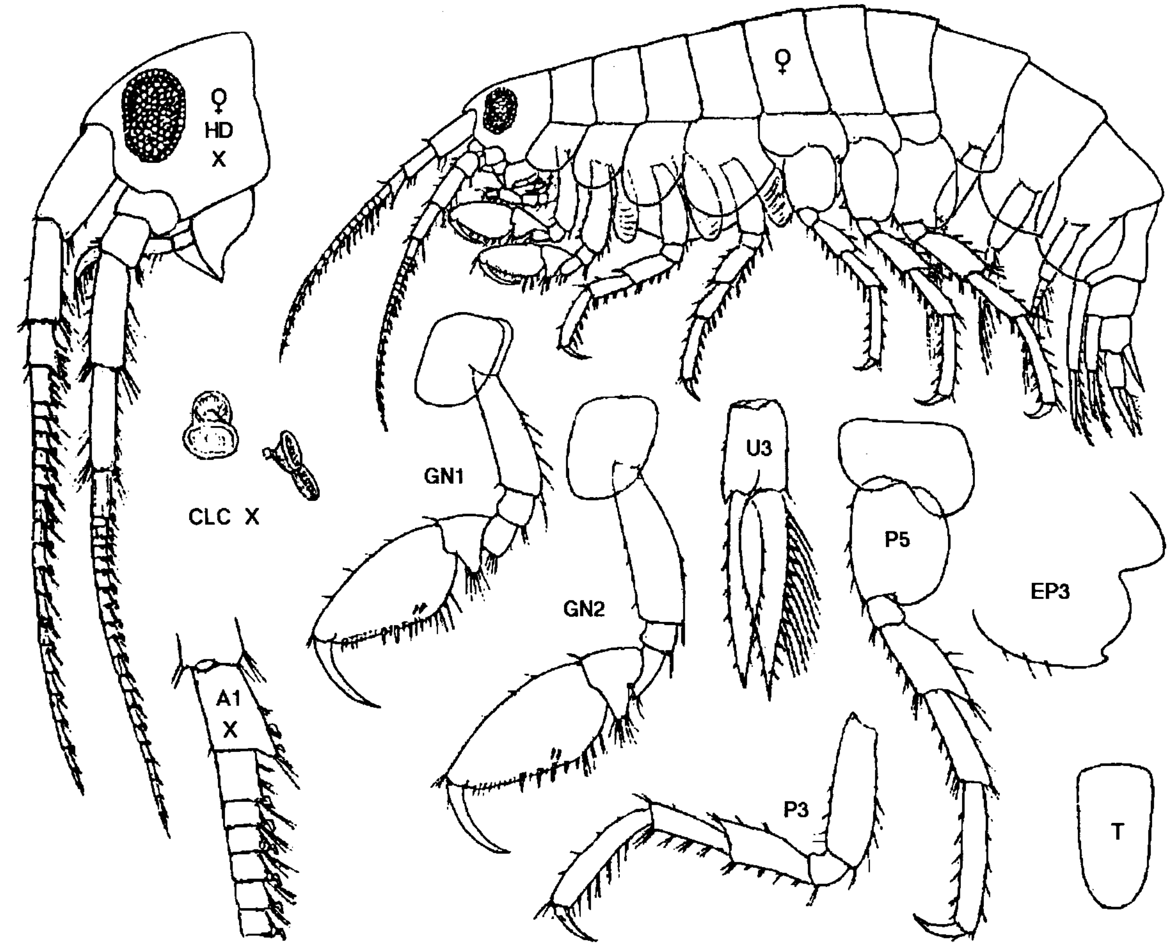


FIG. 2. ***Calliopius rathkii*** **(Zaddach). North Sea. Female (7.0 mm) (after Sars, 1895).**

Distribution. A subarctic and boreal North Atlantic species. Previous records from the North American Pacific region [e. g., Barnard (1954, 1971); Wailes (1933); Dagg, 1975] have not been verified.

Taxonomic commentary: *Calliopius laeviusculus* Kr., as the type species of the genus, is rediagnosed here on the basis of new taxonomic features. Some records from the North American Pacific region (e. g., Wailes, 1931, 1933) were bassed on identifications by the late C. R. Shoemaker. However, the material, possibly still in Smithsonian Institution collections, may contain other species.

Calliopius rathkii (Zaddach)
(Fig. 2)

Amphithoe rathkii Zaddach, 1844: 6.
Calliopius rathkii (Zaddach) Stebbing, 1906: 297.
Calliopius rathkei (Zaddach) G. O. Sars, 1895: 447, pl. 157.
Calliopius laeviusculus (Kr.) Schellenberg, 1942: 89.—Gurjanova, 1951: 618 (part).—Lincoln, 1979: 406 (part).—Barnard & Karaman, 1991: 313.

Material Examined. Nyborg fiord, Denmark (Copenhagen Museum) - male (8.1 mm); female (8.7 mm)..

Diagnosis. Female (8.7 mm): Body nearly smooth dorsally. Head, eyes very large, broadly reniform, black. Antennae 1 & 2 short. Antenna 1, flagellum with 17 regular segments; peduncular segment 3 with very short distal process; accessory flagellum very small, low conical; calceoli large, in single posterior row on peduncular segments 2 & 3, and on flagellum. Antenna 2, peduncular segment 5 shorter than 4; calceoli on peduncular segment 5 and proximal flagellar segments.

Mandible, right palp with 5 setae in main baso-facial "A" cluster, and single supernumerary seta. Other mouthparts not described.

Coxae 1-4 deeper than wide, strongly convex and smooth below. Gnathopods 1 & 2, propods relatively small, palmar margins very oblique, nearly straight, longer than corresponding posterior margins, with 3-4 spines near postero-distal angle; dactyls relatively short.

Peraeopods 3 & 4 slender; segment 5 not reduced; dactyls slender. Peraeopods 5-7 homopodous, bases not wider than deep, gently convex behind. Peraeopod 7, basis regular, lower lobe shallow; segment 4 not broadened; segment 6 longer than basis, anterior margin with 4-5 setal clusters.

Pleon plate 2 with a few facial and submarginal spines, mostly singly inserted; hind corner acuminate. Pleon 3, with 6 lower submarginal spines; hind corner acuminate. Uropod

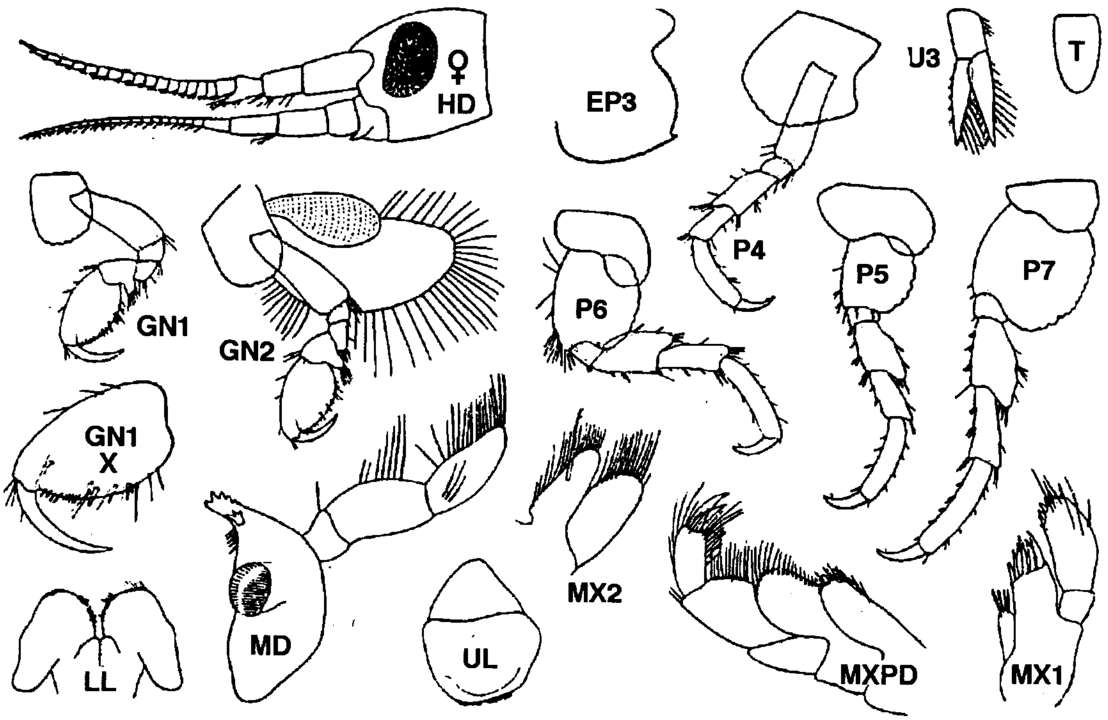


FIG. 3. ***Calliopius crenulatus*** **Chevreux & Fage. Concarneau, France. Female (7.0 mm) (after Chevreux & Fage, 1925).**

1, outer ramus distinctly the shorter. Uropod 2, outer ramus 2/3 length of inner, apical spine not elongate. Uropod 3, inner ramus broad, inner margin setose, outer margin spinose; outer ramus much more slender, margins spinose.

Telson of medium length, slightly less than twice width, slightly narrowing to evenly rounded apex.

Male (8.1 mm): Gnathopod propods more robust than in female. Uropod 3, outer ramus with inner marginal setae.

Distribution. From southern Norway and the British Isles to the Channel coast of France.

Taxonomic commentary. The species is here considered distinct from *C. laeviusculus,* with which it has been synonymized by several authors. *C. rathkii* differs mainly in the short antennal peduncular process, narrow coxae 1-4, and other characters of the key (p. 9)

Calliopius crenulatus Chevreux & Fage

(Fig. 3)

Calliopius crenulatus Chevreux & Fage, 1925: 183, figs. 189, 190.

Calliopius laeviusculus Lincoln, 1979: 406 (part).—Barnard & Karaman, 1991: 313.

Diagnosis. Female (to 7 mm): Body very weakly (or not) carinated on pleon. Head, eyes large, subreniform. Antennae 1 & 2 subequal in length; calceoli large, in single row along posterior margin of distal peduncular and flagellar segments. Antenna 1 peduncular process short; flagellum 19-segmented; accessory flagellum undescribed. Antenna 2, flagellum 18-21-segmented.

Mandibular palp segment not strongly falciform, length ~segment 2. Maxilla 1, inner plate with 4 apical setae; right palp medium stout, with 8 apical conical spines. Maxilla 2, inner plate narrow, facial seta prominent. Maxilliped, outer plate expanded, broader than inner, apical margin with few (6-8?) curved setae.

Coxal plates 1-4 subquadrate, rounded and strongly crenulated below. Gnathopod propods short, deep; palmar margin longer than posterior margin, with 3-4 spines near posterodistal angle.

Peraeopods 3 & 4, segment 5 slightly shorter than 4. Peraeopods 5-7 stout; bases broadly rounded behind, posterior margin coarsely crenulate; segment 4 relatively broad; segment 6 not longer than basis; dactyls strong.

Pleon plates 2 & 3, facial spines weak or lacking, hind margin of 3 convex, hind corner distinctly mucronate. Uropod 2, rami not described. Uropod 3, inner ramus little broader than outer ramus; outer ramus lacking outer marginal setae.

Telson relatively short, length/width ratio ~ 1.6.

Male: Not described.

Distribution. Known only from southwestern Norway to the Channel coast of France and the Brittany peninsula, but apparently not reaching the Mediterranean (Chevreux & Fage, 1925).

Taxonomic commentary. Lincoln (1979) considers *C. crenulatus* merely a small southern variant of *C. laeviusculus* and the present phenetic analysis (Fig. 40, p. 60) confirms a

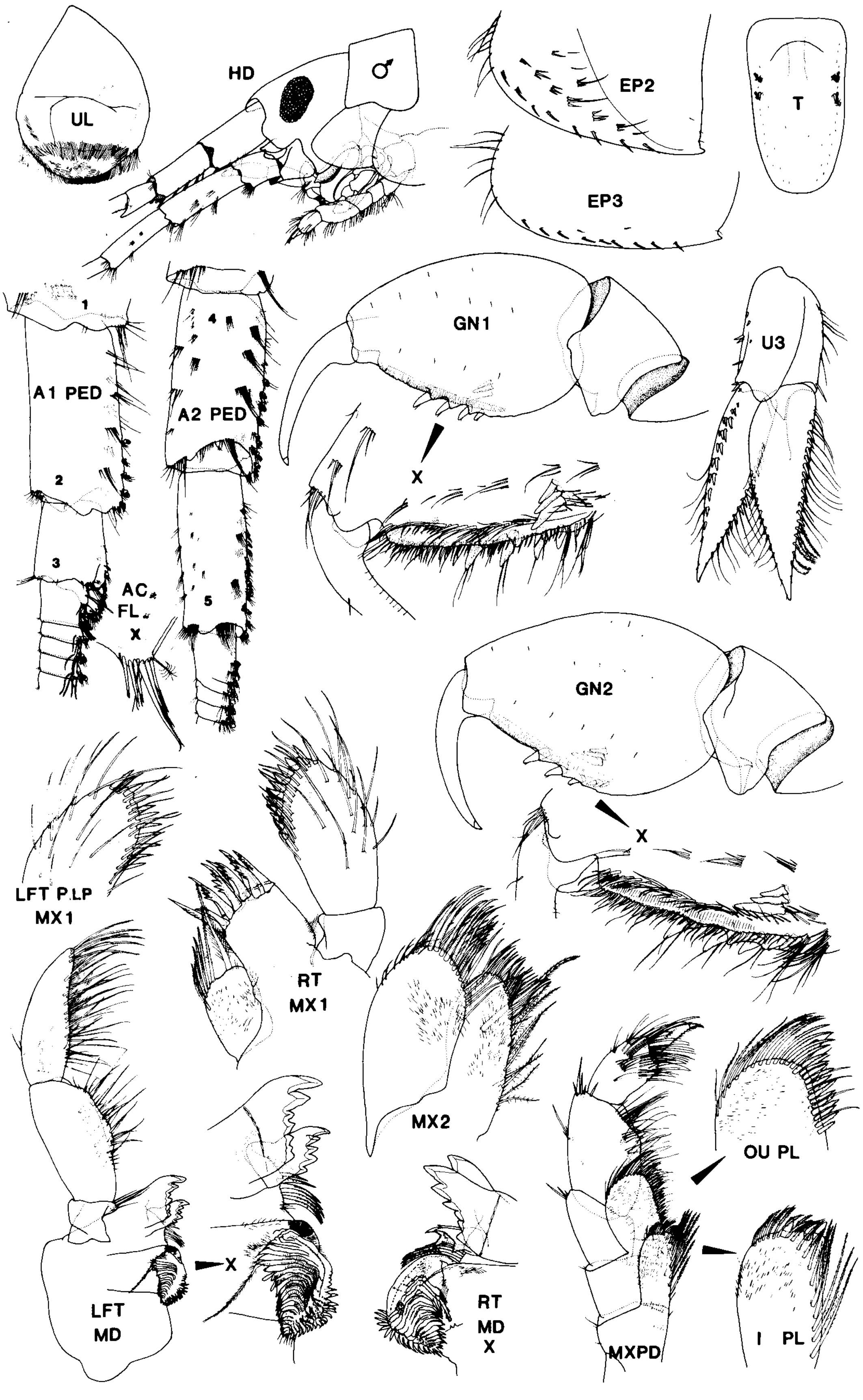


FIG. 4. *Calliopius sablensis,* new species. Salt lake, Sable I. Female (12.5 mm); male (13.0 mm).

close morphological similarity. However, *C. crenulatus* is clearly distinct from *laeviusculus* in characters of the key (p. 7). The strongly and more coarsely crenulated hind margin of the bases of peraeopods 5-7 and the much smaller size at maturity are also diagnostic. *C. crenulatus* differs from *C. rathkii* in the latter's narrower coxae 1-4, more slender segment 4 of peraeopods 5-7, spinose margins of the outer ramus of uropod 3, and more elongate telson.

***Calliopius sablensis*, new species**

(Fig. 4)

Calliopius laeviusculus (Kr.) Bousfield, 1970: 36.—Bousfield, 1973: 80 (part).

Material Examined. Wallace Lake, Sable I., off Nova Scotia, Northwest Atlantic, dip net over sand, JEH Martin coll., July 15, 1967 - 1 male (13.0 mm) **Allotype;** 2 male **Paratypes** (12.5 mm); 1 female ov. (12.5 mm **Holotype**, CMN collections, Ottawa.

Diagnosis. Female (12.5 mm). Pleon weakly mid-dorsally carinate. Head, inferior lobe, margin vertical, slightly sinuous. Eye medium, elongate subovate. Antennae 1 & 2 moderately elongate, flagella ~25-30-segmented, little or not setose; calceoli small, in single posterior marginal row on peduncular segments. Antenna 1, segment 3 short, peduncular process small, shorter than first flagellar segment; accessory flagellum very short, distal margin with 7-8 setae.

Mandible, palp segment 3 not strongly falcate, inner margin strongly setose; right palp, principal baso-facial cluster with 8 " A" setae, and 3 supernumnerary setae; left lacinia irregularly 5-dentate; spine row with 6-7 blades. Maxilla 1, inner plate with 5 apical setae; right palp segment 2 broad, with 11-12 conical apical spines; left palp slender, oblique apical margin with 10 slender spines. Maxilla 2, inner plate with single slender facial seta and 4 proximal marginal setae. Maxilliped, outer plate relatively short, with 12 curved apical setae; inner plate relatively short, narrow.

Coxae 1-4 subquadrate, about as deep as wide, gently rounded below. Gnathopod propods relatively short, deep; palmar margins short, not longer than corresponding posterior margin, with 3-4 proximal spines.

Peraeopods 3 & 4, segment 5 not shortened; segment 6, hind margin with 8-9 spine clusters; dactyls medium. Peraeopods 5-7, bases very broad, hind margin convex, narrowing slightly distally to large lower lobe; segment 4 not strongly broadened; segment 6 with 8-9 anterior marginal spine clusters.

Pleon plate 2, facial setal groups in 3 marginal and submarginal rows. Pleon 3, lower margin with 9-10 short spines, hind corner minutely acuminate. Uropod 2 stout, length of outer ramus 2/3 inner ramus, with 5-6 serially paired marginal spinose; apical spines short. Uropod 3, inner ramus very broad basally,narrowing strongly; inner margin setose and spines; outer ramus with 8-9 short spines and 5-6 distal setae, apex broadly rounded.

Telson little narrowing distally, length barely twice width. Male (13.0 mm). Very similar to female. Gnathopods scarcely more robust; right palp segment 3, main cluster with 11 baso-facial setae.

Distributional ecology. Known only from the type locality, a brackish lake on Sable Island, off Nova Scotia.

Taxonomic commentary. *Calliopius sablensis* is clearly distinct from *C. laeviusculus* and other N. Atlantic species but exhibits plesiomorphic character states of the *C. carinatus* subgroup of the North Pacific region.

***Calliopius carinatus*, new species**

(Figs. 5, 6, 7)

Calliopius laeviusculus Barnard, 1954: 8, plate 8.— Wailes, 1933: 8—Austin, 1985: 589 (part).—Barnard & Karaman, 1991: 313 (part)?
Calliopius carinatus Shaw MS, 1987.
Calliopius sp. Staude, 1987: 378 (part) (<u>non</u> fig. 18.76)?

Material Examined.
ALASKA:
Kenai Peninsula & Prince William Sound. ELB Stns, July, 1961: A136 (2); A130 (6) A121 (9); A140 (3); A153 (5).
NE Gulf of Alaska. ELB Stns, June, 1961: A73 (Icy Bay) (10 spms., slide mount); A71 (~118 males, females, 2 slide mt.); A67 (Yakutat Bay) (2).
.Southeastern Alaska. ELB Stns, 1961: A55 (Icy Strait) (50); A30 (2); A33 (20 spms., slide mt.); A7 (Ketchikan) (1 female + slide). ELB Stns, July-Aug., 1980: S11B3 (5); S10F1 (2); S16B1 (82 specimens, 2 slide mts.).
BRITISH COLUMBIA:
North-central mainland coast. ELB Stn, 1959 N16 (Johnstone Strait) (4). ELB Stns, July, 1964: H16 (Skeena R.) (6) ; H10 (106); H23 (1); H3 (15).
Vancouver Island, inner coast. ELB Stns, Aug., 1959: V7 (Alert Bay)(1); V11 (4); V20 (6); V22 (Oyster Bay - 10 specimens including. **fig'd** male (10.5 mm). ELB Stn F8 (San Juan Is.), July, 1955 - 18 specimens + 2slide mts., incl. **fig'd** male (11.7 mm.),
South end. ELB Stns, Aug., 1959: 017 (Wickaninnish Bay) (20 males, females, 2 slide mts.). ELB Stns, Aug., 1955: P4 (4); P8 (4). ELB Stn, July, 1978: B12b (2). ELB Stn., July, 1970: P707 (3). ELB Stns, July 1964: H44 (1); H41 (2).
.Juan de Fuca Strait. ELB Stn F3 (Witty's Lagoon), Aug.16, 1955.- 26 specimens incl. male **holotype**; female **allotype.** CMN collections.
WASHINGTON & OREGON:
Strait of Juan de Fuca. ELB Stns, July-Aug., 1966: W39 (Cape Flattery) (216 specimens, 2 slide mts.); W42 (7); W36 (Clallam Bay) (10); Puget Sound. ELB Stns, July, 1966: W30 (Fort Flagler Beach) (1 female); W9 (12); W11 (3).
Olympic Peninsula: W24 (2); W22 (Pt Grenville) (13).
Oregon, outer coast. ELB Stns, Aug., 1966: W53 (Neahkannie beach) - 8 spms., incl. male variant (**fig'd**); W66 (10 spms., slide mt.); W63 (10); W61 (Neskowin Beach) (1 female).

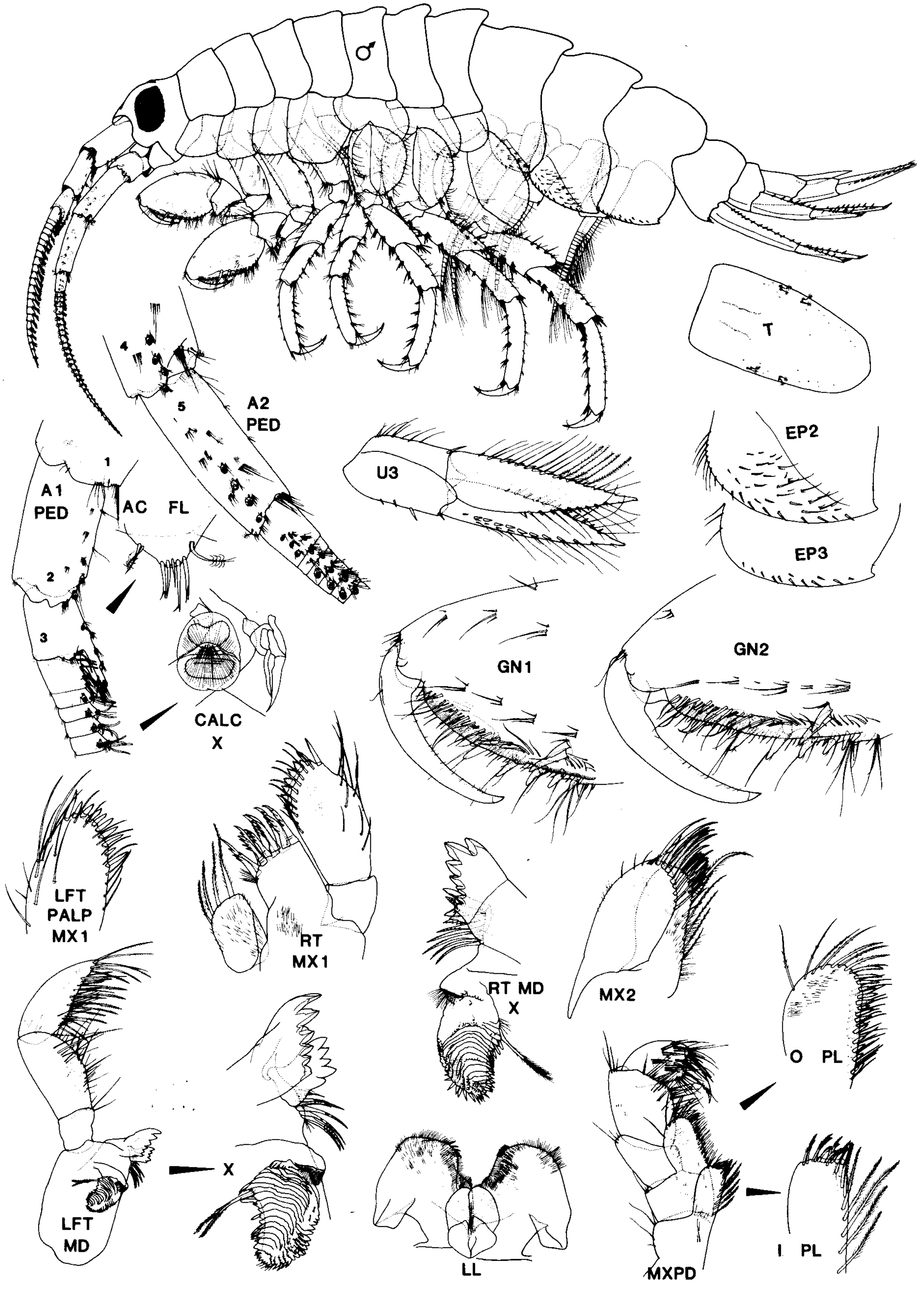


FIG. 5 *Calliopius carinatus*, new species. Witty's Lagoon, V. I., B. C. Male (9.5 mm); female (8.5 mm).

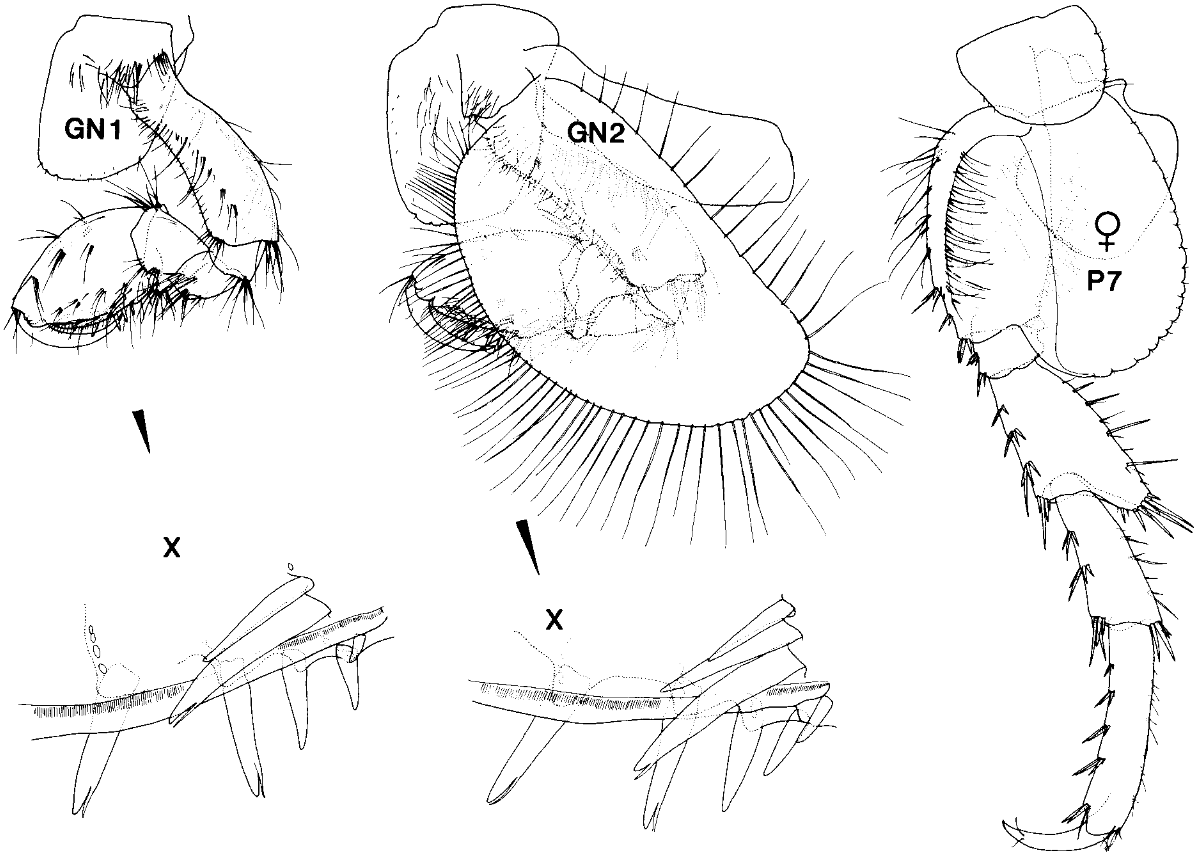


FIG. 6. ***Calliopius carinatus*** **new species. Witty's Lagoon, V. I., B. C. Female (8.5 mm).**

Diagnosis. Male (9.0 mm.): Body variously carinated or tuberculated on posterior peraeonal and pleonal segments. Head, eyes large, black, subrectangular. Antenna 1 2/3 length of antenna 2; flagellum with 22 segments; segment 3, peduncular process shorter than weakly callynophorate basal flagellar segment; accessory flagellum very short, triangular, apex with 4-6 short slender spines; calceoli small, in 2-3 posterior marginal and submarginal rows.

Lower lip, inner lobes distinct. Mandiblular palp segments 2 & 3 subequal in length, 3 lacking basal cluster of "A" setae; spine row with 5 blades. Maxilla 1, inner plate with 4 apical setae; right palp moderately broad, apex oblique, with 8 conical spines; left palp with 7 slender apical spines. Max-illa 2, inner plate with single slender facial seta. Maxilliped, outer plate relatively short, apical margin with ~8 curved setae; inner plate short; palp strong, segment 2 stout.

Coxal plates 1-4 short, subquadrate, gently convex below. Gnathopods 1 & 2, propods large, palmar margin strongly oblique, submarginally setose, longer than posterior margin, with 4-5 stout spines near posterodistal angle; 3-4 weak clusters of distal median facial setae .

Peraeopods 3 & 4 relatively long; segment 5 not shortened; dactyls strong. Peraeopods 5-7 distinctly increasing in length; bases somewhat dissimilar,that of peraeopod 5 distinctly smallest. Peraeopod 7, basis broadening posterodistally, hind margin irregularly crenulated; segment 4 slightly broadened; segment 6 slightly longer than basis, with 4-5 anterior marginal clusters of spines.

Pleon plate 2 with numerous slender facial and marginal spines, nearly all singly inserted. Pleon plate 3 with closely submarginal row of about 10 short spines, and a few supernumerary spines; hind corner acuminate. Uropod 1, rami unequal, much shorter than peduncle. Uropod 2, outer ramus ~2/3 length of inner ramus; apical spine elongate. Uropod 3, inner ramus relatively slender, both margins setose; outer ramus, outer margin with 8-10 pairs of short spines and setae.

Telson elongate, length about twice width, slightly narrowing distally, apex regularly rounded, spade-shaped.

Coxal gills 2-6 elongate sac-like, that of peraeopod 7 large, irregularly plate-like.

Female (8.5-11 mm). Gnathopods 1 & 2 much smaller and less robust, and peraeopods 5-7 shorter than in male. Brood plates very large, broad, margins strongly setose.

Etymology. From the Latin root "carina" or keel, with reference to the carinated body dorsum.

Distributional ecology. Known from eastern Prince William Sound, Alaska, to the central coast of Oregon. Common in the surf swash zone, mainly along rocky shores, from fully marine to mesohaline inshore waters. Usually associated with submerged plants and algae.

Taxonomic commentary. Materials at hand exhibit considerable morphological variation throughout the range. Specimens from outer coast and northern localities tend to be more strongly carinate (Fig. 7A). The species is most closely similar to *C. pacificus* (see Fig.40, p. 60).

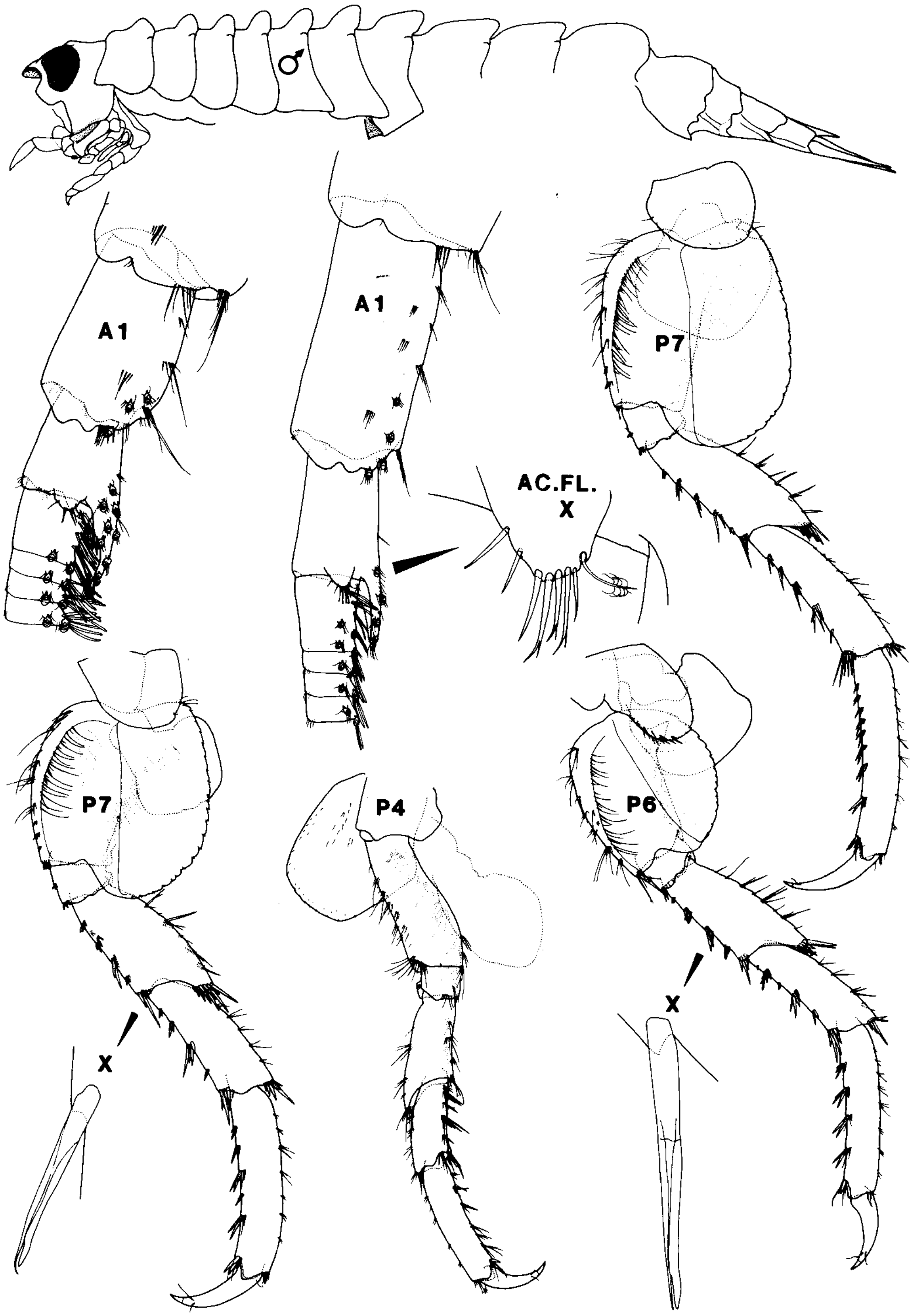


FIG. 7. ***Calliopius carinatus*, new species. Morphological variations. A. Neahkannie Beach (W53), Oregon. Male (10..5 mm); B. Oyster Bay (V22), Georgia Strait, B. C. Male (10.5 mm); C. Friday Harbor (F8), WA. Male (11.7 mm).**

Calliopius pacificus , new species
(Figs. 8, 9)

Calliopius laeviusculus (Kr.) Barnard, 1954: p. 8, pl. 8 (part)

Material Examined. 70 records - SE Alaska to Oregon. CMN collections, Ottawa.

ALASKA.

Southeastern Alaska. Prince William Sound entrances. ELB Stns, July, 1961: A80 (10); A99 (10); A98 (11); A121(1). Southeastern Alaska. ELB Stns, July, 1980: S8B2 (N. Chichigof I.) (19 females); S5B1 (1 female); ELB Stns, June-

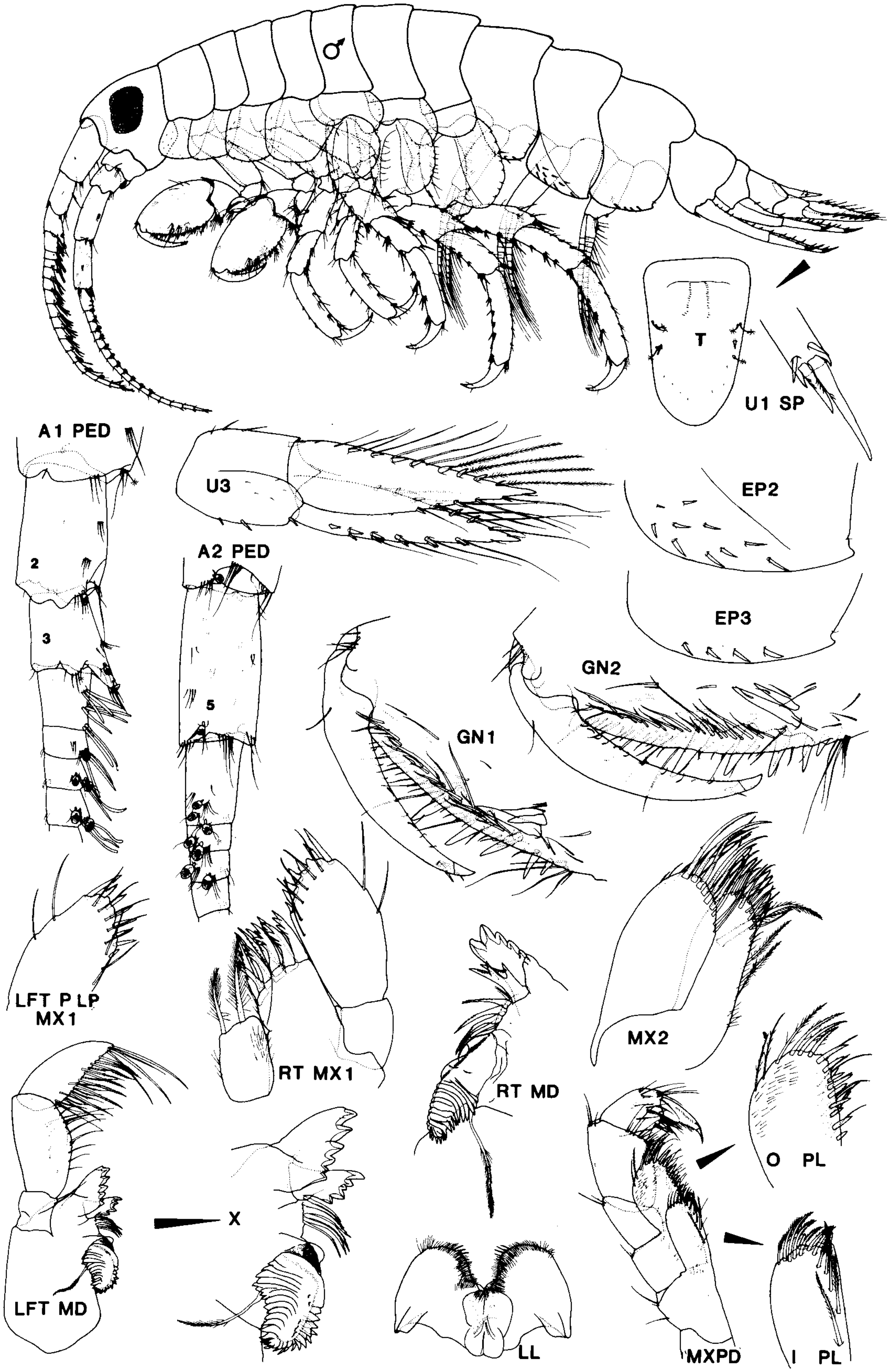


FIG. 8. *Calliopius pacificus*, new species. Off Selma Park (M5), Georgia Strait, B. C. Male (14.3 mm).

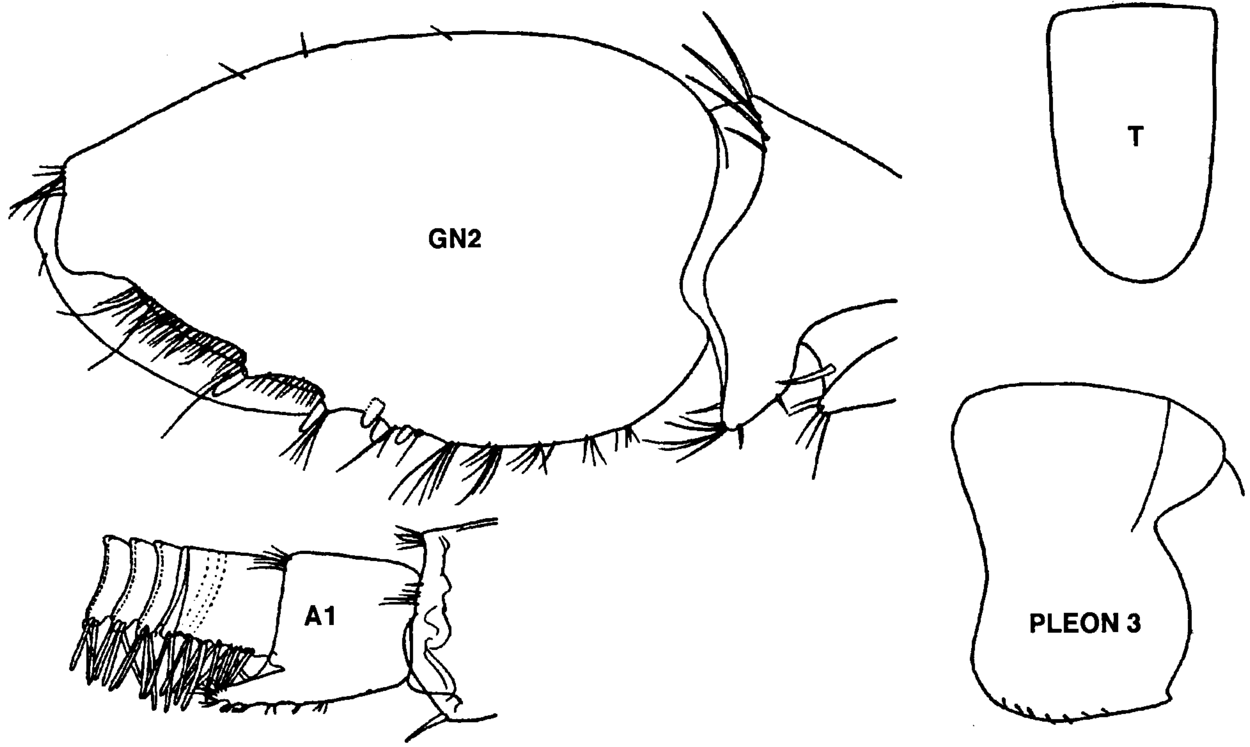


FIG. 9. ***Calliopius pacificus*, new species. Off Depoe Bay, OR. Male (10.0 mm) (after Barnard, 1954).**

July, 1961: A19 (45); A12 (1); A175 (10); A7 (Ketchikan)(3 specimens, slide mount).

BRITISH COLUMBIA.

Queen Charlotte Islands. ELB Stns, July-Aug., 1957: H8a (NE Graham Is.) (3); H5 (1); El (3); E14b (1 female ov.); E17-18 (NE Moresby Is.) (l).

North-central mainland coast. ELB Stns, July, 1964: H10 (Hecate Strait) (10); H7 (2); H4 (> 2); N11 (Queen Charlotte Strait) (25).

Georgia Strait. ELB Stns, July-Aug., 1955: M2 (N. of Powell R.) (2); M5 (Selma Park) - 3 specimens, slide mounts including male (14.3 mm), **holotype**; 2 female ov. (10.0 mm), **allotypes**; M8 - 1 female ov.; M11 - 1 female ov.; G2 - 10 females; Fraser R. Delta, May, 1979 - 1 female ov.

Vancouver Island, inner coast. ELB Stns., 1959: V17 (N. Johnstone Strait) - 1 female ov.; N18 (4); J. Carl Stn (Saturna I.), Aug., 1955 - 40 specimens; R. Long Stn, Saltspring Is. 1977 - 1 female.

Vancouver I., outer coast. ELB Stns, July-Aug., 1959: O3 (Quatsino Sd) (10); O7b (1 female ov); ELB Stn H44 (Bamfield), July, 1964 - 1 specimen.

Juan de Fuca Strait. ELB Stns, Aug., 1955: F4 (7); F5 (6); ELB Stn P716 (Esquimault), July, 1970 - 24 specimens; ELB Stn B5d, May, 1977 - 10 specimens; J. Carl Stn, Victoria, 1949 - 8 specimens; J. Carl Stn (Oak Bay) 1949 -7 specimens.

WASHINGTON:

San Juan Island. ELB Stn F8, July, 1955. - 1 male, 10 females, 1 slide mount.

Puget Sound. ELB Stns, July, 1966: W5 (Whidbey Is.) (10); W10 (Olympia) (60 females ov.).

OREGON:

ELB Stn W57 (Cape Perpetua), Aug., 1966 - 1 female ov.

Diagnosis. Male (4.3 mm): Body weakly carinate on posterior peraeon and pleon. Head, eye large, subrectangular. Antennae 1 & 2, peduncular segments nearly bare of setae. Antenna 1 slightly shorter than 2; flagellum ~16-segmented; peduncular segment 3, process very short, about 1/3 weakly callynophorate flagellar segment 1. Calceoli small, sparse, in double or triple posterior marginal and submarginal rows.

Mandibular palp segments 2 & 3 subequal; baso-facial cluster of setae lacking?; spine row with 5 blades. Maxilla 1, inner plate with 2 setae; right palp segment 2 very broad. Maxilla 2, inner plate slender, facial seta slender. Maxilliped, outer plate regular, apical margin with ~6 curved setae.

Coxal plates 1-4 small, squarish, gently convex below. Gnathopod propods relatively large and stout; palmar margins very oblique, submarginally setose, with 4-5 strong spines near posterodistal angle.

Peraeopods 3 & 4 relatively strong, dactyls powerful, nearly equal to half length of respective propods. Peraeopods 5-7 increasing distinctly in size distally; peraeopod 5, basis much smaller than in peraeopod 7; basis of peraeopod 7 slightly expanded and angled distally behind, margin distinctly crenulated; segment 4 not broadened; segment 6 distinctly longer than basis.

Pleon plate 2 with scattered single facial and submarginal

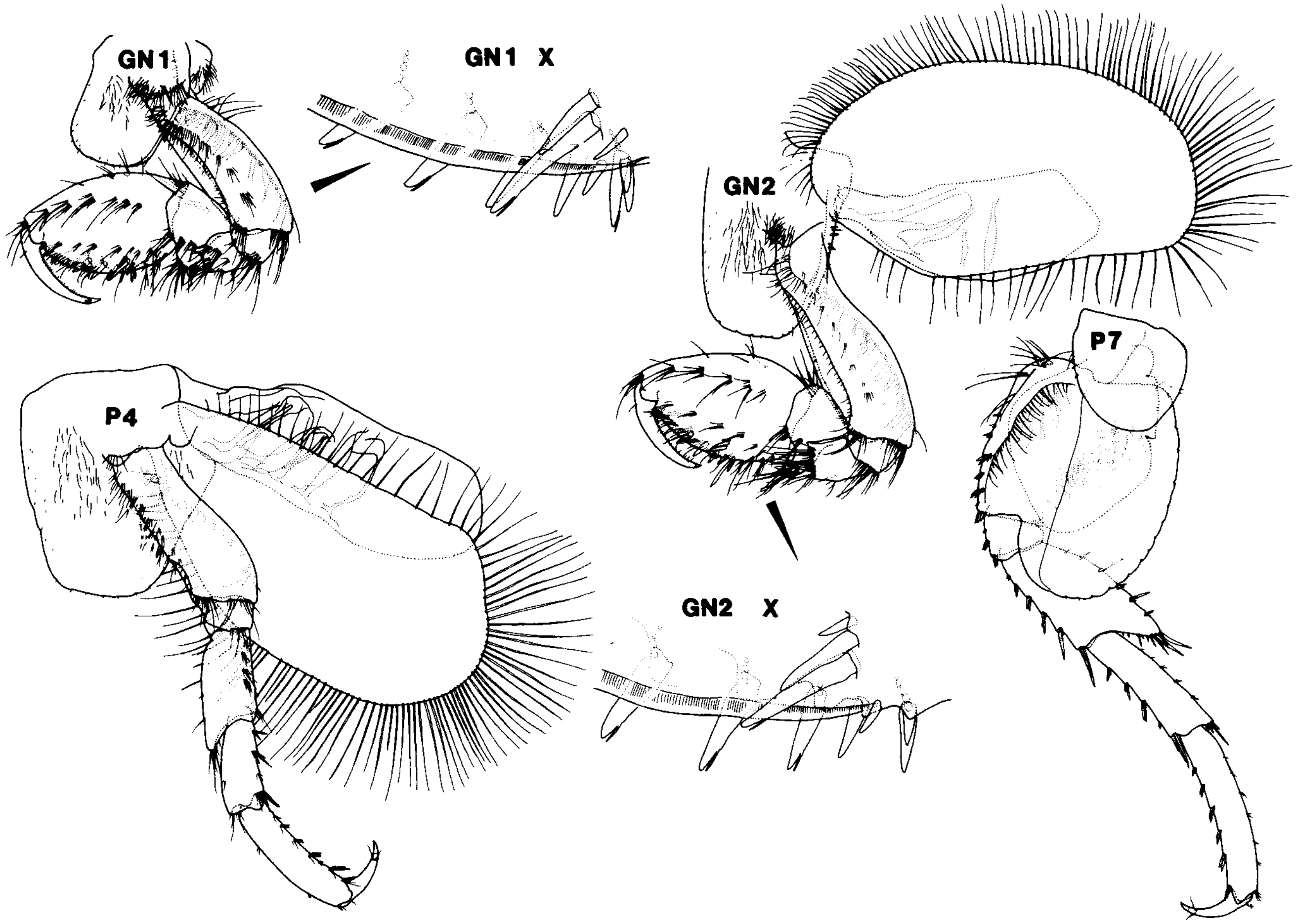


FIG. 10. ***Calliopius columbianus*** **, new species. Brown Bay (V20), V. I., B. C. Female (8.5 mm).**

spines. Pleon 3 with 4 stout submarginal spines; hind corner minutely mucronate. Uropod 2, length of outer ramus about 2/3 inner ramus; apical spine elongate. Uropod 3, inner ramus very broad basally, outer ramus, outer margin with spines and a few setae.

Telson, length less than twice width, slightly narrowing distally and rounded behind.

Female (10.0 mm). Dorsum less strongly carinated and gnathopods 1 & 2 distinctly smaller than in male.

Distribution. Known from Prince William Sound, Alaska to the central coast of Oregon. Dominant in inshore waters of bays and estuaries; apparently moderately euryhaline. Usually associated with submerged plants and algae.

Taxonomic commentary. The material of Wailes (1933) may be this species although the author gives no taxonomic details. This less strongly carinated form is not simply the male of *C. carinatus* because of the morphological differences outlined above and in the key (p. 9).

Barnard (1954) provides figures and limited distributional ecology but no taxonomic commentary. His offshore material checks out most closely with *C. pacificus* which is the most common regional form and thus must likely to occur in his limited material from one station.

Calliopius columbianus, new species
(Figs. 10, 11)

Calliopius laeviusculus (Kr.) Barnard, 1971: 10 (part)? Austin 1985: 589 (part).

Calliopius spp. Staude, 1987: 378 (part)?

Material Examined. ~90 specimens at 18 stations:

ALASKA.

Southeastern Alaska. ELB Stns, June-July, 1961: A22 (Sitka Sd) (2); A177 (Dall Is.) (1 male).

BRITISH COLUMBIA

North-central mainland coast. ELB Stns, 1964: H39 (S.Queen Charlotte Sd) (1).

South-eastern mainland coast. ELB Stn V6 (Burrard Inlet), 1978 - 1 female ov., 10 other specimens, slide mount, photo. Vancouver Island, inner coast. Pam Rock (Queen Charlotte Strait) (10 spms., slide mt.), Dec., 1977; ELB Stn V20 (Brown Bay) June, 1959 - Male (9.5 mm), **holotype**; female ov., **allotype,** (slide mounts); ELB Stn., 1955: G4 (2 females, slide); J. Carl Stn, Departure Bay July, 1938 (1); D.V. Ellis Stn, Saanich Inlet, Apr., 1965 (10 specimens, slide mount); Discovery Passage, May, 1965 (10); Stn B7 Victoria (Georgia Strait) (1 female, slide);

Outer coast. Barkley Sd, May, 1965 (1). Uncertain locations.

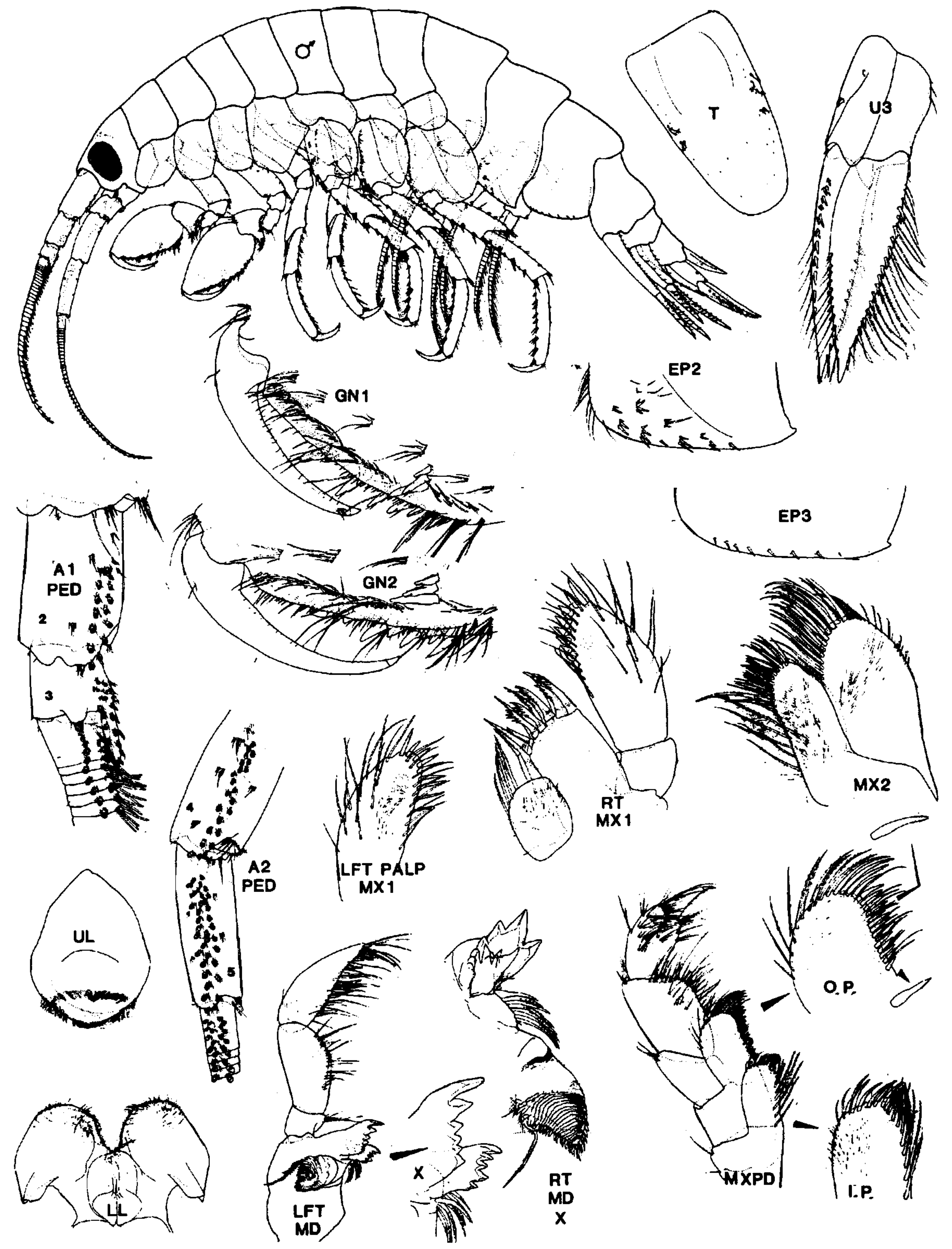


FIG. 11. ***Calliopius columbianus*, new species. Brown Bay (V20), Vancouver Island . Male (9.5 mm).**

1915-1937 (8 specimens, 2 slide mts.); JFLC Stn, Aug., 1938 (2). Coastal B.C., Apr., 1972 (8); Stn 760012, June, 1976 (1); E.Black Stn, May, 1981 (10, slide mount).

Diagnosis. Male (9.5 mm): Body very weakly carinated, on pleon only. Head, eyes large, slightly narrowing below. Antennae 1 & 2 moderate; peduncular segments nearly bare. Antenna 1, peduncular segment 3 very short, with strong distal process; accessory flagellum very short, subconical, with 4-6 apical setae; calceoli small, numerous, in 2-4 posterior marginal and submarginal rows; flagellum of ~40 short segments.

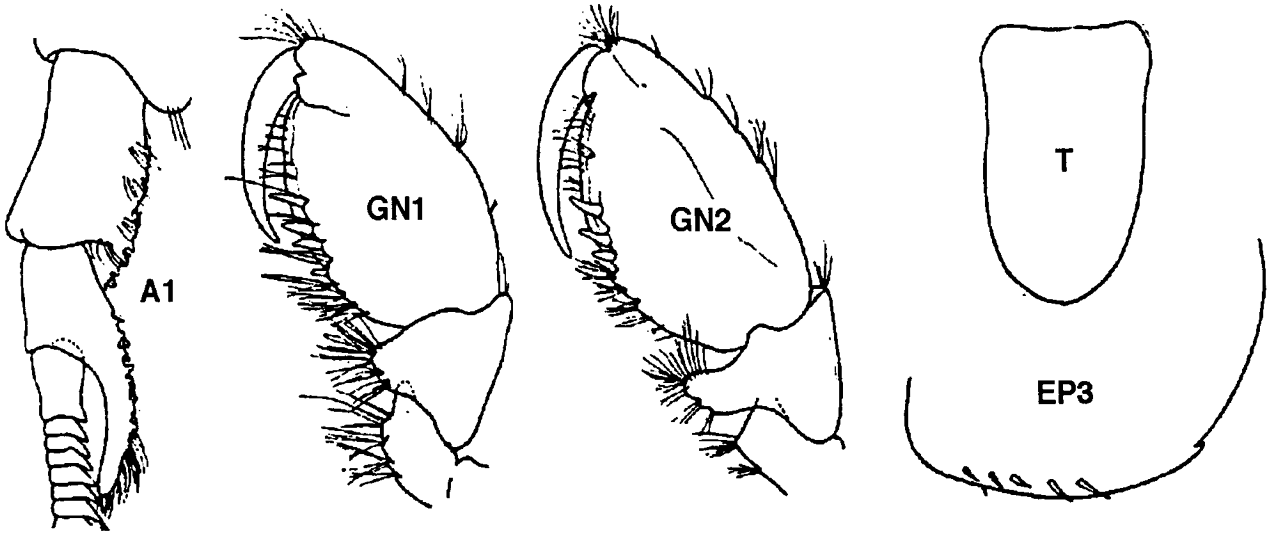


FIG. 12. ***Calliopius behringi*** **Gurjanova. Bering Sea. Female (8-10 mm). (after Gurjanova, 1951).**

Mandibular palp segment 3 subfalciform, distinctly longer than segment 2, with weak basal cluster of "A" setae; spine row with 7-8 blades; left lacinia 5-6 dentate. Maxilla 1, inner plate with 5 apical setae; right palp slightly broadened, oblique apex with ~10 stout spines, outermost longest; left palp slender, apex narrowly rounded, with 6-8 short slender spines. Maxilla 2, inner plate with single slender facial seta and several similar proximal inner marginal setae. Maxilliped, outer plate, apical margin with ~12 slender curved setae.

Coxae 1-4 subrectangular, longer than wide. Coxa 4 strongly tapering distally. Gnathopods 1 & 2, propods stout, palmar margins very oblique, longer than posterior margin, with 4-5 medium spines near posterior angle.

Peraeopods 3 & 4 slender; segment 5 not shortened. Peraeopods 5-7 slender, increasing in length posteriorly. Peraeopod 7, basis broadening posterodistally, hind margin not crenulate; segment 4 slender; segment 6 longer than basis, with 8-10 anterior marginal clusters of spines; dactyls slender.

Pleon segment 2 with 10-12 doubly or triply inserted submarginal and facial spine clusters. Pleon 3 with 7-8 submarginal spines; hind corner weakly acuminate. Uropod 1, rami slender, unequal, shorter than peduncle. Uropod 2, outer ramus 2/3 length of inner ramus, apical spines short. Uropod 3, inner ramus broad, both margins setose and spinose; outer ramus with outer marginal spines and setae.

Telson length 1.8 X basal width, narrowing distally, apex broadly rounded.

Etymology. The species name reflects its centre of distribution along the coast of British Columbia.

Distributional Ecology. Occurring sparsely from southeastern Alaska (Sitka) to southern Vancouver Island, BC (Victoria), from the swash zone along rocky, surf exposed shores, in variable (but mainly higher) salinities, subtidally to depths of 160 m, and deeper off Oregon (Barnard, loc. cit.)

Taxonomic commentary. *Calliopius columbianus* is most similar morphologically to *C. behringi* (Fig. 40, p. 60). These character states include the relatively smooth dorsum, elongate, multi-calceolate antennae, and strongly expanded bases of peraeopods 5-7. Relatively little variation was noted in instar sizes throughout its range. The species may occur in deeper water off Oregon (Barnard, 1971).

Calliopius behringi Gurjanova

(Figs. 12, 13, 14)

Calliopius behringi Gurjanova, 1951: 619, fig.420.—Barnard & Karaman, 1991: 313.
Calliopius sp. Fukida et al., 1971: 63, fig. 1?

Material Examined: 1 lot, CMN collections, Ottawa.
ALASKA:
Bering Strait. King Island. P. Slattery Stn., 1989 - female ov., male imm., slide mounts **(fig'd. specimens).**

Diagnosis. Female (8-10 mm- Kamchatka; 15 mm.- Commander Is.). Body carinated mid-dorsally on peraeon 6-7 and pleosome. Head, eyes large, broadly subovate, black. Antennae 1 & 2 intermediate. Antenna 1, flagellum with 40+ short segments; peduncular process elongate, variously curved, extending to flagellar segment 5 or 6; accessory flagellum very short, with 1-2 apical setae; calceoli very small, in 3-6 posterior marginal and submarginal rows.

Mandible, palp segments 2 & 3 subequal in length; segment 3 not falciform, virtually lacking basal cluster of "A" setae; spine row with 7-9 blades; left lacinia 5-6 dentate. Maxilla 1, inner plate with 3 apical setae; palp segment 2 very broadly expanded, nearly truncate apex with 9-10 short, stout spines. Maxilla 2, inner plate with single slender plumose facial seta, and 4 similar proximal marginal setae. Maxilliped, outer plate slightly broadened, apex with 12+ curved setae.

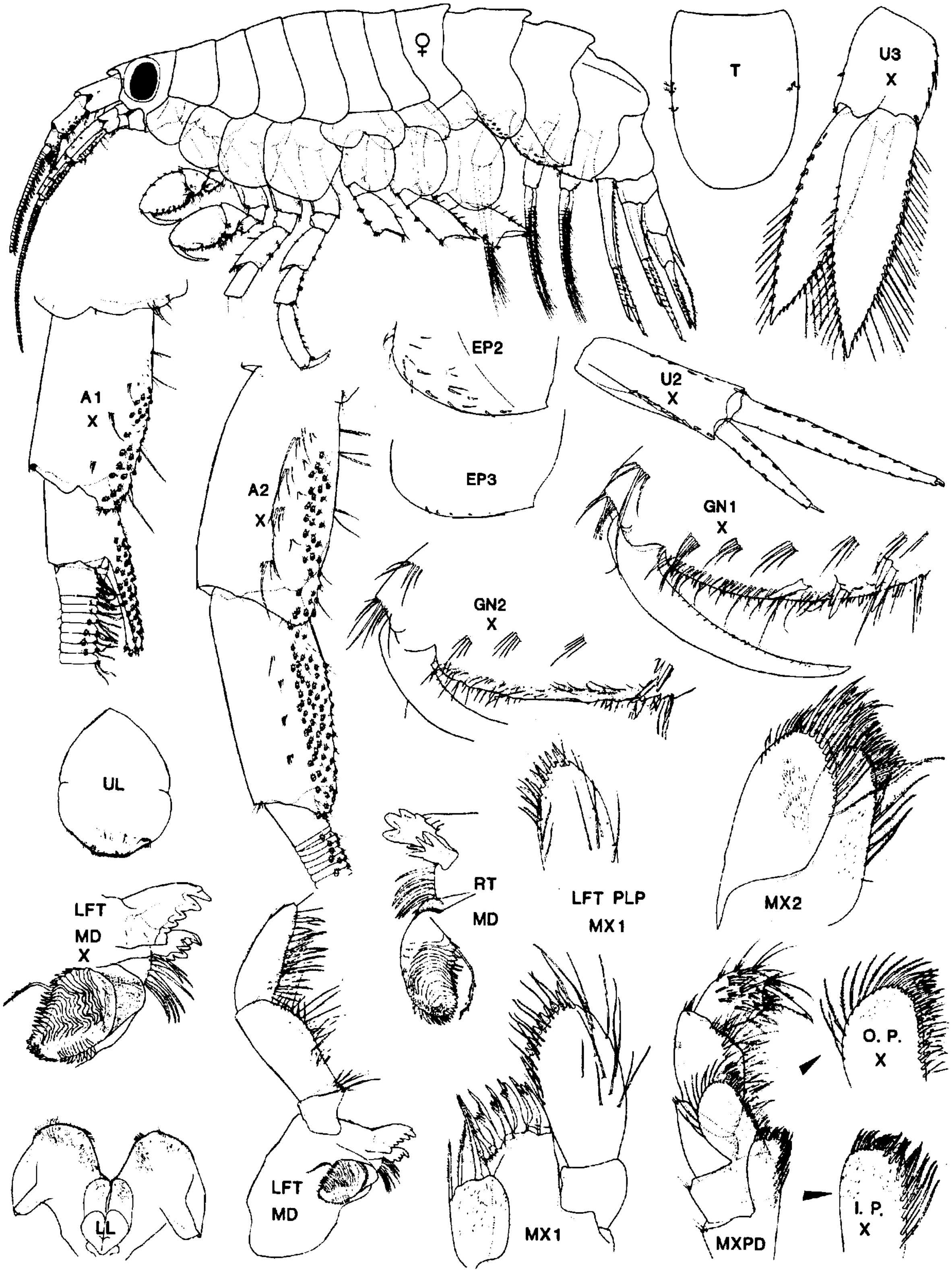


FIG. 13. *Calliopius behringi* Gurjanova. King I., Bering Strait. Female (10.0 mm).

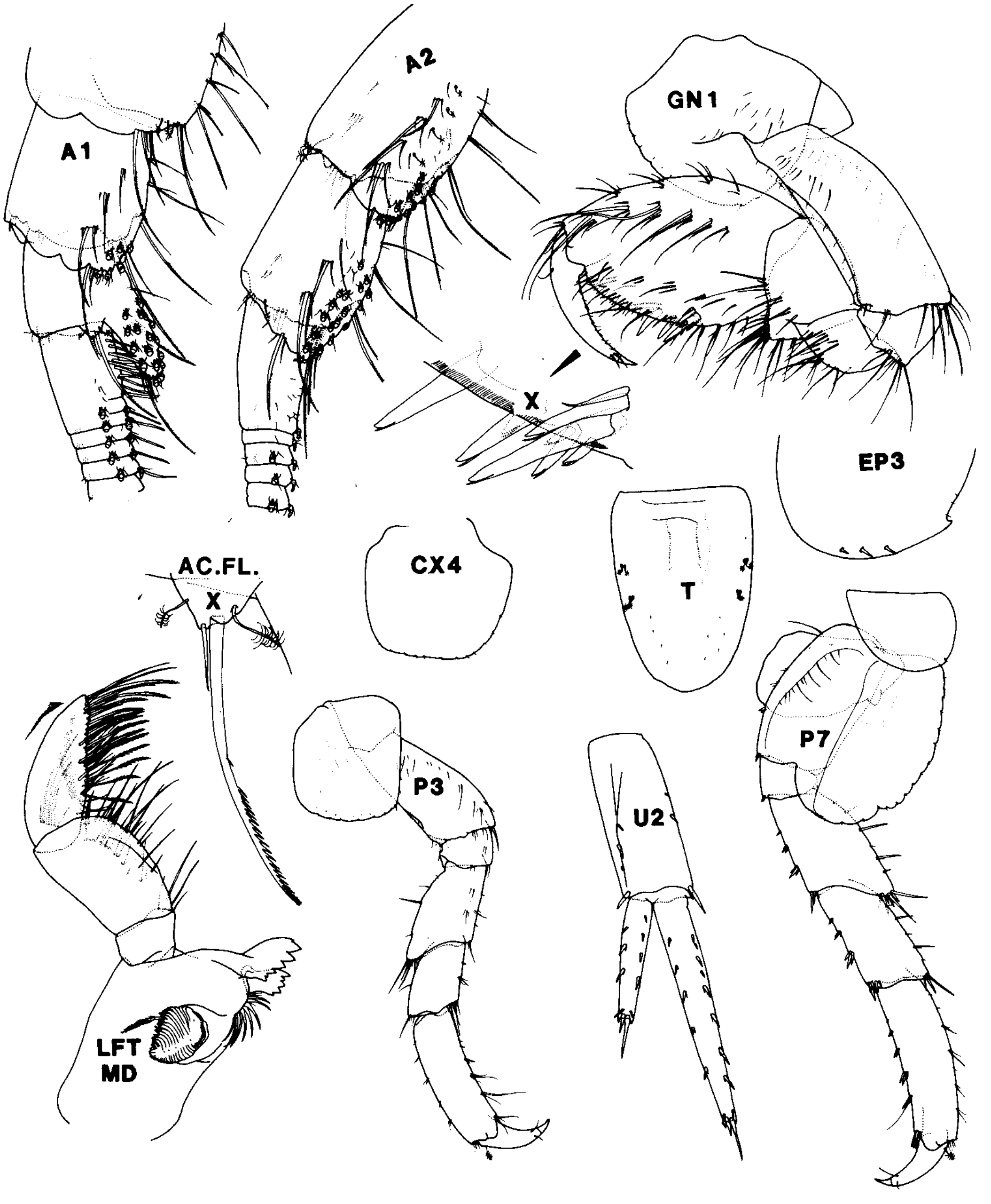


FIG. 14. ***Calliopius behringi*** **Gurjanova. King I., Bering Strait. Male imm. (5.2 mm).**

Coxae 1-4 relatively large, broad, lower margins slightly convex. Gnathopods 1 & 2, propods relatively small, with 5-6 distal median facial clusters of setae; palmar margin oblique, shorter than posterior margin, with 2-4 stout spines near posterodistal angle; dactyls relatively long.

Peraeopods 3 & 4 stout, segment 5 shortened, dactyls short. Peraeopods 5-7 homopodous in form, increasing in size posteriorly; bases very broad, strongly convex behind. Peraeopod 7, basis enlarging posterodistally, hind margin finely crenulate; segment 4 slightly broadened.

Pleon plate 2 with a few submarginal and facial spines, mostly single inserted; hind corner subquadrate. Pleon 3 with 5-4 submarginal single short spines; hind corner obtuse. Uropod 1, rami markedly unequal, shorter than peduncle. Uropod 2, rami slender, length of inner ramus about twice the outer, apices narrowly truncate, spines short.

Telson short, broad, length about 1.4 X width, apex broadly rounded.

Distribution. Bering Sea: Bering Strait, Commander Is., and Kamchatka Peninsula. Littoral zone.

Taxonomic commentary. Antennal peduncles of the immature male specimen are strongly setose posteriorly. The outline figure of *Calliopius* sp. from the Bering Sea region provided by Fukida et al. (1971) is not detailed, but is not incompatible with *C. behringi* as described above.

Oligochinus J. L. Barnard

Oligochinus Barnard, 1969b: 98.—Barnard & Karaman, 1991: 329.

Diagnosis. Body smooth. Rostrum short. Eyes medium, narrow, rectangular. Anterior head margin rounded, broadly notched below. Antennae medium; peduncles short, lacking calceoli and/or callynophore. Antenna 1 shorter than 2; accessory flagellum scale-like, with single large stiff apical seta; clusters of aesthetascs posteriorly on alternate flagellar segments.

Lower lip lacking inner lobes. Mandible normal; palp segment 3 subfalciform, shorter than 2; left lacinia 5-dentate?; right lacinia slender. Maxilla 1, palp normal, inner plate 4-setose. Maxilla 2, inner plate with submarginal and single large facial setae. Maxilliped, outer plate small, palp ordinary, not raptorial.

Coxae 1-4 medium, deeper than wide. Gnathopods weakly subchelate, subsimilar; propod and carpus short; palm oblique, posterior angular spines stout.

Peraeopods 3 & 4 short, stout, spinose; segment 5 shorter than 4; dactyls short. Peraeopods 5-7 regularly homopodous, increasing slightly posteriorly.

Pleon plates 2 & 3 shallow, rounded below, lower margin spinose, hind margin serrate. Uropods 1 & 2 short, stout, rami much shorter than peduncles, marginally and apically spinose. Uropod 1, rami subequal. Uropod 2, outer ramus the shorter. Uropod 3 short, rami broad-lanceolate, margins spinose and setose

Telson short, broad, apex notched. Coxal gills simple, not pleated.

Taxonomic and distributional commentary. *Oligochinus* is apparently monotypic and endemic to the Pacific coast of North America. It is not close to other N. American genera, but is least remote from *Laothoes* (Fig. 39, p. 58).

Oligochinus lighti J. L. Barnard
(Fig. 15)

Oligochinus lighti Barnard, 1969b: 98, figs. 8, 9.—Barnard, 1975: 115, plate 78.—Austin, 1985: 589.—Staude, 1987: 378, fig. 18.13.—Barnard & Karaman, 1991: 329.

Material Examined. Approx. 110 specimens, mostly mature females, in 33 lots. CMN collections, Ottawa.

ALASKA:
Bering Sea.Aleutian Islands (Amchitka Is.). C. E. O'Clair Stn, 1973: B2 (Banjo Pt.) - 3 specimens; IA2(4).
Southeastern Alaska. ELB Stns, July, 1980: S11B2 (NW Chichigof I., north of Sitka) - 2 specimens, photo; S7B3 (2)

BRITISH COLUMBIA:
Queen Charlotte Islands. ELB Stns, 1957: H11 (Masset Hbr.) (2); E21 (North Pt., Moresby I.) - 3 specimens.
North-central mainland coast. ELB Stns., July, 1964: H13 (Prince Rupert) (1); H35 (FitzHugh Sd.) (1).
Vancouver Island, inner coast. ELB Stn, 1955: G13 (north of Nanaimo) - 1 specimen.
Vancouver Island, outer coast. C. Lobban Stns, 1971: CL1022 (Wickaninnish Bay) - 91 specimens, 4 slide mounts; CL1004 (70). C. Lobban Stns., 1971: CL1037 (70); CL1036 (5); 1976-157, Apr., 1976; D. Kittle Stn 73-128, 1972 (8); R.Anderson, 1976 (3); C. Levings Stn, 1975 - 1 female; R. Lee Stn. 5926, 1971 - 1 female.
Vancouver I., south end. ELB Stns, June-July, 1976: B28 (3); B3 (16 specimens, slide mount). ELB Stn, 1970: P704 (4); P719 (Cape San Juan) (2).
Juan de Fuca Strait (Victoria region). ELB Stn, Aug., 1955: F5 (1); D.V. Ellis Stn 5, 1979 (2); R. Long Stn, Victoria, 1977 - 4 females ov.

OREGON:
K. Conlan Stns, Sunset Bay, 1986: 06-9 (6), 06-8 (2).

Diagnosis. Female (8.0 mm)(not fig'd): With the characters of the genus, described as in Barnard, 1969b.

Antenna 1, accessory flagellum with single large stiff apical seta.

Gnathopods 1 & 2, propods subrectangular, posterior margins with 3-4 clusters of setae.

Coxae 1-4, lower margin strongly convex and lined with short spines. Peraeopods 5-7, bases broad, posterior margin strongly convex.

Pleon plates 1 & 2, spinose along lower margin. Uropod 1, outer margin of peduncle with 12-15 stout spines.

Male (5.0 mm): No fully mature males were detected in material examined and are apparently not present in largely summer collections of FHL from Puget Sound (Staude, pers. com.). In the male examined aesthetascs were slightly longer, the slopes of the palms of gnathopods 1 & 2 more oblique, and the telson slightly less deeply notched than in the female.

Distributional Ecology. Recorded sparsely from the Aleutian Islands, Southeastern Alaska (Sitka region), Queen Charlotte Islands, and along the outer coast of Vancouver Island, Puget Sound (Armstrong et al, 1977) and Juan de Fuca strait, south through Oregon to Central California (Pt. Conception). Nestles in *Phyllospadix* clumps and in kelp (*Egregia*) holdfasts, at and immediately below LW level, mainly along surf-exposed and fully marine (>27‰) cold-water coasts.

Taxonomic commentary. Some variation was noted throughout the range of this species, but of a minor nature, not suggesting more than one species is present. The apparent absence of males in summer collections suggests that mature animals are reproducing in late winter and spring in the southern part of its range. *Oligochinus lighti* is a unique species, unlike all other intertidal forms, and differs especially in the notched telson (see phenogram, Fig. 39, p. 58).

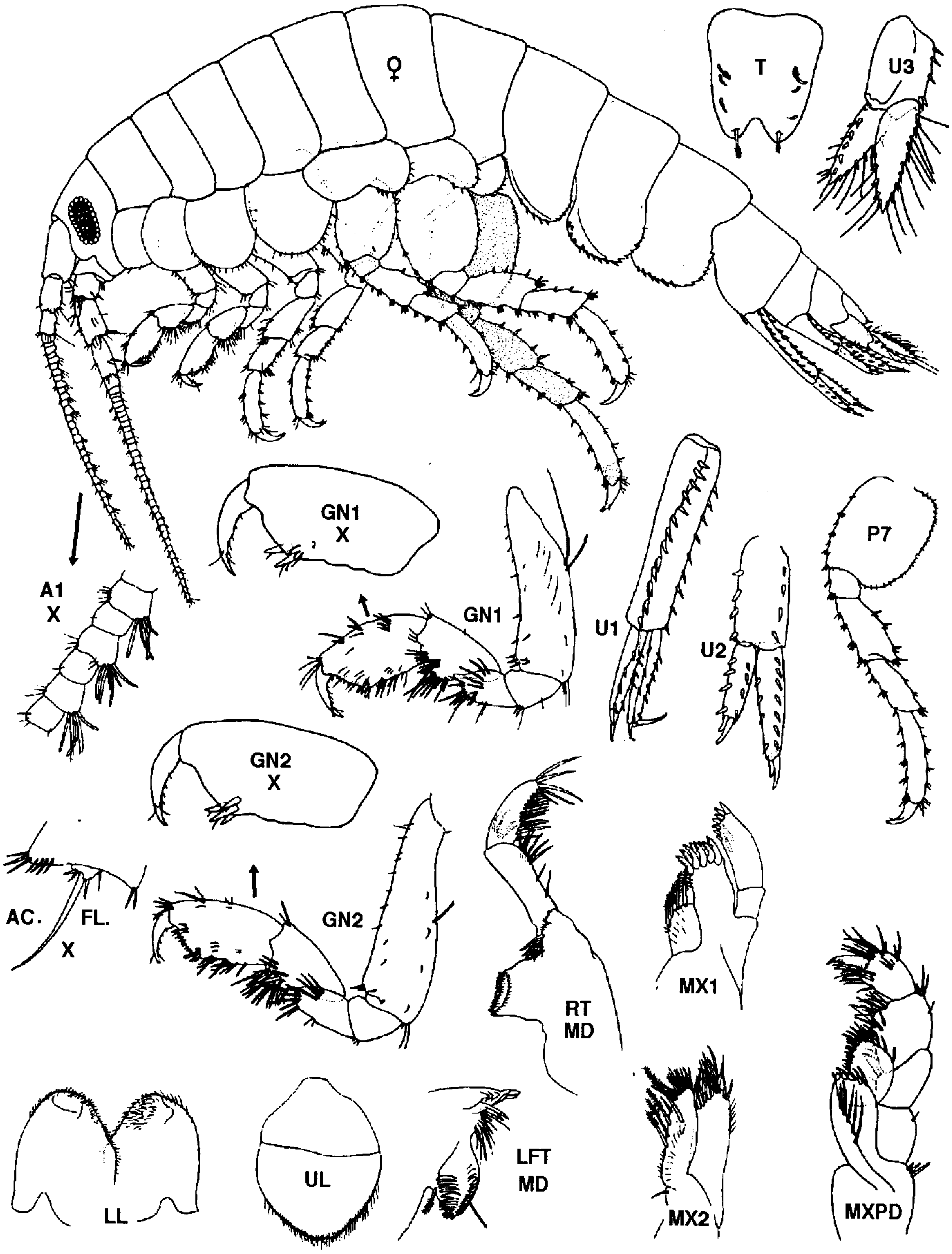


FIG. 15. *Oligochinus lighti* J. L. Barnard. Hazard Canyon Reef, CA. Female (8.0 mm). (after Barnard, 1969b).

Paracalliopiella Tzvetkova & Kudrjaschov

Leptamphopus G.O. Sars, 1895: 458 (part).—Gurjanova, 1951: 311 (part).
Calliopiella Barnard, 1969a: 175 (part).
Callaska J. L. Barnard, 1978: 38.
Paracalliopiella Tzvet. & Kudrj., 1975: 14.—Karaman & Barnard, 1979: 114.—Barnard & Karaman, 1991: 330.

Type species. *Leptamphopus litoralis* Gurjanova, 1938.

Other North Pacific species. *Paracalliopiella pratti* (Barnard, 1954), Coyle & Mueller, 1981; *P. bungei* (Gurjanova, 1951); *P. shoemakeri*, new species (p. 42); *P. haliragoides*, new species (p. 45); *P. beringiensis*, new species (p. 32); *P. pacifica* Tzvetkova & Kudrjaschov, 1975; *P. slatteryi*, new species (p. 37) (female only); *P. tzvetkovae*, new species (p. 35) (male and female) (=*P. litoralis* Tzvetkova & Kudrjaschov, 1975); and *P. kudrjaschovi*, new species (p. 40).

Diagnosis. Body smooth to strongly carinated mid-dorsally on posterior peraeonal segments and pleon. Rostrum short to medium strong. Eyes large, pigmented, larger in male. Inferior antennal sinus shallow, notch small, inferior head lobe little or not produced anteriorly. Antenna 1 shorter than 2; calceoli lacking. Antenna 1, peduncle short; accessory flagellum minute; aesthetascs clustering posteriorly on alternate flagellar segments.

Upper lip broadly rounded. Lower lip, inner lobes weak or lacking. Mandible, palp segment 3 usually shorter than 2, with basofacial cluster of "A" or "B" setae; left lacinia 5-6 dentate, right lacinia trifid. Maxilla 1, inner plate with 2-8 apical setae; outer plate with 11 apical spines, innermost

KEY TO NORTH PACIFIC SPECIES OF *PARACALLIOPIELLA*

1. Body strongly carinated on peraeon segments 6 & 7, and pleon segments 1 & 2; uropod 3, inner ramus, inner margin with spines and setae, usually strongly .setose .... 2.
—Body essentally smooth above or weakly carinated only on peraeon 7 and pleon segments 1 & 2; uropod 3, inner ramus, margins spinose, rarely with a few setae .... 4.

2. Rostrum strong, ~= antennal peduncle 1; pleon segment 3 strongly carinate.. *P. haliragoides* n. sp. (p. 45)
—Rostrum short, <1/2 length of antennal peduncle 1; pleon segment 3 weakly carinate .... 3.

3. Gnathopod 2, propod broadening distally; telson subovate, width <length .... *P. bungei* (Gurj.) (p. 40)
— Gnathopod 2, propod margins subparallel; telson suborbicular, width = length *P. shoemakeri* n .sp. (p. 42)

4. Peraeon 7 and pleon segments 1 & 2 weakly carinate .... 5.
—Peraeon 7 and pleon segment 1 & 2 essentially smooth above .... 6.

5. Uropod 3, rami length <1.5X peduncle, inner margins with a few setae; gnathopod 2, carpus with broad shallow posterior lobe; gnathopods 1 & 2, palms subtransverse .... *P. slatteryi* n. sp. (p. 37)
—Uropod 3, rami length >1.5X peduncle, all ramal margins spinose; gnathopod 2, carpus with narrow, deep posterior lobe; gnathopods 1 & 2, palms oblique .... *P. pacifica* n. sp. (p. 32)

6. Gnathopods 1 & 2 (female), carpus slender, subequal in length to propod; gnathopod 1 (male) not larger than gnathopod 2 .... 7.
—Gnathopods 1 & 2 (female), carpus short, deep, shorter than propod; gnathopod 1 (male) distinctly larger than gnathopod 2 .... 8.

7. Gnathopod propods, distal facial setae singly inserted; mandibular palp segment 3, length < segment 2. .... *P. beringiensis* n. sp. (p. 32)
—Gnathpood distal facial setae clustered; mandibular palp segment 3 =2.... *P. tzvetkovae* n. sp. (p. 35)

8. Antennae 1 & 2, flagellum medium (25+ segments); gnathopod 1 (female), carpus and propod relatively slender, shallow, carpus length >1.5 X width (depth).................... *P. kudrjashovi* n. sp. (p. 40)
—Antennae 1 & 2, flagellum short (<20 segments); gnathopod 1 (female), carpus and propod relatively short, deep, carpus length <1.5 X width (depth) .... 9.

9. Peraeopods 5-7, segment 4 broad, stout, length slightly longer than width; mandibular palp segment 3 , length > segment 2; uropod 3, inner ramus longer than peduncle .... *P. litoralis* (Gurj.) (p. 30)
—Peraeopods 5-7, segment 4 regular, length ~2X width; mandibular palp segment 3 shorter than segment 2; uropod 3, inner ramus not longer than peduncle .... *P. pratti* (Barnard) (p. 28)

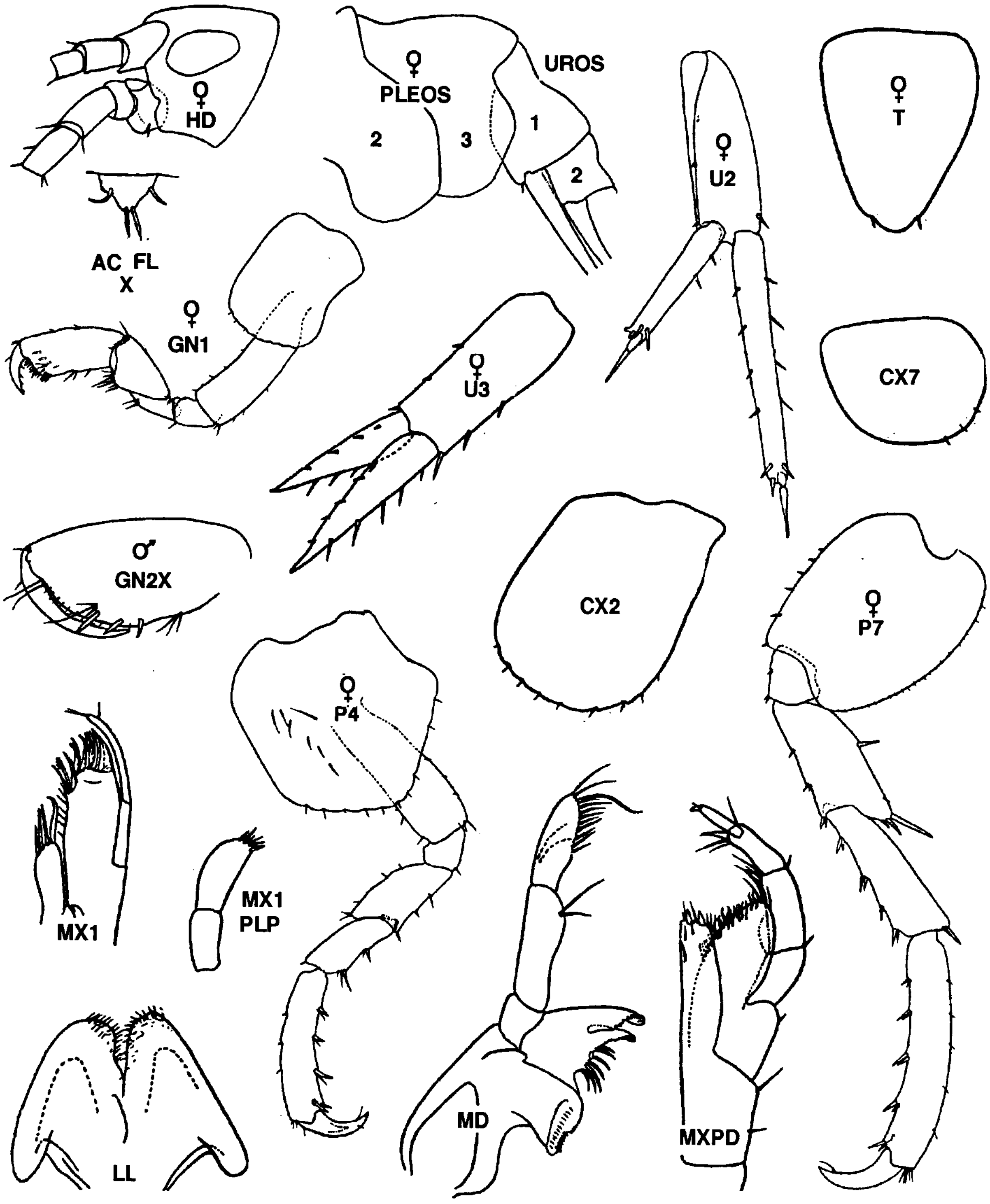


FIG. 16. ***Paracalliopiella pratti*** **(Barnard). Coos Bay, Oregon. Female (5.0 mm) (after Barnard, 1954).**

slender, finely pectinate, outermost heavy, coarsely pectinate; palp segment 1 elongate, right palp segment 2 not broadly expanded. Maxilla 2, inner plate narrow, with 3-6 marginal or submarginal facial setae. Maxilliped, inner plate tall, inner margin setose, apex with 2(3) conical spines; outer plate broad, inner margin angled distally and apex medially incised; palp strong, not raptorial in form.

Coxae 1-4 broad, medium deep, increasing posteriorly. Gnathopods 1 & 2 subsimilar; in female: weakly subchelate, propods narrow; carpus slender not longer than propod, hind lobe shallow; in male: gnathopods strongly subchelate, gnathopod 1 usually larger; propods large, deep, with strong palmar spines; carpus short, deep, lobate behind.

Peraeopods 3 & 4 regular, segment 5 often slightly shorter than 4; dactyls medium. Peraeopods 5-7 regularly homopodous, increasing posteriorly; bases intermediate, rounded behind and distally lobate; segment 4 variously broadened; dactyls medium.

Pleon plate 3, hind margin smooth, rounded, lower margin spinose, hind corner obtuse. Uropods 1 & 2, rami narrowly lanceolate-linear, margins strongly serially spinose; outer ramus distinctly the shorter. Uropod 3, rami lanceolate, attenuating distally, usually longer than peduncle; inner ramus slightly the larger, margins spinose and/or weakly setose. Telson entire, narrowing distally, apex narrowly rounded or truncate.

Coxal gills plate-like, not pleated in male. Brood plates very broad, marginally setose.

Taxonomic commentary. Members of the North Pacific endemic genus *Paracalliopiella* differ from *Calliopius* mainly in the generally smaller body size, more pronounced sexual dimorphism of the gnathopods (weakly subchelate in female), broader and deeper coxal plates, more spinose and less setose uropod 3; shorter distally narrowing telson, and lack of antennal peduncular process and calceoli. *Paracalliopiella* overlaps considerably with *Oligochinus* which also has clusters of aesthetascs on alternating flagellar segments (p. 24). Strongly carinate members may prove distinctive at the subgeneric or perhaps even full generic level (Fig. 41, p. 60).

Paracalliopiella pratti (J. L.Barnard)
(Figs. 16, 17)

Calliopiella pratti (?) J. L. Barnard, 1954: 6, pls. 6, 7.—Barnard, 1969b: 95, figs. 7-8.—Barnard, 1975, figs. 71 (7); 72 (29).—Staude, 1987: 378.
Callaska pratti J. L. Barnard, 1978: 38.
Paracalliopiella pratti (Barnard) Coyle & Mueller, 1981: 10.—Barnard & Karaman, 1991: 331.
Apherusa sp. Park, 1961: fig. 53, & key.

Material Examined: About 1500 specimens in 105 lots. CMN collections, Ottawa (no specimens figured).
ALASKA:
Kenai Peninsula. ELB Stns, June-July, 1961: A130 (15); A136 (4); A129 (4); A131(70).
Prince William Sound. ELB Stns, June-July, 1961: A93 (1); A92 (2); A121 (32).
Southeastern Alaska. ELB Stns. June-July, 1961: A164(31); A168 (4); A171-2(2); A18 (50); A25 (4); A23 (15); A83 (Cordova) (l); A81 (8 females, slide mount); A80 (54); A75 (20); A68 (19); A67 (32); A43(10); A66 (1); A61-62 (1); A57 (29 specimens, slide mount); A48 (29); A32 (3); Al9 (54 specimens,2 slide mounts); A20 (6); A30 (23 specimens, 2 slide mounts); A22 (15); A18 (50) A15 (3); (2); A8 (1); A6(3); A3 (Dall Is.) (39). ELB Stns, July 1980: S11Bl (~52 females ov., photo); S11B3 (1); S8B2(7); S7Bl (30); S7B4 (2); S6L2 (1); S5Bl (1); S4B4 (l female,photo); S4Bl (12); S16Bl (1 female ovig.,photo); S19Bl (l); S18Bl (2 females ov., photo); S20B2 (2 females ov.).

BRITISH COLUMBIA:
Queen Charlotte Islands. ELB Stns, July-Aug., 1957: H13 (NE coast Graham I.); H12 (l00 specimens, slide mount); H2a (30); Wl (l); H11(15); H9 (10); H8a (4); H8b (3); W2 (25); H10 (80); H4a (15); E5 (13); W9 (40); Wll (30); E14a (16); E17 (1); E17-18 (8); E9 (3);W15b (9); E25 (Juan Perez Sound, Masset I.) (11).
North-central mainland coast. ELB Stns, July-Aug., 1964: H13(Prince Rupert) (20); H16 (5); H7 (50); H29 (9); H5 (1); H32 (4); H3 (8); H33 (5); H53 (80); H56(17); H50 (11); H57 (40); H35 (30); Hl (55 spms, slide mount); H46, (2); H39 (1);H65 (100). ELB Stns., July, 1959: Nl(50); N6 (20); N11 (30); N18 (3); N16 (100).
Southeastern mainland coast. ELB Stns, Aug., 1955: M2 (3); M11 (White Rock) (19).
Vancouver Island,inner coast. ELB Stns, July-Aug., 1959: V4b (Hope Is.) (40); V5 (20); V7 (25); V10 (35); V11 (43); V17(32); V18 (~100); Vl9 (32); V20 (70). ELB Stns, May, 1977: B4(3); B4a (60); ELB Stns, Aug.,1955: G2 (46); G4 (Comox) (l).
Vancouver I., outer coast. ELB Stns, Aug., 1955: P4 (5); P6c (20); P8(l); P7 (14); P9 (1). ELB Stns, July, 1959: O1 (Cape Scott) (~20); O4 (14); O3 (4); O5 (2); O11 (~25); O13 (6) ELB Stn,1975: P5a (13); 5b (5); 5c (4); 5d (17); P17a (2); P24 (1). ELB Stns, July, 1976: B7 (161 spmns, slide mount); B3 (47); B5 (4); B12b (4); B11b(l); B13 (fem-ale ov., slide mount); B28 (21). ELB Stns, 1977: B4 (slide mount); Bl9b (1).
Vancouver I., southwestern coast. ELB Stns, July, 1970: P710 (1); P712 (10); P714 (1). ELB Stn, 1964: H40 (Port Renfrew)(150).
Strait of Juan de Fuca. ELB Stns, Aug., 1955: F6 (22); F5 (30). F4(17); F3(16); Fl(30); F2(9); F2a (William Head((1). ELB Stns, July, 1970: P715 (8); P716 (Esquimalt) (2); P717 (4). ELB Stn B6a, May, 1977 (~100).

WASHINGTON & OREGON:
Strait of Juan de Fuca & Puget Sound. ELB Stns, July-Aug., 1966: W42 (Shipwreck Pt.) (10); W36 (35-40 specimens, slide mount), W35 (~20); W34 (9); W44 (4); W30 (24);W7 (7);W8 (Tacoma) (4).
Olympic Peninsula. ELB Stns, July, 1966: W40 (Mukkaw Bay) (2); W16 (Westport)(l).
Oregon outer coast. ELB Stns, Aug., 1966: W66 (Cape Meares) (3); W61 (1); W60 (~80); W58 (1); W57 (21); K.Conlan Stns, Coos Co., July,1986: 06-11 (6); 06-2 (many); 06-10 (13 specimens, 2 slide mounts).

Diagnosis. Female (5.0 mm): Body small, deep, smooth above. Eyes very deep, subreniform. Head, rostrum short; anterior head lobe emarginate; inferior antennal sinus broadly notched. Antenna 1 ~ 2/3 length of antenna 2; peduncle very short; segment 3 short; accessary flagellum minute, shallow, rounded apex with 2-3 setae; flagellum ~18-segmented.

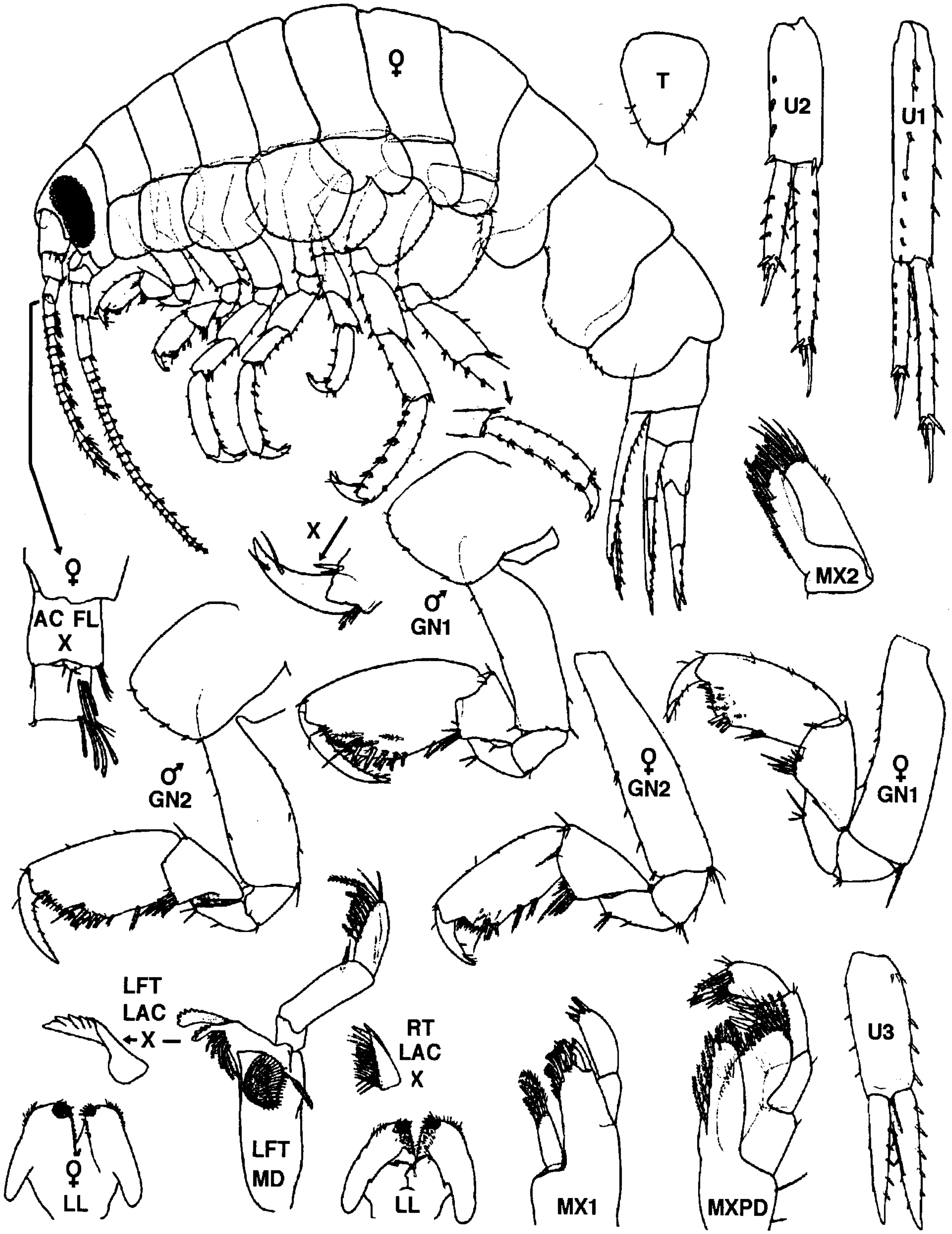


FIG. 17. *Paracalliopiella pratti* (Barnard). Near Carmel Pt., CA. Female (4.2 mm); male (3.9 mm). (after Barnard, 1969b).

Lower lip lacking inner lobes. Mandible, palp segment 3 shorter than 2; left lacinia 5-dentate; right lacina trifid, body apparently finely setulose. Maxilla 1, inner plate with 4 apical setae. Maxilla 2, inner plate with 3 submarginal plumose setae. Maxilliped, inner plate taller than broad, inner margin with 6-7 plumose setae; outer plate not unusually broadened or distally incised, apex with 6-7 curved setae; palp segment 2 relatively short.

Coxal plates 1-4 relatively short and wide, subquadrate, weakly scalloped below. Gnathopods 1 & 2 subsimilar; propods subrectangular; propod of 1 slighter the deeper and stronger; oblique palm much shorter than straight hind margin that is armed with 1-2 setal clusters; carpus shorter and deeper than propod, hind lobe shallow, setose.

Peraeopods 3 & 4, segment 5 little shorter than 4; dactyls stout. Peraeopod 5 markedly smaller than subequal peraeopods 6 and 7; segment 5 reduced. Peraeopods 6 & 7, bases not very broad, hind margins slightly convex, lower lobes shallow; segment 6 with 5 anterior marginal clusters of spines; dactyl moderately strong.

Pleon plates 2 & 3, lower margins with 4-5 spines; hind corner of pleon 3 broadly obtuse. Uropods 1 & 2, outer ramus distinctly the shorter, dominant apical spine more than twice length of others. Uropod 3, rami spinose marginally, inner ramus not longer than peduncle.

Telson normally spade-shaped, little longer than wide; apex sharply rounded.

Male (to 3.9 mm): Gnathopods subchelate, unequal in size and form; carpus shorter and deeper than in female. Gnathopod 1 the larger; propod powerful, 50% longer than deep, palm oblique, convex, slightly emarginate near midpoint; medial face of propod with 5 stout distal marginal spines and a few singly inserted submarginal setae. Gnathopod 2, propod slightly deeper and stronger than in female, posterodistal angle with 2 clusters of spines, hind margin with single setal cluster; dactyl setulose behind.

Distributional ecology. *Paracalliopiella pratti* occurs commonly from the Kenai Peninsula, Prince William Sound and southeastern Alaska, southward through British Columbia, Washington and Oregon to central California. The species is not uncommon in the outer Puget Sound region (Staude, pers. comm.). The animals occupy a variety of habitats through a wide range of temperature (6.3°C-15.9°C) and salinity, from brackish to fully marine. The species is usually associated with submerged plants and algae, organic debris and other substrata, at and just above the LW level, along both surf-exposed and semi-protected shores.

Taxonomic commentary. On the North American Pacific coast, *Paracalliopiella pratti* is unmistakable in its small size and morphological features. It is most closely related to *P. litoralis* of the Asiatic Pacific coast, but is distinctive in its less robust peraeopods and shorter mandibular palp (see key to species, p. 26, and phenogram, Fig. 41, p. 60).

Paracalliopiella litoralis (Gurjanova)

(Figs. 18, 19)

Leptamphopus litoralis Gurjanova, 1938: 311, fig. 26.—Gurjanova, 1951: 615, fig. 418.—Bulycheva, 1957: 100—Tzvetkova, 1967: 170.
Paracalliopiella litoralis (Gurjanova) Tzvetkova & Kudrjaschov, 1975: 17, fig. 2.—Barnard & Karaman, 1991: 330 (part).

Diagnosis. Female (to 5.0 mm): Body smooth above. Head, rostrum medium. Eyes large, subrectangular. Antennae short, flagella 13-20 segmented. Antenna 1 the shorter, accessory flagellum very short (<1/2 flagellar segment 1), apex rounded, with 2 setules.

Upper lip shallow, rounded below. Lower lip lacking inner lobes. Mandible, palp segment 3 slender, >segment 2. Maxilla 1, inner plate with 4 apical setae. Maxilla 2, inner plate with 6(?) inner marginal setae. Maxilliped undescribed.

Gnathopods 1 & 2 subsimilar; carpus short, hind lobe deep, setose below, much shorter than short propod; palmar margin short, oblique, slightly convex, length ~12 posterior margin of propod that is armed with 2 clusters of setae.

Peraeopods 3 & 4 undescribed. Peraeopods 5-7 stout, increasing posteriorly; bases broad, hind margins convex, weakly crenulated, strongly lobate below; segment 4 distinctly broadened; segment 6, anterior margins with 2-3 spine clusters; dactyls strong.

Pleon plate 3, lower margin nearly bare, hind corner rounded or broadly obtuse. Uropods 1 & 2 undescribed. Uropod 3, inner ramus slightly longer than peduncle, inner margin with 4-5 spines.

Telson medium, subtriangular, apex subacute.
Male: undescribed.

Distributional ecology. Recorded authentically only from the intertidal of the northwestern Sea of Japan (Peter-the-Great Bay).

Taxonomic commentary. Gurjanova's original description and illustrations are limited but sufficiently detailed to permit critical distinction from other species treated here. Tzvetkova & Kudrjaschov (1975, Fig. 2) have described a 3.5 mm juvenile lectotype specimen under the name *Paracalliopiella litoralis* (Gurjanova, 1938). However, they also assigned to that species an 8 mm. male and a 10 mm female specimen (Figs. 3 & 4) from the littoral zone of Provideniya Bay, on the Siberian shores of the northwestern Bering Sea. These specimens are here considered very different from Gurjanova's original species, and are redescribed below as *P. tzvetkovae*, new species (p. 35). Bulycheva (1957) and Tzvetkova (1967) assigned specimens from Peter-the-Great Bay to *Leptamphopus litoralis* Gurjanova. The description and figure of a 3.5 mm lectotype juvenile by Tzvetkova & Kudrjaschov (1975) (Fig. 19, this paper) agree fairly closely with the original description and figure of Gurjanova (Fig. 18, this paper).

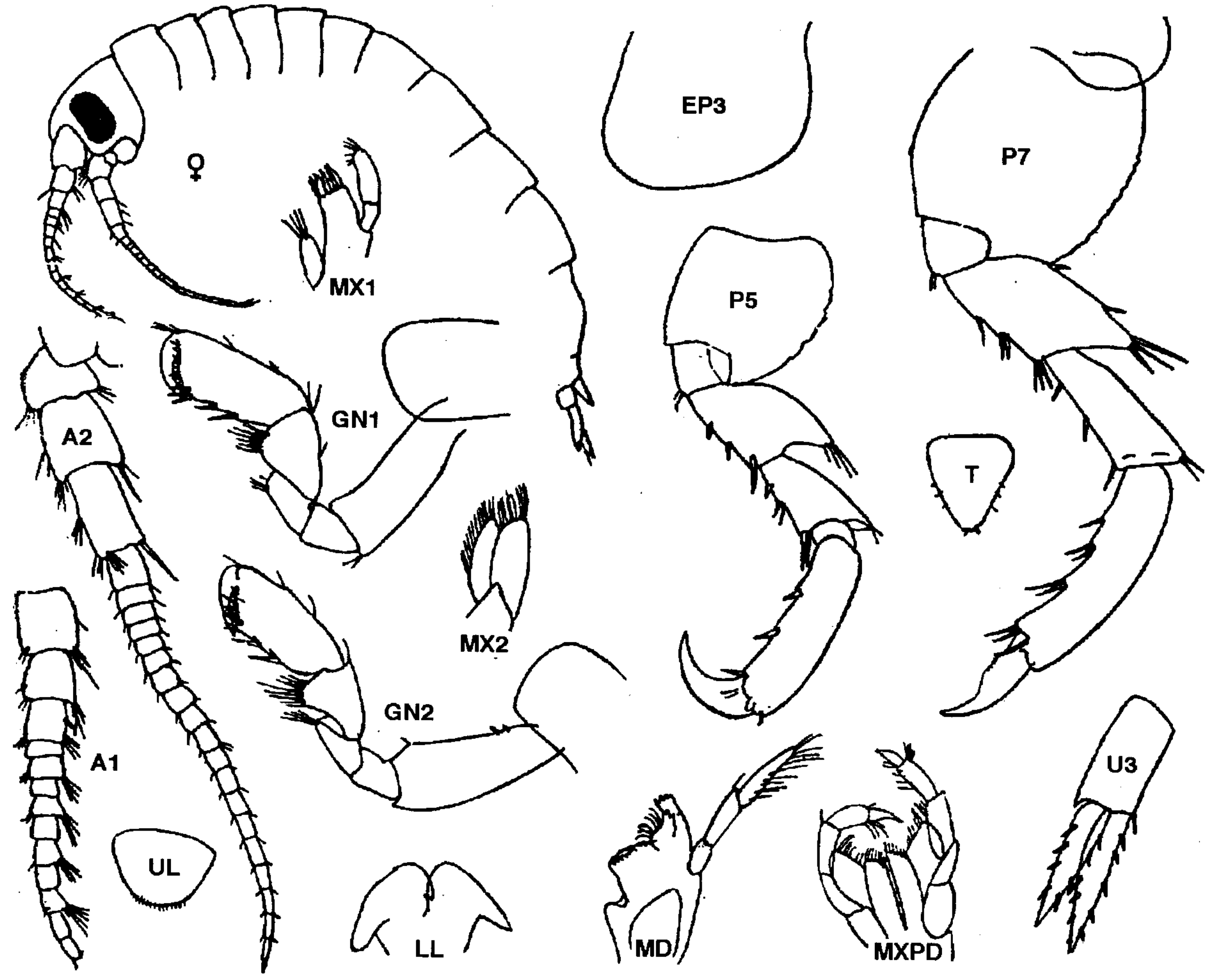


FIG. 18. *Paracalliopiella litoralis* (Gurjanova). Northeastern Sea of Japan to Kamchatka. Female (to 5.0 mm) (after Gurjanova, 1951).

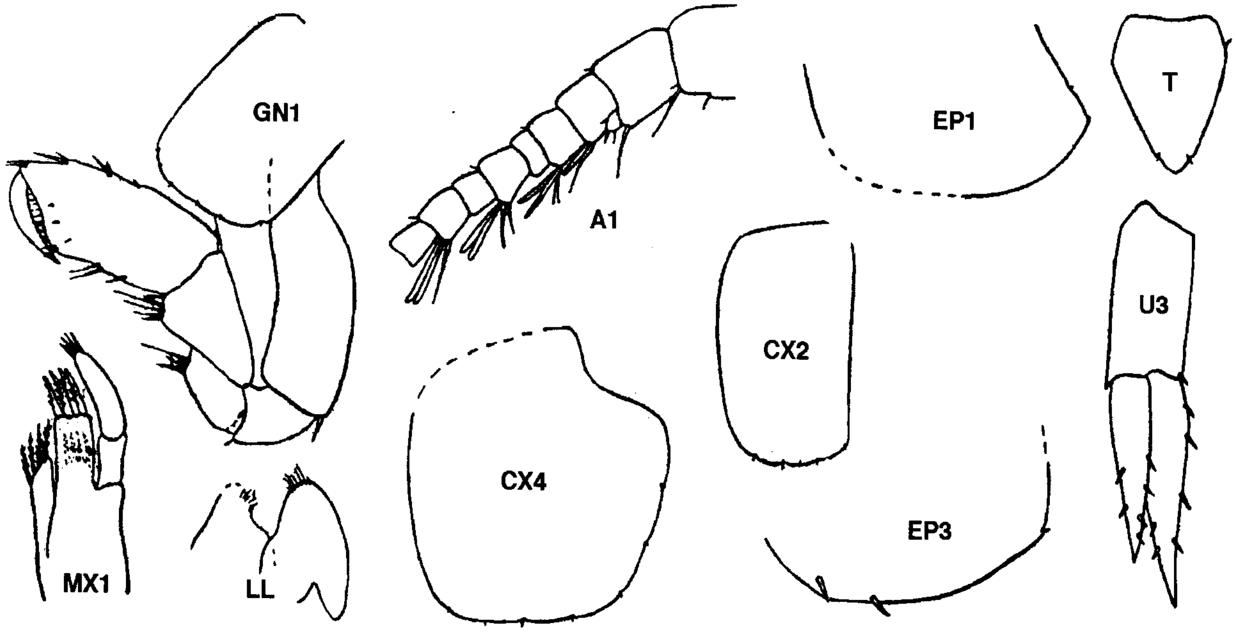


FIG. 19. *Paracalliopiella litoralis* (Gurjanova). Peter-the-Great Bay, Sea of Japan. Lectotype juvenile (3.5 mm) (after Tzvetkova & Kudrjaschov, 1975).

Paracalliopiella pacifica Tzvetkova & Kudrjaschov
(Fig. 20)

Paracalliopiella pacifica Tzvetkova & Kudrjaschov 1975: 15, fig.1.—Barnard & Karaman, 1991: 330.

Material examined.
Aleutian Islands. St. Paul I., P. Slattery Stn., 1983 (2 specimens, 2 slide mounts); Amchitka I., C.E. O'Clair Stn, 1976 - 1 specimen, slide mount. CMN collections, Ottawa.

Diagnosis. Female (to 20.0 mm): Body low-carinate on pleonal and posterior peraeonal segments. Head, rostrum short to medium. Eyes large, dark brown, oblique. Antenna 1 much shorter than 2, both with elongate flagella (28-35 segmented, segments slightly lobate behind). Antenna 1, peduncle 2 not reduced; accessory flagellum minute, with 3 apical setae.

Lower lip with weak inner lobes. Mandible, palp segment 3 shorter than 2. Maxilla 1, inner plate with 5 apical setae; palp slender. Maxilla 2, inner plate broadest medially, inner margin with 6-7 plumose setae. Maxilliped, inner plate stout, apex subtruncate, with 2-3 conical spines, inner margin with several setae; outer plate broad, not disto-medially incised, apex subtruncate, with 8-10 setae; palp strong, segment 2 broad.

Coxae 1-4 shallow, not deeper than broad. Gnathopods 1 & 2 relatively strongly subchelate, subequal; propods expanding distally, palmar margins oblique, convex, merging with hind posterior margin, each with 2 clusters of strong spines at posterodistal angle; inner face distally with few setae; dactyls strong, setulose behind; carpus much shorter than propod, hind lobe of gnathopod 2 deep and rounded, much more pronounced than in gnthopod 1.

Peraeopods 3 & 4 not described. Peraeopods 5-7, segment 4 broadened distally, hind margin wing-like.

Pleon plate 3, with 3-4 lower marginal spines, hind corner obtuse or rounded. Uropods 1 & 2, rami slender, outer ramus shorter, apical spines short. Uropod 3, rami slender, elongate, outer slightly the shorter, both markedly (>1.5X) longer than peduncle, margins distally spinose.

Telson subtriangular, narrowing to an acute apex.

Male: Although the original authors surveyed ~1000 specimens, no male was described. Gnathopods 1 & 2, propods probably larger and carpus shorter and deeper.

Distributional ecology. Common in the middle and lower littoral zone, among algae, on rocky, stony, and pebbly-gravelly sediments, from southwestern Bering Sea (Comander Islands), shores of Kamchatka Peninsula and Kurile Islands to the northwestern Sea of Japan (Posyet Bay).

Taxonomic commentary. As illustrated by Tzvetkova & Kudrjaschov (loc. cit.), the female gnathopods of this otherwise primitive species are relatively strongly subchelate, gnathopod 2 slightly larger, with distinctive short, deep, posteriorly lobate carpus.

Paracalliopiella beringiensis, new species
(Figs. 21, 22)

Material Examined.
ALASKA. Bering Sea. Little Diomede Is. (Bering Strait), P. Slattery Stn, 1984 - 2 females ov., slide mount; King I., P. Slattery Stn, 1986 - female (7.3 mm), **holotype**. St. Lawrence I, Southeast Cape, 8 m. - .male (6.0 mm), **allotype**; female (7.5 mm), **paratype**; 20 additional male and female specimens, 7 slide mounts. St. Matthew I., P. Slattery Stn, 1983. - 2 specimens, 1 slide mount. CMN collections, Ottawa.

Diagnosis. Female (7.3 mm.): Body dorsally smooth, or with slight humping of pleonal and posterior peraeonal segments. Rostrum medium. Eyes large, reniform-rectangular. Antenna 1 short, little more than half antenna 2; peduncular segments stout; accessory flagellum ~20-segmented.

Lower lip, inner lobes weakly defined. Mandible, palp segment 3 slender, short; segment 2 with 6-8 stout distal setae, and 3 basofacial "A" setae; left lacinia 6-7-dentate. Maxilla 1, inner plate with 7 marginal setae. Maxilla 2, inner plate with 5-6 marginal plumose setae. Maxilliped, outer plate broad, apical margin with 8-10curved setae, incised medially; inner plate tall, with 11-12 marginal setae.

Coxal plates 1-3 slightly deeper than wide, rounded and weakly scalloped below; coxa 1 not distally flared; coxa 4 deep, much the largest. Gnathopods 1 & 2 subequal; carpus and propod slender, subequal, posterior lobe of carpus shallow, setose; propod with 5-6 singly inserted mediodistal setae, palm short, oblique, with 5 short spines at posterodistal angle; dactyl nearly lacking posterior marginal setules.

Peraeopods slender, dactyls moderate. Peraeopods 3 & 4, segment 5 slightly shortened. Peraeopods 5-7 regularly increasing; bases moderately broad, hind margins nearly straight; segment 4 little expanded behind; segment 6 with 5 anterior marginal spine clusters.

Pleon plates 2 & 3, hind corners weakly acuminate, lower margins with 2-5 spines. Uropods 1 & 2, inner ramus with 8-9 serially paired spines, apical spines short. Uropod 3, rami distinctly unequal, tapering uniformly distally, margins serially spinose; inner ramus longer than peduncle.

Telson narrowing distally to irregularly truncate apex, length nearly twice width.

Male (6.0 mm): Gnathopod 2, propod larger than in gnathopod 1; palmar margin smoothly convex and contiguous with posterior margin, inner and outer margins each with 4-5 medium spines near posterior angle; inner (median) face distally with 6-7 singly inserted submarginal setae; carpus short, deep, apex of hind lobe subtriangular, weakly setose. Telson, apex gently rounded.

Etymology. The species name recognizes the type locality in the Bering Sea.

Distributional ecology. Known only from the northern Bering Sea region (Little Diomede to St. Lawrence I..).

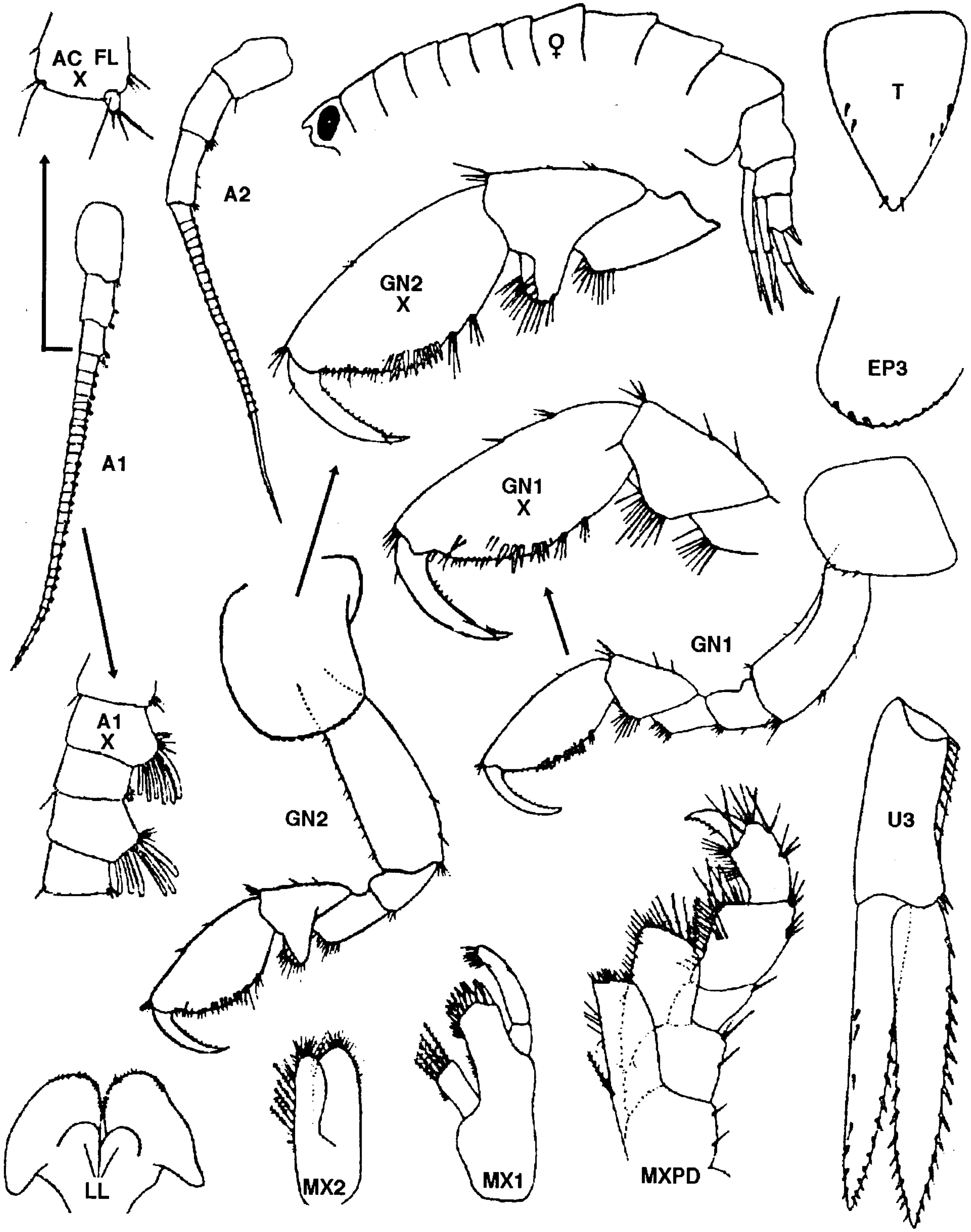


FIG. 20. ***Paracalliopiella pacifica*** **Tzvetkova & Kudrjaschov. Peter-the-Great Bay. Fem. (to 20 mm). (after Tzvetkova & Kudrjaschov, 1975).**

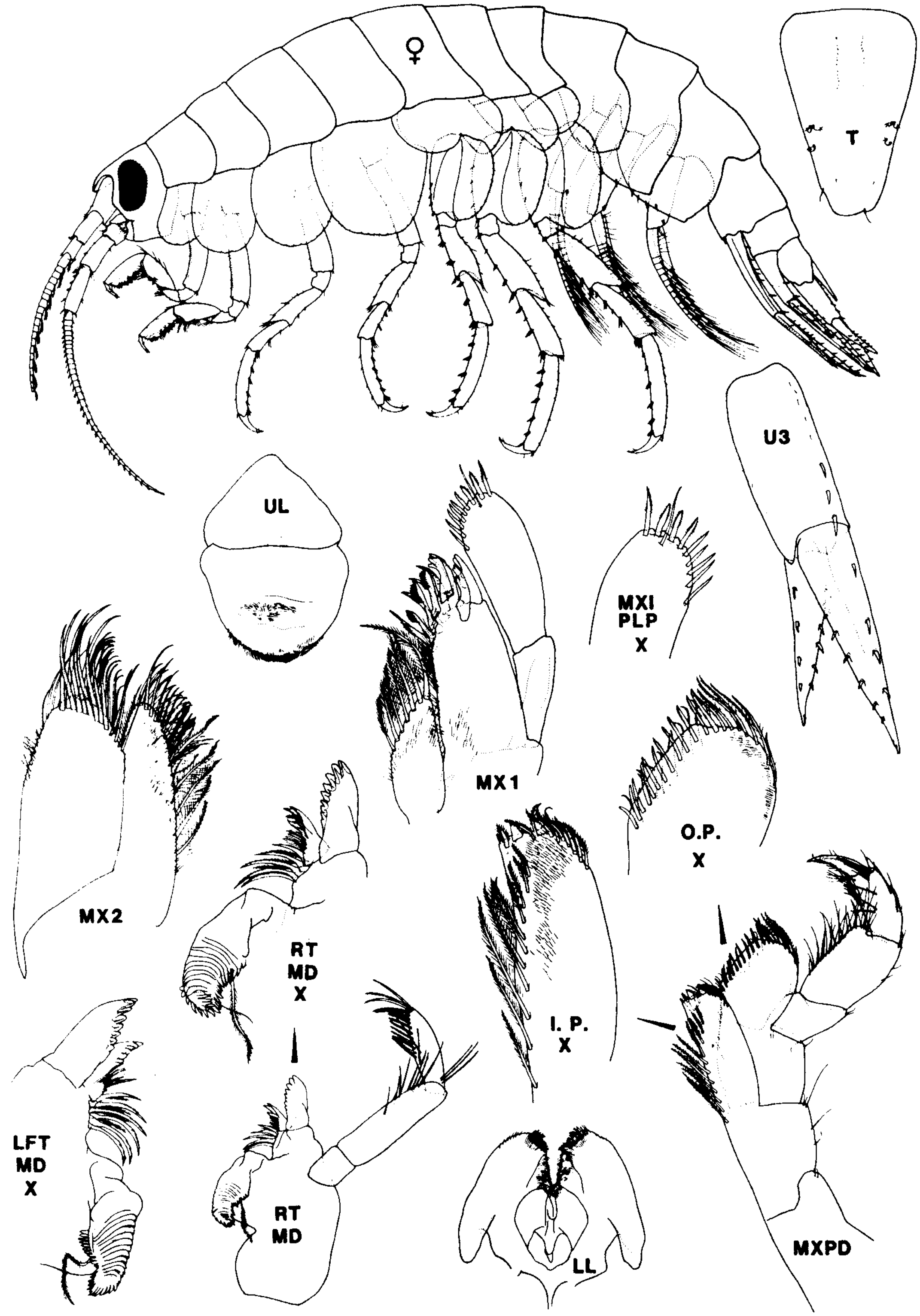


FIG. 21. *Paracalliopiella beringiensis,* new species. King I., Bering Strait. Female (7.3 mm).

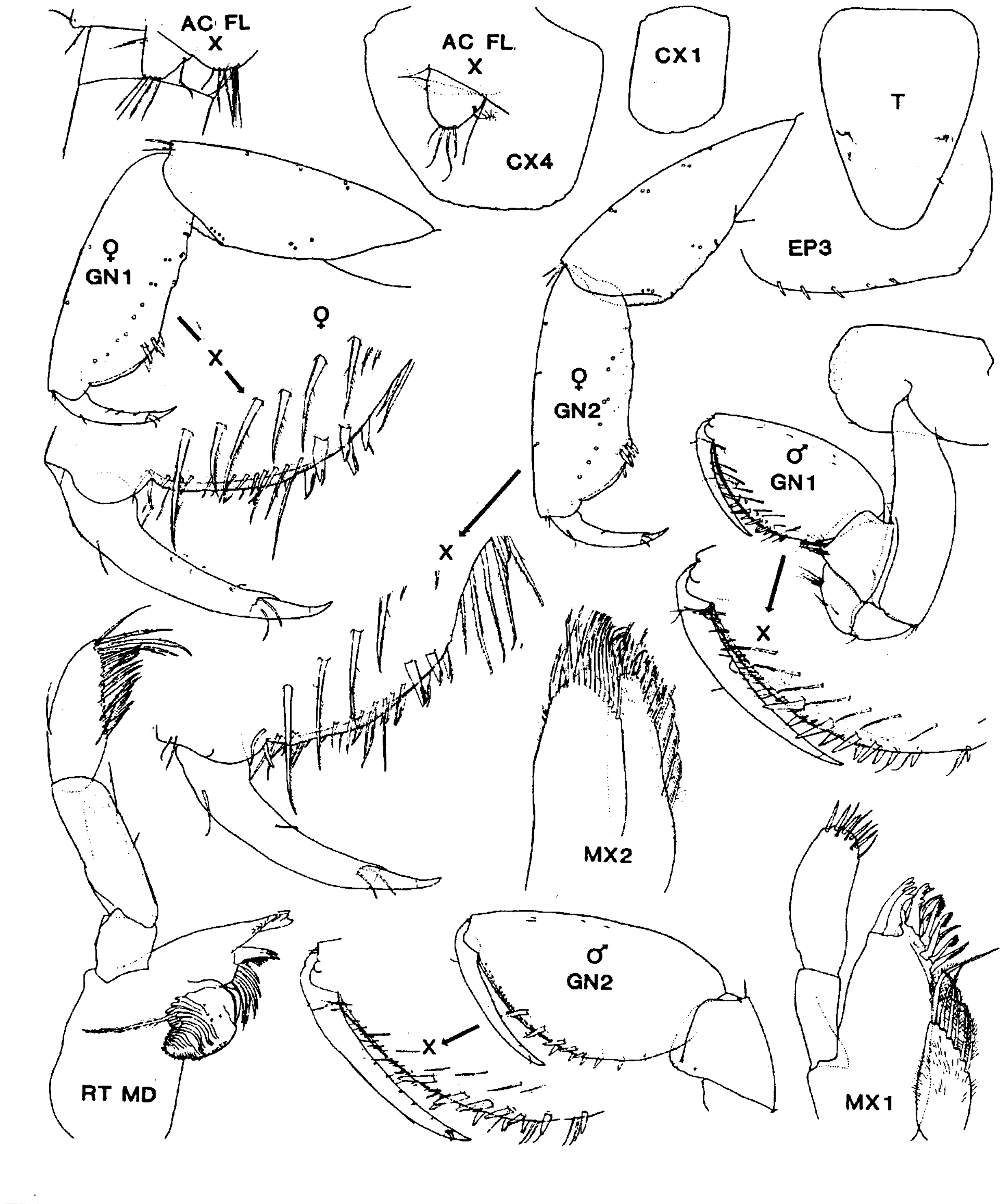


FIG. 22. *Paracalliopiella beringiensis*, new species. St. Lawrence I. Female (7.5 mm); male (6.0 mm).

Taxonomic commentary. *Paracalliopiella beringiensis* is most closely similar to *P. tzvetkovae*. The degree of morphological similarity with other regional species is indicated in Fig. 41, p. 60. *P. beringiensis* is plesiomorphic in nearly every character state, especially in the form of the female gnathopods. Morphological variation is slight.

Paracalliopiella tzvetkovae, new species
(Fig. 23)

Paracalliopiella litoralis (Gurjanova) Tzvetkova & Kudrjaschov, 1975: 17, figs. 3, 4.—Barnard & Karaman, 1991: 330 (part).

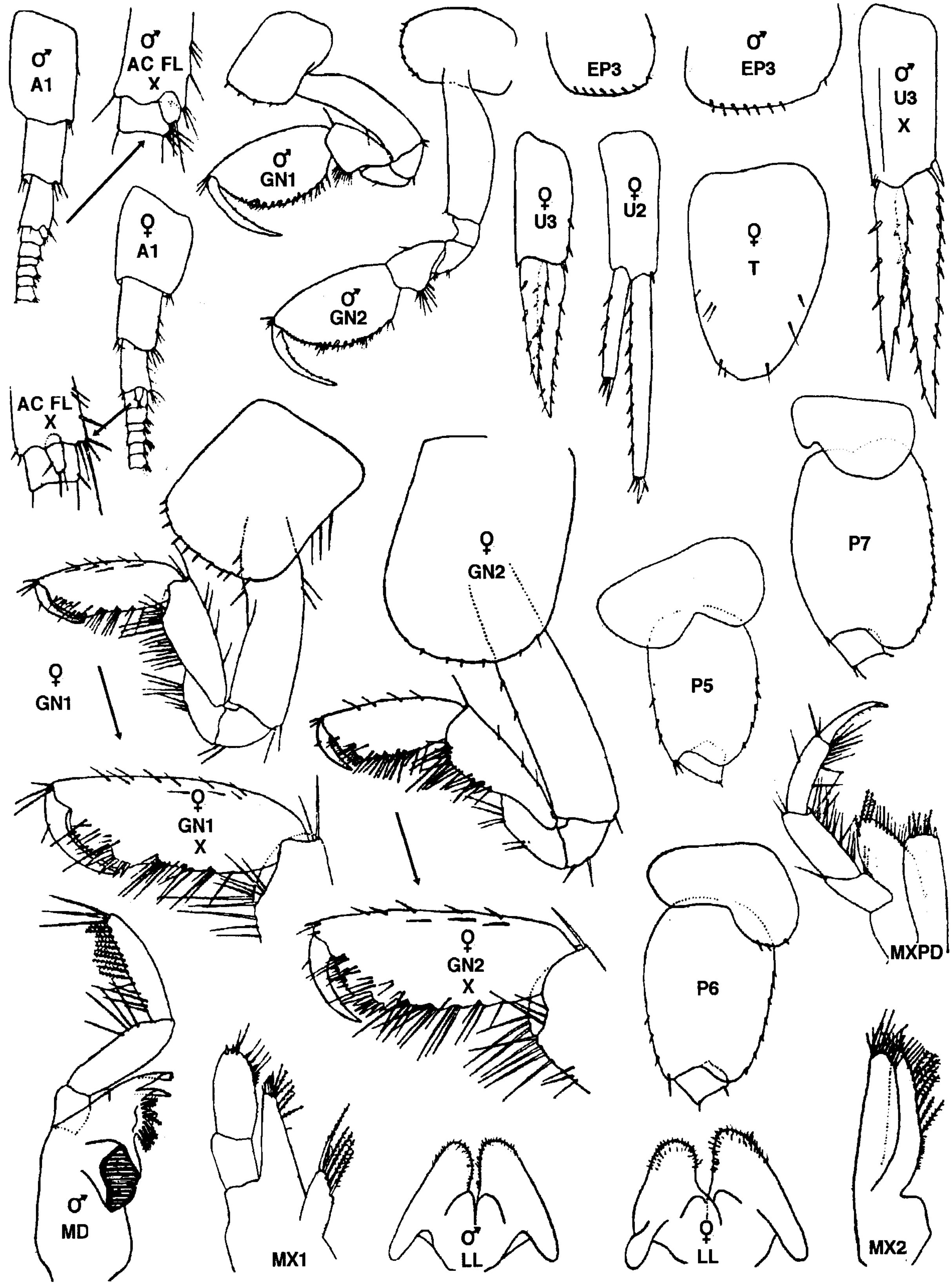


FIG. 23. ***Paracalliopiella tzvetkovae*, new species. Provideniya Bay. Male (8.0 mm); female (10.0 mm). (after Tzvetkova & Kudrjaschov, 1975).**

Material. The holotype female and allotype male material from Provideniya Bay, as figured by Tzvetkova and Kudrjaschov (1975) is deposited in the Zoological Museum, St. Petersburg. Specimens were not examined by the writers.

Diagnosis. Female (10.0 mm): Body smooth or with slight pleonal mid-dorsal elevations. Rostrum short. Eyes very large, reniform. Antenna 1 distinctly shorter than 2, peduncular segments short; accessory flagellum distinct, length nearly equal to flagellum 1, apex with 2-3 setae.

Lower lip, inner lobes weak. Mandible, palp segment 3 long; segment 2 with 4 inner distal setae; left lacinia 5-dentate, spine row with 8 blades. Maxilla 1, inner plate with 5-6 plumose setae; right palp broadened. Maxilla 2, inner plate with 6-8 marginal plumose setae. Maxilliped, inner plate large, truncate; outer plate broad, distal margin rounded with a few curved setae; palp powerful, dactyl long.

Coxal plates 2-4 large, broad, lower margins nearly straight; coxa 1 not splayed distally. Gnathopods slender; carpus shallow, equal in length to propod; propods, margins subparallel, palmar margin short, oblique, with cluster of posterodistal spines.

Peraeopods ordinary, not elongate, dactyls short. Peraeopods 5-7 regularly increasing, bases medium broad, segment 4 little expanded behind.

Pleon plates 2 & 3, lower margins with 7-8 spines, plate 3 rounded behind, hind corner obtuse. Uropods 1 & 2 not extending beyond 3. Uropod 2, outer ramus short (~1/2 inner ramus), outer margins spinose. Uropod 3, rami slender, unequal, margins with serially paired spines only.

Telson broadly linguiform, apex rounded.

Male (8.0 mm): Eyes very large, covering most of the side of the head. Coxa 2 & 3 relatively small, little larger than coxa 1. Maxilla 1, inner plate with 4 plumose setae.

Gnathopods 1 & 2 powerfully subchelate, 1 slightly the larger; propods deep, palm smoothly merging with posterior margin, 4-5 spines at posterodistal angle; carpus short, hind lobe small. Telson medium, apex bluntly rounded.

Distributional Ecology. The type locality is Provideniya Bay, Siberian coast of northeastern Bering Sea. Material from Bering Strait and other regions of the Bering Sea, south to Prince William Sound, southeastern Alaska.

Etymology. Named in honour of Dr. Nina L. Tzvetkova co-author of the genus *Paracalliopiella*, who has contributed much new taxonomic and ecological information on amphipod communities of the Asiatic North Pacific region.

Taxonomic commentary. As noted above (p. 30), this species was previously included under the name *P. litoralis* (Gurjanova, 1938) by Tzvetkova & Kudrjaschov (loc. cit.). However, *P. tzvetkovae* differs from *P. litoralis* in many character states, most of which are relatively plesiomorphic (key, p. 26). *P. tzvetkovae* most closely resembles *P. beringiensis* (p. 32).

Paracalliopiella slatteryi, new species

(Fig. 24)

Material Examined. 2 lots, CMN collections, Ottawa. ALASKA: Bering Sea. St. Paul I., English Bay, one lot only, P. Slattery coll., 1982 - female ov. (9.7 mm), **holotype;** 5 females ov., slide mounts, **paratypes.**
Southeastern Alaska: Elrington I., North Twin Bay, Prince William Sound, K. Conlan coll., July, 1989 - 1 female.

Diagnosis. Female ov. (9.7 mm): Body weakly toothed dorsally on peraeon 7 and pleon segments 1 & 2. Head, rostrum medium; anterior head lobe incised; inferior sinus a narrow slit; lower head lobe slightly produced anteriorly. Eyes very large, reniform-rectangular. Antennae nearly subequal, each with flagellum of 30-35 short segments. Antenna 1, peduncular segment 3 shorter than 2; accessory flagellum short, conical, apex with 5-6 small setae.

Lower lip with very small inner lobes. Mandible; palp segment 3 short; segment 2 with more than 12 short distal setae; left lacinia 5-dentate, right lacinia trifid; spine row with 7-8 blades. Maxilla 1, inner plate with 5 plumose setae; palp slender. Maxilla 2, inner plate with 4-5 marginal plumose setae. Maxilliped, inner plate narrow, inner margin with 9-10 plumose setae; outer plate distally flexed laterally; apical margin slightly emarginate, with 8-9 curved setae.

Coxal plates 2-4 broader than wide, lower margins weakly convex, little scalloped; coxa 4 extremely broad. Gnathopods slender, subequal; carpus shorter than rectangular propod, with marginally setose hind lobe; propod slender, margins subparallel, inner (medial) face with 3 distal submarginal clusters of 2-3 setae; hind margin with 4 groups of setae; palm short, nearly vertical, with 5-6 short spines at posterodistal angle; dactyl slightly overhanging palm.

Peraeopods ordinary; dactyls short. Peraeopods 3 & 4, segment 5 shorter than 4. Peraeopods 5-7 increasing regularly; bases moderately broad, evenly rounded behind.

Pleon segments 1 & 2, lower margins with 6-8 spines; hind margin of pleon plate 3 strongly convex, hind corner obtuse. Uropods 1 & 2 very slender, inner rami with 7-8 serial pairs of spines. Uropod 3, rami subequal, evenly lanceolate, inner margins with a few plumose setae as well as spines.

Telson short, spade-shaped, apex unevenly subtruncate. Brood plates very large, margins with 30-40 short setae.
Male: Unknown.

Etymology: The species is named in honour of Peter Slattery, Moss Landing, California, who has contributed extensively to knowledge of amphipod faunas of the Bering Sea.

Distribution. Intertidally, from St. Paul I., Bering Sea, to Prince William Sound, southeastern Alaska.

Taxonomic commentary. *Paracalliopiella slatteryi* appears most closely similar to *P. kudrjaschovi* and *P. pacifica,* all of intermediate phyletic position (Fig. 41, p. 60).

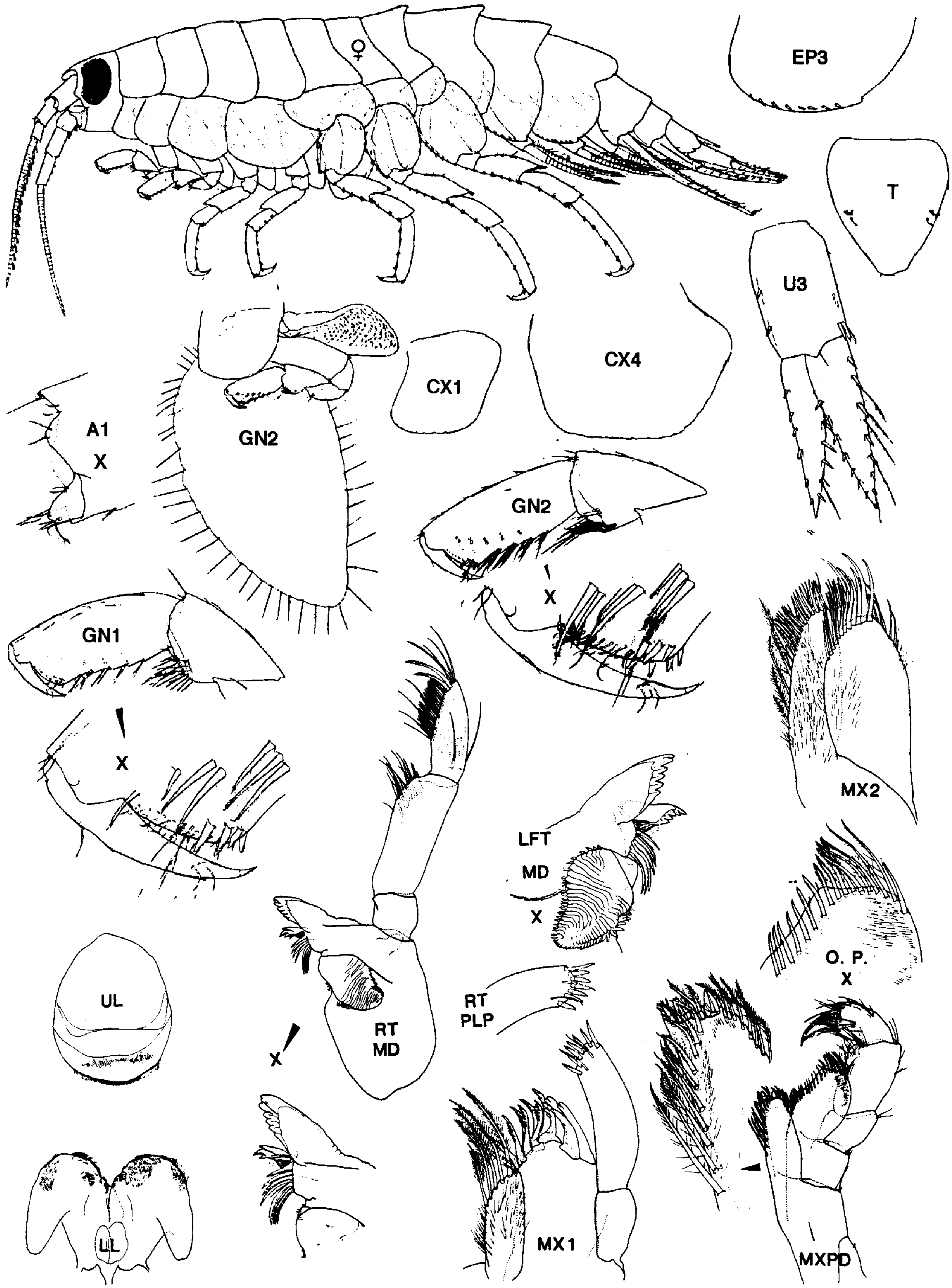


FIG. 24. *Paracalliopiella slatteryi,* new species. St. Paul I., Bering Sea. Female (9.7 mm).

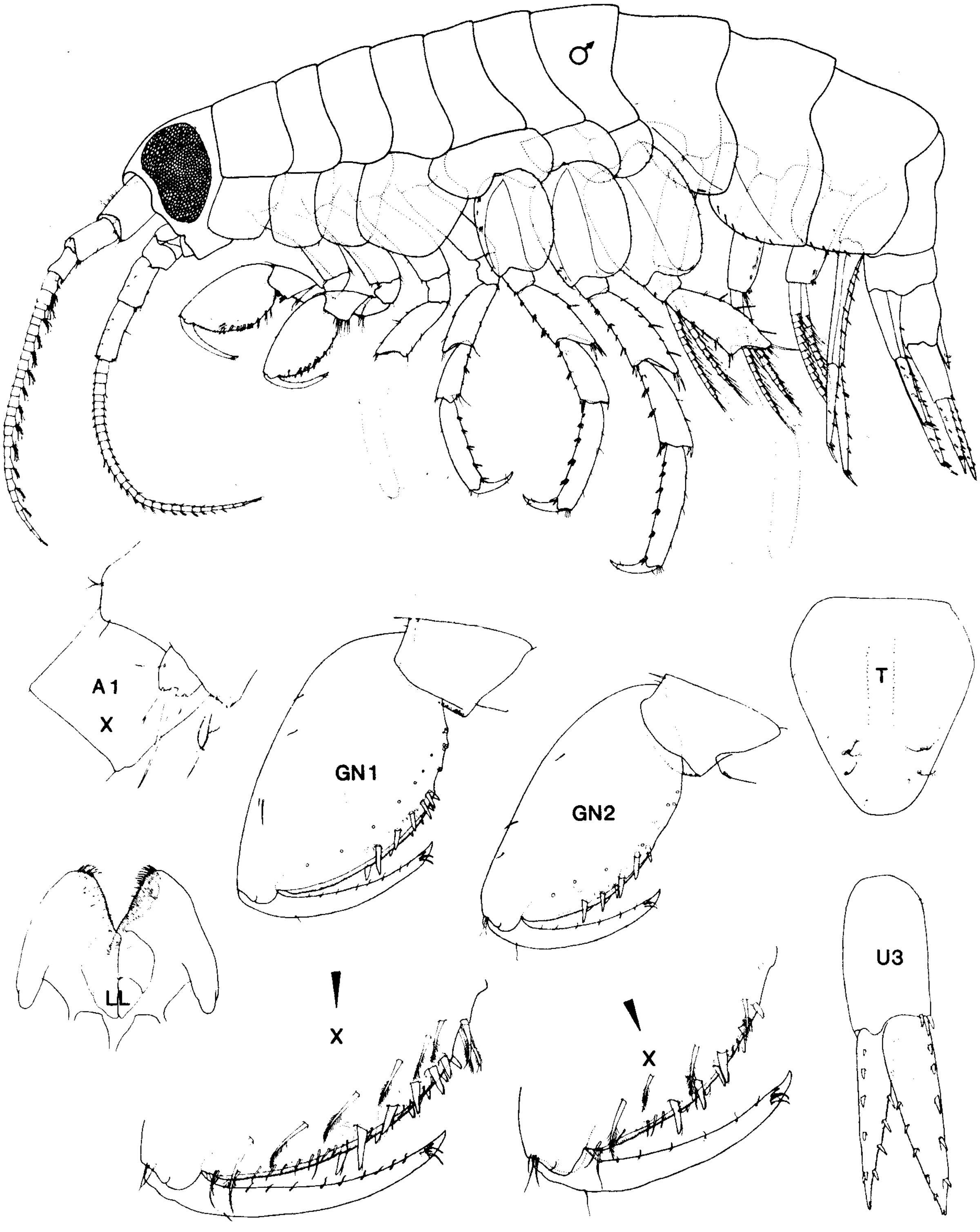


FIG. 25. *Paracalliopiella kudrjaschovi*, new species. Little Diomede I., Bering Strait. Male (5.0 mm).

Paracalliopiella kudrjaschovi, new species
(Figs. 25, 26)

Material Examined. ~150 specimens in 6 lots. CMN collections, Ottawa.
ALASKA. Bering Sea. P. Slattery coll., Little Diomede I., 1984 - 8 specimens, incl. 2 male, female slide mounts; King I. - 41 specimens, incl. males, females, slide mounts; St. Lawrence I., Southeast Cape - 2 females (ov.), slide mounts. Pribiloff Ids., St. Paul I., English Bay, south side - female (8.2 mm), **holotype**; male (5.0 mm), **allotype**; female (7.9 mm), **paratype**, slide mount; >100 additional spmns.
Southeastern Alaska. ELB Stn., 1961: A81 (Hawkins I.) - 1 female spmn, slide mount.

Diagnosis. Female ov. (8.2 mm). Body smooth above, or very slightly raised on pleon segments 1 & 2. Head, rostrum medium; anterior head lobe slightly incised; inferior sinus a short notch; inferior head lobe nearly vertical. Eyes very large, subreniform. Antennae of medium length. Antenna 2 distinctly the longer, flagellum of 22-29 short segments. Antenna 1, peduncle 2 not shortened; accessory flagellum subconical, apex with single large stiff setae and a smaller setule.

Upper lip relatively tall and narrow. Lower lip with weak inner lobes. Mandible; palp segment 3 shorter than 2, with 2 basofacial "A" setae; left lacinia 5-dentate, right lacinia trifid; spine row with 6-7 blades; molar with single lateral seta. Maxilla 1, inner plate with 6 apical setae; palp medium broad. Maxilla 2, inner plate with 3-4 marginal plumose setae. Maxilliped, inner plate tall, outer margin convex, inner margin with 7-8 plumose setae; outer plate relatively broad, deflexed laterally, apical margin slightly incised medially, lined with 7-8 curved setae; palp segment 2 moderately strong.

Coxae 2-4 broader than deep, very weakly crenulated and convex below. Gnathopods slender, subsimilar; carpus shorter than rectangular propod, hind lobes shallow, setose apically; propods slender, margins subparallel, medio-distal submarginal facial setae singly or doubly inserted (not clustered), hind margin with 5 clusters of setae, palmar margin smooth, nearly transverse, with 5-6 spines at posterodistal angle; dactyl strong, tip little exceeding posterodistal angle.

Peraeopods 3 & 4 slender; segment 5 little shortened; dactyl slender. Peraeopods 5-7 regularly increasing posteriorly; bases medium broad and convex behind, lower lobes distinct; segment 4 not broadened; segment 6 with 4-5 anterior marginal spine clusters.

Pleon plate 3, lower margin with 4-5 spines; hind margin rounded to small lower corner. Uropods 1 & 2, rami slender, inner ramus longer than peduncle, one apical spine of each strong. Uropod 3, rami unequal, narrowing regularly; inner ramus longer than peduncle, inner margin spinose.

Telson short, subtriangular, apex subacute.

Male (5.0 mm): Body very low-carinate posterodorsally on peraeon 7 and pleon segments 1 & 2. Eyes large, approximated above. Antennal flagella with 25-20 short segments. Gnathopods 1 & 2 strongly subchelate. Gnathopod 1, propod distinctly larger and deeper than in gnathopod 2; palm convex, strongly oblique, margin smoothly merging with posterior margin, inner face with 5 marginal spines near posterior angle and 4-5 submarginal setae; dactyl slender, setulose behind; carpus short, relatively shallow, apex of hind lobe obtuse, weakly setose.

Telson basally broad, narrowing distally, apex rounded.

Etymology. The species is named in honour of Dr. V. A. Kudrjaschov, co-author of the genus *Paracalliopiella*, who has extensively investigated amphipod communities of boreal and subarctic shores of the western North Pacific region.

Distributional Ecology. Widely distributed in the northeastern Bering Sea region, from Bering Strait and Pribilof Islands south to Prince William Sound. Occurring mainly at and below LW level of hard rock and sand beach interfaces, to depths of 20 m.

Taxonomic commentary. The female of *Paracalliopiella kudrjaschovi* is, in many details, similar to the female of *P. slatteryi*. However, the latter is larger at maturity, the dorsum is distinctly mucronate, the gnathopod propods are shorter and stouter, the inner ramus of uropod 3 is marginally setose, and the telson is relatively long and broad.

As noted above, *P. kudrjaschovi* appears most closely similar to P. *pacifica* and *P. slatteryi* (Fig. 41, p. 60).

Paracalliopiella bungei (Gurjanova)
(Fig. 27)

Halirages bungei Gurjanova, 1951: 611, fig. 414.
Paracalliopiella bungei (Gurjanova) Barnard & Karaman, 1991: 331 (part).

Material examined.
ALASKA.
Bering Sea. Aleutian Islands (Amchitka Is.), K. Chew, G. Tutmark, K. Kimura, 1968 (3); 1969 - 7 spmns, 2 slide mts.

Diagnosis. Female (to 18 mm): The description and illustrations, particularly of the mouthparts (Gurjanova, loc. cit.) are limited. Distinguishing features are provided in the key to species (p. 26).

Peraeon weakly carinated on each of peraeonal segments 2-6, more strongly on peraeon 7 and pleon segment 1, and most conspicuously on pleon segment 2, with a raised mid-dorsal ridge on segment 3. Head, rostrum medium; anterior head lobe gently convex; inferior antennal sinus a broad notch. Eye narrow, subreniform. Antennae medium long, subequal; each flagellum with ~40+ short segments.

Accessory flagellum and mouthparts not described, but probably similar to those of *P. shoemakeri* (below).

Coxae 1-4 relatively shallow, broader than deep, convex and weakly crenulated below. Gnathopods 1 & 2 weakly

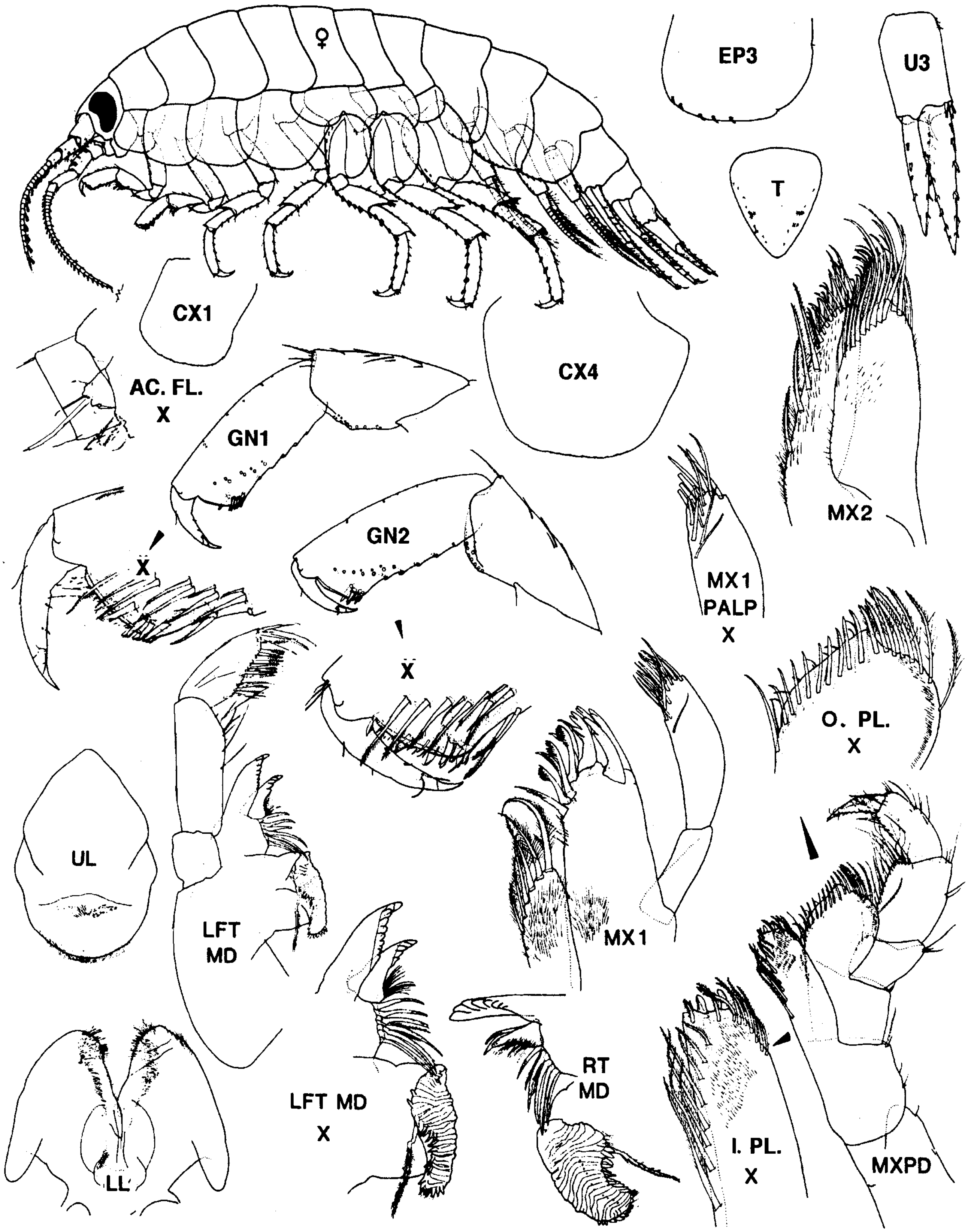


FIG. 26. ***Paracalliopiella kudrjaschovi*, n. sp. Little Diomede I., Bering Strait. Female (8.2 mm).**

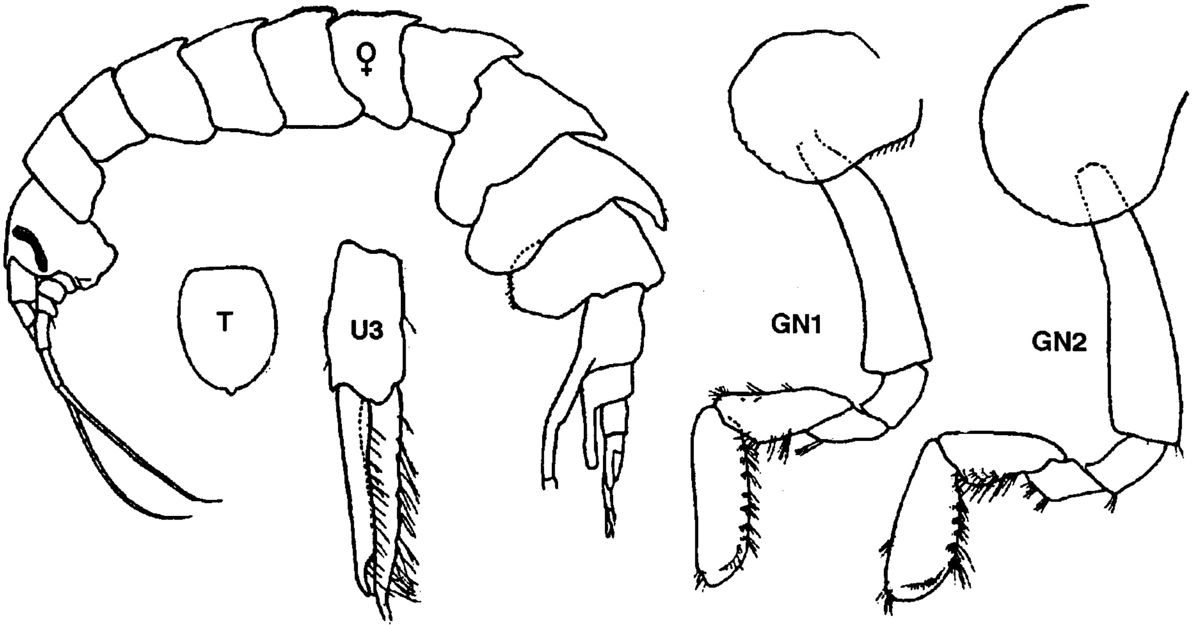


FIG. 27. *Paracalliopiella bungei* (Gurjanova). Bering Sea. Female (18 mm). (after Gurjanova, 1951).

subchelate, with slender elongate carpus and propod, but differing slightly in form and size. Gnathopod 1, propod slender, longer than carpus, margins subparallel, lower margin with 7-8 setal clusters; palm short, convex, oblique; carpus, hind lobe shallow, setose, length about half the anterior margin. Gnathopod 2, propod slightly broadening distally to medium palm that is less steeply oblique than in gnathopod 1; hind margin with 6-7 clusters of setae.

Peraeopods 3-7 undescribed (probably stout, with short dactyls, and similar in form to those of *P. shoemakeri*).

Pleon plates 2 & 3, lower margin spinose; hind corner obtuse, not mucronate. Uropods 1 and 2 slender, incompletely described. Uropod 3, rami slender, narrowing distally, distinctly longer than peduncle, inner margins strongly setose.

Telson broad but longer than wide, rounding apically to small subacute apex.

Male not described.

Taxonomic and distributional commentary. *Paracalliopiella bungei* is known from the Bering Sea, and along the eastern shores of the Kamchatka Peninsula, among algae and on fine sand, in depths to 60 m.

Paracalliopiella shoemakeri, new species
(Fig. 28)

Haliragesbungei Gurjanova, Shoemaker, 1964: 406, fig. 8.
Paracalliopiella bungei (Gurjanova) Barnard & Karaman, 1991: 331.

Material Examined. The 13.0 mm female specimen from the Bering Sea, illustrated by Shoemaker (loc. cit.) is here design-ated as **holotype**, USNM collections, Washington.

Diagnosis. Female (13 mm): Body mid-dorsally carinated, weakly on peraeon 3-5, more strongly on 6-7, very strongly on pleon segments 1 & 2, but reduced to a short ridge posteriorly on pleon 3. Head, rostrum short, wide; anterior head lobe short, slightly emarginate; inferior antennal sinus a broad notch. Eyes narrow, subreniform. Antennae intermediate, subequal; flagella with ~40 short segments. Antenna 1, peduncular segment 3 with slight posterodistal cusp or process; accessory flagellum minute, subconical, with 3 apical setae. Antenna 2, peduncular segment 5 slightly longer than segment 4.

Lower lip simple, lacking inner lobes. Mandible; left lacinia 5-dentate; spine row with 9 blades; palp segment 2 with posterodistal setal cluster; segment 3 distinctly shorter than segment 2, with basofacial cluster of 3 "A" setae. Maxilla 1, inner plate subtruncate, with 5 apical setae; inner plate with 11 apical spines; palp medium broad, apex with 12+ spines and some setae. Maxilla 2, inner plate with 4 inner marginal plumose setae. Maxilliped, inner plate tall, slender, apex with 3 short conical spines, inner margin with 6-8 plumose setae; outer plate large, broad, apex rounded, slightly emarginate medially; palp relatively short, stout, segment 2 distinctly exceeding outer plate.

Coxae 1-4 relatively small and shallow, rounded below. Gnathopods 1 & 2 subsimilar in form and size; propod and carpus slender, weakly subchelate, palms convex, oblique; hind margins with many clusters of short setae, distal median facial setae in clusters of three; dactyls richly setulose behind; carpus, hind lobe shallow, margin setose.

Peraeopods 3 & 4, segment 5 slightly shorter than 4; dactyls short, curved. Peraeopods 5-7 homopodous in form, slightly increasing in length posteriorly; bases broadly rounded, hind lobes not projecting below; dactyls short.

Pleon plates 1 & 2, hind corners weakly acuminate.

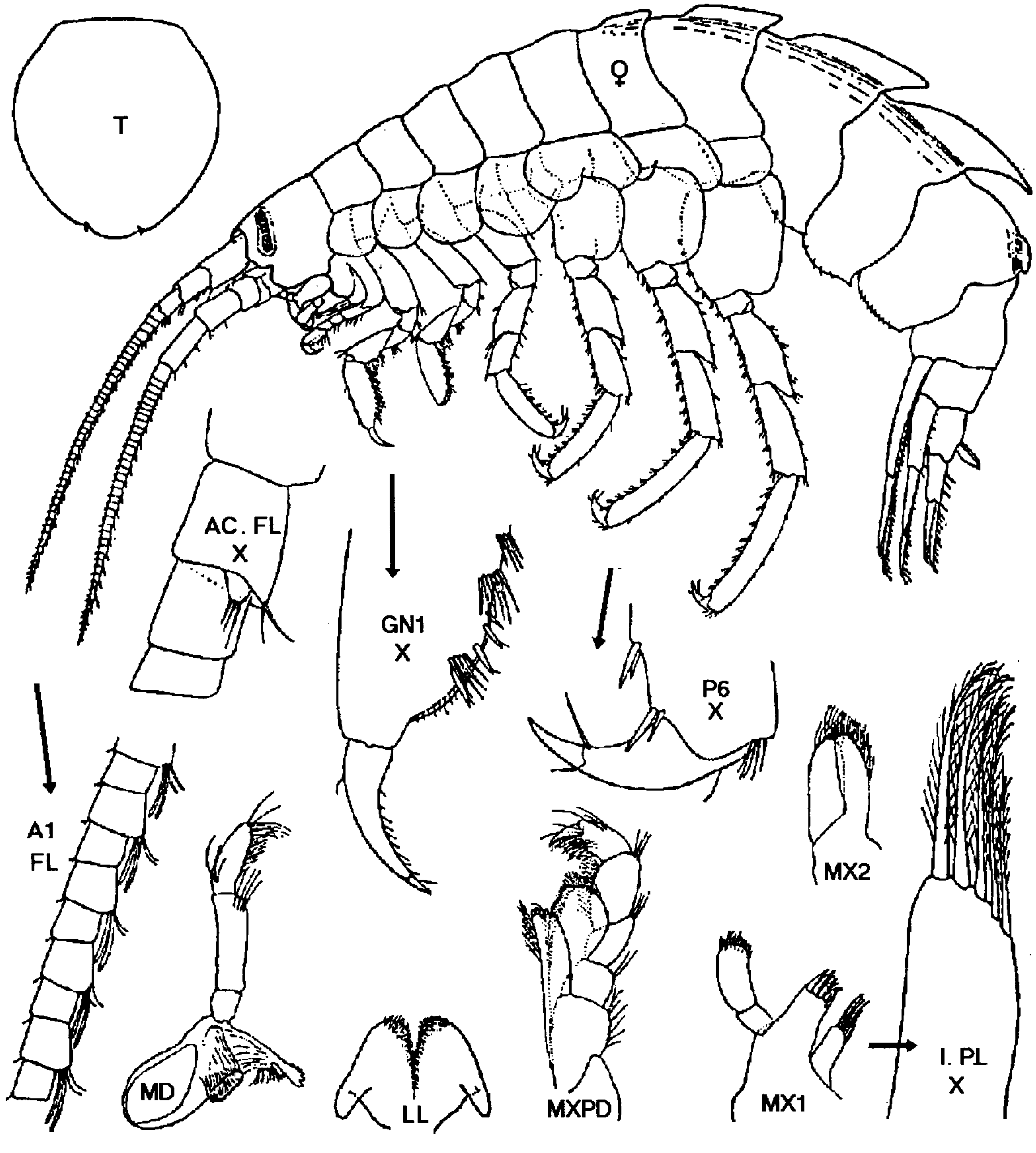


FIG. 28. ***Paracalliopiella shoemakeri*, new species. Bering Sea (Commander Is.). Female (13.0 mm). (after Shoemaker, 1964).**

Pleon 3, hind corner slightly obtuse. Uropods 1 & 2 slender, outer ramus the shorter; with numerous serial marginal spines and stronger apical spines. Uropod 3, rami longer than peduncle, inner ramus the longer, inner margins setose and spinose.

Telson broad, suborbicular, broadly rounded apically. Male unknown.

Distributional ecology. Records from the Commander Islands, Bering Sea (Shoemaker, 1964) are based on a total of 12 specimens.

Taxonomic commentary. Shoemaker (loc. cit.) had synonymized his material with that of Gurjanova's *C. bungei.* However, it is here considered sufficiently different from *C. bungei,* in characters of the key and in size at maturity, to justify separate species recognition. Barnard & Karaman's decision to transfer both forms to the genus *Paracalliopiella,* based solely on the presence of an accessory flagellum, is considered invalid because of the instability of this character state and the need to define calliopiid taxa on the basis of multiple character states (cf., *Calliopius,* p. 7). The strongly carinated *bungei* subgroup, including *P. shoemakeri,* and *P. haliragoides,* may merit separate generic recognition (p. 61).

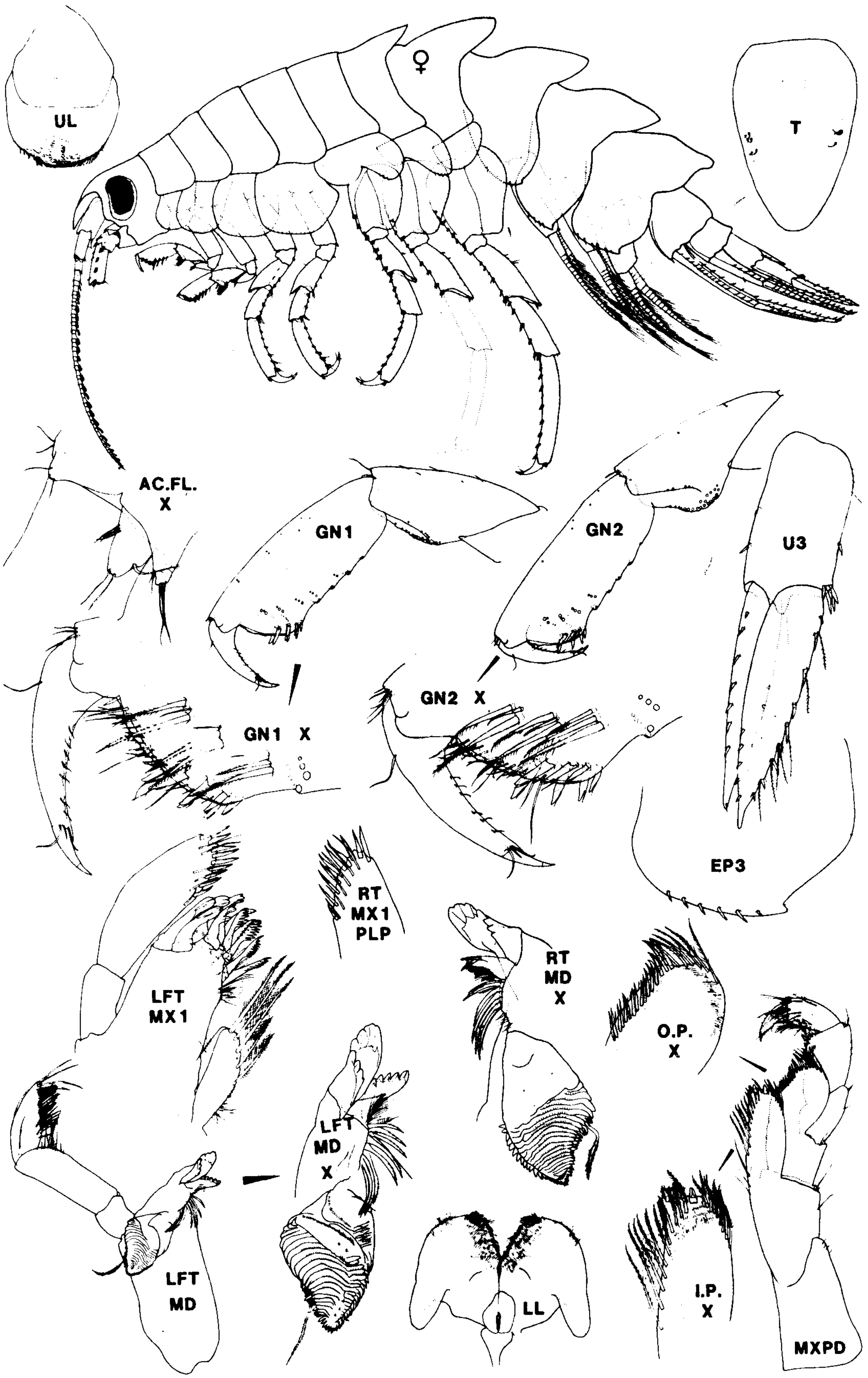


FIG. 29. *Paracalliopiella haliragoides,* new species. Bering Sea. Female (12.5 mm).

Paracalliopiella haliragoides, new species
(Fig. 29)

Material examined. About 100 specimens from a single station. CMN collections, Ottawa.
ALASKA:
Southeastern Alaska. ELB Stn A33, Holkham Bay, at spit off Sumdum Glacier, among stones on sand at LWlevel, 6.3°C., June 12, 1961. Lot # 1 - Female (13.5 mm), **holotype**; male (9.0 mm), **allotype**; 50 immatures, **paratypes.** Lot #2 - 2 females ov. (12.0 mm), 1 male (8.0 mm), slide mounts, 40 immature specimens.

Diagnosis. Female (12.5 mm). Body strongly carinated mid-dorsally on peraeon segments 6 & 7 and pleon segments 1-3. Head, rostrum strong, length about equal to antenna 1, peduncle 1. Inferior head lobe not produced. Eye large, reniform. Antenna 1, flagellum with 40+ short segments, alternate segments with short aesthetascs; accessory flagellum minute, conical.

Lower lip lacking inner lobes. Mandible, spine row with 8 blades. Maxilla 1, inner plate with 3 stout and 2 slender apical setae; outer plate with 11 strongly pectinate apical spines. Maxilliped, outer plate longer than wide, slightly incised medio-apically.

Gnathopods 1 & 2, propods parallel-sided, not broadening distally, inner face armed distally with 3 clusters of stiff setae; palms regularly oblique, with 3-4 clusters of spines at posterodistal angle, extending variously along both sides of the palmar margin.

Peraeopods 3 & 4, segment 6 with 5-6 posterior marginal spine clusters. Peraeopods 5-7, bases normally broad, narrowing distally, lower hind lobes angled or sharply rounded; segment 6 with 6 anterior marginal clusters of short spines.

Pleon segment 2 & 3, lower margins weakly spinose, hind corners acuminate. Uropods 1 & 2, rami unequal, margins serially spinose. Uropod 3, rami medium lanceolate, margins each with 7-9 small spines and short plumose setae.

Telson linguiform, distinctly longer than wide, apex sharply rounded.

Coxal gills and brood plates regular.

Mature male (9.0 mm). Head strongly rostrate. Eye medium, subrectangular. Gnathopods 1 & 2 powerfully subchelate; carpus short, deep, hind lobe triangular; propod deep, palmar margin strongly convex, with ~6 pairs of strong spines. Peraeopod dactyls short, strongly curved. Pleon plate 3, hind corner with small tooth. Telson linguiform.

Etymology. A combining form, referring to its superficial resemblance to some species of the genus *Halirages.*

Distributional ecology. Known only from the type locality, a glacial fiord in southeastern Alaska, among stones over sand at LW level.

Taxonomic commentary. The species is unlike *C. bungei* and *C. shoemakeri* in lacking any trace of dorsal carination on pereaon segments 2-5, in its much stronger rostrum, and in its relatively narrow linguiform telson. At maturity, *C. haliragoides* is similar in size to *C. shoemakeri* but apparently significntly smaller than *C. bungei* .

Halirages Boeck
(see Fig. 30)

Halirages Boeck, 1971: 194.—Stebbing, 1906: 290.—Gurjanova, 1951: 605.—Barnard, 1969a: 177.—Barnard & Karaman, 1991: 322.

Species. 7 world species of which *Halirages nilssoni* Ohlin, 1895 and *H. fulvocincta* (M. Sars) are regional.

Diagnosis. Body mid-dorsally toothed or strongly mucronate, mainly on pleon segments 1 & 2, and posterior peraeon. Head, rostrum short, inferior head lobe little producef. .Antennae elongate, often calceolate (pontogeneiid type). Antenna 1, peduncle 3 with short distal process; accessory flagellum present, minute; aesthetascs small, singly inserted on alternate segments of primary flagellum.

Mouthparts basic. Lower lip lacking inner lobes. Mandible, palp segment 3 strong, falciform. Maxilla 1, inner plate multisetose; outer plate with 11 apical spines; palp normally 2-segmented. Maxilla 2, inner plate with row of facial setae. Maxilliped plates and palp regular, strong.

Coxae 1-4 medium, lower hind margins serrate. Gnathopods slender, weakly subchelate, not sexually dimorphic; carpus shallow, not longer than propod.

Peraeopods 3-4 slender; dactyls short; segments 4 & 5 subequal in length. Peraeopods 5-7 slender, homopodous, bases not broadly expanded; dactyls short.

Pleon plates 2 & 3, hind corners acuminate, pleon 3 (and often 2) serrate behind. Uropods 1 & 2, rami lanceolate, margins spinose, outer ramus slightly the shorter. Uropod 3 large; rami subequal, lanceolate, margins spinose and setose.

Telson elongate, variable, narrowing distally, apex notched truncate, or acute.

Coxal gills unpleated.

Brood plates large, margins setose.

Taxonomic commentary. The genus *Halirages* is superficially similar to some species of *Apherusa*, and *Paracalliopiella* (Barnard & Karaman (loc. cit.). Differences in the mouthparts, dorsal carination, and generally larger size of component species are the most obvious differences. The generic type species, *H. fulvocincta,* has been recorded from the western Canadian Arctic (Shoemaker, 1920) and the northwestern Pacific south to the northeastern Sea of Japan (Gurjanova, loc. cit.). *Halirages nilssoni* has been taken in the Beaufort Sea (Shoemaker, loc. cit.) and from the Chukchi and Bering Seas, and northwestern Sea of Japan, in depths to 30 m. (Gurjanova, loc. cit.). *H. nilssoni* has a triply carinate abdominal dorsum, a triply toothed hind margin of the posterior peraeonal and anterior pleonal segments, and the telson is unusually elongate.

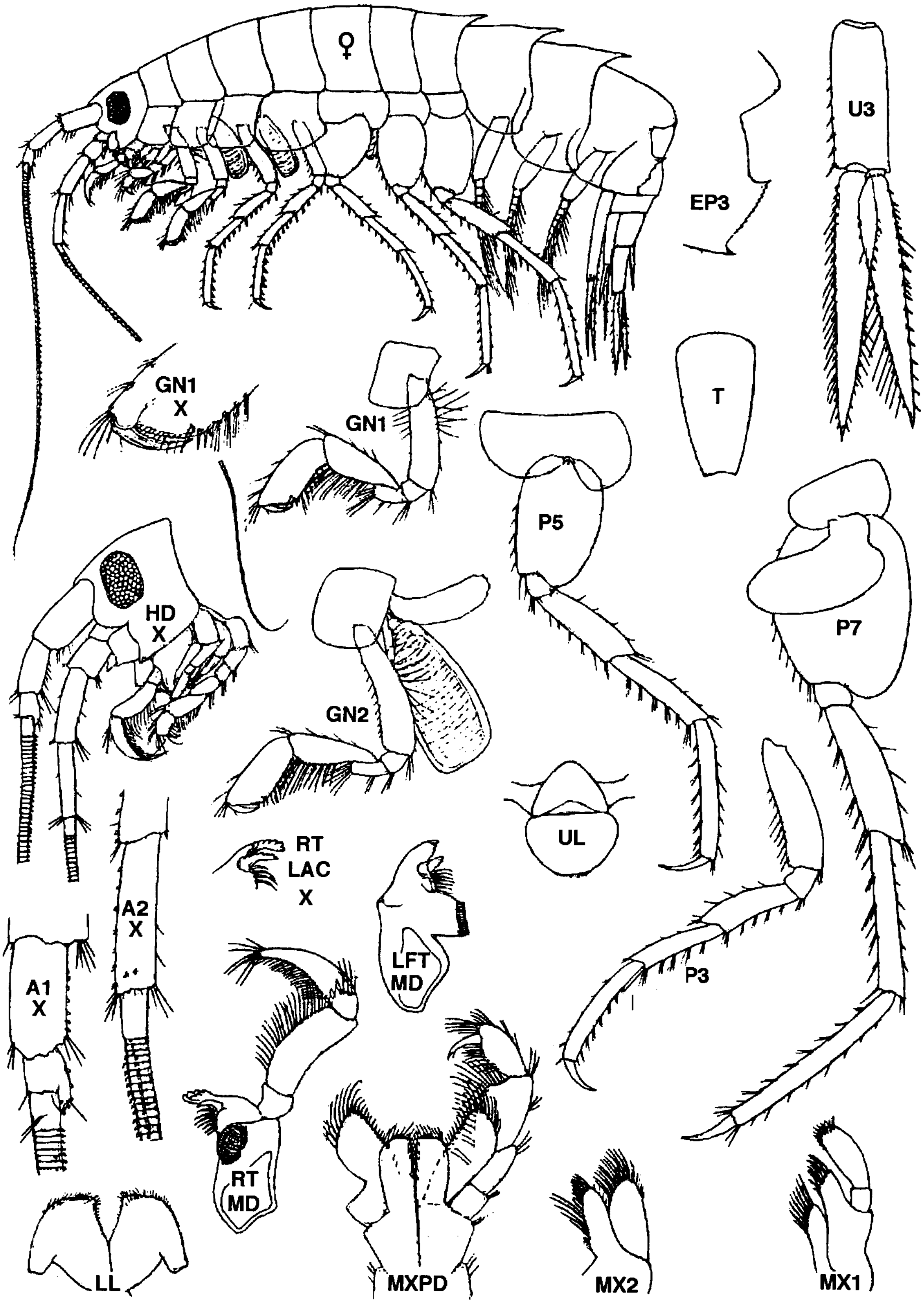


FIG. 30. ***Halirages fulvocincta*** **(M. Sars). Arctic Norway. Female (19.0 mm) (afters Sars, 1895).**

Laothoes Boeck

Laothoes Boeck, 1971: 202.—Stebbing, 1906: 286.—Gurjanova, 1951: 602.—Barnard, 1969a: 177.—Barnard & Karaman, 1991: 324.

Type species. *Laothoes meinerti* Boeck, 1971.

North Pacific species. *Laothoes polylovi* Gurjanova, 1946; *L. pacificus* Gurjanova, 1938 (=*L. macrocheir* Oldevig, 1959, fide Barnard & Karaman, 1991).

Diagnosis. Body dorsally smooth. Head, rostrum short; inferior head lobe not produced. Eyes small, round. Antennae slender, elongate; flagella with numerous short segments lacking calceolae (both sexes). Antenna 1, peduncular segments short, segment 3 unproduced; flagellum not basally callynophorate; accessory flagellum lacking.

Lower lip lacking inner lobes. Mandibular palp normal, segment 3 little shorter than 2; left lacinia 5-dentate. Maxilla 1, inner plate with few (4-5) apical setae; outer plate with 9(?) tall apical spines; palp typically much shortened, 2-segmented. Maxilla 2, plates narrow, inner plate lacking facial setae. Maxilliped, outer plate very large, broad, inner margin with strong close-set spines; palp slender, short, little exceeding outer plate; inner plate relatively short, broad.

Coxae 1-4 medium, rounded below. Gnathopods slender, weakly subchelate, not sexually dimorphic; propods parallel-sided; palms short, nearly vertical; dactyls toothed behind; carpus variably shorter than propod, with shallow hind lobe.

Peraeopods 3 & 4 regular, stout, spinose; segment 5 <4; dactyls strong. Peraeopods 5-7 homopodous, larger posteriorly; bases broad, hind lobes shallow; dactyls medium.

Pleon plates 2 & 3 smooth behind. Uropods 1 & 2, rami sublinear, outer ramus shortened. Uropod 3, rami broad-lanceolate, subequal; margins spinose.

Telson short, apex truncate or slightly emarginate.

Taxonomic commentary. *Laothoes* has specialized mouthparts and is otherwise relatively advanced (see phenogram, Fig. 39, p. 58).

Laothoes pacificus Gurjanova
(Fig. 31)

Laothoes pacificus Gurjanova, 1938: 309, fig. 25.—Gurjanova, 1951: 602, fig. 406.—Barnard & Karaman, 1991: 324.

Material Examined. None from study region.

Taxonomic and distributional commentary. The species has been recorded from Asiatic shores of the Bering and Chukchi Seas, at depths of less than 100 m, but not yet from the North American coast.

Laothoes polylovi Gurjanova

Laothoes polylovi Gurjanova, 1946: 287, fig. 20.—Gurjanova, 1951: 601, fig. 405.—Barnard & Karaman, 1991: 324.

Taxonomic and distributional commentary. *L. polylovi* differs from *L. pacificus* in its more slender gnathopods, less reduced palp of maxilla 1, and much smaller size at maturity (to 7.0 mm). The species is recorded from the Sea of Okhotsk and Bering Sea, at depths to 360 m.

Apherusa Walker

Apherusa Walker, 1891: 83.—Stebbing, 1906: 304.—Chevreux & Fage, 1925: 176.—Gurjanova, 1951: 626.—Barnard, 1969a: 174.—Barnard & Karaman, 1991: 304.

Type species. *Amphithoe jurinei* Milne-Edwards, 1830.

North Pacific regional species. *A. retovskii* Gurjanova; *A. glacialis* (Hansen, 1887); *Apherusa* sp. Park, 1961: 10—Austin, 1985: 589?

Diagnosis. Body smooth or weakly mucronate, especially on pleon segments 1 & 2. Head, rostrum small, short; inferior head lobe usually acutely produced. Eye roundish. Antennae slender. Antenna 1 distinctly the shorter; peduncular segments 2 & 3 short, lacking distal process; accessory flagellum lacking; calceoli usually lacking but present on antennae 1 & 2 in the type species (fide Chevreux & Fage, 1925).

Mouthparts little modified. Lower lip, inner lobes weakly developed. Mandibular palp segment 3 shorter than 2; lacinia 5-dentate; spine row medium. Maxilla 1, inner plate with 4-8 apical setae; outer plate with 11(9?) apical spines; palp normally 2-segmented. Maxilla 2, inner plate with submarginal and a few stout facial facial setae. Maxilliped regular, plates large; palp weakly unguiform.

Coxae 1-4 relatively small, shallow. Gnathopods weakly subchelate and subsimilar (both sexes), weakly to medium strongly sexually dimorphic; carpus shallow, not strongly shortened.

Peraeopods 3-7 regular, slender, segments 4 & 5 subequal in length; dactyls medium. Peraeopods 5-7 homopodous in form, regularly increasing in size posteriorly; bases relatively narrow, rounded behind, lower lobes small.

Pleon plates 2 & 3, hind corners acuminate, hind margins usually serrate or toothed, rarely smooth. Uropods 1 & 2, rami slender, linear; outer ramus of uropod 2 short. Uropod 3 large, rami lanceolate, margins spinose and variously (usually weakly) plumose-setose.

Telson entire, apex often acute. Coxal gills simple, not pleated.

Taxonomic and distributional commentary. About 20 species are recorded from the Mediterranean, North Atlantic and eastern Arctic regions, but few are recorded from

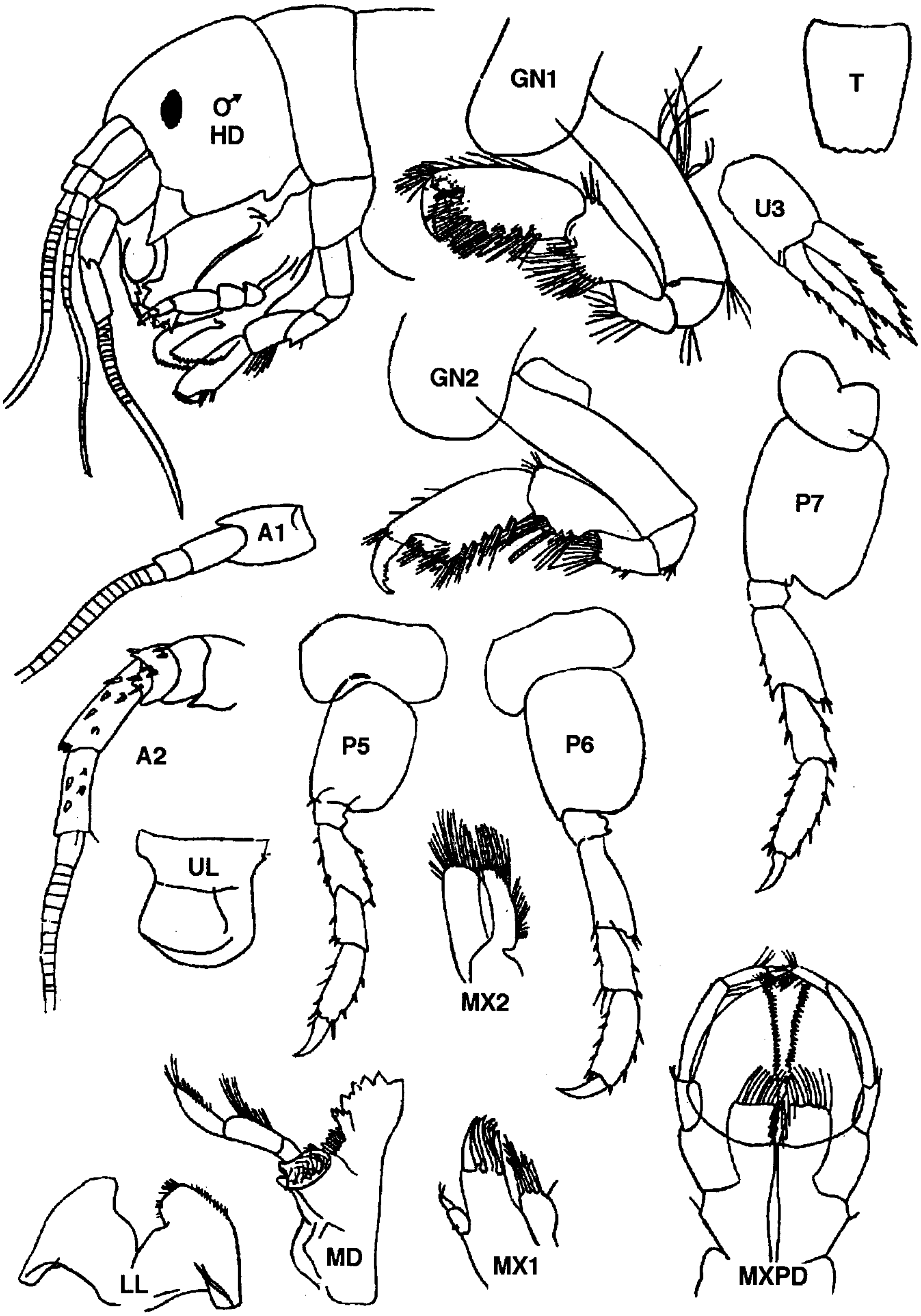


FIG. 31. *Laothoes pacificus* Gurjanova. Northeastern Sea of Japan. Male subadult (13.0 mm) (after Gurjanova, 1951).

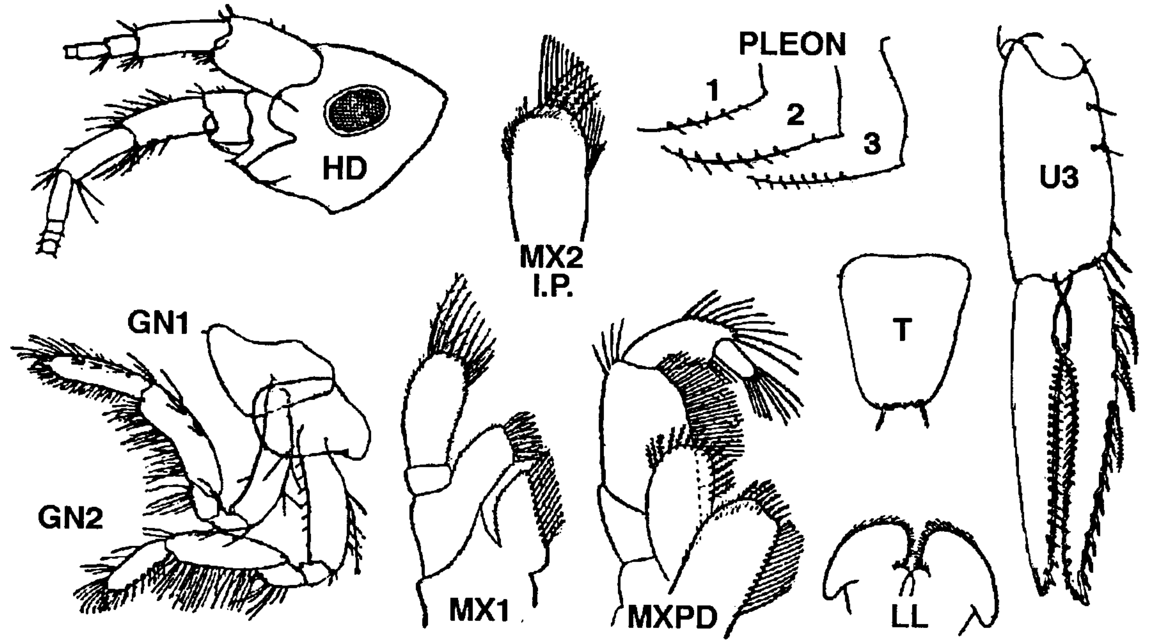


FIG. 32. ***Apherusa glacialis*** **(Hansen). Female (to 20 mm). Arctic Seas (after Stephensen, 1931).**

the western Nearctic or Siberian arctic and none authentically from the Bering Sea region. Of the20 described species only 3 are characterized by a simple pleon plate 3 (not serrate or toothed behind), large marginally setose uropod 3, and truncate telson. The other 15 species, represented by A. megalops (fig. 33), show more advanced character states, including distinctly sexually dimorphic gnathopods, short spinose uropod 3 rami and apically acute telson. They are confined mainly to the Mediterranean and the boreal northeastern (European) Atlantic coastal marine region.

This southern group actually possesses only a few features in common with the northern group, including a processiferous inferior head margin and partially developed inner lobes of the lower lip. These species appear to be a southern, warmer water counterpart of the genus *Paracalliopiella* of the boreal North Pacific region. Full review might lead to their separate generic recognition.

Apherusa glacialis (H.J. Hansen)
(Fig. 32)

Apherusa glacialis (Hansen, 1887) Shoemaker, 1920: 12.—Stephensen, 1931: 277, fig. 79.—Gurjanova, 1951: 632, fig. 432.—Shoemaker, 1955: 39.—Barnard & Karaman, 1991: 304.

Taxonomic and distributional commentary. This moderately large (to 20 mm) High Arctic species has been recorded sparsely from the Point Barrow region, from the under side of ice cakes, in shallow water (Shoemaker, 1955), and is marginally included here. The record of *Apherusa* sp. of Park (1961), repeated in Austin (1985), is problematical. It may represent a misidentification of *Oradarea longimana* which it resembles superficially in gnathopods, uropod 3, and other character states.

Apherusa glacialis is a member of the primitive subgroup of calliopiids of which *A. jurinei* is the type, in which pleon side plate 3 is simple (not serrate or toothed behind), and the gnathopods are slender and the carpus elongate.

Apherusa megalops (Buchholz)
(Fig. 33)

Apherusa megalops (Buchholz, 1874) Shoemaker, 1930: 293, figs. 32-34.—Gurjanova, 1951: 631, fig. 430.—Barnard & Karaman, 1991: 304.

Taxonomic and distributional commentary. *A. megalops* typifies the largest generic subgroup having serrated pleon plate 3, gnathopods more or less medium strongly subchelate and sexually dimorphic, and telson variously modified (usually triangular and apically subacute).

This relatively small species is holarctic in distribution, including the Beaufort Sea, but but has not yet been recorded from the Bering Sea region.

Oradarea Walker

Oradarea Walker, 1903: 40, 56.—Stebbing, 1906: 799.—Barnard, 1969a: 178 (part).—Shoemaker, 1930: 81.—Shaw, 1988: 942 (Table 1).—Barnard & Karaman, 1991: 330. *Leptamphopus* G. O. Sars, Gurjanova, 1951: 612 (part).

Type species. *Oradarea walkeri* Shoemaker, 1930 (= *O. longimana* Walker, 1903, homonym).

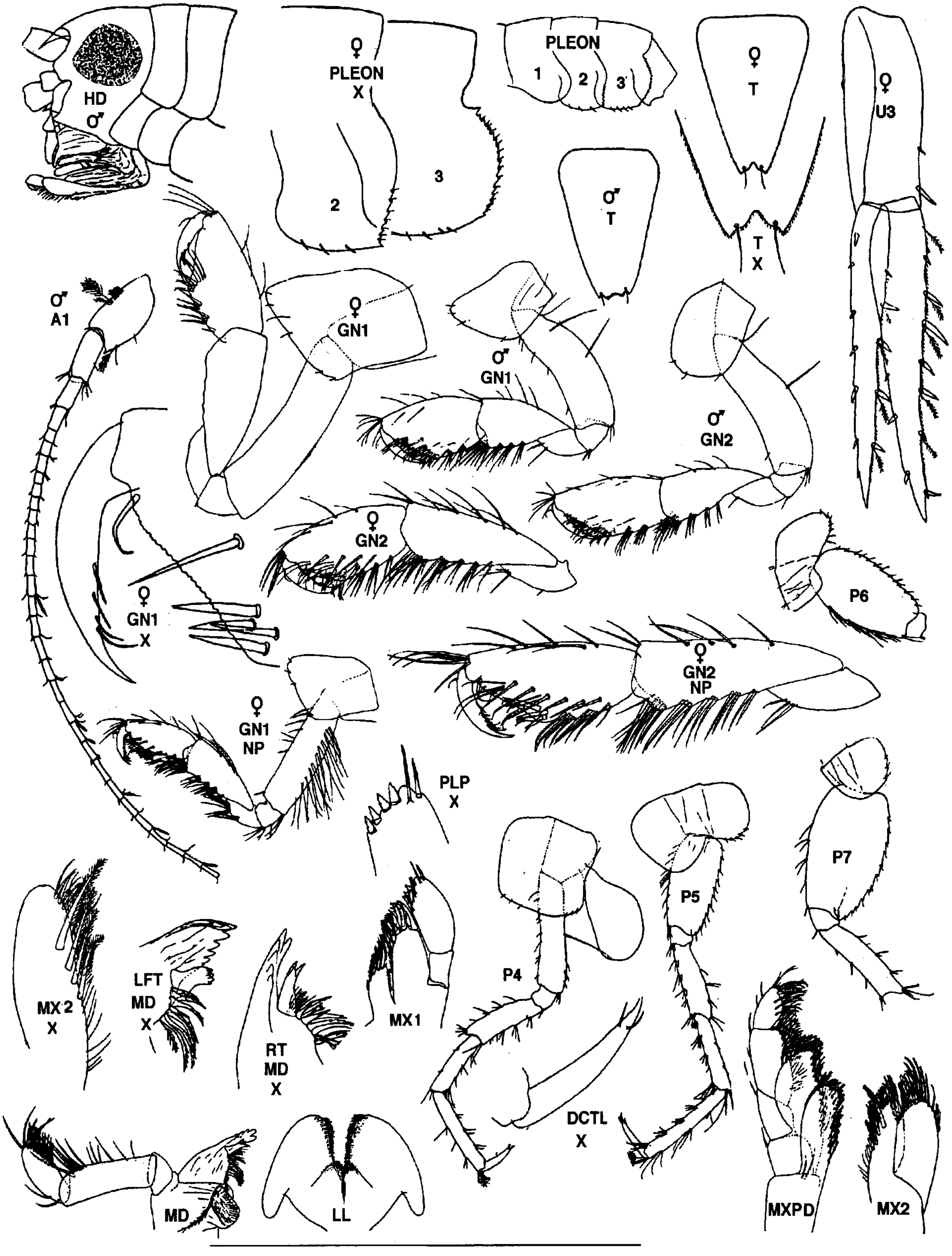


FIG. 33. ***Apherusa megalops*** **(Buchholz). Gulf of St. Lawrence. Female (7.0 mm); male (5.0 mm). Legend NP - from original specimen of Deutsche Nordpolar Expediton (after Shoemaker, 1930).**

Diagnosis. Body weakly mucronate on pleon and peraeon segment 7. Rostrum short. Eye small. Lower head process acute. Antennae slender, elongate. Antenna 1, peduncle short; accessory flagellum short, apex setose; flagellum weakly callynophorate, but lacking calceoli.

Mouthparts modified. Lower lip with distinct inner lobes. Mandibular palp segment 3 short, apex blunt; lacinia mobilis 5-dentate. Maxilla 1, inner plate multisetose. Maxilla 2, inner plate with facial setae. Maxilliped, inner plate broad; outer plate normal; palp, dactyl short.

Coxae 1-4 regular, deeper than broad. Gnathopods weakly subchelate, slender, very unequal. Gnathopod 2 much the longer, carpus and propod elongate (both sexes).

Peraeopods regular, slender, dactyls small. Peraeopods 5-7 elongate, homopodous; dactyls short.

Pleon plates 2 & 3 lacking facial spines, hind corners not acuminate. Uropods 1 & 2, rami slender, elongate, weakly spinose, outer ramus much the shorter. Uropod 3, rami very unequal (inner longer), margins spinose only.

Telson short, length slightly greater than width, apex very weakly notched.

Coxal gills plate-like, not pleated.

Taxonomic commentary. Shoemaker (1930) submerged *Leptamphopus longimanus* within Walker's genus *Oradarea*, a decision not accepted by Gurjanova (1951). Barnard & Karaman (1991) regard the species *walkeri*, newly named by Shoemaker (loc. cit.), as the type of the genus *Oradarea*. Paradoxically, of the 14 species currently recognized in the genus *Oradarea*, all but the type species are antarctic, antiboreal, or deep-sea tropical in distribution.

Oradarea longimana (Boeck)
(Fig. 34)

Amphithopsis longimana Boeck, 1871: 200.
Oradarea longimana (Boeck, 1971) Stebbing, 1906: 799.—Shoemaker, 1930: 298, figs. 35-37.—Austin, 1985: 589.—Staude, 1987: 378.—Shaw, 1989: 1889.—Barnard & Karaman, 1991: 330.
Leptamphopus longimanus (Boeck, 1871) Gurjanova, 1951: 614, fig. 416.
?*Leptamphopus novaezealandiae* (Thomson) Nagata, 1965: 174.—Ishimaru, 1994: 44.

Material examined. Specimens detailed by Shaw (1989) from Endeavour Segment, Juan de Fuca Ridge vent site, 2200 m, ~200 km west of Vancouver Island, B. C.
This species has also been recorded from San Juan Channel (Staude, pers. comm.).

Taxonomic and distributional commentary. *Oradarea longimana* is panboreal at sublittoral to abyssal depths in the North Atlantic and North Pacific Oceans. The species is believed to be an obligate scavenger or commensal with larger crustaceans,on bottoms of mixed mud, sand, and shell.

Bouvierella Chevreux

Bouvierella Chevreux, 1900: 70.—Barnard, 1969a: 175.—Barnard, 1969b: 95.—Shaw, 1988: 939.—Barnard & Karaman, 1991: 311.

Diagnosis. Body smooth, without dorsal processes or carina. Rostrum short; anterior head lobe subacute. Pigmented eyes lacking. Antenna 1 slightly longer than 2. Antennal peduncles short; accessory flagellum very short or lacking; callynophore and calceoli lacking.

Mouthparts basic. Upper lip slightly notched. Lower lip simple. Mandible, palp normal, left lacinia 7-dentate. Maxilla 1 normal, inner plate with numerous marginal setae. Maxilla 2, inner facial setae numerous, regular. Maxilliped, inner plate short; outer plate broadened.

Coxae 1-4 large, deep. Gnathopods 1 & 2 slender, weakly subchelate, sexually alike; carpus of gnathopod 2 elongate.

Peraeopods 3-7 regular, weakly subchelate, dactyls short. Peraeopods 5-7 closely homopodous; bases broad.

Pleon large; plates 2 & 3, hind corners obtuse ; pleopods powerful. Uropods 1 & 2, rami sublinear, serially spinose, with weak apical spines, outer ramus shorter. Uropod 3, rami narrowly lanceolate, margins spinose. Telson plate-like, apex with V-cleft.

Coxal gills plate-like, simple, on peraeopods 2-7. Brood plates moderately broad to narrow.

Taxonomic commentary. The genus *Bouvierella* is closest to *Oradarea*, and other "long wristed" leptamphopid genera of calliopiids, but differs in its weakly prehensible peraeopods. The species from Japanese waters, identified by Nagata (1965) and Inaba (1988) as *O. novaezelandiae* (Thomson, 1879), appears synonymous with *O. longimana* (Boeck).

Bouvierella carcinophila (Chevreux)
(Fig. 35)

Bouvierella carcinophila Chevreux, 1889.—Shaw, 1988: 939, figs.1, 2.—Barnard & Karaman, 1991: 311.
Leptamphopus paripes Stephensen, 1931: 280, fig. 80.

Material examined. Material of P. Shaw (loc. cit.) from head and mouth of Alice Arm, Vancouver I., in shrimp and crab pots set at 95 m (possibly associated with the spider crab *Chionoecetes* sp.

Taxonomic and distributional commentary. *Bouvierella carcinophila* is a small to medium, slender species known from sublittoral to abyssal depths in the North Atlantic and North Pacific regions. In the North American Pacific region, the species has been recorded by Shaw (1988) from Olga Bay, Alaska, to Alice Arm, B. C., from crab pots set at depths of ~75-180 m. Shaw (loc. cit.) has synonymized this species with *Leptamphopus paripes* Stephensen (1931), originally described from Danish Ingolf material off E.

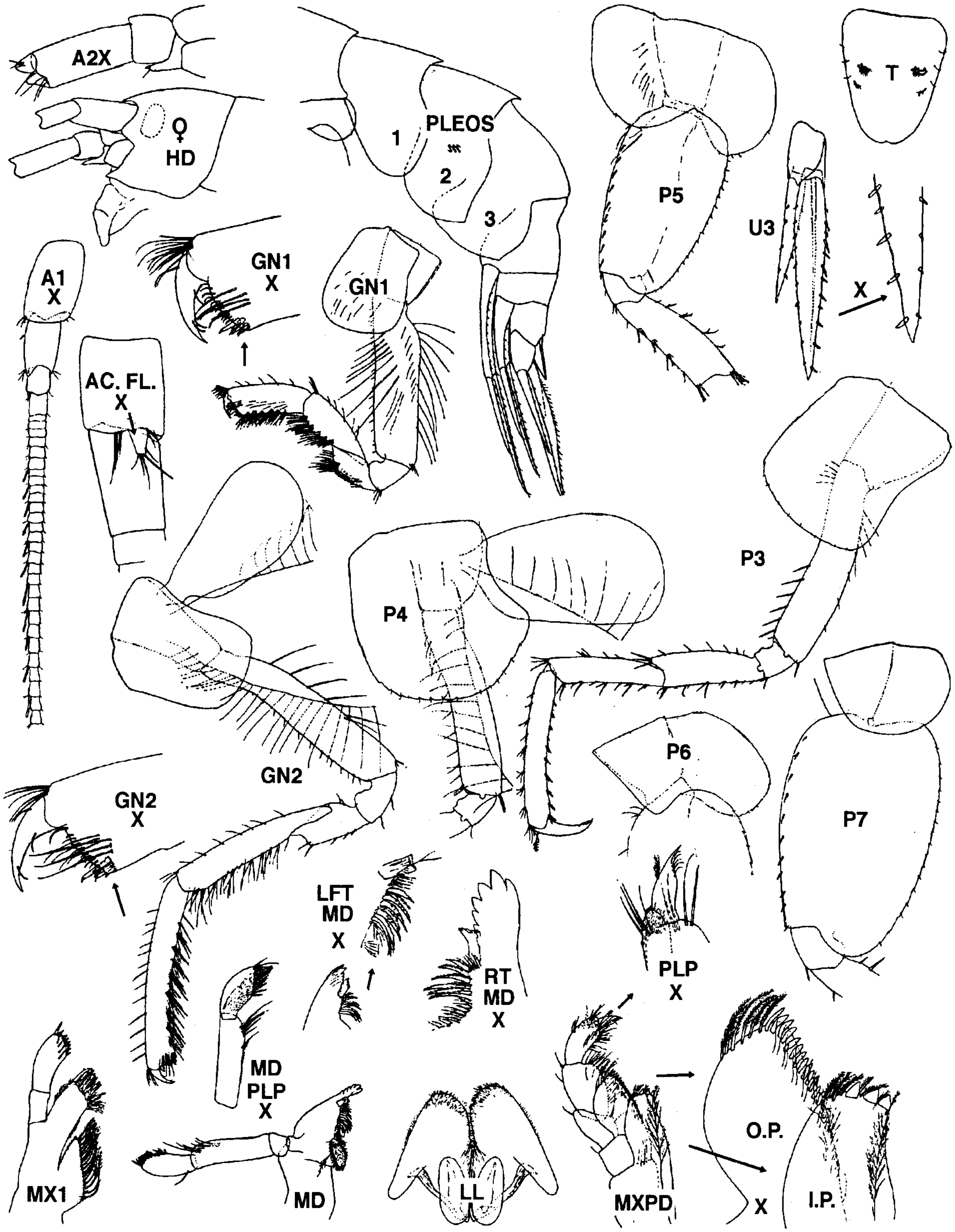


FIG. 34. ***Oradarea longimana*** **(Boeck). Gulf of St. Lawrence. Female (11.0 mm) (after Shoemaker, 1930)**

Greenland, a decision tentatively accepted here. Vader (1983) has discussed the significance of prehensile peraeopods in gammaridean amphipods, including those associated with decapod crustaceans. *B. carcinophilus* appears to be associated with decapod crabs, possibly as a scavenging commensal.

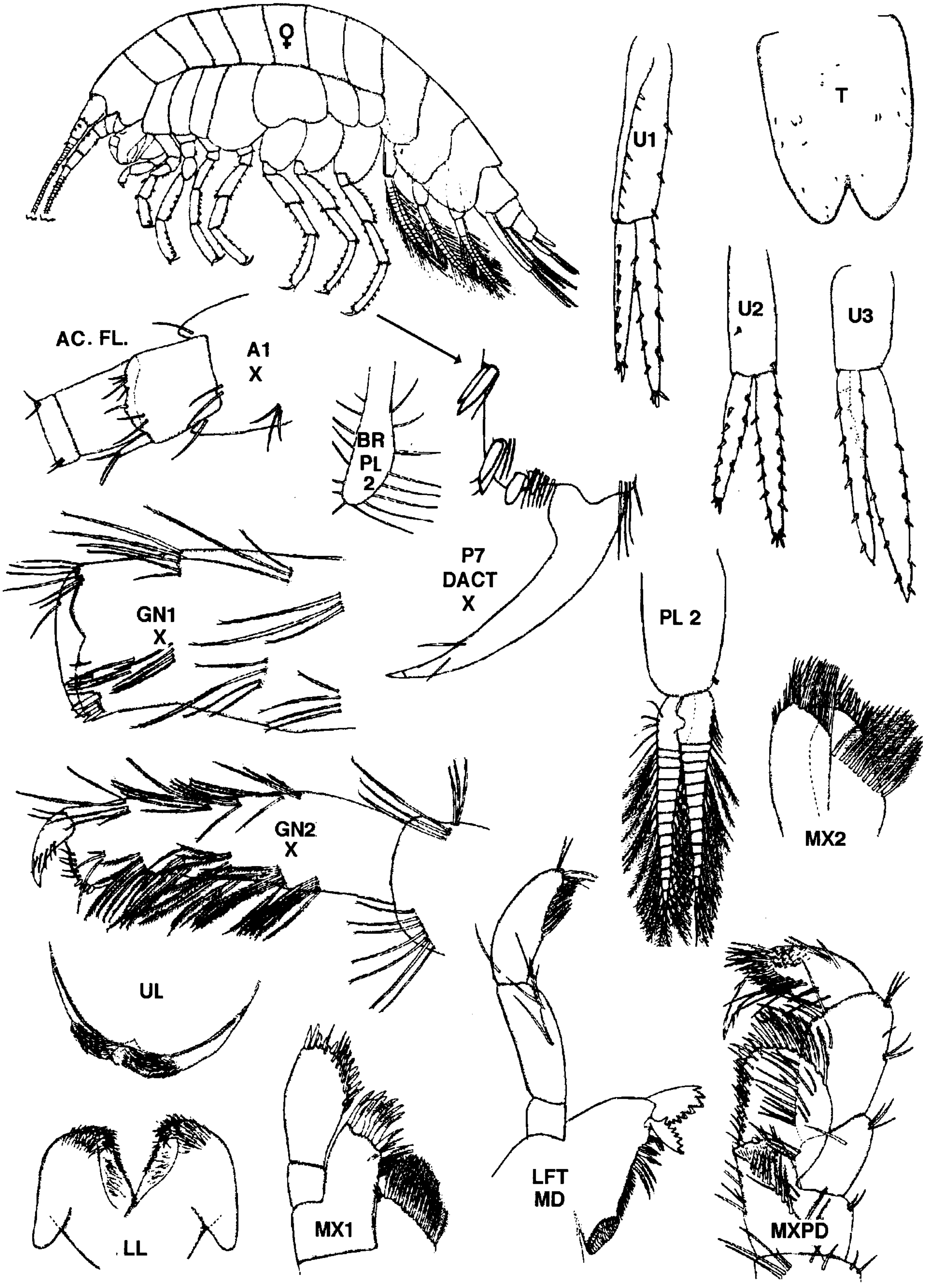


FIG. 35. *Bouvierella carcinophila* (Chevreux). Alice Arm, B. C. Female (7.3 mm) (after Shaw, 1988).

Weyprechtia Stuxberg

Weyprechtia Stuxberg, 1880: 27.—Stebbing, 1906: 380.—Gurjanova, 1951: 735.—Barnard & Barnard, 1983: 595, figs. 39, 40.—Barnard & Karaman, 1991: 26.

Type species. *Amathilla heugleni* Buchholz, 1874.

North Pacific regional species. *Weyprechtia heugleni* (Buchholz, 1874); *W. pinguis* (Kroyer, 1838).

Diagnosis. Body dorsally smooth. Head, rostrum short; inferior antennal sinus shallow, inferior head lobe not produced. Eye medium. Antennae medium, slender, 2 the longer, calceolate in male. Antenna 1, peduncle 3 not distally produced; accessory flagellum well developed (3+ segmented).

Mouthparts basic. Upper lip deep, rounded below, epistome produced. Lower lip lacking inner lobes (present?). Mandibular palp, segment 3 larger than 2. Maxilla 1, inner plate strongly setose; outer plate withh 11 apical spines; palp strong, 2-segmented. Maxilla 2, inner plate with strong row of facial setae. Maxilliped plates and palp regular.

Coxae 1-4 medium, deeper than long, lower hind margin serrate. Gnathopods weakly subchelate, subsimilar, not sexually dimorphic; propod, palm oblique; posterodistal spines few; dactyls smooth behind; carpus shallow, usually longer than propod.

Peraeopods 3 & 4 regular, segment 5 <4; dactyls medium. Peraeopods 5-7 regularly homopodous; bases medium broad, hind lobes distinct; dactyls moderately long.

Pleon plate 3 singly toothed behind, lower corner acute. Uropods 1 & 2, rami lanceolate, margins sparsely spinose; outer ramus shortened. Uropod 3, rami lanceolate, subequal, margins spinose.

Telson medium, subtruncate or weakly notched apically.

Coxal gills large, not pleated. Brood plates broad.

Taxonomic and distributional commentary. The genus was transferred from Gammaridae to Calliopiidae by Bousfield (1977) although still retained within the gammaroidean family complex by Barnard & Barnard (1983). The overall dorsally smooth body, weakly rostrate head, weakly subchelate, not sexually dimorphic gnathopods, homopodous, posterolobate peraeopods, lanceolate uropods, plate-like telson, and pontogeniid-like calceolus are character states that are basically eusiroidean (see Bousfield & Shih, 1994). The two known species are described as arctic-boreal littoral marine endemics (Barnard & Karaman, 1991). They are among the most primitive members of family Calliopiidae. The genus *Weyprechtia* is isolated phyletically from all other genera but *Halirages* (Fig. 39, p. 58).

Weyprechtia pinguis (Kroyer)
(Fig. 36)

Weyprechtia pinguis (Kroyer, 1838) Gurjanova, 1951: 737, fig. 509.—Shoemaker, 1955: 48.—Just, 1970: 28, figs. 13-15.—Barnard & Barnard, 1983: 596.—Bousfield & Shih, 1994, fig. 9 (part).

Material Examined. None from the study region.

Taxonomic and distributional commentary. This medium large species (to 29 mm) occurs mainly in the North Atlantic and eastern Nearctic regions, but has neen recorded from Pt. Barrow, Alaska (Shoemaker, 1955), and sparsely from the Sea of Okhotsk (Gurjanova, 1951).

Weyprechtia heugleni (Buchholz)
(Figs. 37, 38)

Weyprechtia heugleni (Buchholz, 1874) Derzhavin, 1930: 328.—Stebbing, 1894: 41, pl. 7.—Gurjanova, 1951: 735, fig. 508.—Shoemaker, 1955: 49.—Barnard & Barnard 1983: 596, figs. 39C, 40 A.

Material examined. None from the study region.

Taxonomic and distributional commentary. This very large species (to 52 mm) is common at Pt. Barrow, Alaska, and widely distributed in the Chukchi Sea and northern part of the Bering Sea region (Gujanova, 1951).

Weyprechtia heugleni is sufficiently unlike the type species, *W. pinguis,* that the former could well merit generic distinction of its own. Especially significant are the reported inner lobes of its lower lip, strong development of the mandibular palp, the epimerid-like development of coxa 4, and the broadly lanceolate form of the uropod rami that lack apical spines. Lack of regional study material prevents further analysis here.

KEY TO NORTH PACIFIC SPECIES OF *WEYPRECHTIA*

1. Coxal plate 4 normal, not produced laterally; antennae 1 & 2 subequal; uropod 3, rami narrowly lanceolate .... *W. pinguis* (p. 54)

—Coxa 4 produced laterally; antenna 2 elongate; uropod 3, rami broad .... *W. heugleni* (p. 54)

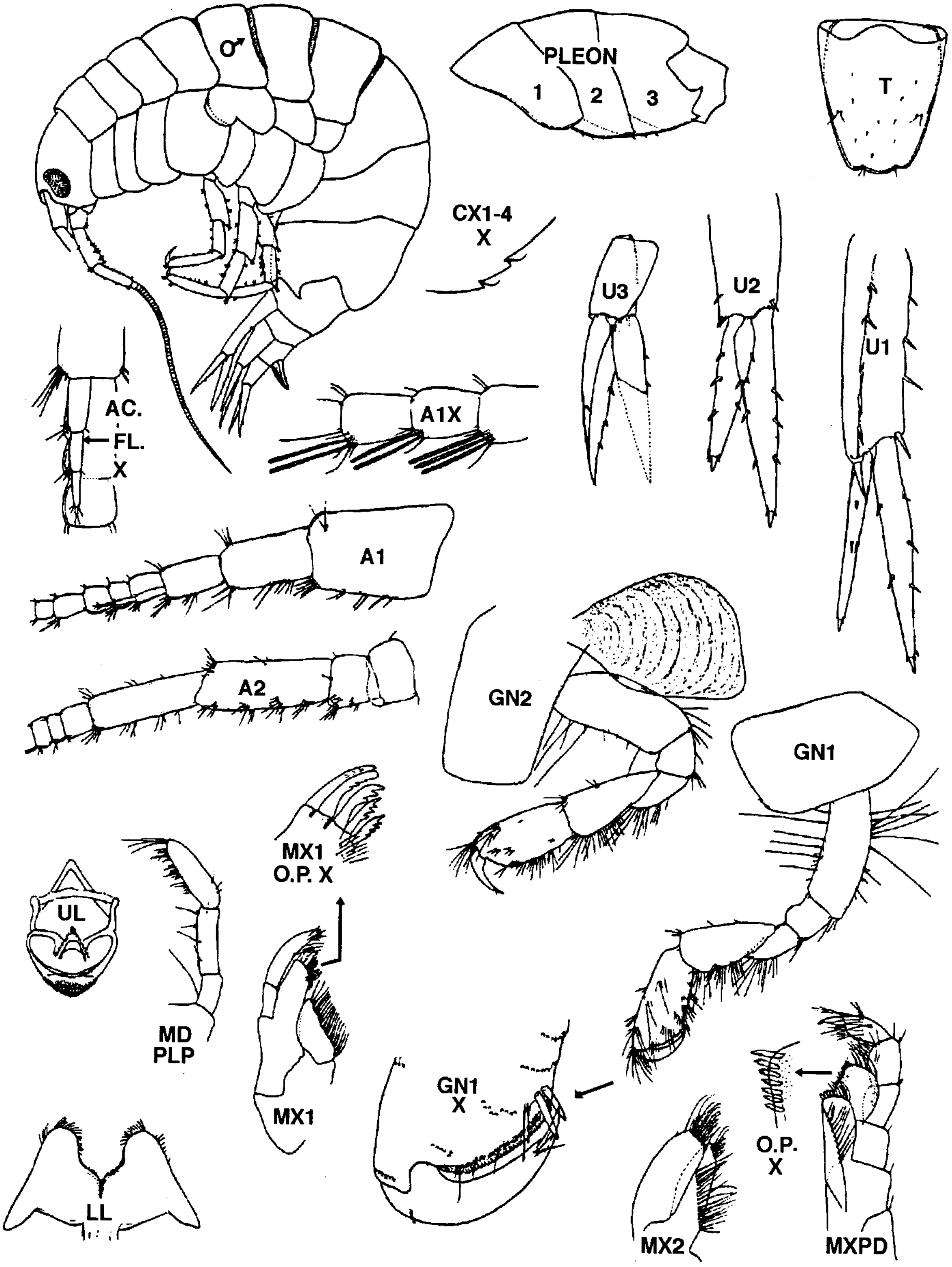


FIG. 36. *Weyprechtia pinguis* (Kroyer). Danish Ingolf Stn 49, off Greenland. Male (13-15 mm) (after Just, 1970).

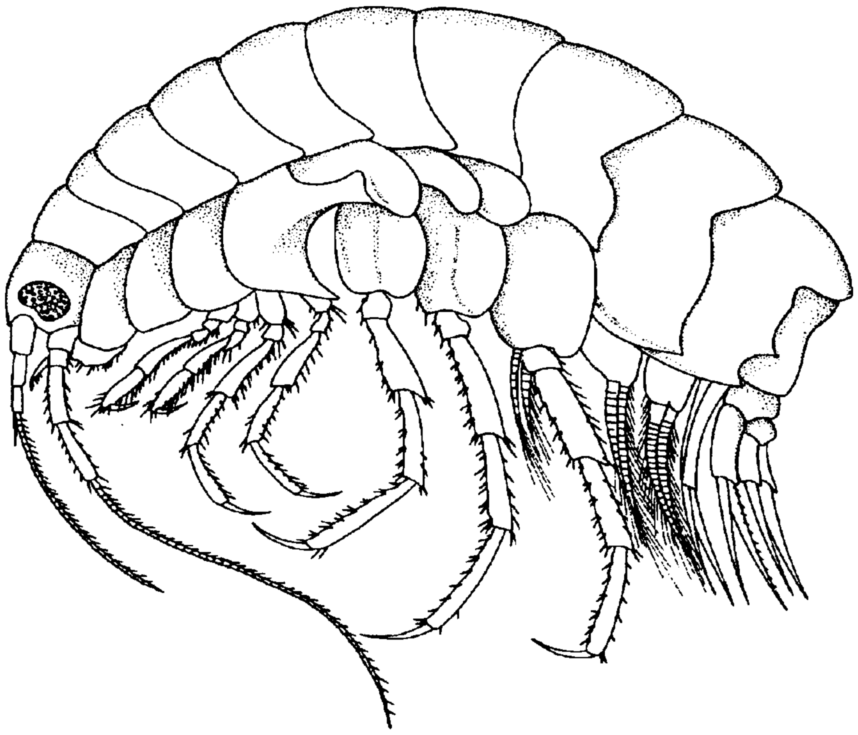


FIG. 37. Weyprechtia heugleni (Buchholz) Arctic Ocean, littoral. Female (30 mm) (after Barnard & Barnard, 1983)

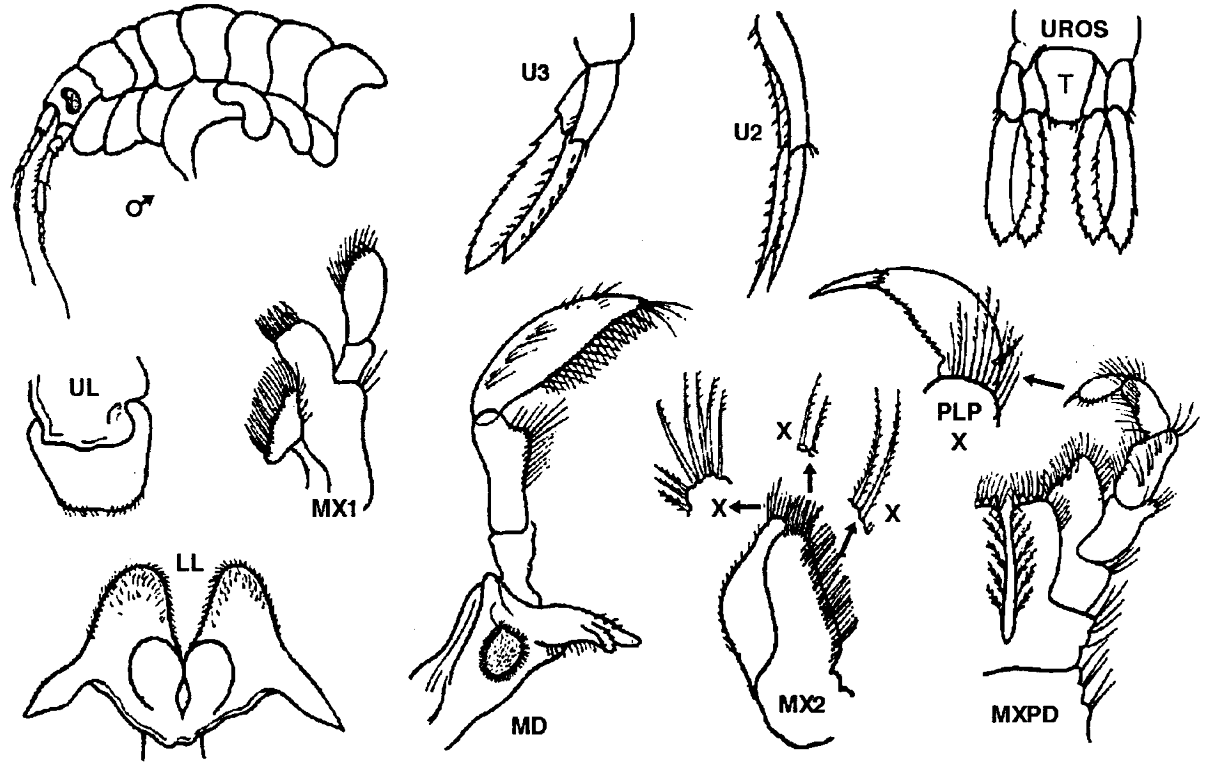


FIG. 38. *Weyprechtia heugleni* (Buchholz). Male (52 mm). Arctic Ocean to Bering Sea (after Gurjanova, 1951).

TABLE I. CHARACTERS AND CHARACTER STATES: GENERA OF CALLIOPIIDAE

CHARACTER	CHARACTER STATE VALUE		
	Pleiomorphic 0	Intermediate 1	Apomorphic 2
1. Antennal calceoli	present, both sexes	present males only	lacking both sexes
2. Antenna 1, accessory flagellum	present, 3+ segmented	present, minute	lacking
3. Antenna 1, segment 3 postero-distal process	lacking	present, small	present, well developed
4. Lower lip, inner lobes	lacking	trace	partly developed
5. Mandibular palp ratio: segment 3/ segment 2	>1	~1	<1
6. Maxilla 1, number of inner plate setae	10+	7-9	4-6
7. Maxilla 2, inner plate, row of facial setae	present , strong (5+)	present, few (1-4)	lacking, or marginal only
8. Maxilliped, outer plate	Normal		much enlarged or short, broad
9. Gnathopods 1 & 2 sexual dimorphism	lacking	slight	distinct
10. Gnathopods 1 & 2, form of propod	slender		short, deep
11. Gnathopod 2, form of carpus	slender not lobate		short, lobate below
12. Peraeopods 3-7 dactyls	short or weak		elongate or strong
13. Pleon plate 3, hind margin	smooth normal	single stout tooth	strongly serrate
14. Uropods 1 & 2, rami	lanceolate, apical spines lacking		linear, apical spines strong
15. Uropod 3, rami	subequal margins setose		unequal, margins spinose
16. Telson, form	elongate, apex notched	shorter, apex subtruncate	short, apex subacute

TAXONOMIC DISCUSSION

In this systematic study of calliopiid amphipods, as the family is diagnosed herein (p. 4), we have examined survey material of 13 species in 5 genera from the North American Pacific coastal region, from the Bering Sea to central California. An additional 13 species in 6 genera, occurring in Arctic waters immediately adjacent to the Bering Sea, or in the Asiatic North Pacific regions, are included in the following taxonomic and biogeographical analyses. These numbers represent about one-third of the species recorded to date from the Northern Hemisphere, and about one-fifth of the total marine calliopiid fauna world-wide.

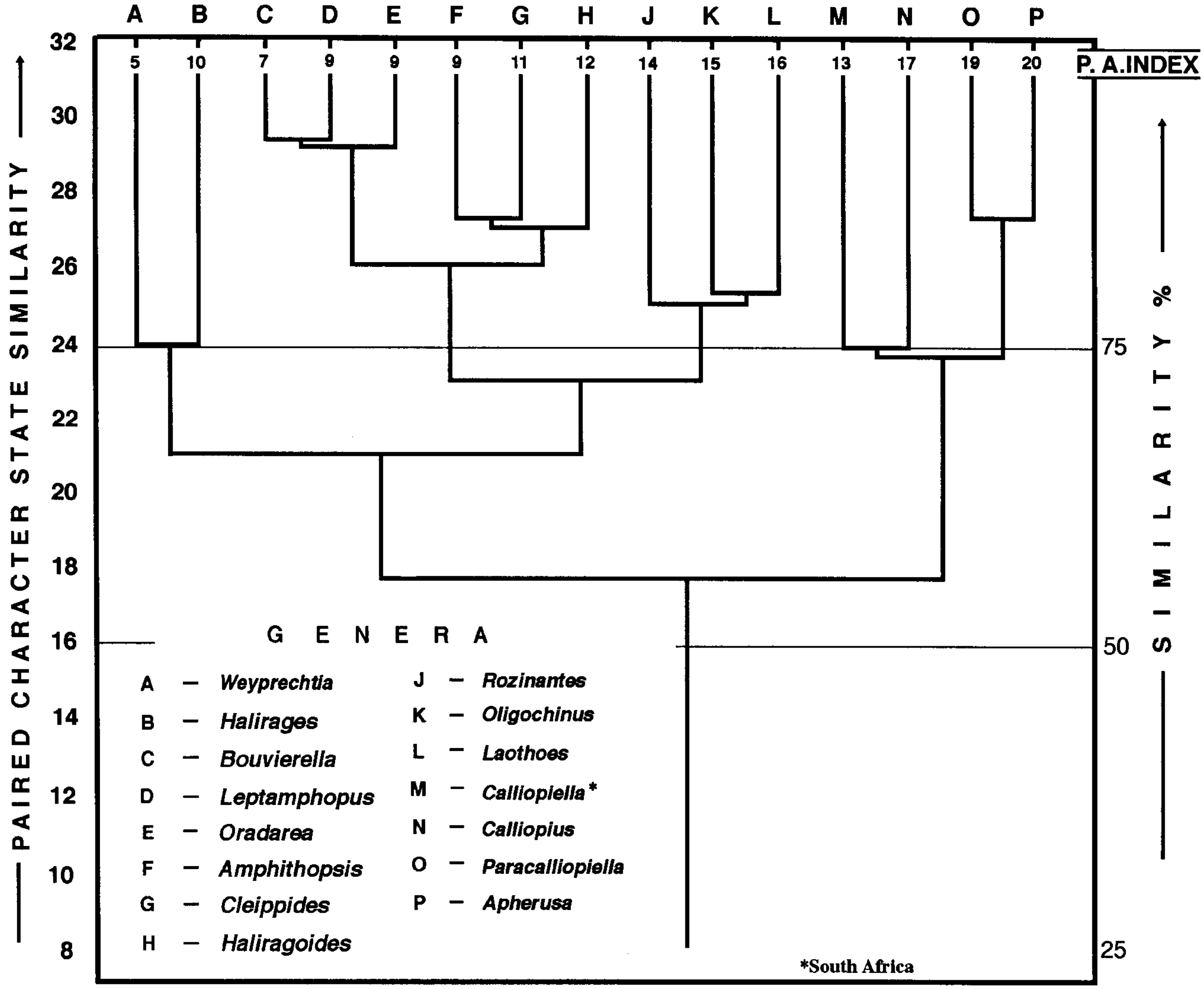


FIG. 39. PHENOGRAM: MAINLY HOLARCTIC GENERA OF CALLIOPIIDAE.

Morphological similarities as a basis for phyletic relationships.

Despite the relatively limited scope of the material at hand, the pertinent morphological and distributional data assembled here may be analyzed, on a numerical basis, for possible broader phyletic and biogeographical significance. A modification of the phenetic UPGMA (cluster analysis) system of Sneath and Sokal (1973) has been employed previously in similar regional faunistic studies (e.g., Jarrett & Bousfield, 1994; Bousfield & Hendrycks, 1995) and is utilized here. In this system, the character states are ordered on a presumed phyletic basis. Thus, the plesiomorphic condition (state) of a character is given a numerical value of 0, the advanced or apomorphic state a value of 2, and an intermediate condition, where applicable, a value of 1. By totalling the numerical values for individual character states, an overall criterion of morphological similarity termed the Plesio-Apomorphic (P.-A.) Index is obtained. Low P.-A. values signify phyletically primitive, and high numbers relatively advanced, taxa.

Within a restricted definition of the family Calliopiidae (p. 4), analysis of morphological similarities of genera, mainly of the Northern Hemisphere, is based on 16 characters and corresponding 32 paired character state extremes (Table I, p. 57). The characters selected include a mixture of conspicuous body features, usually embodied in descriptions and figures of the previous literature, as well as more cryptic, but possibly more phyletically significant features, especially those of the mouthparts.

Similarities in the ordered character states of mostly northern calliopiid genera are phenetically analyzed (Fig. 39, above). Phyletic relationships are suggested by the four main groupings in which genera are relatively closely similar (at and above 75% similarity level). These are: (1) a primitive *Weyprechtia-Halirages* subgroup on the extreme left (P.-A. Indices of 5-10); (2) a primitively intermediate *Bouvierella-Haliragoides* subgroup of six genera in the centre left (P. A. Indices of 7-12), and (3) an intermediate but relatively advanced *Oligochinus* cluster in the centre right (P.-A. values of 14-16); and (4) a cluster of four advanced genera (including *Calliopius*) on the right (P. A. Indices of 13-20).

With respect to (1), character states are almost uniformly plesiomorphic, including calceolate antennae, basic mouthparts and strongly toothed pleon plates. These are large species, confined to arctic littoral and sublittoral substrata.

Within cluster (2) are two subclusters, viz., a relatively primitive *Leptamphopus* complex that includes *Bouvierella* and *Oradarea*. These deep-water species are characterized strikingly by elongate, weakly subchelate gnathopods with slender wrists, by short peraeopod dactyls, apically notched telson, and basic mouthparts. They are linked at the 80% similarity level with the more advanced sublittoral *Amphithopsis-Haliragoides* complex, mainly of the North Atlantic region, in which the mouthparts are more specialized, the gnathopod wrists shorter, and the telson plate-like.

The intermediate cluster (3) links distantly, and perhaps unnaturally, the eastern North Pacific littoral genus *Oligochinus*, with two arctic and subarctic sublittoral genera, *Rozinante* and *Laothoes*.

Cluster (4) encompasses the holarctic genus *Calliopius* and the South African genus *Calliopiella*. However, their advanced character state similarities (e. g., powerful gnathopods in both sexes) are probably homoplasious. More closely, and probably more naturally, linked are the two most advanced genera, the littoral North Pacific *Paracalliopiella* and its mainly Arctic and North Atlantic counterpart *Aphherusa*. Their more apomorphic character states, especially of mouthparts and uropods, plate-like telson, and sexually dimorphic gnathopods, are associated with the more benthic-epibenthic life styles and more southerly distributions of holarctic littoral species.

Relationships between species within the genus *Calliopius* are suggested by the phenetic analysis of Fig. 40 (p. 60). In the phenogram, three major subgroups cluster at or above the 75% similarity level: (1) to the left, a primitive North Pacific *behringi -columbianus* pair (P.-A. values of 8-9); (2) in the centre left, an intermediate North Pacific *carinatus-pacificus* species pair (P. A. values of 14-18); and (3) to the right, an advanced North Atlantic *laeviusculus-rathkii* complex of four species (P.-A.Indices of 16-22).

With respect to the species pair of (1), character states are mainly plesiomorphic and include multi-segmented antennal flagella, minute antennal calceoli that occur in three or more posterior (inner) facial rows; maxilla 2, inner plate with weak facial seta(e); coxa 4 very broad; basis of peraeopod 7 broadly lobate, and the outer ramus of uropod 3 broadly lanceolate.

Within intermediate group (2), species have relatively few but large antennal flagellar segments; antennal calceoli are larger and concentrate along segmental posterior margins; maxilla 2, inner plate with single stout facial seta; coxa 4 is relatively narrow and rounded below; the basis of peraeopod 7 is more narrowly lobate, and the rami of uropod 3 more narrowly lanceolate.

Within advanced subgroup (3), the clustering tends to support the species distinctiveness of the *laeviusculus-crenulatus* taxonomic pairing, and continued recognition of *C. rathkii* (Zaddach) that G. O. Sars (1895) had so ably demonstrated in his monographic study of the Norwegian amphipod fauna a century ago.

The phenetic analysis further indicates that the most primitive subgroup is sufficiently distinctive (at ~50% level of similarity) to warrant subgeneric recognition. However, *Calliopius sablensis*, the most primitive member of the advanced Atlantic subgroup, exhibits some character states (e.g., small antennal peduncular process, broad coxae 3 & 4) variously in common with Pacific species, and its single record of occurrence is from the western North Atlantic. Thus, in comparing the plesio-apomorphic ratings of component species, the most primitive species occur only in the North Pacific and the most advanced only in the eastern North Atlantic. Thus, the North Pacific appears to be a plausible centre of origin and evolution of the genus *Calliopius*. Ancestral forms may have penetrated the North Atlantic secondarily, via an eastward arctic pathway.

Probable phyletic relationships of ten described species within the North Pacific genus *Paracalliopiella* are suggested by the closeness of morphological similarities shown in Fig. 41 (p. 60). The analysis employed a slightly different and more numerous suite of characters and corresponding character states. These included the degree of dorsal carination of peraeon and pleon; number of flagellar segments of antenna 1; size of the accessory flagellum of antenna 1; and degree of setation of the rami of uropod 3.

Four major subgroupings at and above 75% similarity can be recognized: (1) on the left, a very primitive, closely related *bungei - shoemakeri -haliragoides* trio (P.-A. Index of 7-11); (2) on the centre left, an intermediate pair of *beringiensis-tzvetkovae* (P.-A. Index of 14-17); (3) on the centre right, a less closely similar intermediate trio of *pacifica-slatteryi-kudrjaschovi* (P. A. Index of 18-20); and (4) on the right, a very advanced *litoralis-pratti* species pair (P.-A. Index of 28-31).

Subgroup (1) consists of relatively large species having strongly carinated dorsum, elongate antennae, elongate carpus and propods of gnathopods 1 & 2, elongate and setose inner ramus of uropod 3, and other plesiomorphic character states.

Subgroup (2) retains mainly plesiomorphic character states, including elongate gnathopod carpus (female), gnathopod 2 stronger than 1 (male), and telson elongate. More advanced characters states include weakly developed inner lobes of the lower lip, very weakly carinate pleon and smaller size at maturity.

With respect to (3), the pleon and posterior peraeon remain slightly carinated, and the antennal flagella and uropod 3 rami are elongate. However, more apomorphic character states include a medium to short carpus in gnathopod 2 (female); gnathopod 2 (male) slightly more strongly subchelate than gnathopod 1; and uropod 3 margins are spinose or, if setose, very weakly so.

Subgroup (4) embraces two small intertidal species having mostly apomorphic character states. These include a

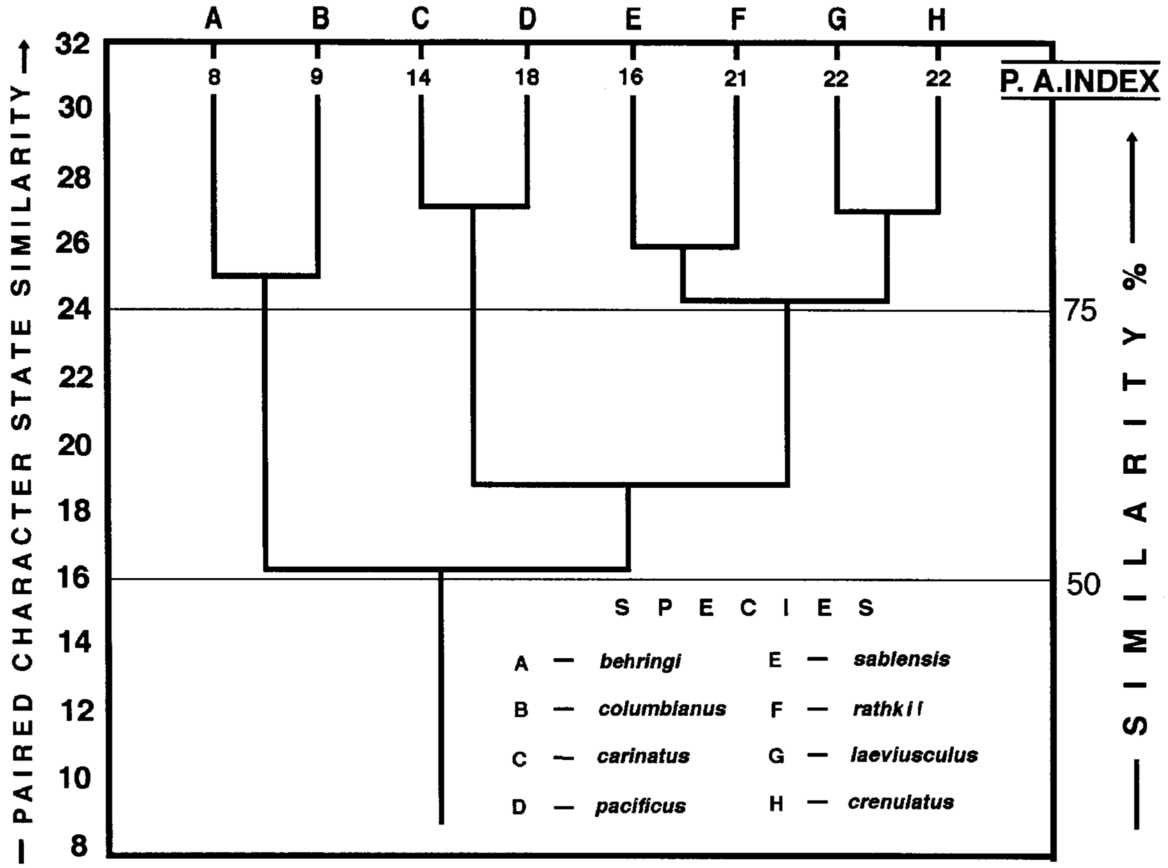


FIG. 40. PHENOGRAM: HOLARCTIC SPECIES OF *CALLIOPIUS*

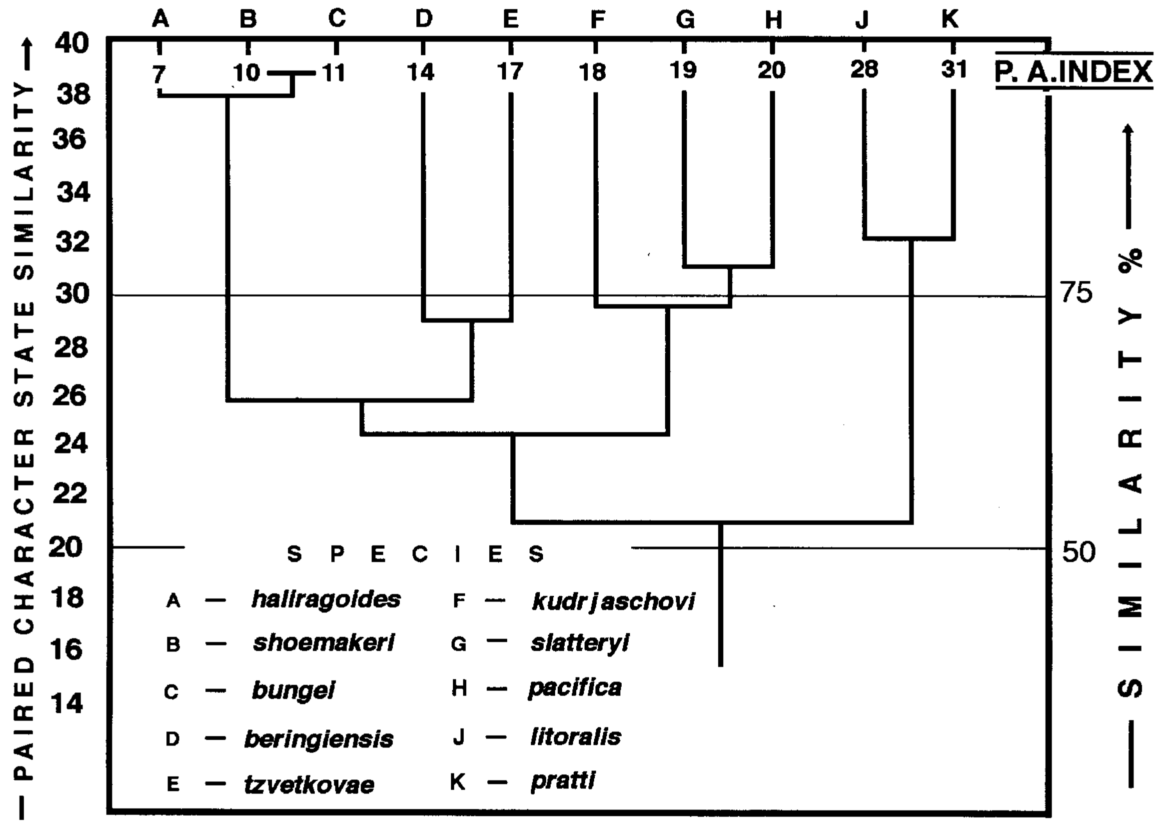


FIG. 41. PHENOGRAM: NORTH PACIFIC SPECIES OF *PARACALLIOPIELLA*

smooth dorsum, short antennal flagella, short rami of uropod 3, short telson, and strong peraeopod dactyls. In addition, the gnathopod carpus (female) is short, and gnathopod 1 (male) is more strongly subchelate than gnathopod 2.

Species within subgroups of *Paracalliopiella* exhibit disconcerting morphological anomalies. Thus, within subgroup (2), *P. beringiensis* has a short mandibular palp segment 3, and squarish hind corner of pleon plate 3, character states that are reversed in *P. tzvetkovae.* Within subgroup (3) (above), *P. pacifica* has an elongate mandibular palp, strongly setose posterior margin of gnathopod propods, and elongate telson, but the reverse is true in *P. slatteryi.* Within subgroup (4), *P. litoralis* has an elongate mandibular palp segment 3, and maxilla 2 inner plate is strongly marginally setose, character states that are reversed in its North American counterpart, *P. pratti.* However, until more thorough examination of type material can be undertaken, these cross-subgroup inconsistencies are here considered indicators of convergent evolution rather than phyletic significance.

Family Calliopiidae: a broader concept?

The present study may shed some light on broader aspects of calliopiid classification and phylogeny. The taxonomic basis for submergence of Pontogeneiidae Stebbing, 1906, and possibly Bateidae Stebbing, 1906, within Calliopiiidae Sars, 1895, remains moot. As noted above (p. 5), Barnard & Karaman (1991) have united calliopiids and pontogeneiids within a much broadened concept of family Eusiridae. However, they retained Bateidae as a separate family based solely on the degenerate condition of gnathopod 1. Some character states, especially of mouthparts, in some "classically" pontogeneid genera such as *Accedomoera* J. L. Barnard, 1969b, and bateid genera such as *Carinobatea* Shoemaker, 1926, overlap considerably. These genera might readily be classified as calliopiid, perhaps closest to *Paracalliopiella* and *Oligochinus*, except for the more deeply separated telson lobes (see also Ortiz, 1991). Thus, *Accedomoera* has a notched inferior antennal sinus, short antennal peduncles, minute accessory flagellum, and strong bundles of aesthetascs on alternating segments of the flagellum of antenna 1. In addition, its mouthparts are similar, peraeopods 5-7 are similarly homopodous, and the rami of uropods 1 & 2 are linear and unequal. In *Accedomoera*, too, the antenna, are strongly calceolate, segment 3 of the mandibular palp is strongly subfalciform, the lower lip shows incipient inner lobes, and the lanceolate, marginally plumose-setose rami of uropod 3 are reminiscent of the condition in the calliopiid type genus *Calliopius*. However, until full examination of representative species of all pertinent genera can be undertaken, sufficient real taxonomic differences remain, singly or in combination, especially of the gnathopods, coxal gills, and telson, that continued recognition of the Calliopiidae as a distinct family within superfamly Eusiroidea remains justifiable.

Relationships of Calliopiidae and Gammarellidae

Largely on the basis of micromorphology of the antennal calceolus, J. L. Barnard (1989) resurrected family Gammarellidae, which had been submerged within family Calliopiidae by Bousfield (1983). Barnard expanded its generic composition to embrace the arctic-subarctic genus *Gammarellus* Herbst and the antarctic genera *Gondogeneia, Austroregia* and *Chosroes.* His lead has been followed by recent authors including DeBroyer & Jazdzewski (1993) and Palerud & Vader (1991). Encompassed taxa share the following (mostly plesiomorphic) character states: medium to large body size, strongly dorsally carinate bodies (especially pleon), basic mouthparts, homopodous peraeopods, fully developed uropods with lanceolate rami, and plate-like telson with median setae and emarginate apex. Antennal calceoli are usually present, and of a complex form having stalk and bulla, large receptable, and distal elements separated into 3 (or more) units. *Gammarellus* is especially primitive in having a well-developed accessory flagellum (vestigial in all others), pleated coxal gills, present on peraeopod 7, and multicalceolate antennae. Other character states typical of the Gammarellidae are: uropod 3, rami elongate, marginally setose, outer ramus the longer; maxilliped, palp segment 2 distally broadest; aesthetascs in bundles on alternate segments of antennal flagellar segments; anterior head notch deep, broad; mandibular palp segment 3 falciform; gnathopods strongly subchelate but little sexually dimorphic; gnathopod carpus shorter than propod; maxilla 1 with 9-11 apical spines (9 in *Austrogia regias* which may prove to be a pleustid!)

The *bungei* subgroup within the North Pacific genus *Paracalliopiella* variously bears a strong superficial resemblance to these genera. Similarities are especially close to *Gammarellus* on the one hand, and *Austroregia* on the other. However, calceoli are lacking in all species of *Paracalliopiella,* so a critical "Barnardian" comparison at family level cannot be made at present. However, it is unlikely that the similarities of the *bungei* subgroup (above) can be entirely convergent. This subgroup links the calliopiids and the gammarellids rather closely. Perhaps a further species of the *bungei* group bearing antennal calceoli will yet be discovered, and thereby facilitate full taxonomic evaluation of these genera at family level.

One final point of "spinoff" from this study might be raised. Steele (1995) has queried the concept of a pelagic, ancestral amphipod type, as developed by the senior author [e.g. in Bousfield and Shih (1994)]. Evidence amassed by Steele, mainly from eusiroidean examples, points to an essentially benthic ancestral type with pre-amplexing reproductive behaviour, from which various lines of pelagic and/or otherwise free-swimming morphotypes arose. While evidence from the present study on calliopiid amphipods is not critical, the characters and character states analyzed here suggest that evolutionary trend within component North Pacific genera is from a free-swimming body form, with

TABLE II. DISTRIBUTION OF SPECIES OF CALLIOPIIDAE: NORTH PACIFIC REGION

SPECIES	BIOGEOGRAPHIC ZONES								
	1	2	3	4	5	6	7	8	9
1. ***Weyprechtia***									
heugleni (Buchholz)		*x*	*X*						
pinguis (Kroyer)			*X*						
2. ***Apherusa***									
megalops (Buchholz)			?						
glacialis (Hansen)			*X*			?			
3. ***Laothoes***									
pacificus Gurjanova		*X*	*X*						
polylovi Gurjanova		*X*	*X*						
4. ***Halirages***									
fulvocincta (M. Sars)		*x*	*X*						
nilssoni Ohlin		*x*	*X*						
5. ***Bouvierella***									
carcinophila Chevreux		?		?	*X*				
6. ***Oradarea***									
longimana (Boeck)		?			*X*	*X*	*X*		
7. ***Calliopius***									
laeviusculus (Kroyer)		?	?		?				
behringi Gurjanova		*X*	*X*	?					
columbianus, n. sp.			*x*	*X*	*X*	*X*			
carinatus, n. sp.				*X*	*X*	*X*	*X*		
pacificus, n. sp.				*X*	*X*	*X*	*X*		
8. ***Paracalliopiella***									
litoralis (Gurjanova)		*X*	*X*						
bungei (Gurjanova)		*X*	*X*						
pacifica Tzvetk. & Kudr.		*X*	*X*						
tzvetkovae, n. sp.		*X*	*X*						
shoemakeri, n. sp.			*X*						
beringiensis, n. sp.			*X*						
slatteryi, n. sp.			*X*						
haliragoides, n. sp.			?	*X*					
kudrjaschovi, n. sp.			*X*	*X*					
pratti (J. L. Barnard)			*X*	*X*	*X*	*X*	*X*		
9. ***Oligochinus***									
lighti J. L. Barnard			*x*	*X*	*X*	*X*	*X*	*X*	

Legend: 1. SE Japan Sea; 2 NW Sea of Japan & Sea of Okhotsk ; 3. S. Chukchi & Bering Seas; 4. S.E. Alaska; 5. Northern B. C.; 6. Southern B. C.; 7. Wash.-Oregon; 8. Northern and Central California; 9. Southern and Baja California. Occurrence: X - common; x - rare or marginal; ? - questionable occurrence.

calceolate antennae, natatory uropods, and slender, sexually similar gnathopods, to a benthic crawling or nestling body form. During the process of changing life style, antennal calceoli are gradually reduced and eventually lost, uropods transform from lanceolate and setose to linear and spinose, suitable for ambulation or saltation, and gnathopods become increasingly powerfully subchelate, sexually dimorphic, and pre-amplexing in the male. The primary "swimming-perching" nature of amphipod crustaceans, proposed by Steele (1988), and pelagic reproductive searching, remain the probably most correct ancestral behaviour patterns and best fit the morphological evidence within extant members of the Calliopiidae.

Biogeographical discussion.

The distribution of 26 species and 9 genera of family Calliopiidae in the North Pacific region is outlined in Table II. Twenty-one of these species are essentially intertidal and/or littoral in bathymetric range; only three species (*Halirages fulvocincta, Laothoes polylovi,* and *Apherusa megalops*) might be considered fully sublittoral, and only two (*Bouvierella carcinophila* and *Oradarea longimana*) are deep sublittoral to bathyal. As noted above (p. 57), the North Pacific assemblage represents about one-third of the known holarctic calliopiid fauna of 70+ species, in 15 genera, most species of which occur along Arctic and North Atlantic coastlines (Palerud & Vader, 1991) south to the Mediterranean (Lincoln, 1979; Krapp-Schickel, 1982) and middle Atlantic states regions (Bousfield, 1973; Watling, 1981). More than 50 calliopiid species, in 16 mostly antiboreal genera, are also known from Antarctic waters (DeBroyer & Jazdzewski, 1993; Barnard & Karaman, 1991) where, in the absence of gammaroideans, they dominate rocky intertidal and littoral marine habitats.

North Pacific calliopiids can be grouped regionally into: (1) an essentially Beringian fauna (in biogeographical zone 3) of 19 species, in 8 genera, of which 6 species have not been recorded elsewhere; (2) an Asiatic North Pacific assemblage (in zones 1 & 2) of 11 species, in 6 genera, none of which is endemic and occurs also in the Beringian region; and (3) a North American Pacific fauna (in zones 4-9) of 9 species, in 5 genera, of which 5 species are apparently endemic and only four occur also in the Beringian region. The western and eastern North Pacific calliopiid faunas appear to be approximately equal in numbers of species, and extend southward over coastlines of comparable length and latitudinal range (S. Korea, to lat. 36° N., and California, to Pt. Conception, at 34° N., respectively). The southern limit of littoral marine calliopiids in the western North Pacific conforms with the discontinuity belts of distribution of northern and southern faunas in the Sea of Japan outlined by Nishimura (1965). Until the faunas are more extensively known, full explanation of the apparently higher percentage of calliopiid endemics along North American shores may be premature. However, as outlined in earlier regional comparisons (e.g., Bousfield & Hoover, 1995), year-round thermal stability and ice-free winter climate of the eastern North Pacific contrast with the harsher temperature regime and severe winter icing along northwestern Pacific shores, and in the Bering Sea region. Such edaphic differences, effective over long geological periods, may have mirrored by corresponding differences in niche diversity and stability in the two regions. The North American Pacific boreal coastline may have been less suitable for cold-adapted Beringian species on the one hand, but more amenable to new evolutionary "opportunities" on the other, thus contributing to the observed faunal differences.

We may conclude, therefore, that the North Pacific calliopiid fauna is centred in the Beringian region. It extends southward virtually unchanged along Asiatic Pacific shores to the limit of cool-temperate (boreal) inshore marine climates. Along the North American coastline, however, the Beringian fauna is replaced almost entirely by regionally endemic counterpart species.

REFERENCES*

Alderman, A. L., 1936. Some new or little known amphipods of California. Univ. Calif. Publ. Zool. 41: 53-74, 51 figs.

Armstrong, J. W., C. P. Staude, R. M. Thom, and K. K. Chew, 1976. Habitats and relative abundances of the intertidal macrofauna at five Puget Sound beaches in the Seattle, Washington, area. Syesis 9: 277-290.

Austin, W. C., 1985. An annotated checklist of marine invertebrates of the cold temperate northeast Pacific. Khoyatan Marine Laboratory, Cowichan Bay, B. C. Vol. I-III: 682 pp.

Barnard, J. L., 1954. Marine Amphipoda of Oregon. Oregon State Monographs, Studies in Zoology 8: 1-103, 33 pls.

————, 1958. Index to the families, genera, and species of the gammaridean Amphipoda (Crustacea). Publ. Allan Hancock Foundation. Occ. Pap. 19: 1-146.

————, 1969a. The families and genera of marine gammaridean Amphipoda. U. S. Natl. Mus. Bull. 271: 1-535.

————, 1969b. Gammaridean Amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. U. S. Nat'l. Mus. Bull. 258: 1-230. 173 figs.

————, 1971. Gammaridean Amphipoda from a deep-sea transect off Oregon. Smiths. Contr. Zool. 61:1-86, 48 figs.

————, 1975. Amphipoda: Suborder Gammaridea. pp. 313-366, pls.70-85. in R. I. Smith & J. T. Carlton (eds). Light's Manual: Intertidal Invertebrates of the Central California Coast, 3rd ed., 716 pp. Univ. California Press, Berkeley, California.

————, 1978. Redescription of the amphipod *Calliopiella michaelseni* Schellenberg from South Africa, with comparison to a new genus from the Pacific Ocean. Ann. S. Afr. Mus. 754: 33-40, 3 figs.

————, 1989. Rectification of *Halirages regis* and *H. huxleyanus* (Crustacea: Amphipoda) from marine Antarctica, with description of a new genus, *Austroregia*. Proc. Biol. Soc. Wash. 102: 701-715, 7 figs.

————, & C. M. Barnard, 1983. Freshwater Amphipoda of the World, Vols. I & II. 830 pp., 50 figs. Hayfield Associates, Mt. Vernon, VA.

————, & M. M. Drummond, 1978. Gammaridean Amphipoda of Australia, part III. The Phoxocephalidae. Smiths. Contr. Zool. 245: 1-551, 269 figs.

————, & G. S. Karaman, 1987. Revisions in classification of gammaridean Amphipoda (Crustacea), part 3. Proc. Biol. Soc. Wash. 100: 856-875.

————, 1991. The Families and Genera of Marine Amphipoda (Except Marine Gammaroids), Pts. 1 & 2. Rec. Austral. Mus., Suppl. 13: 866 pp, 133 figs.

Barnard, K. H., 1930. Amphipoda. British Antarctic Expedition, 1910. Nat. Hist. Repts., Zool. 8: 307-454, 63 figs.

————, 1931. Diagnosis of new genera and species of amphipod Crustacea collected during the "Discovery" investigations, 1925-1927. Ann. Mag. Nat. Hist. 10(7): 425-430.

Bate, C. S. 1857. A synopsis of the British eridriophthalmous Crustacea. Ann. Mag. Nat. Hist, ser. 2, 19:135-152, 2 figs.

Birstein, J. A., and M. E. Vinogradov, 1964. Pelagicheskie gammaridy severnoi chasti Indiiskogo Okeana. Akad. Nauk SSSR, Inst. Okeanol., Trud. 65:152-195, 10 figs.

Boeck, A., 1861. Bemaerkninger Angaaende de Ved de Norske Kyster forekommende Amphipoder. Forh. Skand. Naturf. Ottende 8: 631-677.

————, 1871. Crustacea Amphipoda Borealia et Arctica. Forh. Selsk. Christiana 1870: 83-280.

Bousfield, E. L., 1958. Ecological investigations on seashore invertebrates of the Pacific coast of Canada. Natl. Mus. Canada Bull. 147: 104-115.

————, 1963. Investigations on seashore invertebrates of the Pacific coast of Canada, 1957 and 1959. I. Station List. Nat'l. Mus. Canada Bull. 185: 72-89.

————, 1968. Studies on littoral marine invertebrates of the Pacific coast of Canada, 1964. I. Station List. Nat'l. Mus. Canada Bull. 223: 49-57.

————, 1970. Amphipod and isopod crustaceans. Pp. 34-37, in Fauna of Sable Island and its zoogeographic affinities - a compendium. Nat'l. Mus. Nat. Sci., Publ. Zool., No. 4: 45 pp.

————, 1973. Shallow-water Gammaridean Amphipoda of New England. 312 pp., 13 figs., 69 pls. Cornell University Press. Ithaca & London.

————, 1977. A new look at the systematics of gammaroidean amphipods of the world. Crustaceana Suppl. 4: 282-316, 1 fig.

————, 1979. A revised classification and phylogeny of amphipod crustaceans. Trans. Roy. Soc. Can. 4: 343-390.

————, 1980. Studies on the freshwater amphipod crustaceans of New Zealand and Tasmania. Proc. Int. Conf. Biol. Evol. Crustacea. Australian Museum, Sydney, May, 1980. Oral presentation and Abstract.

————, 1982a. Amphipoda. Gammaridea. In: S. B. Parker (ed.). Synopsis and Classification of Living Organisms. McGraw-Hill, New York, vol. 2: 245-285.

————, 1982b. Amphipoda (palaeohistory). McGraw-Hill Year Book of Science & Technology, 1982-1983: 96-101. New York.

————, 1983. An updated phyletic classification and palaeohistory of the Amphipoda. Pp. 257-277, 2 figs. in F. R. Schram (ed.). Crustacean Phylogeny. San Diego: Museum of Natural History.

————, & E. A. Hendrycks, 1994. The amphipod superfamily Leucothoidea on the Pacific coast of North America. Family Pleustidae: subfamily Pleustinae. Systematics and biogeography. Amphipacifica I (2): 3-69.

————, ————, 1995. The amphipod superfamily Eusiroidea in the North American Pacific region. I. Family Eusiridae. Amphipacifica I (4): 3-59.

————, & N. E. Jarrett, 1981. Station lists of marine biological expeditions of the National Museum of Natural Sciences in the North American Pacific coastal region, 1966 to 1980. Syllogeus 34: 1- 66.

————, & D. E. McAllister, 1962. Station list of the National Museum Marine Biological Expedition to southeastern Alaska and Prince William Sound. Nat'l. Mus. Can., Bull. 183: 76-103.

————, & C.-t. Shih, 1994. The phyletic classification of amphipod crustaceans: problems in resolution. Amphipacifica I (3): 76-140.

Bowman, T. E., 1974. The "sea flea" *Dolobrotus mardeni* n. gen., n. sp., a deep-water American lobster bait scavenger (Amphipoda: Eusiridae). Proc. Biol. Soc. Wash. 87: 129-138, 27 figs.

Buchholz, R., 1874. 8. Crustaceen. Die Zweite deutsche nordpolarfahrt in den Jahren 1869 und 1870 unter Fuhrung des Kapitan Karl Koldewey. 2, Zoologie: 262-399, 15 pls.

Bulycheva, 1957. Amfipody (Amphipoda) severnozapadnoi chasti Japonskogo Morja. Akad. Nauk SSSR, Issled. Dal' nevostoch Morei 4: 85-126, 3 figs.

Bushueva, I. V., 1986. New representatives of the Antarctic fauna of scuds (Amphipoda:Gammaridea). Zool. Zhurn. LXV(9):1296-1302. (In Russian).

Chevreux, E., 1889. Amphipodes nouveaux provenant des campagnes de l'Hirondelle 1887-1888. Bull. Soc. Zool. France, 14: 284-289, 3 figs.

————, 1900. Amphipodes provenant des campagnes de l'Hirondelle (1885-1888). Resultats des Campagnes Scientifiques Accomplis par le Prince Albert I. Monaco 16: 195, 18 pls.

————, 1911. Sur les amphipodes des Expeditions Antarctiques Francaises .Acad. Sci., Paris, Comptes Rendus 153: 1166-1168.

————, & F. Fage, 1925. Amphipodes. Faune de France. 9: 488 pp., 438 figs.

Conlan, K. E., 1991. Precopulatory mating behaviour and sexual dimorphism in the amphipod Crustacea. Hydrobiologia 223: 255-282.

Coyle, K. O., & G. J. Mueller, 1981. New records of Alaskan marine Crustacea, with descriptions of two new gammaridean Amphipoda. Sarsia 66: 7-18, 5 figs.

Dagg, M. J., 1975. Complete carbon and nitrogen budgets for the carnivorous amphipod *Calliopius laeviusculus* (Kroyer) PhD thesis, Univ. washington, Seattle, WA, 175 pp., ill.

DeBroyer, C., & K. Jazdzewski, 1993. A checklist of the Amphipoda (Crustacea) of the Southern Ocean. Doc Trav. Inst. Roy. Sci. Nat. Belgique 73: 154 pp.

Derzhavin, A., 1930. Arctic elements in the fauna of the Sea of Japan. Hydrobiological Journal SSSR 8(10-12): 326-329. (In Russian).

Enequist P., 1949. Studies on the soft-bottom amphipods of the Skagerak. Zool. Bidr. fran Uppsala. 28: 297-492.

Fukida, M., Y. Yoshida, & A. Hara, 1971. An observation on the feeding behaviour of macrozooplankton. Bull. Plankton Soc. Japan 18(2): 62-64.

Gurjanova, E. F, 1938. Amphipoda. Gammaroidea of Siaukhu Bay and Sudzuhke Bay (Japan Sea). Reports of the Japan Sea Hydrobiological Expedition of the Zoological Institute of the Academy of Sciences USSR in 1934 1: 241-404, 59 figs. (in Russian).

——————, 1946. New species of Isopoda and Amphipoda from the Arctic Ocean. Works of the Drifting Ice Expedition in the Central Arctic Ocean in Icebreaking Steamer G. Sedov: 272-297, 26 figs. (in Russian).

——————, 1951. Bokoplavi moreii SSSR i sopredelnikh vod (Amphipoda: Gammaridea). Akad. Nauk SSSR. Opred. po Faune SSSR 41: 1029 pp., 705 figs.

Halcrow, K. E., and E. L. Bousfield, 1986. Scanning electron microscopy of surface microstructures of some gammaridean amphipod crustaceans. J. Crust. Biol. 7(2): 274-287.

Hansen A., 1887. Malacostraca marina Groenlandiae occidentalis. Oversigt over det vestlige Gronlands faunaaf Malakostrake Havkrebsdyr. Vidensk. Medd. Dansk Nat. Foren. Kobenhaven 1887: 5-226, pls. 2-7.

Holmes, S. J., 1904. Amphipod crustaceans of the expedition. Harriman-Alaska Expedition: 233-246, 11 figs.

——————, 1908. The Amphipoda collected by the USBF Steamer "Albatross" off the west coast of North America in 1903-04. Proc. U. S. Nat. Mus. 35: 489-543, 46 figs.

Inaba, 1988. Flora and Fauna of the Seto Inland Sea, 2nd ed., II. Spec. Publ. Mukaishima Mar. Biol. Stn: 1-475.

Ishimaru, S. 1994. A catalogue of Gammaridean and Ingolfiellidean Amphipoda recorded from the vicinity of Japan. Rept. Sado Mar. Biol. Sta., Niigata Univ., No. 24: 29-86.

Jarrett, N. E., & E. L. Bousfield, 1994. The amphipod superfamily Phoxocephaloidea on the Pacific coast of North America. Family Phoxocephalidae. Part I. Metharpiniinae, new subfamily. Amphipacifica I (1): 58-140.

Just, J., 1970. Amphipoda from Jorgen Bronlund Fiord, North Greenland. Medd. Gronl. 184 (6): 39 pp. 20 figs.

Karaman, G. S., & J. L. Barnard, 1979. Classificatory revisions in gammaridean Amphipoda (Crustacea), Part I. Proc. Biol. Soc. Wash. 92: 106-165.

Krapp-Schickel, G., 1982. Family Calliopiidae. Pp.164-178. in S. Ruffo (ed.). The Amphipoda of the Mediterranean. Mem. Inst. Oceanogr., Monaco No. 13. 1982.

Krøyer, H., 1838. Gronlands amfipoder beskrevne af Henrik Kroyer. Det Konigelige Danske Videnskabernes Selskabs Naturvidenskabelige og Mathematiske Afhandlinger 7: 229-326, 4 pls.

——————, 1842. Une nordiske Slaegter og Arter af Amfipodernes Orden, henhorende til familien *Gammarina* (Forelobigt Uddrag af et storre Arbejde). Naturh. Tidsskr. 4: 141-166.

Krøyer, H., 1846. Karcinologiske Bidrag (Fortsaettelse). Naturhistorisk Tidsskrift 2: 1-211, pls. 1-2.

Liljeborg, V., 1865. Bidrag till kannedomen om underfamiljen Lysianassina. inom underordningen Amphipoda bland kraftdjuren. Nova Acta Regia Soc. Scient. Upsaliensis III Ser. 6: 1-38, 5 pls.

Lincoln, R. J., 1979. British Marine Amphipoda: Gammaridea. Brit. Mus. (Nat. Hist.), London. 658 pp, 280 figs.

——————, & D. E. Hurley, 1981. The calceolus, a sensory structure of gammaridean amphipods (Amphipoda: Gammaridea). Bull. British Mus. Nat. Hist. (Zool.) 40: 103-116, 4 figs.

Milne Edwards, H., 1830. Extrait de recherches pour servir a l'histoire des crustaces amphipodes. Ann. Sci. Natur. 20: 353-399.

Nagata, K., 1965. Studies on marine gammaridean Amphipoda of the Seto Inland Sea. II. Publ. Seto Mar. Biol. Lab., 13(3): 171-186.

Nishimura, S., 1965. The zoogeographical aspects of the Japan Sea. Part I. Publ. Seto Mar. Biol. Lab. XIII(1): 35-75.

O'Clair, C. E., 1977. Marine invertebrates in rocky intertidal communities. The environment of Amchitka Island, Alaska, 1977. Tech. Information Center, NOAA, Auk Bay, Alaska, Ch. 18: 395-449.

Ohlin, A., 1895. Bidrag til Kannendomen om Malakostrakfaunan i Baffin Bay och Smith Sound. Acta Univ. Lund, 31(6): 70 pp, 1 pl.

Oldevig, H., 1959. Arctic, subarctic and Scandinavian amphipods in the collections of the Swedish Natural History Museum in Stockholm. Goteborgs Kungl. Vetensk. Handl. (6B) 8(2): 132 pp., 4 pls.

Ortiz, M., 1991. Amphipod Crustacea II. Family Bateidae. Mem. Hourglass Cruises. Florida Mar. Res. Inst., Dept. Nat. Res., St. Petersburg, Florida. VIII(I): 1-31, 21 figs.

Palerud R., & W. Vader, 1991. Marine Amphipoda Gammaridea in Northeast Atlantic and Norwegian Arctic. Tromura 68: 2-96.

Park, T. S., 1961. Tentative keys to the gammarid amphipods of the San Juan area. Zoology 533 Student Report (unpubl. MS), Friday Harbor Laboratories, Univ. Washington, 10 pp., + 7 plates.

Pfeffer, G., 1888. Die Krebse von Sud-Georgien nach der Ausbeute der deutschen station 1882-83. 2. Teil. Die Amphipoden. Jahrb. Wissensch. Anst. Hamburg 5: 76-142.

Sars, G. O., 1895. An account of the Crustacea of Norway. Amphipoda. I: 711 pp., 240 pls , 8 suppl. Christiania.

Sars, M., 1858. Oversigt over de i den norsk-arctiske Region forekommende Krebsdyr. Forh. Vidensk. Christiania, for 1858: 122-163.

Schellenberg, A., 1925. Crustacea VIII: Amphipoda. In:

W. Michaelsen, (ed.). Beitrage zur Kenntnis der Meersfauna Westafrikas 3, 4: 11-204.

——————, 1942. Krebstiere oder Crustacea IV: Flohkrebse oder Amphipoda. Die Tierwelt Deutschlands, Jena 40: 252 pp., 204 figs.

Shaw, D. P., 1988. Redescription of *Bouvierella carcinophila* (Chevreux, 1889) (Eusiroidea: Calliopiidae) from northern British Columbia and its proposed synonomy [sic!] with *Leptamphopus paripes* Stephensen, 1931. Can. J. Zool. 66: 939-943.

——————, 1989. New amphipods from geothermal vent sites off the west coast of Vancouver Island, British Columbia, with a reappraisal of the amphipod family Sebidae. Can. Jour. Zool. 67: 1882-1890.

Shoemaker, C. R., 1920. The amphipods of the Canadian Arctic Expedition, 1913-1918. Report of the Canadian Arctic Expedition 1913-1918. 7E:1-30, 6 figs., appendix.

——————, 1926. Amphipods of the family Bateidae in the collections of the United States National Museum. Proc. U. S. Nat'l. Mus. 68(2626): 26 pp., 16 figs.

——————, 1930. The Amphipoda of the Cheticamp Expedition of 1917. Contr. Can. Biol. Fish, new ser., 5(10): 221-359, 54 figs.

——————, 1955. Amphipoda collected at the Arctic laboratory, Office of Naval Research, Point Barrow, Alaska, by G. E. McGinitie. Smiths. Misc. Coll. 128(1):1-78, 20 figs.

——————, 1964. Seven new amphipods from the west coast of North America with notes on some unusual species. Proc. U. S. Nat'l. Mus. 115: 391-430, 15 figs.

Sneath, P. N., & R. R. Sokal, 1973. Numerical Taxonomy. Freeman and Co., San Francisco. 573 pp.

Stapleton, J. L., W. D. Williams, & J. L. Barnard, 1988. The morphology of the calceolus of an Australian crangonyctoid freshwater amphipod. Crustaceana 55: 157-162.

Staude, C. P., 1987. Amphipoda Gammaridea. Pp. 346-391. In E. N. Kozloff (ed.). Marine Invertebrates of the Pacific Northwest. Univ. Wash. Press., Seattle. 511 pp.

——————, J.W. Armstrong, R.M. Thom, & K. K. Chew, 1977. An illustrated key to the intertidal gammaridean Amphipoda of Central Puget Sound. College of Fisheries, Univ. Washington, Seattle, Contrib. 466, 27 pp.

Stebbing, T. R. R., 1888. Report on the Amphipoda collected by H.M.S. Challenger during the years 1873-76. Zoology 29: 1737 pp., 210 pls. London.

——————, 1894. Amphipoda, William Barents Expedition, 1880-1884. Bidj. tot Dierk. (17): 48 pp., 7 pls.

——————, 1897. Amphipoda from the Copenhagen Museum and other sources. Trans. Linn. Soc. London (2 Zool.) 7: 25-45, pls. 6-14.

——————, 1899. Revision of Amphipoda (continued). Ann. Mag. Nat. Hist. 7(4): 205-211.

——————, 1906. Amphipoda. I: Gammaridea. Das Tierreich 21: 1-806, figs. 1-127.

Steele, D. H., 1988. What is the amphipod life style? Crustaceana Suppl. 13. Studies on Amphipoda: 107-121.

——————, 1995. Sexual dimorphism in mature gammaridean amphipods. Polskie Archiwum Hydrobiologii 42 (4): 303-317, 24 figs.

Stephensen, K., 1931. Crustacea Malacostraca. VII. (Amphipoda. III). Danish Ingolf-Expedition 3: 179-290.

Stout, V. R., 1913. Studies in Laguna Amphipoda. Zool. Jahrb. Systematik 34: 633-659, 3 figs.

Stuxburg, A., 1880. Evertebratefaunan Sibiriens Ishaf., 1878-79. Bih. Kungl. Sv. Vetensk. Handl. 5(22): 76 pp.

Thomson, G. M., 1879. Additions to the amphipodous Crustacea of New Zealand. Ann. Mag. Nat. Hist. ser. 5, 4: 329-333. pl. 16.

Tzvetkova, N. A., 1967. K faune ekologii bokoplavov (Amphipoda: Gammaridea) Zaliva Posyeta (Japonskoye Morye). Akad. Nauk SSSR, Zool. Inst. Issled. Fauny Morei 5: 160-195, 7 figs.

——————, 1975. Pribrezhnye gammaridy severnykh i dal'nevostochnykh morei SSSR i sopredel'nykh vod. Akad Nauk SSSR, Zool. Inst. Izd. Nauka Leningrad. Otd., pp. 1-256, 89 figs.

——————, & V. A. Kudrjaschov, 1975. Novyi rod amfipod semeistva Calliopiidae iz severnoi chasti Tikhogo Okeana. Biol. Morya 4: 13-23, 5 figs.

Vader, W., 1983. Prehensile peraeopods in gammaridean Amphipoda. Sarsia 68: 139-148, 11 figs.

Vanhoffen, E., 1897. Die Faune und Flora Gronlands. Gronland Expedition der Gesellschaft fur Erdkunde zu Berlin 1891-1893, 2(1): 383 pp., 8 pls.

Wailes, G. H., 1931. Amphipoda from British Columbia. Museum & Art notes, Vancouver, 6(1): 40-41.

——————, 1933. The plankton of the west coast of Vancouver Island, British Columbia. Mus. & Art Notes, Vancouver, Suppl. 7(9): 11 pp.

Walker, A. O., 1891. On *Pherusa fucicola* Leach. Ann. Mag. Nat. Hist. ser. 6, 8: 81-83.

——————, 1903. Amphipoda of the "Southern Cross" Antarctic Expedition. Jour. Linn. Soc. London 29: 38-64, pls. 7-11.

Watling, L., 1979. Zoogeographic affinities of the northeastern North American Gammaridean Amphipoda. Bull. Biol. Soc. Wash. 3: 256-282, 1 fig.

Zaddach, E. G., 1844. Synopseos crustaveorum prussicorum prodromus. Dissertatio zoologica, quam scripsit et ex auctoritate amplissimi phiposophorum ordinis in academia Albertina pro facultate docendi adipiscenda die XI. M. Decembris ...; 39 pp. Regiomonti: E. J. Daljowski.

---

*Referencing of Russian papers follows the general format of Barnard & Karaman (1991).

AMPHIPACIFICA VOL. II NO. 3 MAY 15, 1997. 67

THE AMPHIPOD SUPERFAMILY COROPHIOIDEA ON THE PACIFIC COAST OF NORTH AMERICA. PART V. FAMILY COROPHIIDAE: COROPHIINAE, NEW SUBFAMILY. SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

by E. L. Bousfield[1] and P. M. Hoover[2]

ABSTRACT

Based on extensive new material from North American Pacific coastal marine waters, and on the previous literature, the nominate subfamily, Corophiinae, is newly proposed within family Corophiidae Dana, 1849, to encompass the polymorphic genus *Corophium* Latreille, 1806 sens. lat. World-wide, the new subfamily embraces 13 genera world-wide of which 6 relatively primitive genera have unfused urosomal segments and member species are primarily free-burrowing in soft sediments, and 7 relatively advanced genera that have fused urosomal segments and component species typically construct open-ended tubes on hard substrata. The following 10 genera are represented in the North Pacific region: ***Eocorophium***, new genus [Type species - *E. kitamori* (Nagata, 1965)]; ***Sinocorophium***, new genus [Type species- *S. sinensis* (Zhang, 1974)]; ***Americorophium***, new genus [Type species - *A. spinicorne* (Stimpson, 1857)]; ***Microcorophium***, new genus [Type species- *M. miospinulosum* (Hirayama, 1986)]; ***Lobatocorophium***, new genus (Type species - *L. lobatum* (Hirayama, 1987)]; ***Crassicorophium***, new genus (Type species - *C. crassicornis* (Bruzelius, 1859)]; ***Hirayamaia***, new genus [Type species - *H. mortoni* (Hirayama, 1986)]; ***Monocorophium***, new genus [Type species - *M. insidiosum* (Crawford, 1937)]; ***Apocorophium***, new genus [Type species - *A. acutum* (Chevreux, 1908)]; and ***Laticorophium***, new genus [Type species - *L. baconi* (Shoemaker, 1934a)]. The following 3 genera are restricted variously to the northeastern North Atlantic, Mediterranean and Aralo-Caspian regions: *Corophium* Latreille, 1908 [Type species - *C. volutator* (Pallas, 1776)]; ***Medicorophium***, new genus [Type species - *M. aculeatum* (Chevreux, 1908)], and ***Chelicorophium***, new genus [Type species- *C. chelicorne* Sars, 1895b)].

In the present study of the subfamily in coastal marine and brackish waters, from Alaska to northern California, the following species are recorded, redescribed, variously refigured, and keyed. *Americorophium spinicorne* (Stimp.), *A. salmonis* (Stimp.), *A. stimpsoni* (Shoem.), *A. brevis* (Shoem.), *Crassicorophium crassicorne* (Bruz.), *Monocorophium insidiosum* (Crawf.), *M. steinegeri* (Gurj.), *M. acherusicum* (Costa), *M. californianum* (Shoem.), and *Laticorophium baconi* (Shoem.). Newly described within *Monocorophium* and recorded here is ***M. carlottensis***, new species. Five other regionally peripheral species, *Crassi-corophium* clarencense (Shoem.) and C. *bonelli* (M.-E.), arctic and subarctic shallow-water species, *Monocorophium oaklandense* (Shoem.), a cool water Californian endemic, and *M. uenoi* (Nagata) and *Sinocorophium alienense* (Chapman), synanthropic in San Fancisco Bay, are also redescribed, figured and keyed.

Taxonomically, previously employed character states such as the degree of fusion of the urosomal segments, form of the mandibular palp, and degree of ventral insertion of uropods were found to exhibit homoplasious similarity in otherwise distantly related genera, and thus appear unreliable as a basis for cladistic classification within the subfamily. Phyletically, the endemic North American Pacific corophiin fauna exhibits strong affinities to that of the western North Atlantic, but little to that of the eastern North Atlantic and Mediterranean regions, and apparently none to the Asiatic North Pacific fauna. Of the warm-temperate species of *Monocorophium* from central and southern California, only *Corophium californianum* ranges northward to British Columbia. The three species of *Crassicorophium* occurring in northern parts of the study region are arctic-subarctic in biogeographic affinities and may be closest phyletically to the primitive, mainly sublittoral Mediterranean endemic genus *Medicorophium*. We may conclude that the Corophiinae are relatively recently evolved, and have two main centres of origin and dispersal, viz., primarily in the western North Pacific, from whence they have apparently radiated, post-Tethyan, to the North Atlantic, and secondarily in the North Pacific region wherein most advanced generic types have recently radiated.

INTRODUCTION

Studies on North American Pacific corophiid amphipods commenced with William Stimpson's (1857) description of *Corophium spinicorne* and *C. salmonis* from San Francisco Bay and Puget Sound. Knowledge of the biology of the two species in Central California was extended by Bradley (1908). In a pioneering series of systematic accounts, C. R. Shoemaker (1934a, 1941, 1949, 1955), described all seven remaining species known to be endemic to the eastern North Pacific region, from Alaska to Central America. Taxonomic features and range extensions of these and several introduced species were extended chiefly by J. L. Barnard (1952, 1954,

---

1. 611-548 Dallas Rd., Victoria, B. C. V8V 1B3.

2. Research Associate, Dept. Biology, University of Victoria, Victoria, B. C. V8W 2Y2.

1958, 1962, 1964, 1969b, 1973), Carlton (1979, 1985), Coyle & Mueller (1981), Austin (1985), Cadien (1991) and Chapman (1988), the latter containing a description of a new species probably synanthropic from the western North Pacific. Further, popular and semi-popular works by Ricketts and Calvin (1948), Aldrich (1961), Barnard (1975), Otte (1976), and Staude (1987) expanded knowledge of the ecology and life style of these mostly littoral and estuarine species, and provided illustrated keys to their identification. The systematics of species introduced from the North America Atlantic coast, or otherwise related to the North Pacific endemics, had been developed chiefly by Shoemaker (1934b, 1943, 1947), and Bousfield (1973), and that from western Europe mainly by Crawford (1937).

With respect to the corophiid fauna of the western North Pacific, Stimpson (1856) had briefly described the enigmatic *Corophium contractum* from the East China Sea and Sea of Japan, but the species was not recorded nor recognized subsequent to the world-wide compendium of Stebbing (1906). A few corophiid species were recorded from the far eastern USSR, mainly by Gurjanova (1951) and Kudrjaschov (1979), including a description of *Corophium steinegeri* Gurjanova from the Kamchatka Peninsula. Descriptions of new and introduced corophiid species from Japanese waters were initiated by Stephensen (1932), and continued by Irie (1958), Nagata (1965), Hirayama (1984, 1987a) and many others, all of which is usefully summarized by Ishimaru (1994). Hong (1983) and Kim (1991) treated the largely synanthropic corophiids of Korean coastal waters. A rich fauna of mainly primitive burrowing corophiids was described from coastal waters of the East China and South China Seas mainly by Yu (1938), Shen (1955), Ngoc (1965), Zhang (1974) and Hirayama (1986).

Despite these relatively recent and intensive studies, a significant hiatus in knowledge of corophiid amphipods of the northeastern Pacific region remained. The primary purpose of this study was therefore to treat the sytematics and distributional ecology of this little known fauna, based mainly on extensive regional survey material of the senior author since 1955, now contained in the crustacean collections of the CMN (Canadian Museum of Nature) in Ottawa. However, as discussed below (p. 69), new taxonomic insights revealed by the initial investigation, and attempts to place the fauna in a global context, necessitated expansion of its scope to a semi-phyletic revison of the genus *Corophium* Latreille, 1806, sens. lat. and its elevation to subfamily status.

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 CMN), Ottawa, and received vital technical assistance and ship time from Canadian Pacific research centres and their staffs. The help of these individuals and agencies, and of many others, is gratefully acknowledged in the station lists of these surveys [see Bousfield (1958, 1963, 1968); Bousfield & McAllister (1962), Bousfield & Jarrett (1981)]; we again express our deepest appreciation to them. These agencies include, in Canada, the Pacific Biological Station (Nanaimo), the Bamfield Marine Station, the Pacific Environmental Institute (West Vancouver), the Royal British Columbia Museum (RBCM) (Victoria), the University of Victoria, the University of British Columbia (Vancouver), and the Institute of Ocean Sciences (Sidney) and, in the United states of America, the Friday Harbor Laboratories and the College of Fisheries of the University of Washington. We are grateful to Dr. Peter Slattery, Moss Landing, CA, who supplied vital material from the Bering Sea region, and to Drs. Hiroshi Morino and Akira Hirayama who kindly supplied recent comparative material from Japan. Dr. John Chapman, Newport, Oregon, generously supplied further notes on *Corophium alienense* and related species, copies of western Pacific literature unavailable from other sources, and commented on an earlier draft of this paper.

We are especially grateful to Dr. D. V. Ellis and the University of Victoria for extensive support and encouragement, and provision of laboratory facilities for the work. For advisory assistance we are also grateful to CMN colleagues Kathleen E. Conlan and Ed Hendrycks, and for curatorial assistance to Judith C. Price. Regrettably, unavailability of CMN collections and records (in late preparation stages) prevented full cataloguing of material. Line illustrations were prepared most capably by Susan Laurie-Bourque, Hull, Quebec. Marjorie Bousfield, Wolfe Island, Ontario, translated pertinent Russian literature and reviewed a late draft of the text. The work was also supported by operational grants from the Royal Ontario Museum, Toronto, and the Natural Sciences and Engineering Research Council, Ottawa.

SYSTEMATICS

COROPHIIDAE Dana, 1849

Corophiidae Dana, 1849: 139.—Stebbing, 1906: 662 (part).—Gurjanova, 1951: 944 (part).—Barnard, 1969a: 184 (part).—Barnard, 1973: 17 (part).—Bousfield, 1973: 198 (part).—Lincoln, 1979: 520 (part).—Myers, 1982: 185 (part).—Ishimaru, 1994: 35 (part).
Corophioidea Barnard & Barnard, 1983: 220 (part).—Barnard & Karaman, 1991: 137.

Type Genus. *Corophium* Latreille, 1806, monotypy.

Genera. Corophiinae, new subfamily (p. 70.): *Corophium* Latreille, 1806 (sens. lat.).

Siphonoecetinae*: *Siphonoecetes* Kroyer, 1845: 491; *Australoecetes* Just, 1983: 128; *Bubocorophium* Karaman, 1981: 19; *Borneoecetes* Barnard & Thomas 1984: 873; *Rhinoecetes* Just, 1983: 125; *Africoecetes* Just, 1983: 17; *Concholestes* Giles, 1888: 238; *Caribboecetes* Just, 1983:130; *Carocubanus* Ortiz & Nazabal, 1984: 5.

---

*(Full references provided in Just,1983).

Diagnosis. Body depressed, cylindrical. Urosome segments separate, fused in advanced taxa. Head, rostrum usually distinct, short; inferior antennal sinus large. Antenna 1 short, slender, lacking accessory flagellum. Antenna 2 large, pediform, often sexually dimorphic; segments 4 and 5 stout; flagellum short.

Upper lip notched below. Lower lip, inner lobes prominent; mandibular lobes various. Mandible, molar strong, incisor moderate; palp short, appearing 2-(rarely 3-) segmented; left lacinia 3-4-dentate. Maxilla 1, inner plate small, unarmed; outer plate with 7 apical spines. Maxilla 2 strong, inner plate lacks facial setae. Maxilliped, outer plate medial margin straight, setose or spinose; palp, dactyl short, weak.

Coxal plates 1-4 small, non-overlapping. Gnathopods 1 & 2 dissimilar, basically not sexually dimorphic. Gnathopod 1 weakly subchelate or simple; carpus elongate. Gnathopod 2 subchelate or simple, stronger than gnathopod 1; merus and carpus elongate and variously fused; carpus, hind (free) lobe very short or lacking.

Peraeopods 3 & 4, short, segments 2 and 4 broadened ("glandular"); segment 5 usually short. Peraeopods 5 & 6 subsimilar, segment 5 with posterior marginal hook spines; segment 6 and dactyl reversed. Peraeopod 7 elongate, dissimilar in form to 5 & 6; distal segments not reversed.

Pleon plates shallow. Pleopod peduncles strongly broadened medially; outer ramus shorter than inner. Uropods 1 & 2 variously modified; rami short, unequal. Uropod 3 short, uniramous. Telson short, broad. Coxal gills sac-like, on peraeopods 3(4)-6. Brood lamellae strap-like, margins with long setae.

Taxonomic commentary. Just (1983) summarized recent major reclassifications and generic inclusions of the Corophiidae. Subsequent to the basic or "classical" compendia of Gurjanova (1951) and Barnard (1969a), Just noted a general trend to increasing refinement of classification within superfamily Corophioidea and a more restricted concept of the family Corophiidae. Thus, Myers (1981) provided solid taxonomic basis for continued distinction of Isaeidae, Aoridae, Ischyroceridae and Corophiidae, and created Neomegamphopidae for several mainly tropical genera allied to Isaeidae; and Lincoln (1979) restricted British genera of Corophiidae to *Corophium* Latreille, *Siphonoecetes* Kroyer, and *Unciola* Say. *Unciola* (and allied genera) were removed from Aoridae (below), but in the world fauna of Corophiidae, Bousfield (1982) included the genera *Kamaka* Derzhavin, *Gaviota* Barnard (now *Ampelisciphotis* Pirlot), *Janice* Griffiths, and *Paracorophium* and related genera.

However, in his revision of the superfamily Corophioidea, Barnard (1973) departed from the previous views and combined Corophiidae, Photidae (now Isaeidae) and Aoridae within family Corophiidae, and recognized no subfamilies. Barnard and Barnard (1983) continued this classification as applied to freshwater genera and species. In further expansion of the "lumper" philosophy, Barnard and Karaman (1991) submerged Ischyroceridae and Neomegamphopidae within Corophiidae, but maintained separate recognition of one subfamily, Siphonoecetinae Just, 1983. The presumed basis for their decision was the difficulty of recognizing clearly defined taxonomic "break-points" between families in the presence of morphologically "intermediate" genera, and in constructing workable keys to separate families that would rigidly apply to all component taxa.

However, in view of the work of Lincoln (1979), Just (1983, 1988), Myers (1981, 1982), and the senior author (Bousfield, 1978, 1982, 1983; Bousfield and Shih, 1994), the present authors cannot justify subordinating or fusing higher taxa on the basis that one (or a few) component lower taxa may appear "intermediate" in some character states. As opined elsewhere (Bousfield, 1983), Darwin's theory of biological evolution implies the existence of intermediate stages between all living organisms at one time or another. The taxonomic convenience of modern classification at family and subfamily level within valid (natural) superfamily concepts is not facilitiated by inability to treat, in a pragmatic manner, the so-called internal "exceptions". Cladistic and cluster analyses (Sneath & Sokal, 1973), and use of multiple-character diagnoses and "best-fit" criteria (Bousfield, 1983), provide more than adequate methodologies for treating such problems more realistically. We therefore continue to recognize family Corophiidae Dana as a natural family unit, here restricted to two component subfamilies, Siphonoecetinae and Corophiinae, as defined and keyed below. Subfamily Cerapiinae Budnikova, is removed to family Ischyroceridae. The present systematic treatment of the Corophiinae follows, in numerical analytical fashion, a revision of the Siphonoecetinae by Just (1983, et seq.), wherein similar numbers of species and global distributions are involved.

Taxonomic exclusions. The present authors have followed Myers (1981, 1982); Conlan (1983, 1991), Ishimaru (1994) and several other recent authors in continued separate recognition of families Aoridae, Isaeidae, and Ischyroceridae within superfamily Corophioidea. Aorids are characterized mainly by: the dominance of gnathopod 1 and peraeon 1 (in both males and females), an elongate antenna 1 with accessory flagellum, a generally non-pediform antenna 2 (male) and the use of gnathopod 1 in pre-amplexing (mate-guarding) behaviour. Lincoln (1979) also validated the family Corophiidae but included the genus *Unciola* Say, 1818. However, *Unciola* appears more naturally included within family Aoridae, as defined by Myers (1988), because it conforms with the major aorid character states (above). Moreover, the mouthparts are regular and unmodified; the bases of peraeopods 3 & 4 are of minimum "glandular" form and segments 4 & 5 normal; segment 5 of peraeopods 5 & 6 is not reduced nor does it bear hook spines; peraeopod 7 is not elongate and differs little in form or size from peraeopods 5 & 6; the pleopod peduncles are not expanded medially; uropods 1 & 2 are regularly linear; the telson is a simple plate without dorsal hooks; the brood lamellae are broad; and some peraeon segments bear a sternal spinose process (lacking in true corophiids).

KEY TO SUBFAMILIES OF COROPHIIDAE

1. Antenna 2 (male), segments 4 & 5 processiferous, often sexually dimorphic; uropods 1 & 2 inner ramus not markedly shortened; gnathopod 2, merus elongate; fused to elongate carpus .... Corophiinae (p. 70)

—Antenna 2, peduncular segments 4 & 5 not processiferous, little sexually dimorphic; uropods 1 & 2, inner ramus reduced or lacking; gnathopod 2, carpus short, deep, with free hind lobe ..... Siphonoecetinae Just

Ischyrocerids are fairly reliably distinguished from corophiids in their overlapping coxae 1-4; strongly setose filter-feeding antennae; antenna 1 with accessory flagellum; gnathopod 2 strongly subchelate (male) used in pre-amplexing mate-guarding; pleopod peduncles little broadened; and uropod 3, ramus with terminal hook spines. Isaeids (photids) are similar but generally deeper bodied, with deeper coxal plates, and uropod 3 is typically biramous and lacks terminal hooks. The genera *Paracorophium*, *Chaetocorophium*, and *Stenocorophium* exhibit several corophiin character states such as a weakly subchelate gnathopod 1 and elongate and setose merus of gnathopod 2, but are here considered essentially isaeid in form of antennae, deep coxae 1-4, unmodified pleopods, linear uropods, and overall morphology. Moreover, component species are antiboreal in distribution, remote from clusters of primitive corophiin genera.

COROPHIINAE, new subfamily

Corophium Latreille, 1806 (sens. lat.).—Stebbing, 1906: 662.—Gurjanova, 1951: 974.—Barnard, 1969a: 190.—Barnard, 1973: 17.—Bousfield, 1973: 198.—Lincoln, 1979: 522.—Barnard & Barnard, 1983: 162.—Barnard & Karaman, 1991: 184.—Ishimaru, 1994: 35.
Corophiinae (informal category) Just, 1983: 120.

Type genus. *Corophium* Latreille, 1806.

Genera of component subgroups.

1. Urosome segments unfused:
Eocorophium, new genus (p. 75); *Sinocorophium*, new genus (p. 75); *Corophium* Latreille, 1806 (p. 85); *Medicorophium*, new genus (p. 82); *Americorophium*, new genus (p. 90); *Chelicorophium*, new genus (p. 88).
2. Urosome segments fused: *Microcorophium*, new genus (p. 98); *Lobatocorophium*, new genus (p. 100); *Hirayamaia*, new genus (p. 108); *Crassicorophium*, new genus (p. 102); *Monocorophium*, new genus (p. 111); *Apocorophium*, new genus (p. 123); *Laticorophium*, new genus (p. 125).

Diagnosis. Body slender, elongate, smooth, depressed. Head broad, weakly rostrate. Urosome segments trending to fusion. Antenna 2 large, pediform, usually sexually dimorphic, with spines and processes for ambulation, burrowing (female and subadults) or mate guarding (adult males).

Mandibular palp, distal segment slender but distinct; proximal segment formed by fusion of embryonic segments 1 & 2, and distally bearing a single median plumose seta. Maxilliped, inner plate short, narrowing distally, apex setose; outer plate, inner margin setose, lacking masticatory spade spines.

Coxae 2-4 smaller and shallower than coxa 1; coxa 1 with 3-4 setae arising from subacute anterior corner. Gnathopods strongly dissimilar. Gnathopod 1 weakly subchelate. Gnathopod 2 simple; merus and carpus elongate, fused medially, bearing numerous filter setae that, with those of the opposing gnathopod, form a food-filtering basket.

Peraeopods 3 & 4, basis linear to inflated and glandular; segment 4 often broadened anterodistally; segment 5 variously shortened. Peraeopods 5 & 6 subsimilar in form, 6 distinctly the larger; segment 5 bearing 2 posterolateral clusters of hooked spines; segment 6 and dactyl usually reversed. Peraeopod 7 elongate, ambulatory, margins of basis strongly plumose-setose.

Pleon plates rounded or squared behind, seldom acuminate. Pleopods short, strong; peduncles deep, strongly broadened medially. Uropods 1 & 2 regular, subequally biramous, rami spinose mainly or exclusively on outer margin. Uropod 3, ramus sublinear or broadened, often not longer than the peduncle, distally setose. Telson free, with subapical dorsal spinules.

Coxal gills on peraeopods 3-6. Brood plates large, strap-like, with long marginal setae.

Distributional ecology: Essentially holarctic in temperate and warm temperate littoral and sublittoral shelf waters; dominant in the North Pacific; overlapping with Siphonoecetinae mainly in the North Atlantic-Mediterranean region; several species (of advanced tube-builders) are widely synanthropic, including the Southern Hemisphere.

Behaviour. Corophiins are primarily burrowers in fine soft sediments, using antennae, peraeopods 3 & 4, and uropods, aided by water currents set up by the powerful pleopods. More advanced species live in fixed open-ended abodes cemented to solid bottom objects. Some species (e.g., *Corophium insidiosum*) can do both (Stock, 1952). Animals crawl slowly along the bottom using antenna 2, peraeopod 7, and uropods. . Advanced corophiids are adept at reversing their bodies quickly within the tube and are thereby able to face into the intermittently reversing tidal currents or confront unwelcome intruders at the rear of the tube.

By contrast, siphonoecetins do not burrow, but form mobile abodes by cementing together tiny mollusk shells and/or relatively coarse sediments. Both sexes may crawl slowly by means of their powerful ambulatory antenna 2, dragging their abodes with them (Just, 1988). Males may cement the abodes of one or more females to their own, all facing in the same direction which, not being fixed, can be turned about to face reversing feeding currents. Antenna 2 is employed in a flipping action in some highly mobile species. In corophiins, however, antenna 2 is strongly pediform in the male, the distal segments with specialized processes that serve in mate-guarding and holding the female during amplexus (Conlan, 1991).

Just (1983, p. 120) opined that *Corophium* (then with some 50 species) (is a) "logical sister group [for Siphonoecetinae, new subfamily]" and "a candidate for subfamily ranking", but he hesitated to formally recognize it as such. Although the present authors have examined material of only half the genera newly proposed, classificatory decisions are to large extent based on the excellent taxonomic accounts and figures provided by previous authors, including Shoemaker (1947, 1949), Barnard and Karaman (1991), Lincoln (1979), Myers (1982), and Hirayama (1984, 1986, 1987a). We now believe Just's reservations are largely "put to rest" in the following considerations and have herewith fulfilled his initial suggestion in formally proposing Corophiinae, new subfamily.

CHARACTERS AND CHARACTER STATES

Taxonomic and classificatory analysis of subfamily Corophiinae is based mainly on characters and character states illustrated in Figs. 1 & 2 (pp. 72-73). The plesiomorphic state is shown in the left-hand column, the apomorphic state in the right-hand column, and a representative intermediate state (when suitable) in the middle column. As in previous numerical analyses of this type (e. g., Bousfield & Chevrier, 1996), the three character states are given phyletically ordered values of 0, 2 and 1, respectively (see also pp. 130-133, Fig. 38, and Table I, this paper).

The following commentary elucidates the illustrations. The lower margin of the inferior antennal sinus (1) is plesiomorphically projecting, apomorphically strongly regressed. Antenna 1 (2) is plesiomorphically slender, peduncular segments elongate, unmodified, and flagellar segments numerous; apomorphically it is relatively short, the peduncular segments variously thickened, spinose or setose, and flagellar segments few. In antenna 2 (male) (3, 4, 5), plesiomorphically the gland cone is elongate and/or prominent, segment 4 is moderately thickened, the distal process is small and single toothed (or lacking), segment 5 lacks a median marginal tooth, the distal process is small (or lacking), and the flagellum is relatively long and slender; apomorphically the gland cone is short or inconspicuous, segment 4 is broad (stout), the distal process is large and bidentate, segment 5 has strong median and distal processes, and the flagellum is short and thick. In antenna 2 (female of sexually dissimilar species) (6), the gland cone is large, peduncular segments 4 & 5 are slender, little modified, and the flagellum is slender; apomorphically, the gland cone is inconspicuous, peduncular segments 4 & 5 are short, thick, and marginally spinose, and the flagellum is short. In antenna 2 of a sexually similar female or hermaphrodite (7), plesiomorphically, as in the male (3-5, above); apomorphically, the appendage is much less stout, the distal process of segment 4 is single-toothed, and segment 4 lacks median and distal processes.

The lower lip (9) plesiomorphically has very short mandibular lobes; apomorphically the lobes are strong, distinct. The mandibular palp (8) plesiomorphically consists of two apparent segments aligned linearly (the proximal segment is composed of the two fused primary segments that are occasionally not fused) (Type P1 of Hirayama, 1987b); apomorphically the distal segment is set at an angle to the proximal segment which bears a terminal seta on a triangular prominence (Type P5 of Hirayama, 1987b). In the primitive maxilliped (10), the inner plate is relatively large, with mumerous marginal setae, the outer plate large, and palp segment 2 elongate; in the apomorphic condition, the inner plate is short, with few marginal setae, the outer plate small, and palp segment 2 short, little longer than segment 1.

In gnathopod 1 (11), the propodal palm is plesiomorphically distinct, vertical, little exceeded by the simple short dactyl; apomorphically, the palm is short, oblique, distinctly exceeded by a dactyl that may bear a posterior marginal denticle. In gnathopod 2 (12), the dactyl is plesiomorphically simple and strong; apomorphically it is short, with 2-4 posterior marginal teeth; in the intermediate condition the dactyl bears a single posterior marginal tooth, and the propod bears a distinct posterodistal cusp.

In peraeopods 3 & 4 (13, 14), plesiomorphically the basis is slender, segment 4 is little expanded distally, segment 5 is subequal in length to 4, and the dactyl is elongate; apomorphically, the basis is broad and glandular, segment 4 is broadened distally and overhangs the short segment 5 , and the dactyl is shorter than segment 6. In peraeopods 5 & 6 (15, 16), plesiomorphically the basis is little broadened, segment 5 is not shortened, the posterodistal "hook spines" are elongate, and segment 6 and dactyl are not reversed; apomorphically, the basis is broadened, segment 5 is very short, with short hook spines, and segment 6 and dactyl are reversed. Peraeopod 7 (17) is plesiomorphically elongate, with narrow basis and elongate dactyl; apomorphically it is relatively short, the basis broadened, and the dactyl short and curved.

In pleon plate 3, plesiomorphically the hind corner (18) is produced and acute, but apomorphically broadly obtuse or rounded, and weakly acuminate or squared in the intermediate condition. In the urosome (19), pleisomorphically the segments are separate, with sharp notches for full lateral insertion of uropod 1; apomorphically, the segments are totally fused,the lateral margins convex, and uropod 1 is inserted ventrally; in the intermediate condition, the segments are fused, the notch is shallow, the lateral margin is straight or incised, and uropod 1 is inserted partly ventrally. In uropod 3 (20), the ramus is apomorphically slender, elongate and spinose, and the peduncle lacks a lateral process; apomorphically, the ramus is short, suborbicular, and the peduncle usually bears a lateral process. Character states of other appendages (e. g., coxal gills, brood plates, and pleopod peduncles) have also been considered in the analysis.

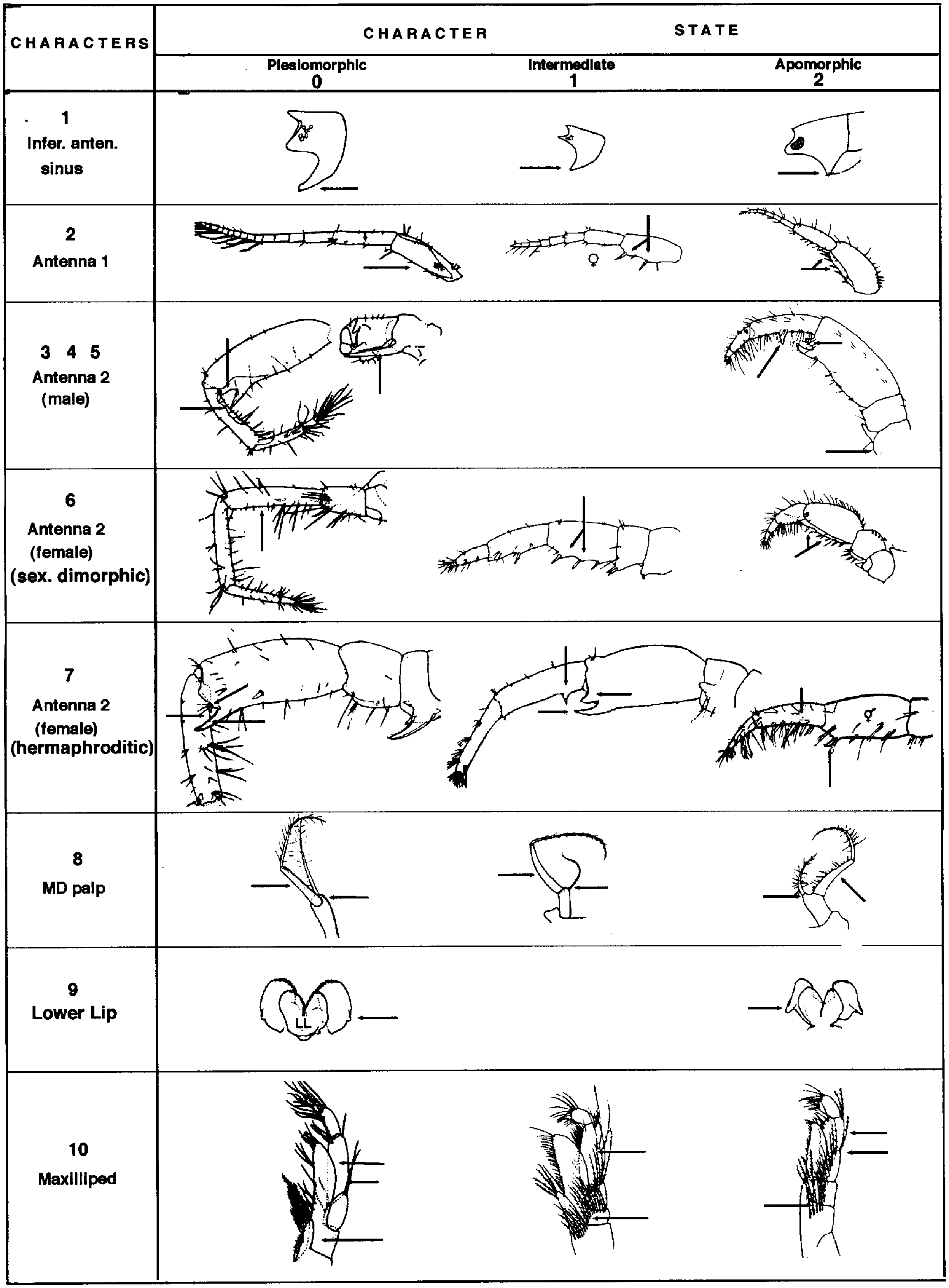


FIG. 1. CHARACTERS AND CHARACTER STATES OF GENERA OF COROPHIINAE.

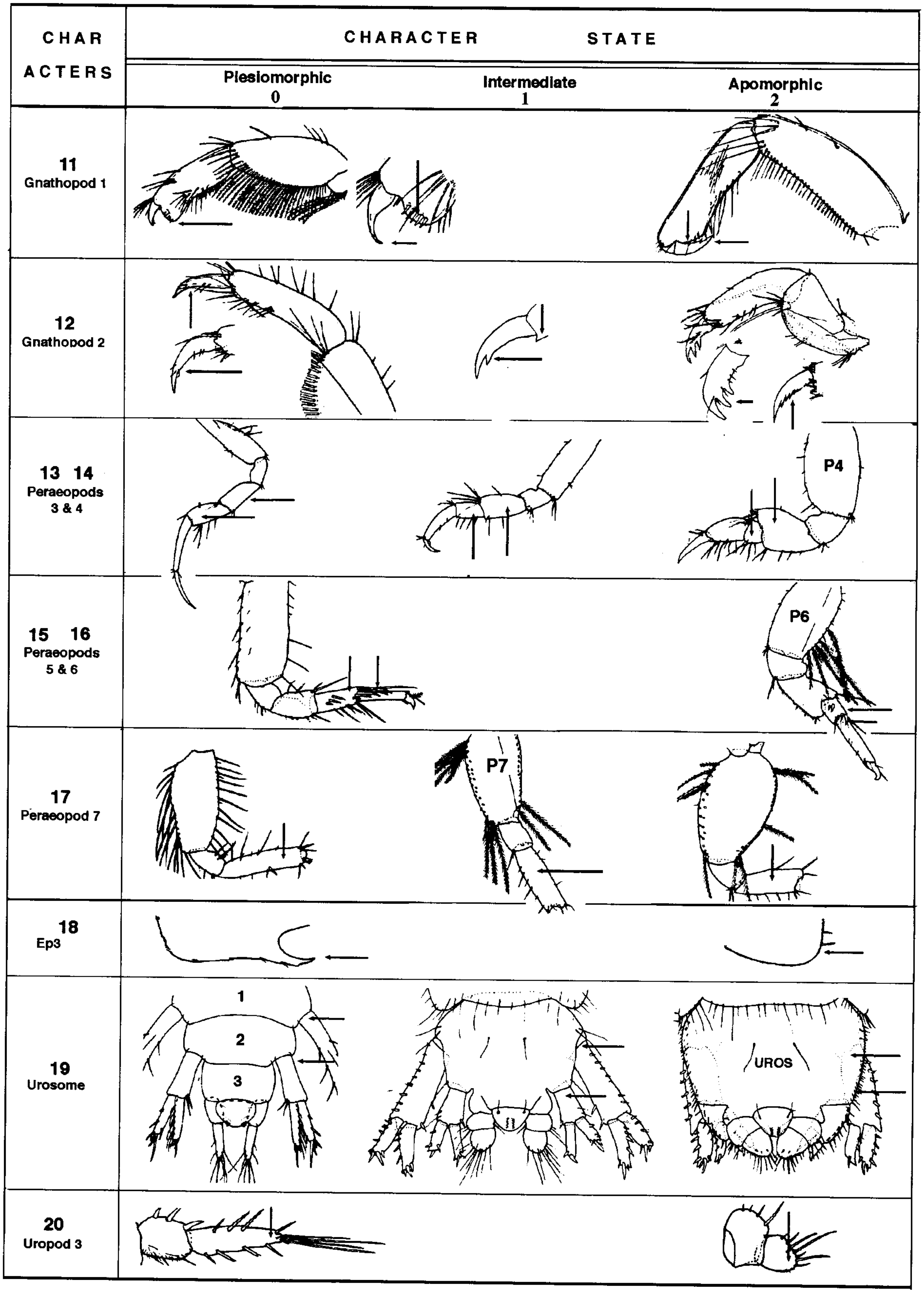


FIG. 2. CHARACTERS AND CHARACTER STATES OF GENERA OF COROPHIINAE (cont.)

KEY TO WORLD GENERA OF COROPHIINAE

1. Urosome segments separate (except *C. ellisi*), uropod 1 variously laterally inserted (Fig. 2:19 P)..... 2.

—Urosome segments fused; uropod 1 often partly or totally ventrally inserted (Fig. 2:19 A).......... 7.

2. Antenna 2, gland cone of segment 2 large, conspicuous (Fig. 1: 3 P); maxilliped palp segment 2 elongate (Fig. 1: 10 P).. 3.
—Antenna 2 gland cone small to medium, not prominent (Fig. 1: 3 A); maxilliped palp segment 2 short to medium (Fig. 1: 10 A).. 6.

3. Pleon plate 3, hind corner strongly produced, acute (Fig. 2:18 P).......... *Eocorophium*, n. g. (p. 75)

—Pleon plate 3, hind corner rounded, subquarate or weakly acuminate (Fig. 2:18 A)................ 4.

4. Peraeopods 3 & 4, segment 5 shortened (<< segment 4) (Fig. 2:14 A).......................... 5.

—Peraeopods 3 & 4, segment 5 not shortened (~ segment 4)(Fig. 2:14 P)...... *Sinocorophium*, n. g. (p. 75)

5. Uropod 3, ramus short, broad, little longer than peduncle .(Fig. 2:19 I)..... *Corophium* Latreille (p. 85)

—Uropod 3, ramus slender, longer than peduncle ..(Fig. 2: 19 P).......... *Medicorophium*, n. g. (p. 82)

6. Uropods 1 & 2, rami with medial spines (setae) (Fig. 2:12 U1, U2): antenna 2 powerful, similar in both sexes, segment 4 and flagellum short (Fig. 1: 4, 5 A); Aralo-Caspian.......... *Chelicorophium* , n. g. (p. 88)
—Uropods 1 & 2, rami lacking medial spines or setae (Fig. 17:UROS); antenna 2 usually sexually dissimilar (Fig. 1: 6 I) (includes *C. ellisi* with urosome segments fused); American-Atlantic and eastern N. Pacific ....*Americorophium* (p. 90)

7 Urosome segments with strong lateral notch for mainly lateral insertion of uropod 1 (Fig. 2:19 I)... 8.

—Urosome segments, lateral notches weak or lacking, uropod 1 arising mainly ventrally (Fig. 2:19 A). 10.

8. Peraeopods 3-4, basis and segments 4 & 5 slender (FIG. 2:13 P)....... *Microcorophium* , n. g. (p. 98)

—Peraeopods 3-4, basis and segments 4 & 5 variously broadened, "glandular" in form (Fig. 2:13 A).... 9.

9. Gnathopod 2, dactyl with 2-3 posterior marginal teeth (Fig. 2:12 A); mandibular palp segment 1 with unproduced distal shelf (Type P4) (Fig. 1:8 I)......................... *Monocorophium*, n. g. (p. 111)

—Gnathopod 2, dactyl with single posterior marginal tooth (Fig. 2:12 I); mandibular palp with distal process (Type P5) Fig. 1: 8 A).. *Crassicorophium* , n. g. (p. 102)

10. Uropod 2 large, broad, larger than uropod 1 (FIG. 25:UROS)...........*Lobatocorophium*, n. g. (p. 100)

—Uropod 2 relatively inconspicuous, distinctly smaller than uropod 1 (Fig. 2:19 I, A)............. 11.

11. Urosome, lateral margins straight or slightly indented (Fig. 24:UROS); gnathopod 2, propod with minute palm and cusp; dactyl with 1(2) posterior marginal tooth (Fig. 2:12: I)........ *Hirayamaia*, n. g. (p. 108)

—Urosome, lateral margins convex (FIG. 2:19 A); gnathopod 2, propod lacking palm or minute cusp; dactyl with 2-4 posterior marginal teeth. (Fig. 2:12 A).. 12.

12 Urosome, lateral margins smooth (Fig. 2:19 A).......................*Apocorophium* , n. sp. (p. 123)

—Urosome, lateral margins each with small notch .(Fig. 37:UROS)......... *Laticorophium* , n. sp. (p. 125)

***Eocorophium*, new genus**
(see Fig. 3)

Corophium Latreille, Hirayama, 1986: 449 (part: *C. kitamori* Nagata).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1994: 35(part).

Type species. *Corophium kitamori* Nagata, 1965 (monotypic)

Diagnosis. A primitive genus, endemic to Hong Kong regional waters. Urosome segments unfused. Uropods arising from lateral notches. Head, rostrum short, broad; inferior antennal sinus with anteriorly directed lower margin. Antenna 1 short; peduncular segment 3 medium. Antenna 2 pediform in male (slender, unlike in female); gland cone elongate; segment 4 with single posterodistal process; segment 5 with strongly developed apical process, but median tooth lacking; flagellum medium, 3-segmented, shorter than peduncle 5, apex lacking curved spines.

Mouthparts basic. Upper lip, epistome produced. Lower lip, mandibular lobes very short. Mandibular palp of type P3 (fide Hirayama, 1987b). Maxilla 1, inner plate broad; palp broadened distally. Maxilla 2, plates narrow. Maxilliped, inner plate short, blunt, strongly setose; outer plate slender, inner margin intermittently setose; palp segment 2 slender, elongate.

Gnathopod 1, carpus and propod subequal in length; palm short, oblique; dactyl strong exceeding palm. Gnathopod 2, fused merus and carpus longer than propod; dactyl thin, elongate, simple.

Peraeopods 3 & 4, segments linear; segment 4 not shortened. Peraeopods 5 & 6, basis not broadened, segment 5 not shortened, with elongate posterodistal spines; segment 6 and short dactyl not reversed. Peraeopod 7 slender, elongate, dactyl moderately long.

Pleon plate 3, hind corner acutely produced. Pleopod peduncles little broader than long. Uropod 1, peduncle linear, slender; rami linear, margins spinose, apex with long spines. Uropod 2 not shortened; rami linear, margins and apex spinose. Uropod 3, ramus linear, elongate, margins spinose. Telson rounded, lacking dorsal spines.

Coxal gills short, sac-like, on peraeopods 2- 6. Brood lamellae undescribed.

Etymology. From the Greek "eo" - dawn or early, and the generic root *Corophium*, with reference to the plesiomorphic nature of its generic character states.

Distribution. Endemic to the Sea of Japan and East China Sea, western North Pacific region.

Taxonomic commentary. *Eocorophium* is remotely allied to the western North Pacific cluster of *Sinocorophium* via species such as *C. sinense.* Hirayama (1986, 1987a) considers this species to represent a distinct evolutionary branching pathway within *Corophium* sens. lat. Such appears convergently similar to *Stenocorophium* Karaman, 1979, within the Isaeidae. Thus, because of the autapomorphic form of gnathopod 2 in *Stenocorophium* and the plesiomorphic form of its coxal plates, antennae, uropod 3, etc., *Stenocorophium* is an unlikely candidate for direct ancestry to *Eocorophium.*

***Sinocorophium*, new genus**
(see Figs. 4, 5)

Corophium Latreille, Hirayama, 1986: 449 (part).—Hirayama, 1987a: 175 (part).—Hirayama, 1987b: 569 (part).—Barnard & Karaman, 1991: 185 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium sinensis* Zhang, 1974 (present designation).

Species. *Sinocorophium heteroceratum* (Yu, 1938); *S. lamellatum* (Hirayama, 1984); *S. minutum* (Ngoc, 1965); *S. homoceratum* (Yu, 1938); *S. triangulopedarum* (Hirayama, 1986); *S. intermedium* (Ngoc, 1965); *S. alienense* (Chapman, 1988); *S. japonicum* (Hirayama, 1984, new status); *S. monospinum* (Shen, 1955).

Diagnosis. Urosome segments uncoalesced. Head, rostrum distinct; inferior lateral sinus large, regressed below. Antenna 1 elongate (usually exceeding antenna 2, peduncular segment 4); peduncular segment 3 shortened (<1/2 segment 2). Antenna 2 strong, pediform (often subsimilar in female), segment 4 with simple (occasionally bifid) posterodistal tooth; segment 5, median tooth and posterodistal process lacking (or weak); flagellum 2-3-segmented, shorter than peduncular segment 5; gland cone large, prominent.

Mouthparts basic. Upper lip, epistome produced, acute. Lower lip, mandibular lobes small. Mandibular palp basic (types P1, P1r of Hirayama, 1987b). Maxilla 1, palp longer than outer plate. Maxilliped, inner plate, apex rounded, setose; outer plate broad, inner margin variously setose; palp segment 2 elongate, often broadened, outer margin with long filter setae.

Gnathopod 1 primitively subchelate; palm of propod short, vertical; dactyl short. Gnathopod 2, merus not occluding distal free margin of carpus; dactyl large, simple.

Peraeopods 3 & 4, basis sublinear; segment 4 little broadened distally, segment 5 little (or not) shorter than 4; dactyl medium, curved. Peraeopods 5 & 6, bases little broadened, posterior margin (especially of P6) setose, segment 4 long, with anterodistal lobe; segment 5 distinct, posterodistal spines elongate; segment 6 and dactyl not reversed. Peraeopod 7 elongate, basis little broadened; dactyl long.

Pleon plate 3, hind corner acuminate or squared. Pleopod peduncles little broader than deep. Uropod 1, rami sublinear, inner ramus the shorter. Uropod 2 not shortened, rami linear, both margins spinose. Uropod 3, ramus linear to subovate, usually longer than peduncle. Telson short, subtriangular.

Coxal gills medium, slender sac-like, on peraeopods 3-6. Brood lamellae medium, marginal setae short.

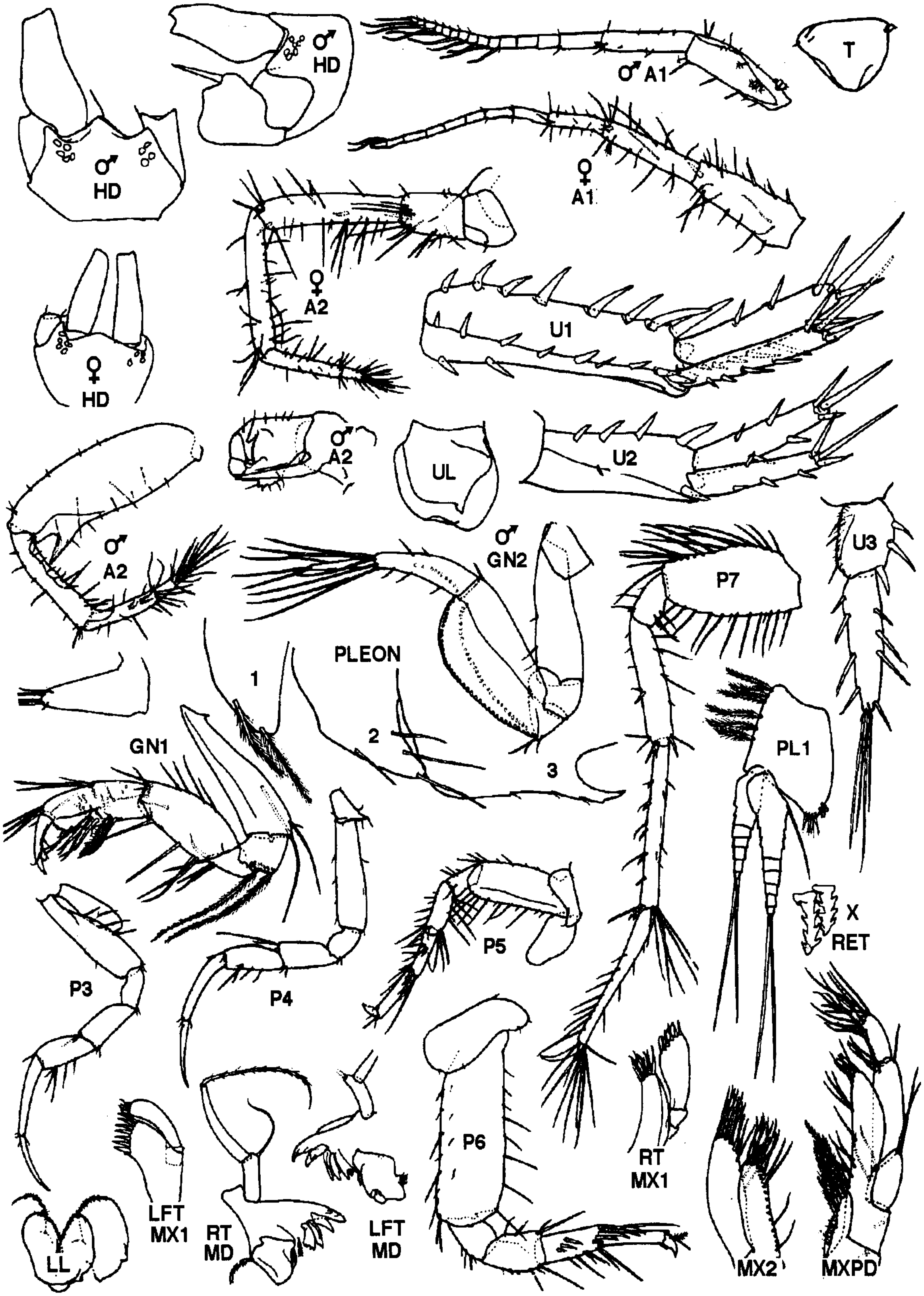


FIG. 3. *Eocorophium kitamori* (Nagata, 1965). South China Sea (after Hirayama, 1986).

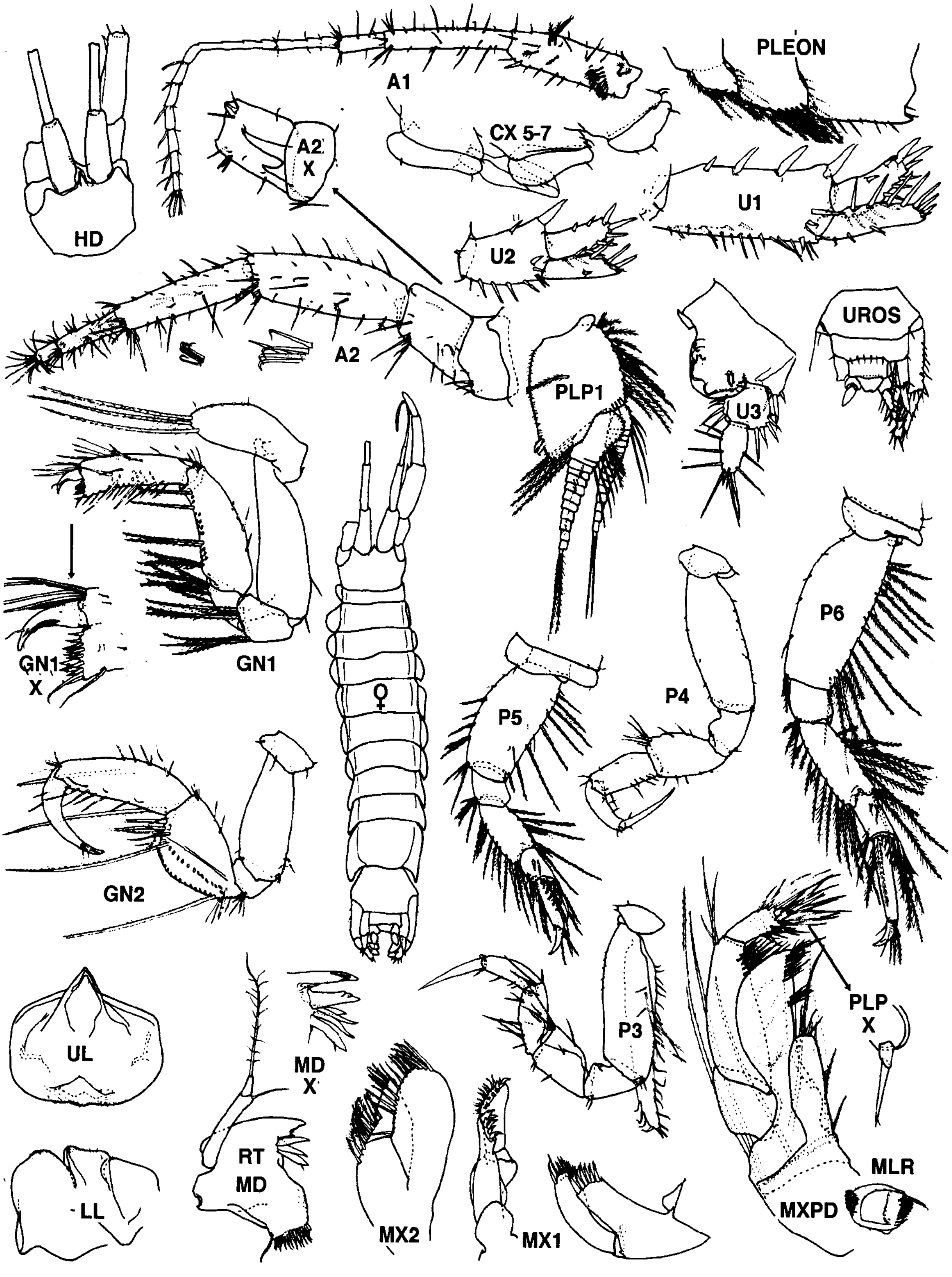


FIG. 4. *Sinocorophium sinense* (Zhang). Seto Inland Sea. Female (6.5 mm) (after Hirayama, 1987a).

KEY TO NORTH PACIFIC SPECIES OF *SINOCOROPHIUM*

1. Antenna 2 sexually dimorphic, pediform in male only; gnathopod 1 subchelate, palm nearly vertical; peraeopods 3 & 4, segment 5, length ~segment 4; uropod 3, ramus sublinear, longer than peduncle . . . 2.
—Antenna 2 sexually subsimilar; gnathopod 1 weakly parachelate, palm reverse-oblique; peraeopods 3 & 4, segment 5 relatively short, <2/3 length of segment 4; uropod 3, ramus short, broad . . . . 5.

2. Uropod 3, peducle with setose lateral process; mandibular palp, terminal segment very short . . . . . . 3.
—Uropod 3, peduncle lacking distinct lateral process; mandibular palp, terminal segment normal . . . . . . 4.

3. Antenna 1, peduncular segment 1 with posterior marginal process . . . . *S. heteroceratum* (Yu)
—Antenna 1, peduncular segment 1 lacking posterior marginal process . . . . *S. sinensis* (Zhang)

4. Gnathopod 1, propod broad, palm oblique; uropod 2, inner ramus fully spinose. *S. lamellatum* (Hirayama)
—Gnathopod 1, propod regular, palm vertical; uropod 2, inner ramus spinose laterally . . *S. minutum* (Ngoc)

5. Uropod 1, rami subequal in length, nearly straight . . . . *S. intermedium* (Ngoc)
—Uropod 1, inner ramus short, curved medially . . . . 6.

6. Antenna 2 (male), segment 4 with bidentate posterodistal process; maxilliped outer plate elongate, exceeding palp segment 2 . . . . *S. homoceratum* (Yu)
—Antenna 2 (male), posterodistal process of segment 4 unidentate; maxilliped, outer plate medium, not reaching distal margin of palp segment 2 . . . . 7.

7. Peraeopod 5, basis, posterior margin setose; gnathopod 2, dactyl long . . . . . *S. alienense* (Chapman) (p. 80)
—Peraeopod 5, basis lacking posterior marginal setae; gnathopod 2, dactyl medium . . . . 8.

8. Uropod 3, ramus suborbicular in form, shorter than peduncle; peraeopods 3 & 4, posterodistal margin of basis with 1-2 long setae only . . . . *S. triangulopedarum* (Hirayama)
—Uropod 3, ramus oblong, subequal to peduncle; peraeopods 3 & 4, basis with several posterodistal setae; . . . . *S. japonicum* (Hirayama)

Etymology. A combining form of the Latin prefix "sino"- Chinese, and the generic root *Corophium*, with reference to the endemism of component species in the East China Sea and adjacent regions.

Distributional ecology. The ten described species are endemic to warm temperate and subtropical shallows of the southeastern Sea of Japan, East China Sea and the South China Sea, south to Vietnam, where they burrow in soft marine and brackish substrata. One species occurs synanthropically in San Francisco Bay.

Behaviour. Virtually nothing is known. All species are presumed to be free-burrowing, mainly in muddy substrata, the tubes of which may be lined with the cemented grains of the substratum. Males are presumed to mate-guard.

Taxonomic commentary. Within subfamily Corophiinae, *Sinocorophium* demonstrates mostly plesiomorphic character states that appear to link it with presumed ancestral isaeids such as *Paracorophium* on the one hand, and (less likely) *Kamaka* on the other. Its plesiomorphic character states (e. g., large antennnal gland cone, short mandibular lobes of the lower lip, elongate maxillipedal palp segment 2, linear uropod rami, elongate maxilliped palp segment 2) suggest closest phyletic relationship with the western European genus *Corophium*, linked by species of the Indian Ocean (e. g., *C. madrasensis*?).

Reasonable grounds for formal subgeneric treatment of species within *Sinocorophium* is provided by numerical taxonomic analysis (Fig. 39 p. 132). A relatively primitive subgroup might include *S. sinensis, S. heteroceratum, S. lamellatum,* and *S. minimum.* A more advanced assemblage includes *S. homoceratum, S. intermedium, S. triangulopedarum, S. japonicum, S. alienense,* and possibly *S. monospinum.* In the latter cluster of species, antenna 2 is not sexually dimorphic, segments 2 and 4 of paired peraeopods 3 & 4 and 5 & 6 are more "glandular" (broadened), the rami of uropods 1& 2 are more unequal, and spinose mainly on the outer margin, and the ramus of uropod 3 is relatively short and broad. Formal taxonomic recognition of these differences, however, awaits the collection and analysis of more extensive and more complete materials.

Corophium contractum Stimpson, 1856, was imperfectly described and is not distinguishable from more recent species with urosome segments fused. Since the type may have been lost in the great Chicago fire of 1871 (Manning, pers. comm.) and material has not been subsequently identified, the species is here considered a nomen nudum [Stebbing (1906) suggested it may have been a female of *C. bonelli*].

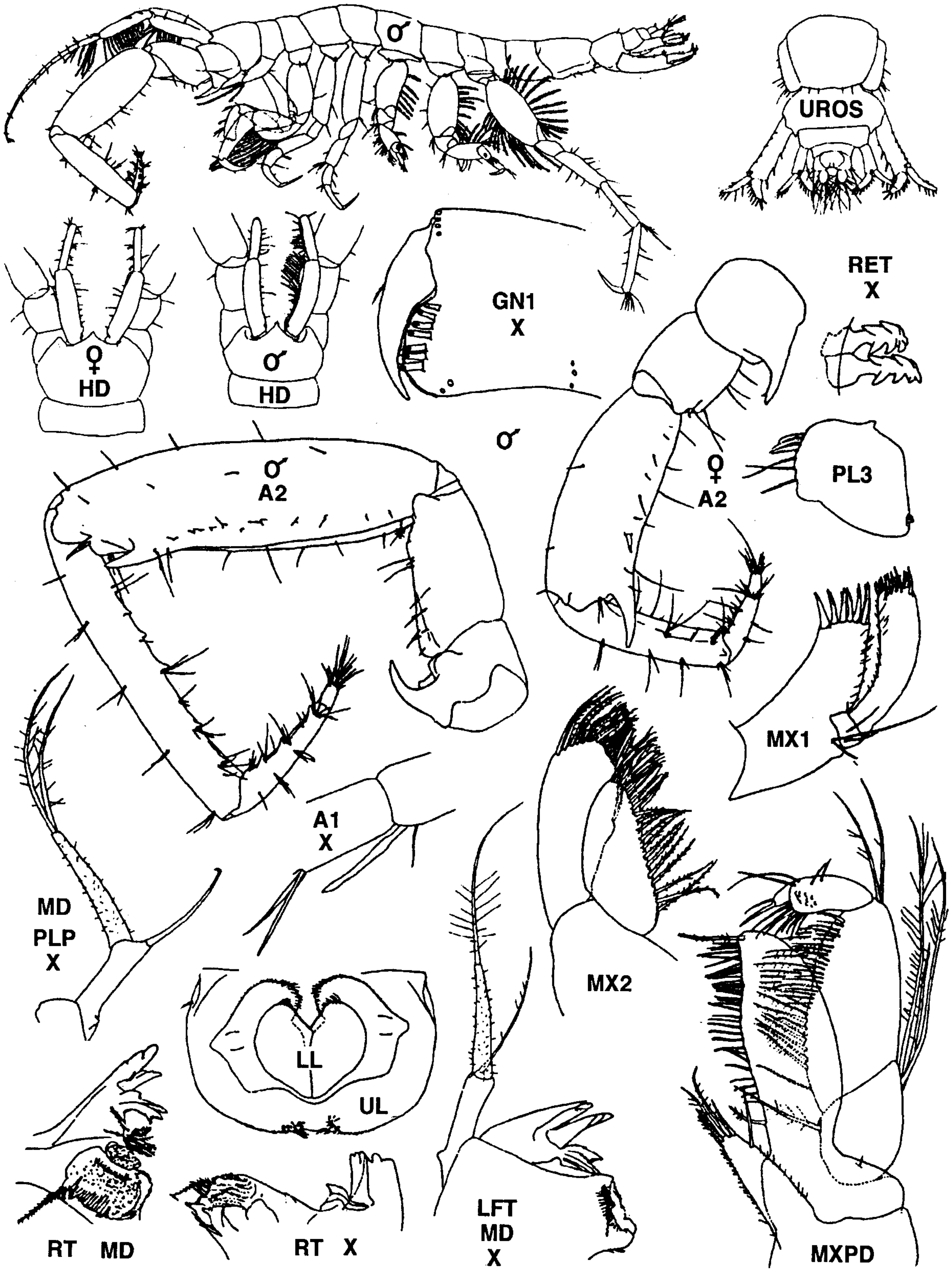


FIG. 5. *Sinocorophium alienense* (Chapman). San Francisco Bay. Male (6.5 mm); female (6.0 mm) (after Chapman, 1988).

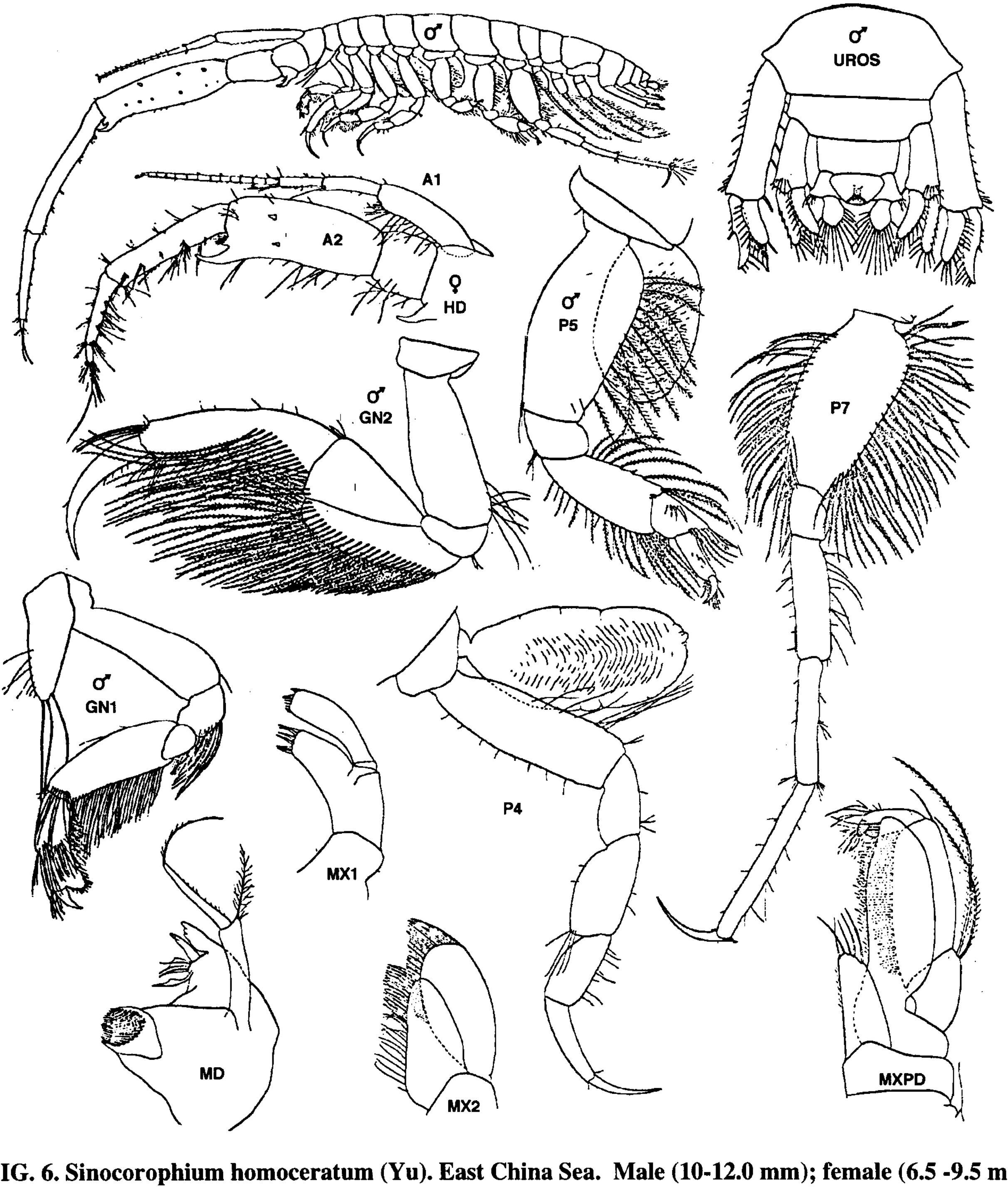


FIG. 6. Sinocorophium homoceratum (Yu). East China Sea. Male (10-12.0 mm); female (6.5 -9.5 mm) (after Yu, 1938).

Sinocorophium alienense (Chapman)
(Fig. 5)

Corophium alienense Chapman, 1988: 368, figs. 3-5.

Material examined. None from the study region.

Distributional Ecology. The species is unknown outside the San Francisco Bay area and is closely similar to *S. triangulopedarum* (Hirayama, 1986) and other species of the western North Pacific (key, p. 78). These factors led Chapman (loc. cit.) to conclude that the species is probably native to the western North Pacific and synanthropic in the eastern North Pacific.

Sinocorophium homoceratum (Yu)
(Fig. 6)

Corophium homoceratum Yu, 1938: 84, figs, 1-5.—Ngoc, 1965: 150, table I.—Barnard & Karaman, 1991: 185.

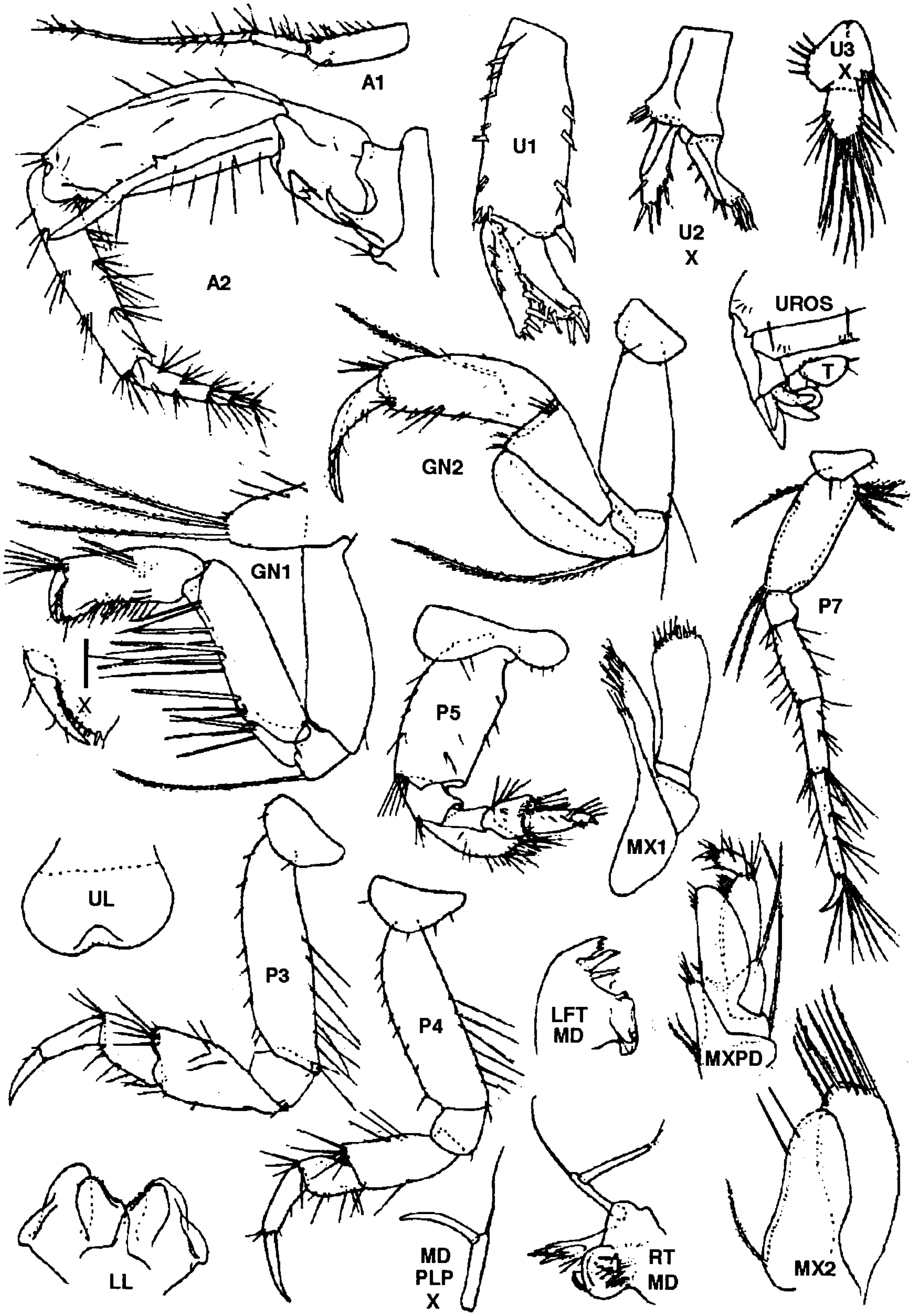


Fig. 7. *Sinocorophium japonicum* **(Hirayama). Tomioka Bay, Japan. Female (6.0 m) (after Hirayama, 1984).**

Medicorophium, new genus

(see Figs. 8, 9)

Corophium Latreille, 1806, Chevreux & Fage, 1925: 363 (part).—Crawford, 1937: 592 (part).—Gurjanova, 1951: 974 (part).—Myers, 1982: 185 (part).—Barnard & Karaman, 1991: 185 (part).

Type species. *Corophium aculeatum* Chevreux, 1908 (present designation).

Species. *Medicorophium rotundirostre* (Stephensen, 1915); *M. minimum* (Schiecke, 1978); *M. annulatum* (Chevreux, 1908); *M. runcicorne* (Della Valle, 1893); *M. affine* (Bruzelius, 1859).

Diagnosis. Small to medium corophiids (1.5-6.0 mm). Urosome segments separate. Head, rostrum short or rounded; inferior sinus deep, regressed. Antenna 1 relatively elongate; segment 3 not shortened. Antenna 2 sexually dimorphic. Antenna 2 (male) pediform; segment 4 with single or bidentate distal process; segment 5, median tooth small or lacking, distal process lacking; gland cone medium strong.

Mouthparts incompletely known (limited for *M. rotundirostre*). Upper lip, epistome produced(?). Lower lip, mandibular lobes weak(?) Mandibular palp advanced (type P4-P5 of Hirayama, 1987b). Maxilla 1, palp not exceeding outer plate. Maxilliped, palp segment 2 elongate(?).

Gnathopod 1 very weakly subchelate; dactyl pectinate behind, overlapping short, oblique propodal palm. Gnathopod 2, merus fused along entire lower length of carpus; dactyl simple or weakly bidentate distally.

Peraeopods 3 & 4, basis and segment 4 little broadened; segment 5 short, little overhung by segemnt 4; dactyls slender, elongate. Peraeopods 5 & 6, basis little broadened; segment 4 short, little broadened anterodistally; segment 5 with weak, elongate, posterodistal spines; segment 6 and dactyl not reversed(?). Peraeopod 7 slender, elongate.

Pleon plate 3, hind corner rounded. Uropod 1, peduncle slender; rami straight, subequal, outer margin spinose, apices with long spines. Uropod 2 not reduced. Uropod 3, ramus slender, longer and narrower than peduncle. Telson broad, rounded, with dorsal hook spines.

Coxal gills slender, sac-like. Brood lamellae medium, sublinear (*M. runcicorne*).

Etymology. A combining form of the Latin prefix *medi* - middle, and the generic root *Corophium*, with reference to the Mediterranean-endemic nature of component species.

Distribution. Largely endemic to the Mediterranean and Black Seas, burrowing in fine sediments, littoral-sublittoral to depths of 80 m.

Taxonomic commentary. Crawford (loc. cit.) treated *M. aculeatum, M. annulatum, M. runcicorne* and *M. affine* as "a natural group of small burrowing forms (1.5-5 mm) of slender build, and with uropod 3 linear in shape". *M. affine* is somewhat intermediate between *Corophium* sens. str. and *Medicorophium*, n. g., but is here included within the latter (Fig. 38, phenogram). Members of the genus *Medicorophium* overlap distributionally in northwestern Europe with *Corophium* sens. str., and with *Chelicorophium*, n. g., in the

KEY TO SPECIES OF *MEDICOROPHIUM*, NEW GENUS

1. Gnathopod 1 normally subchelate, palm distinct, little exceeded by dactyl . . . . 2.
—Gnathopod 1 simple or weakly subchelate, palm short, greatly exceeded by dactyl . . . . 5.

2. Antenna 2 subsimilar in both sexes, peduncular segment 4 toothed posterodistally . . . . 3.
—Antenna 2 sexually dissimilar, pediform in male only . . . . 4.

3. Antenna 2, flagellum elongate (10+ segments); rostrum projecting, apex rounded; uropod 1, rami spinose on both margins . . . . *M. rotundirostre* (Stephensen)
—Antenna 2, flagellum short (5-6 segments); rostrum recessed, apex subtruncate; uropod 1, rami spinose on lateral (outer) margins only . . . . *M. annulatum* (Chevreux)

4. Antenna 2, peduncular segment 4 lacking posterodistal process; uropod 2, margins of rami smooth; head, frontal margin with low rounded rostrum . . . . *M. minimum* (Schiecke)
—Antenna 2, peduncular segment 4 with bidentate posterodistal process; uropod 2, rami with lateral marginal spine(s); head, frontal margin broadly convex, lacking distinct rostrum. . . . *M. affine* (Bruzelius)

5. Antenna 2 (male), peduncular segment 4 thick, deep; peduncular segment 3 short; rostrum low, triangular, projecting little beyond head lobes; uropod 1, inner ramus spinose. . *M. runcicorne* (Delle Valle)
—Antenna 2 (male), peduncular segment 4 relatively slender; peduncular segment 3 elongate; rostrum acute, extending beyond frontal margin; uropod 1, inner ramus setose . . . . . *M. aculeatum* (Chevreux)

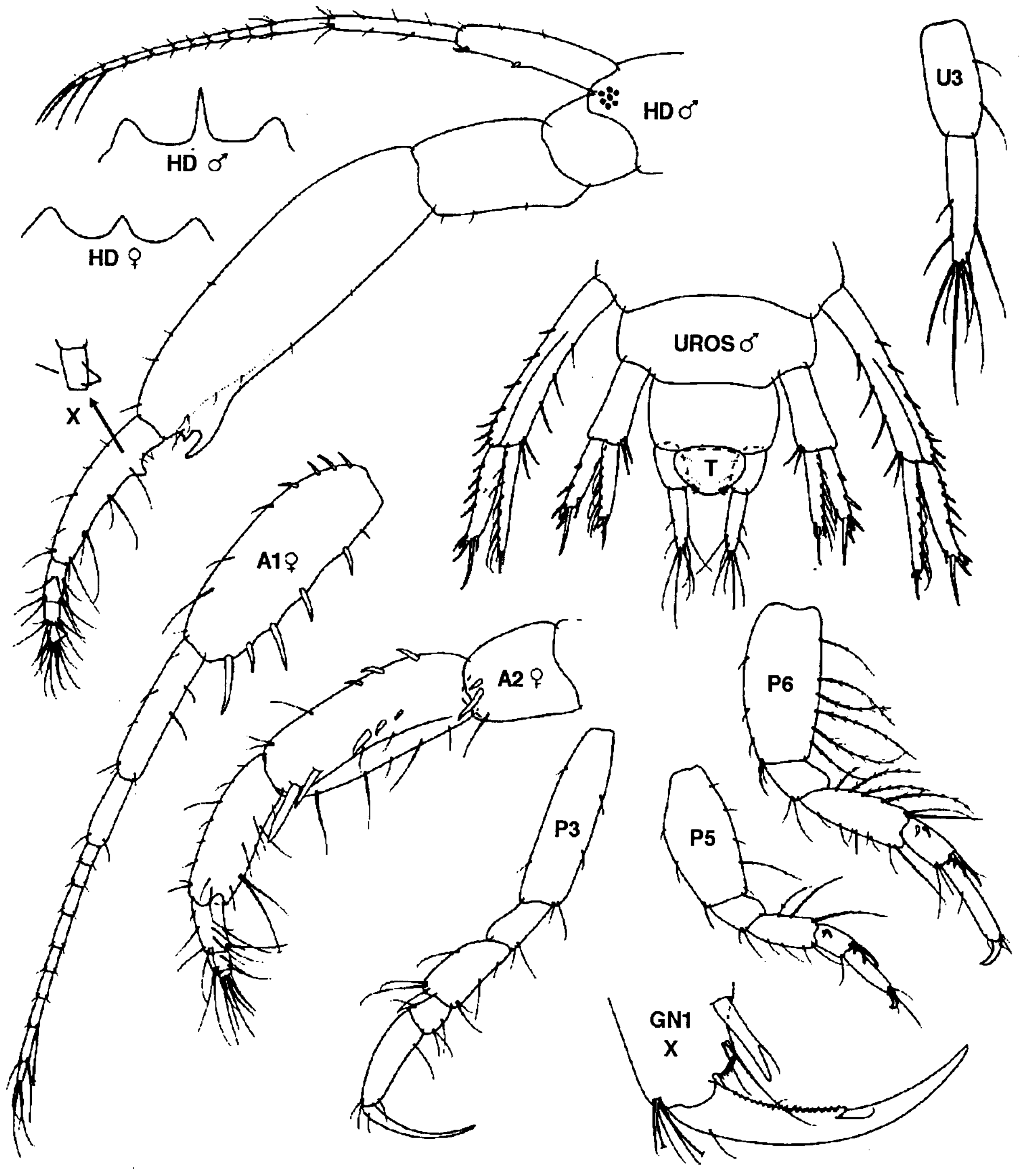


FIG. 8. *Medicorophium aculeatum* (Chevreux). Mediterranean Sea. Male (3.0 mm); female (3.0 mm). (after Myers, 1982).

eastern Mediterranean. However, in ordered character states of symplesiomorphic value, *Medicorophium* appears most closely similar to *Sinocorophium* (Fig. 38, phenogram). As noted elsewhere (p. 102), in the slender form of the urosome and uropods, lateral insertion of uropods 1 & 2, and the elongate apical spines of the uropod rami, among other character state similarities, *Medicorophium* may have given rise to an independent "cold-water" line of corophiins with fused urosome segments, conceivably ancestral to the genus *Crassicorophium*.

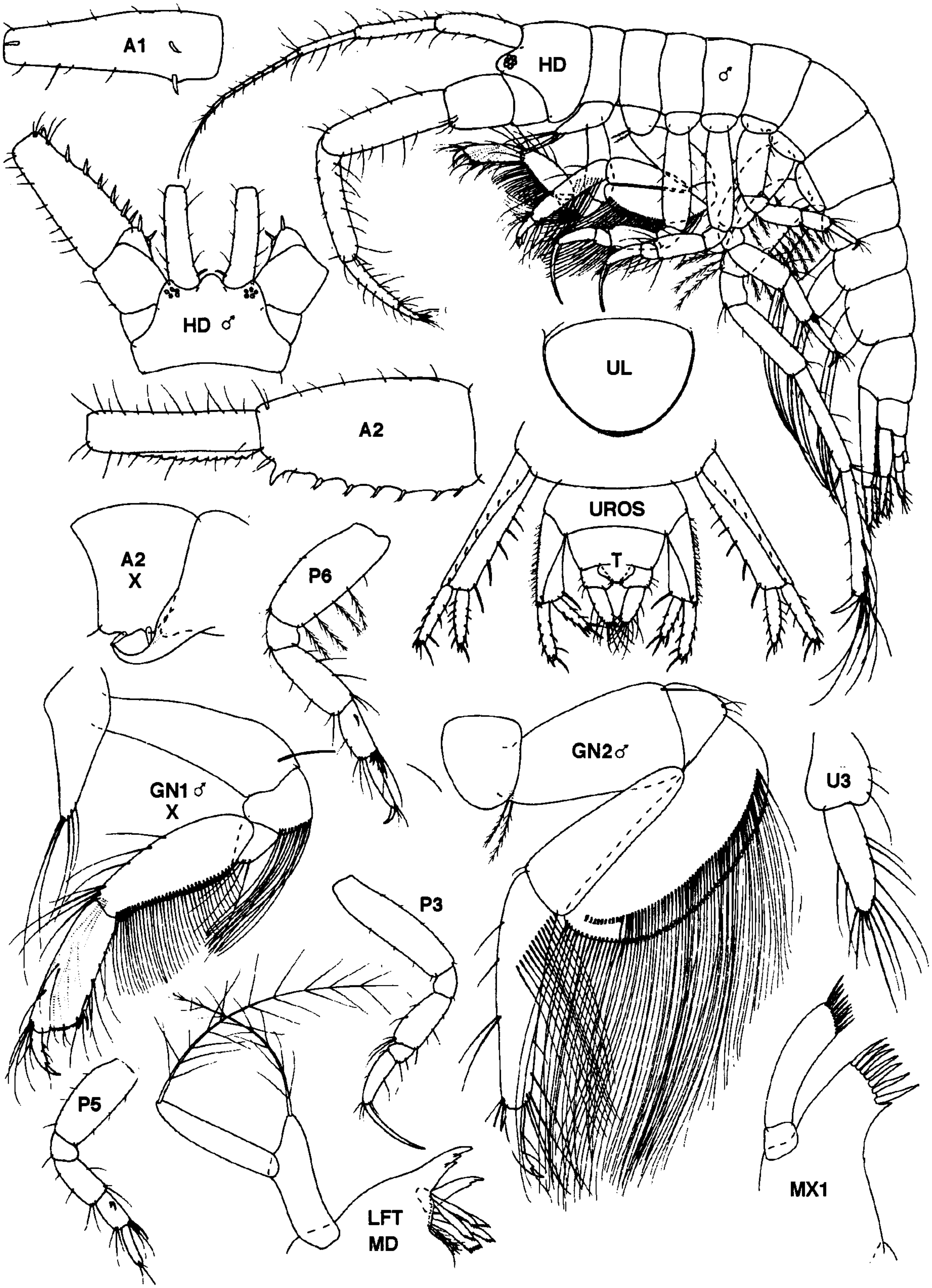


FIG. 9. ***Medicorophium rotundirostre*** **(Steph.). Mediterranean Sea. Male (6.0 mm); female (5.5 mm). (after Myers, 1982).**

Corophium Latreille
(See Figs. 10, 11)

Corophium Latreille, 1806: 58.—Stebbing, 1906: 685 (part).—Crawford, 1937: 595 (Section A, *volutator-arenarium* subgroup).—Gurjanova, 1951: 974 (part).—Bousfield, 1973: 198 (part).—Lincoln, 1979: 522 (part).—Myers, 1982: 185 (part).– Barnard & Karaman, 1991: 184 (part).

Type species: *Oniscus volutator* Pallas, 1766 (North Sea & English Channel).

Species. *Corophium multisetosum* Stock, 1952; *C. arenarium* Crawford, 1937; *C. orientale* Schellenberg, 1928.

Diagnosis. A relatively primitive complex of species, but more advanced than western North Pacific counterparts. Urosome segments not coalesced. Head, rostrum usually distinct; inferior antennal sinus recessed. Antenna 1 elongate, peduncular segment 3 medium. Antenna 2 large, pediform in male, less strong and often lacking process in female; segment 4 with single-toothed posterodistal process; segment 5 lacking median tooth and distal process; flagellum shorter than peduncle 5, proximal segment elongate; gland cone medium, not conspicuous.

Mouthparts plesiomorphic: Upper lip, epistome little produced. Lower lip, mandibular lobes short. Mandibular palp basic (type P1 of Hirayama, 1987b). Maxilla 1, palp slightly broadened distally, longer than outer plate. Maxilliped, inner plate medium, subacute; outer plate large, inner margin strongly setose; palp segment 2 elongate.

Gnathopod 1, propod regular, palm vertical; dactyl short, simple. Gnathopod 2 not greatly larger; propod slender; dactyl medium, simple, lacking posterior marginal teeth.

Peraeopods 3 & 4, basis slightly broadened; segment 4 little broadened distally; segment 5 medium short; dactyls medium. Peraeopods 5 & 6 basis setose behind; segment 4 long, broadened anterodistally; segment 5 shortened, posterodistal hook spines elongate, segment 6 and dactyl reversed. Peraeopod 7 elongate; basis, margins strongly setose; segment 4 shortened; dactyl short.

Pleon plate 3, hind corner obtuse or rounded. Pleopod peduncles broader than deep. Uropods 1 & 2, peduncles medium; rami straight, outer margins spinose; apices rounded. Uropod 3, ramus short, longer but less broad than peduncle. Telson broadly subtriangular, with few dorsal hook spines.

Coxal gills medium, sac-like, on peraeopods 3-6. Brood lamellae short, slender with relatively few (<20) marginal setae.

Distributional ecology: These medium to relatively large species burrow directly into muddy or sandy substrata where they construct sediment-lined U-shaped abodes. Species are endemic to the northeastern Atlantic and Mediterranean regions where they overlap with the *Medicorophium* and *Chelicorophium* subgroups.

Taxonomic commentary. Most species conform closely to the diagnosis above. However, *Corophium affine* Bruz.. is unique in lacking a well-defined rostrum, and other distinct features. It appears closest to the *volutator* type, but connects slightly below the 75% similarity level with genus *Medicorophium* (*aculeatum* type) (see phenogram, p. 130). Its character states are a mixture of the two: head rounded, linear uropod 3; antenna 1 short segment 3; antenna 2 (male) segment 4 bi-toothed; uropods 1 & 2, rami straight, etc.

Note: All previous records of *Corophium volutator* (and subspecies) from the western North Pacific (e.g., Hiray-ama, 1984, 1986) are probably attributable to one or more species of *Sinocorophium.* (p. 75).

KEY TO NORTH ATLANTIC SPECIES OF *COROPHIUM* LATREILLE (sens str.)

1. Antenna 2 sexually subsimilar, large, pediform in both sexes .... 2.
—Antenna 2 sexually dissimilar, pediform in male only .... 3.

2. Antenna 1 (male), peduncular segment 1 crenulate along lower inner margin; antenna 2, posterodistal process short, main tooth projecting slightly beyond end of segment 4; uropod 3, lateral lobe of peduncle weakly developed .... *Corophium volutator* (Pallas)

—Antenna 1 (male), lower medial margin of peduncular segment 1 strongly setose, not crenulated; antenna 2, segment 4, large tooth of posterodistal process extending more than half its length beyond end of segment 4; uropod 3, lateral peduncular process strongly developed .... *C. multisetosum* Stock

3. Antenna 1 (male), peduncular segment 1 crenulate along lower inner margin; uropod 1, outer margin of peduncle spinose throughout; uropod 3, ramus weakly setose .... *C. orientale* Schellenberg
—Antenna 1 (male), peduncular segment 1 not crenulate along lower medial margin; uropod 1, proximal portion of outer margin of peduncle setose, distal portion spinose; uropod 1, inner ramus proximally strongly broadened; uropod 3, ramus strongly setose (10+ setae) .... *C. arenarium* Crawford

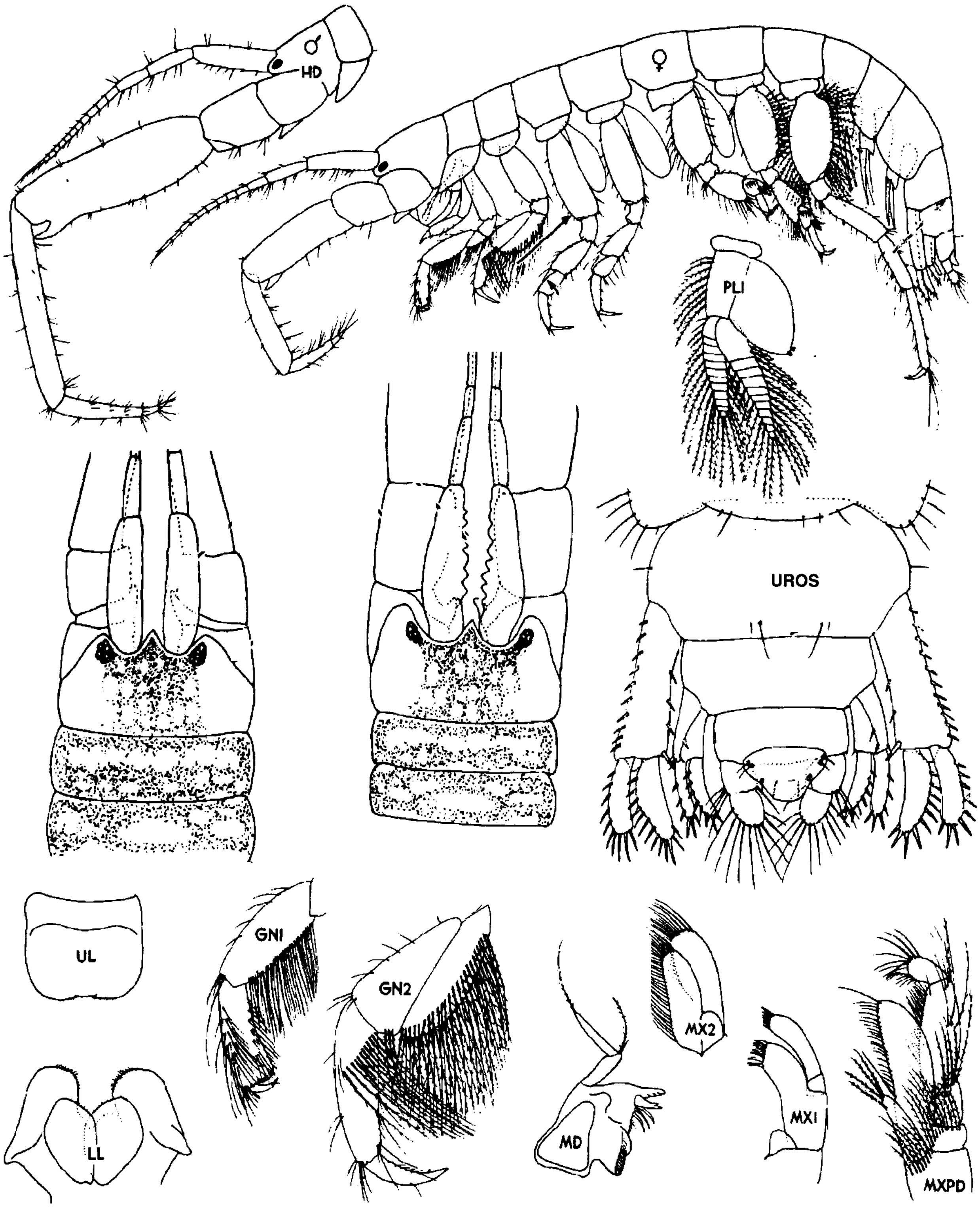


FIG. 10. ***Corophium volutator*** **(Pallas). Bay of Fundy. Male (6.0 mm); female 5.5 mm) (after Bousfield, 1973)**

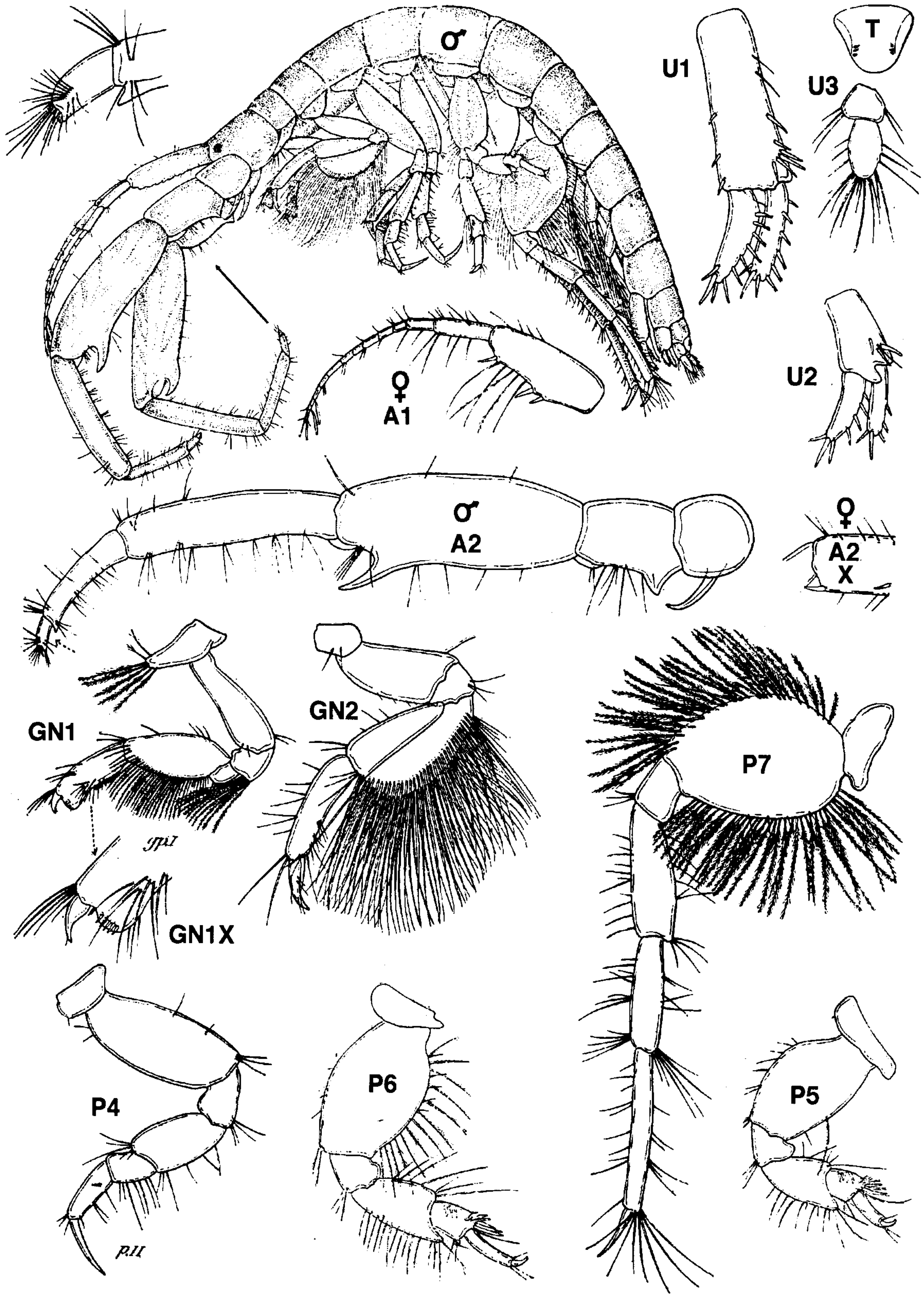


FIG. 11. *Corophium orientale* (Schellenberg). Black Sea. Male (4.0 mm); female (to 7.5 mm) (after Carausu et al., 1955).

Chelicorophium, new genus

(see Fig. 12)

Corophium Latreille, 1806, Stebbing, 1906: 685 (part).—Miloslawskaja, 1931: 61, Table, key).—Crawford, 1937: 594 (Section A, part).—Carausu et al., 1945: 359 (most).—Barnard & Karaman, 1991:185 (part).

Type species. *Corophium curvispinum* Sars, 1895b (present designation).

Species: *Chelicorophium chelicorne* Sars, 1895b; *C. robustum* Sars, 1895b; *C. maeoticum* Sowinsky, 1898; *C. monodon* Sars, 1895b; *C. mucronatum* Sars, 1895b; *C. spinulosum* Sars, 1895b; *C. spongicolum* Welitchkovsky, 1914; *C. sowinsky* Martynov, 1924 ; *C. villosus* Carausu 1943; *C. nobile* Sars, 1895b; (?)*C. madrasensis* Nayar, 1950.

Diagnosis. Urosome segments not coalesced. Head, rostrum short, not exceeding anterior head lobes; inferior antennal sinus deeply regressed. Antenna 1 elongate, segment 3 medium. Antenna 2 strongly pediform and well developed (clasping) in both sexes; peduncular segment 4 with strong bidentate posterodistal process; segment 5 short, usually with median tooth near mid-point, distal process various; flagellum medium, ~ segment 5; gland cone short, inconspicuous.

Mouthparts variably plesiomorphic. Upper lip, epistome produced. Lower lip, mandibular lobes medium. Mandibular palp basic (type P1 of Hirayama, 1987b). Maxilla 1, palp sublinear, longer than outer plate. Maxilliped, inner plate short, apex subacute, inner margin with basal spine; outer plate regular, inner margin strongly setose; palp segment 2 medium to long.

Gnathopod 1, regularly subchelate; dactyl short. Gnathopod 2, propod slender, not longer than combined merus and carpus; dactyl short, typically tridentate.

Peraeopods 3 & 4, basis broad (glandular); segment 5 medium to short, not overhung by segment 4; dactyl short-medium. Peraeopods 5 & 6 short, basis setose behind; segment 4 short, lacking anterior lobe; segment 5 short, posterior hook spines strong; segment 6 and dactyl reversed (usually?). Peraeopod 7, basis strongly setose; segment 5 not elongate; dactyl short.

Pleon plate 3, hind corner rounded. Pleopod peduncles wide, broader than deep. Uropods 1 & 2 medium, peduncles broadening distally; rami short, straight; inner (as well as outer) margins often spinose or setose, apex little out-curved. Uropod 3, ramus longer than peduncle, slightly broadened, setose apically.

Telson short, broad, spinose hooks at hind corners and dorsally. Coxal gills medium broad, sac-like, on peraeopods 3-6. Brood lamellae short, sublinear, marginal setae not elongate.

Etymology. A combing form of the Greek prefix "cheli" - claw, and the generic root *Corophium*, with reference to the strongly pincer-like form of peduncular segments 4 & 5 of antenna 2.

Distributional ecology. Component species are endemic to the Aralo-Caspian region, confined mainly to the Black and/or Caspian Sea Basins, with a few outliers in the Mediterranean to the west, and Aral Sea to the east (formerly). Animals construct sediment-lined abodes in the shallow substratum, in salt, brackish, and tidal fresh waters.

Taxonomic commentary. Crawford (loc. cit.) included all species of this genus, except *C. villosus*, within section I of *Corophium* sens. lat. (segments of the urosome separate). He placed them phyletically between the *volutator-arenarium*, and the *salmonis-spinicorne* subgroups, the rationale for which is generally confirmed in the present study.

KEY TO BLACK SEA SPECIES OF *CHELICOROPHIUM*

1. Antenna 2, peduncular segment 5 lacking median tooth and distal process; peraeopods 3 & 4, segment 5 of medium length, distinctly longer than broad .... *C. nobile* (G. O. Sars)
—Antenna 2, peduncular segment 5 with conspicuous median tooth and distal process; peraeopods 3 & 4, segment 4 short, not longer than broad .... 2.

2. Gnathopod 2, dactyl bidentate posteriorly; uropod 2, inner ramus fully spinose .. *C. chelicorne* (G. O. Sars)
—Gnathopod 2, dactyl with 3-4 posterior marginal spines; uropod 2, inner ramus, inner margin bare ... 3.

3. Peraeopods 3 & 4, basis setose posteriorly; uropod 1 peduncle, outer margin setose .. *C. robustum* (Sars)
—Peraeopods 3 & 4, basis nearly bare posteriorly; uropod 1, outer margin of peduncle spinose .... 4.

4. Antenna 2, segment 4 thickly and deeply incrassate, length <2Xwidth; uropod 1, outer margin of peduncle weakly spinose (4+); uropod 1, inner ramus spinose on outer margin only......... *C. maeoticum* (Sowinski)
—Antenna 2, segment 4 moderately stout, length > 2X width; uropod 1, outer margin of peduncle strongly spinose (10+); uropod 1, inner ramus spinose on both margins............... *C. curvispinum* (G. O. Sars)

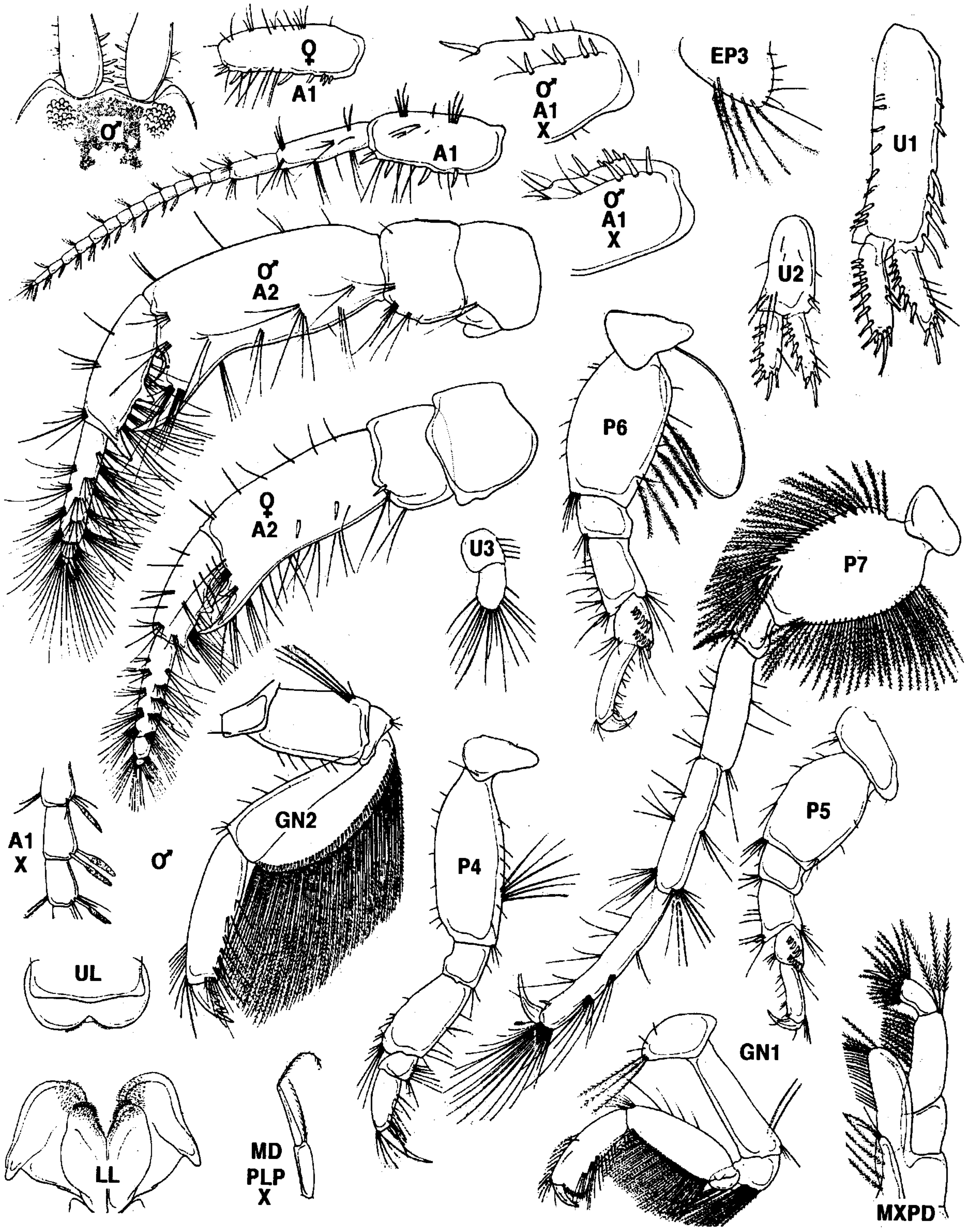


FIG. 12. *Chelicorophium chelicorne* (G. O. Sars). Black Sea. Male (8.0 mm); female (7.5 mm) (after Carausu et al., 1955).

Americorophium, new genus

Corophium Lateille, 1806, Stebbing, 1906: 685 (part).—Crawford, 1937 (Section A, part).—Shoemaker, 1949: 66 (part + key).—Barnard, 1969a: 190 (part).—Barnard, 1973: 17 (part).—Otte, 1976: 2 (part + key).—Barnard & Karaman, 1991: 184 (part).

Type species. *Corophium spinicorne* Stimpson 1857 (present designation).

Species. *Americorophium salmonis* (Stimpson, 1857); *A. brevis* (Shoemaker, 1949); *A. stimpsoni* (Shoemaker, 1941); 1949; *A. panamense* (Shoemaker, 1949); A. *setosum* (Shoemaker, 1949); *A. rioplatense* (Giambiagi, 1929); *A. aquafuscum* (Heard & Sikora, 1972); *A ellisi* (Shoemaker 1943)(?); *A. triaeonyx* (Stebbing, 1904)(?).

Diagnosis. Generally medium to large corophiins. Urosome segments unfused. Head, rostrum flat, rounded,or weakly produced; inferior antennal sinus large, regressed. Antenna 1, peduncular segment 3 variously shortened. Antenna 2, large, pediform, variously sexually dimorphic, often strongly setose posteriorly; gland cone short; segment 4 with bidentate posterodistal process; segment 5, posteromedian tooth and distal process variously developed; flagellum 2(3)-segmented, distal segments very short.

Lower lip, mandibular lobes pronounced. Mandibular palp basic (type P1 of Hirayama, 1987b). Maxilla 1, palp little (or not) exceeding outer plate. Maxilla 2, plates large, inner margins fully setose. Maxilliped, inner plate straight, setose apico-medially; outer plate regular, inner margin fully setose; palp segment 2 medium to short.

Gnathopod 1 regularly weakly subchelate; dactyl slightly exceeding palm. Gnathopod 2 strong; merus not occluding postero-distal free margin of carpus; dactyl moderately strong, spinose or toothed behind.

Peraeopods 3 & 4, bases broadened, glandular; segment 4 broadened distally,variously overhanging shortened segment 5. Peraeopods 5 & 6, bases broadened, that of peraeopod6 setose behind; segment 5 shortened, with short posterodistal hook spines; segment 6 and dactyl reversed. Peraeopod 7; segment 5 not longer than 4; dactyl moderate.

Pleon plate 3, hind corner obtuse. Pleopod peduncles strongly broadened medially. Uropods 1 & 2 stout, peduncles broadened distally; outer ramus shorter than inner ramus; lateral margins of rami spinose, apices acute, curved outward. Uropod 3, ramus medium broad, slightly longer than peduncle. Telson broad,narrowing distally, apex subtruncate.

Brood plates large, strap-like, marginal setae long, numerous (>40). Coxal gills large, sac-like, on peraeopods 3-6.

Etymology. A combining form of the prefix "Ameri"- and the generic root *Corophium*, reflecting the essentially North American and neotropical distribution of known species comprising the genus.

Distributional commentary. Component species occur in North American Pacific boreal to warm-temperate and tropical coastal waters; also in North and South American Atlantic warm-temperate brackish estuaries. One species (*A. triaeonyx*) is endemic to the Indian Ocean.

Taxonomic commentary. Crawford (1937) linked *Corophium salmonis* Stimpson and *C. spinicorne* Stimpson and placed them between the Aralo-Caspian *C. chelicorne*, and the Mediterraean-endemic sublittoral *C. aculeatum* assemblages. He also linked *Corophium triaeonyx* Stebbing, redescribed fom Madagascar by Ledoyer (1982), most closely with *C. rioplatense* on the basis of similarities in antenna 2. These decisions find some supported here (Fig. 39, p. 132). In addition, the posterior margins of the peduncle and flagellum of antenna 2 are strongly setose in these Atlantic regional species of *Americorophium,* which include *A. aquafuscum* and *A. panamense. A. setosum* Shoemaker,1949, a small species with segmented urosome from the Pacific coast of Mexico, may be referable here but is excluded from the analysis because all character states of the male, and many critical features of the female, are unknown. In the medium-large sexually dimorphic Floridian species, "*Corophium*" *ellisi* Shoemaker, 1943, the urosome is unsegmented, but on the basis of most other character states it is assignable to the genus *Americorophium.* Its primitive features include a relatively shallow inferior antennal sinus, a 3-segmented mandibular palp (type P1), and the dactyl of gnathopod 2 that is posteriorly setose rather than toothed.

Americorophium spinicorne Stimpson
(Fig. 13)

Corophium spinicorne Stimpson, 1857: 514.—Bradley, 1908: 227, pls. 9, 10.—Shoemaker, 1949: 74, fig 6.—Aldrich, 1961: 21, fig 2.—Barnard, 1975: 340 (key), fig. 141.—Otte, 1976: 9, figs. 4, 5.—Austin, 1985: 615.—Staude, 1987: 349 (+ key).— Barnard & Karaman, 1991: 186.

Material Examined: About 85 lots comprising more than 300 specimens, from SE Alaska through B. C. to Washington, Oregon, and Central California, mostly in low-brackish estuaries, as follows:
ALASKA.
Southeastern Alaska. ELB Stns, 1961: A1 (21), A7(3), A9(3), A11(6), A27(26), A37(71), A74(1), A78(~50), A88(18), A153 (1), A159(10).

BRITISH COLUMBIA.
Queen Charlotte Islands. ELB Stns., 1957: H2a(2), H4 (67), H5(14), W6(6), W7a(1), H8(8), W9(6), W9b(11), W12b(2), H5(30), H15(1), E17-18(15), E25(4).
North-central mainland coast. ELB Stns, 1964: H4(1), H6(6), H7(1), H14(2), H18 (16), H46(2), H51(6), H54(12), H56(4), H57(5), H58(1).
Vancouver Island, north end and adjacent mainland. ELB

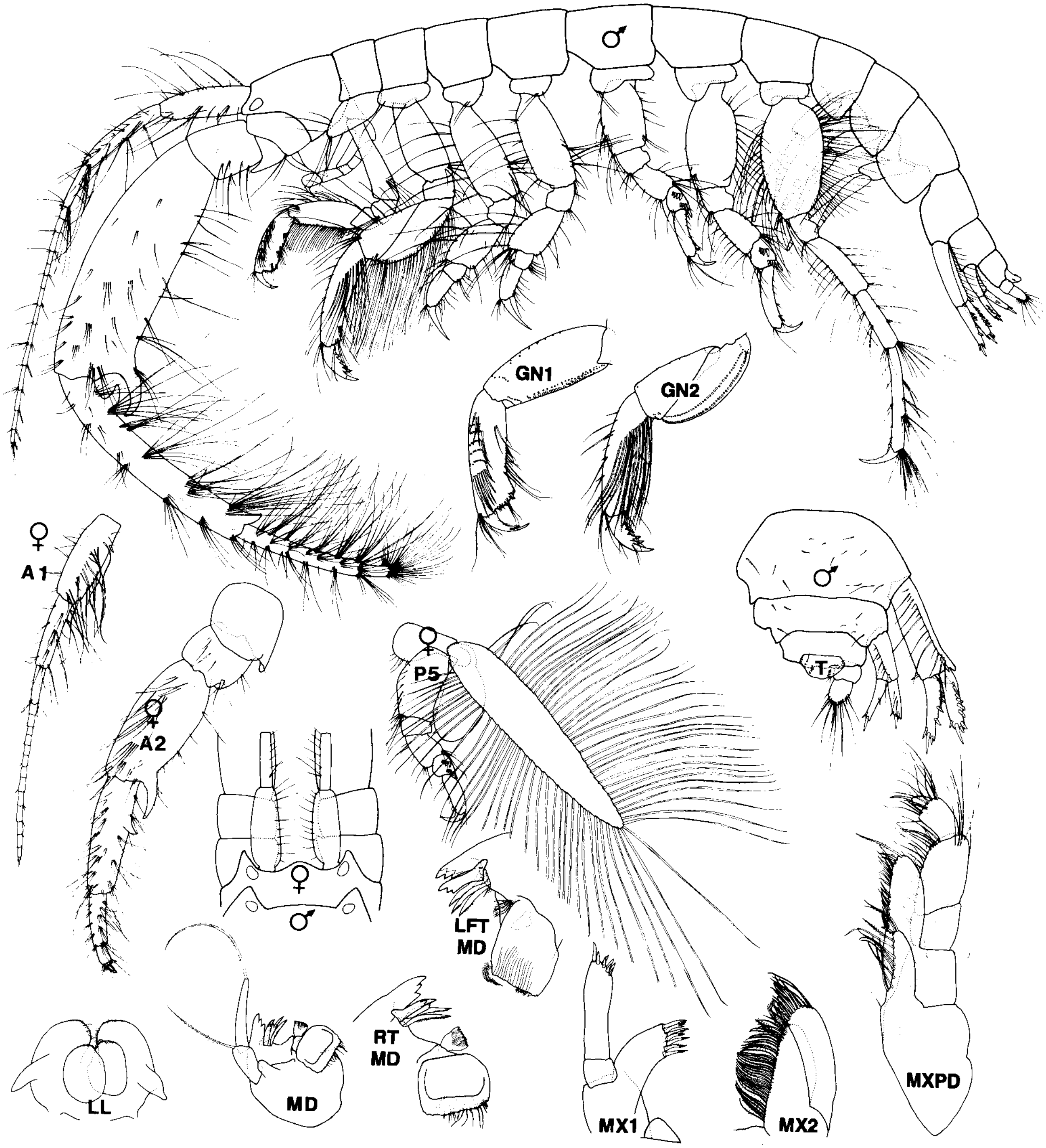


FIG. 13. ***Americorophium spinicorne*** **(Stimpson). Chinook, WA. Male (6.5 mm); female (7.0 mm).**

Stns, 1959: O1(1), O4(22), O7(13), O17(16), V13(4), V17(1), V21(several, damaged), N10(1), N11(22), N13(16), N15(12), N18(3), N21(8).

Southern Vancouver Island and adjacent mainland. ELB Stns, 1955: F3(17), F4(1), F9(29), G5(13), G11(25), G21(18), G22(2), P2(5), P5(20), P5b(2), P7(1), M3(16), M5(18). ELB Stn., 1964: H43(2). ELB Stn., 1970: P713(11). ELB Stns 1975: P6c(3); P16a(1), P19a(~200). F. Rafi coll., Campbell River estuary, 1984: B4(6).

WASHINGTON-OREGON

Washington. ELB Stns, 1966: W11(25); W12(1); W34 (20); W36(18); W44(1); W48 (Chinook) - 67 spms., incl. male (6.5 mm)(**fig'd**); female ov (7.0 mm) (**fig'd**), CMN Cat. No. NMCC1992-0798.

Oregon. ELB Stn W57 (Cape perpetua) - 7 spmns.

Diagnosis. Male (6.5 mm): Antenna 1, peduncular segment 1 regular, inner margin setose; flagellum 12-14

KEY TO SPECIES OF *AMERICOROPHIUM*

1. Antenna 2 (male), posterior margin of peduncular segment 4 sparsely setose, or setose distally only; uropod 2, rami with 2 (or more) outer marginal spines . . . . 2.
—Antenna 2 (male), posterior margin of peduncular segment 4 lined throughout with clusters of long setae; uropod 2, rami with 0-1 outer marginal spines . . . . 6.

2. Antenna 2, similar (large, pediform) in both sexes; posterior margin of segment 5 and flagellum strongly setose; uropod 1, outer margin of peduncle lined with setae. . . . . 3.
—Antenna 2 strongly sexually dimorphic, pediform in male only; posterior margin of segment 5 and flagellum weakly (or not) setose; uropod 1, outer margin of peduncle lined with short spines. . . . . 4.

3. Uropod 1, outer margin of outer rami with numerous (10+) close-set spines; mandibular palp 3-segmented; North American Atlantic . . . . *A. aquafuscum* (Heard & Sikora)
—Uropod 1, outer margin of outer ramus with 6-7 short spines; mandibular palp 2-segmented; North American Pacific . . . . *A. spinicorne* (Stimps.) (p. 90)

4. Urosome segments fused; gnathopod 2, posterior margin of dactyl lined with setae; mandibular palp 3-segmented; N. American Atlantic. . . . . *A. ellisi* (Shoemaker)
—Urosome segments separate; gnathopod 2, posterior margin of dactyl lined with 4-5 teeth or spines as well as setae; mandibular palp 2-segmented; North American Pacific . . . . .5.

5. Antenna 1 (male), peduncular segment 1 expanded medially into broadly rounding lobe; gnathopod 2, propod with small posterodistal cusp . . . . *A. salmonis* (Stimps.) (p. 94)
—Antenna 1 (male) peduncular segment 1 not expanded medially, but with small ventral hook-like process; gnathopod 2, propod lacking cusp . . . . *A. stimpsoni* (Shoem.) (p. 94)

6. Gnathopod 2, posterior margin with 4-6 teeth; uropod 3, ramus short, as broad as long . . . . *A. brevis* (Shoem.) (p. 95)
—Gnathopod 2, posterior margin with 2 teeth; uropod 3, ramus longer than broad . . . . 7.

7. Antenna 2 (both sexes), segment 5 with strong curved distal process; uropod 1, outer margin lined with slender spines; uropod 3, ramus broadened . . . . *A. setosum* (Shoem.)
—Antenna 2 (both sexes), segment 5 lacking distal process; uropod 1, outer margin with short spines; uropod 3, ramus slender, distinctly longer than wide . . . . 8.

8. Antenna 2 (male), posterior margin of peduncular segment 3 strongly setose; antenna 2 (female), segment 4 not produced posterodistally; Indian Ocean . . . . *A. triaeonyx* (Stebbing)
—Antenna 2 (male), posterior margin of peduncular segment 3 nearly bare; antenna 2 (female), segment 4 produced posterodistally; Neotropical . . . . 9.

9. Antenna 2 (female), peduncular segment 4 produced distally as a large triangular spinose process; antenna 1, peduncular segment 1, dorsal margin strongly setose; uropod 1, inner ramus bare . . . . *A. panamense* (Shoemaker)
—Antenna 2 (female) distal process of segment 4 short, weakly spined; antenna 1, peduncular segment 1, dorsal margin normal; uropod 1, inner ramus with outer marginal spine(s). . . *A. rioplatense* (Giambiagi)

---

segmented. Antenna 2 large, pediform; segment 3 weakly setose posteriorly; segment 4 hind margin sparsely setose, posterodistal process appearing single-toothed; segment 5 not shorter than 4, posterior margin with strong proximal tooth, 4-5 clusters of long setae, and strong distal process; flagellum not shortened, 3(4)-segmented, hind margin with numerous long setae.

Gnathopod 1, dactyl with small posterior marginal tooth; tip exceeding oblique palm. Gnathopod 2, basis little broadened; carpus medium, with distinct posterodistal free margin; propod lacking distal cusp; dactyl with 4-5 posterior marginal teeth.

Peraeopods 1 & 2, basis and segment 4, anterior margins loosely lined with long setae; dactyls slender, slightly longer than segment 6. Peraeopod 5, basis, margins weakly setose. Peraeopod 7, basis medium broad, margins of distal segments moderately setose; dactyl medium.

Pleon plate 3, hind corner subquadrate. Uropod 1, outer

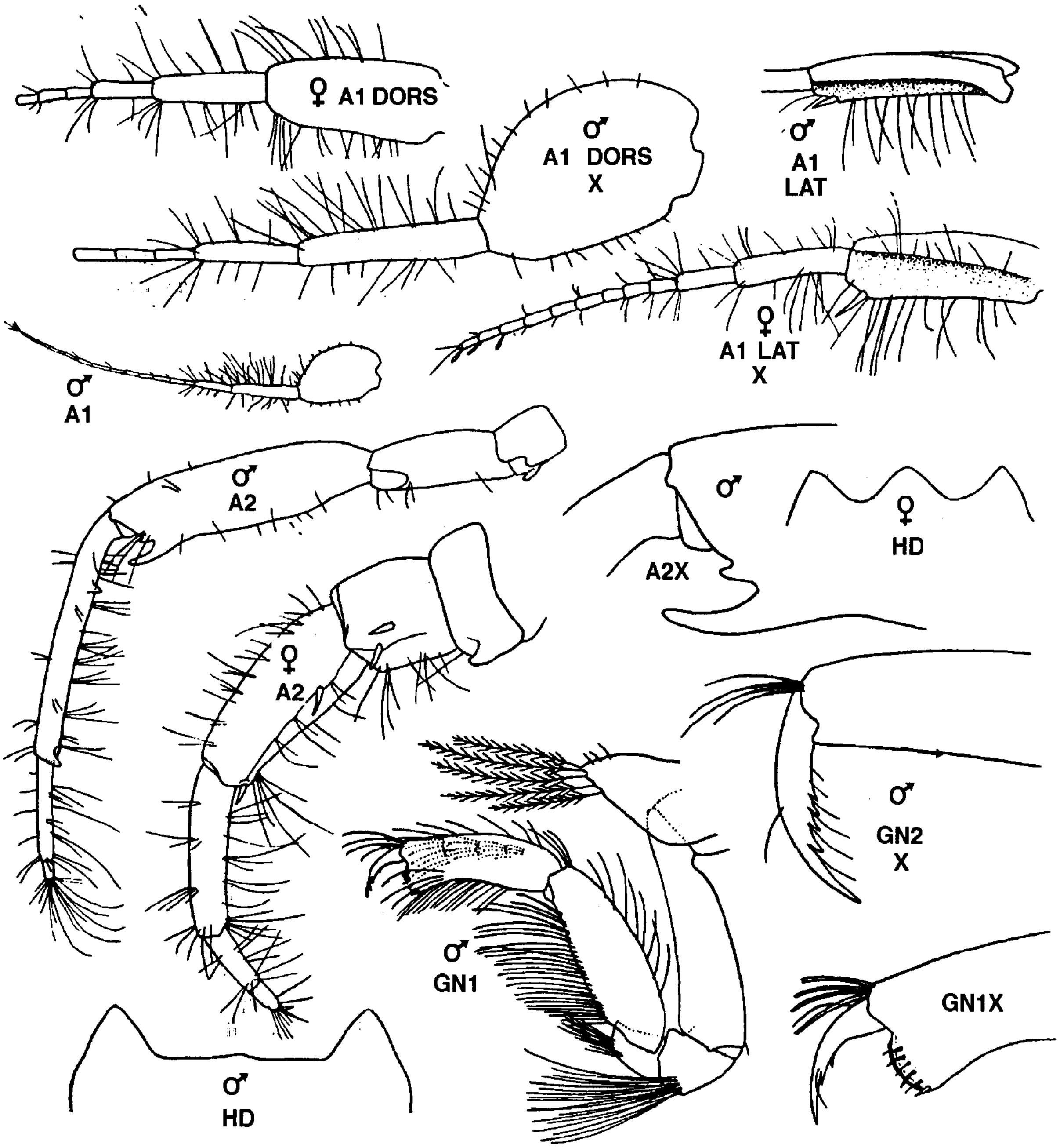


FIG. 14. *Americorophium salmonis* (Stimpson). Puget Sound, WA. Male (6.0 mm); female (7.0 mm). (after Shoemaker, 1949).

margin of peduncle lined with numerous setae of unequal length; rami unequal, outer margins with 5-6 spines. Uropod 2, rami unequal, outer ramus, outer margin setose; inner ramus, outer margin with 1-2 spines. Uropod 3, ramus and peduncle broadened, ramus nearly as wide as long. Telson wider than long, dorsally with 4 pairs of short hook spines.

Female (6.0 mm): Head, rostrum short, rounded. Antenna 2 similar in form (strongly pediform) but less robust than in male.

Brood plate large, strap-like, narrowing distally, margins lined with numerous (>60) long setae.

Taxonomic and distributional commentary. *Americorophium spinicorne* is the most commonly encountered estuarine corophiin amphipod of the northeastern Pacific region. The species occurs in a variety of intertidal habitats, but is most frequent in stream run-offs over shingle and mud flats, from the upper MW to LW levels.

Taxonomically, *A. spinicorne* exhibits mainly plesiomorphic character states, some in common with *A. aquafuscum* (Heard & Sikora) of American Atlantic warm-water estuaries (see Fig. 39, p. 132, and key, p. 92).

Americorophium salmonis (Stimpson)
(Figs. 14, 15)

Corophium salmonis Stimpson, 1857: 514.—Stebbing, 1906: 692.—Bradley, 1908: 235, pls. 11,12.—Shoemaker, 1949: 66, fig. 1.—Otte, 1976: 6 (key), figs. 4, 5.—Austin, 1985: 615.—Staude, 1987: 349 (key), 386, fig. 18.26.—Barnard & Karaman, 1991: 186.

Material Examined. About 250 specimens in 20 lots, mostly from high salinity outer coast locations, from Washington-Oregon north to the Queen Charlotte Islands; not recorded from SE Alaska.

BRITISH COLUMBIA.
Queen Charlotte Islands. ELB Stns, 1957: H5(5), H8a(35), H9(7), H10(4).
North-central mainland coast. ELB Stns, 1964: H13(1), H23(27).
Vancouver Island, north end. ELB Stns, 1959: O4(2), O12(10).
Vancouver Island, south end. ELB Stns, 1955: F3(5); F6(27), G11(3). ELB Stn., 1975: P20(3).

WASHINGTON.
San Juan Islands. ELB Stn, 1955: S5(1).
Washington, outer coast. ELB Stns, 1966: W15(7), W17(2), W29(2), W36(10), W40(1), W41(3), W48(13 spmns including male (6.0 mm)**(fig'd)**, female (7.0 mm) **(fig'd),** CMN Cat. No. NMCC1992-0798.

Diagnosis. Male (to 6.0 mm): Head, rostrum very short, little protruding beyond frontal margin. Antenna 1 peduncular segment 1 greatly broadened dorsomedially, inner margin weakly setose, flagellum slender, 12-14-segmented. Antenna 2 large, pediform; segment 3 elongate, posterior margin nearly bare; segment 4, surfaces and hind margin with scattered clusters of short setae, posterodistal process appearing single-toothed; segment 5 relatively slender, little shorter than 4, posterior margin with median proximal tooth, a few clusters of short setae, and medium-sized distal process; flagellum 3-segmented, ~1/2 length of segment 4, margins not strongly setose.

Coxa 1 with 5-6 antero-distal plumose setae. Gnathopod 1, dactyl with small posterior marginal tooth; tip exceeding rounded, nearly vertical palm. Gnathopod 2, basis little broadened; carpus medium, with distinct posterodistal free margin; propod with weak distal cusp; dactyl slender, with 4 small posterior marginal teeth and slender interdentate setae.

Peraeopods 1 & 2, basis, anterior margin loosely lined with longish setae; segment 4 broadened distally, partly overhanging short segment 5, anterodistal margin (of 4) richly long-setose; dactyl slender, curved, longer than segment 6. Peraeopod 5, basis setose anteriorly and posterodistally. Peraeopod 7 not unusually elongate, basis subovate; margins of distal segments moderately setose; dactyl medium, curved.

Pleon plate 3 shallow, hind corner tightly rounded. Uropod 1, outer margin of peduncle proximally with a few short setae, distally with short spines; rami strong, subequal, outer margins with 4-7 stout spines. Uropod 2 strong; rami subequal, outer margin with 2-3 spines. Uropod 3, ramus and peduncle little broadened, ramus distinctly longer than wide, margins setose. Telson very broad, short, hook spines short, indistinct.

Female (to 7.0 mm): Head, rostrum slightly stronger and more acute than in male. Antenna 1, peduncular segment 1 not strongly broadened, posterior margin with distal spine. Antenna 2 much shorter and strongly dissimilar in form to that of male; peduncular segments 4 & 5 short and stout, margins and surfaces with scattered short setae, but lacking stout spines; flagellum short, margins with short setae.

Brood plates broadly strap-like, margins lined with moderate numbers (~40) long setae.

Taxonomic and distributional commentary. *Americorophium salmonis* has been recorded subtidally from Puget Sound to the south coast of Alaska (Kodiak Island), on muddy bottoms in high salinity estuaries and fiords. It shows a mixture of character states, and clusters most closely with *A. stimpsoni* and other intermeiate species of the genus (see Fig. 39, p. 134).

Americorophium stimpsoni (Shoemaker)
(Fig. 16)

Corophium stimpsoni Shoemaker, 1941: 184.—Shoemaker, 1949: 68, fig. 2.—Barnard, 1975: 340 (key).—Barnard & Karaman, 1991: 186.

Material Examined: None in present collections.

Taxonomic and ecological commentary. This species ranges narrowly from San Francisco Bay north to Mendocino Bay, northern California, and possibly southern Oregon. The species was not listed by Otte (1975), Austin (1985), nor Staude (1987) from coastal waters of British Colombia or Puget Sound. It was not taken in at any of the present study sites in Washington and Oregon north to British Columbia. However, it is included in the key to species of *Americorophium* (p. 92) where it pairs closely with *A. salmonis* (Stimpson).

Americorophium stimpsoni shows several plesiomorphic character states, and clusters among the primitive to intermediate members of the genus (Fig. 39, p. 134). It was only partially described and figured by Shoemaker (1941, 1949). He found few reliable features for distinguishing females from those of *A. salmonis*. The males are readily distinguishable by: (1) the form of the rostrum which is much stronger, with apex rounded, in *A. stimpsoni*; (2) the form of peduncular segment 1 of antenna 1, that is not medially expanded but bears a ventral hook-like process in *A. stimpsoni*; and (3) by the form of antenna 2 in which segment 3 is shorter, the median tooth of segment 5 is more proximally positioned and the flagellum shorter than in *A. salmonis*.

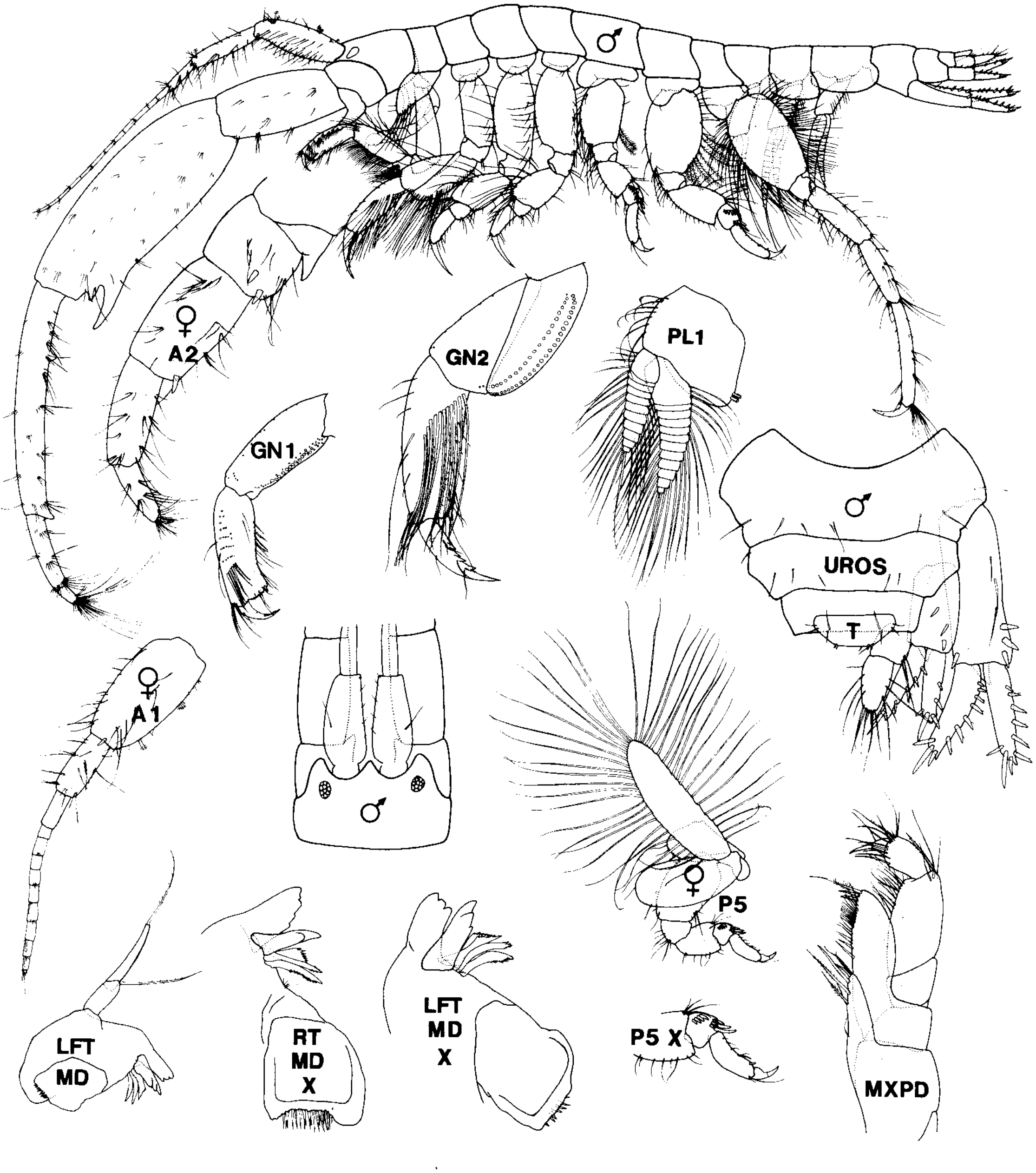


Fig. 15. ***Americorophium salmonis*** **(Shoem.). Chinook, WA. Male (6.0 mm); female (7.0 mm).**

Females of the two species do show slight overall difference in the antennae. In *A. stimpsoni*, the peduncular segments of antenna 1 are somewhat less strongly setose, and in antenna 2, peduncular segments 4 & 5 are relatively short and slender. However, despite the smaller overall size of *A. stimpsoni*, in gnathopod 1 the antero-distal setae of the coxa are more numerous, and the propod is less strongly broadened distally and the palm less strongly convex. In gnathopod 2, the dactyl is shorter and stouter, with fewer posterior marginal setae, than in *A. salmonis*.

Americorophium brevis (Shoemaker)
(Fig. 17)

Corophium brevis Shoemaker, 1949: 70, fig. 4.—Barnard, 1975: 340 (key), figs. 148, 149.—Otte, 1976: 6 (key), figs. 4, 5.—Coyle & Mueller, 1981: 9.—Austin, 1985: 615.—Staude, 1987: 349 (key), 386.—Barnard & Barnard, 1991: 185.

Material Examined. Nearly 200 specimens in 42 lots, mostly from interidal habitats of outer coast localities, from

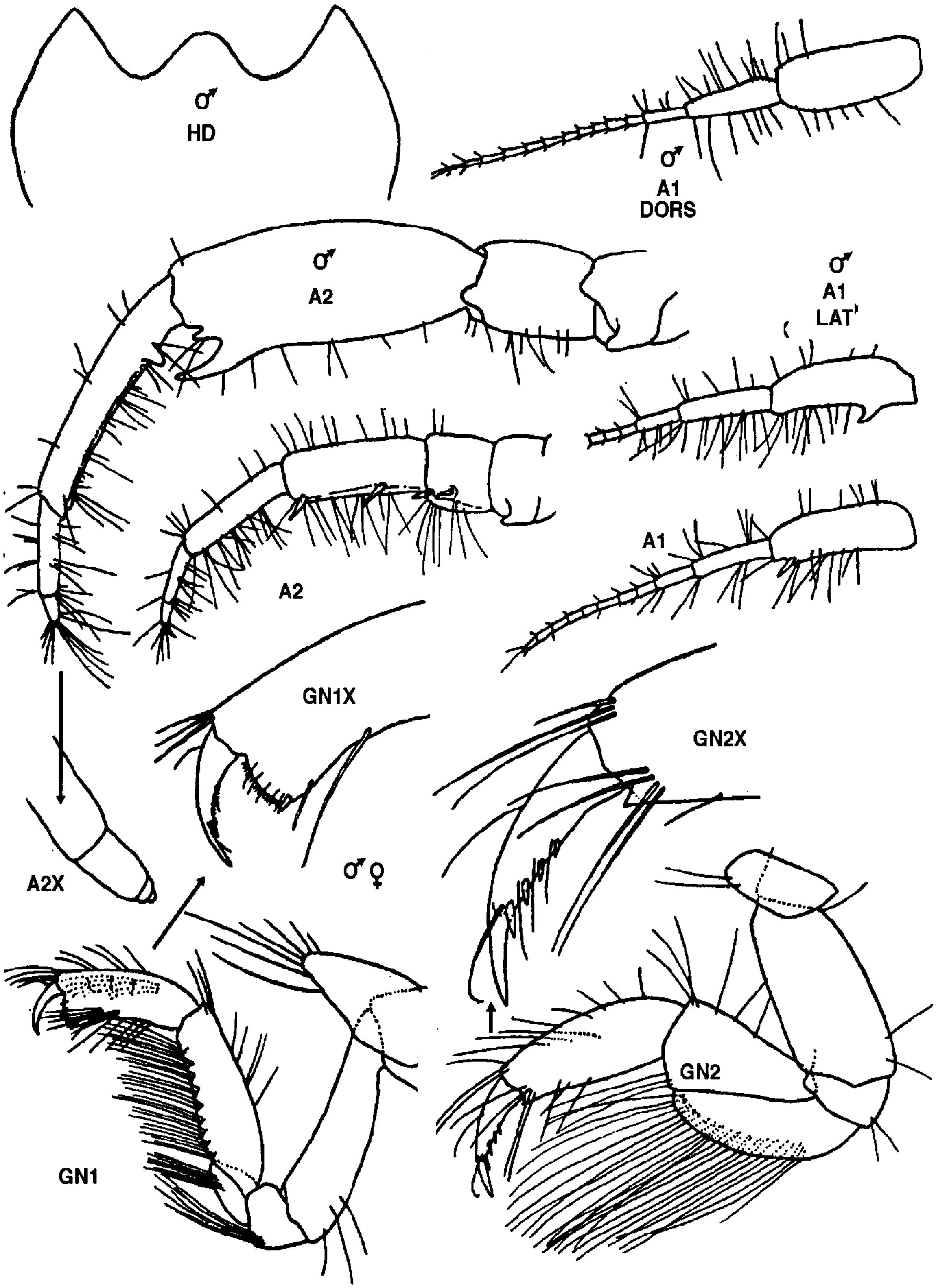


FIG. 16. *Americorophium stimpsoni* (Shoemaker). Dillon Beach, CA. Male (5.0 mm); female (6.0 mm) (after Shoemaker, 1949).

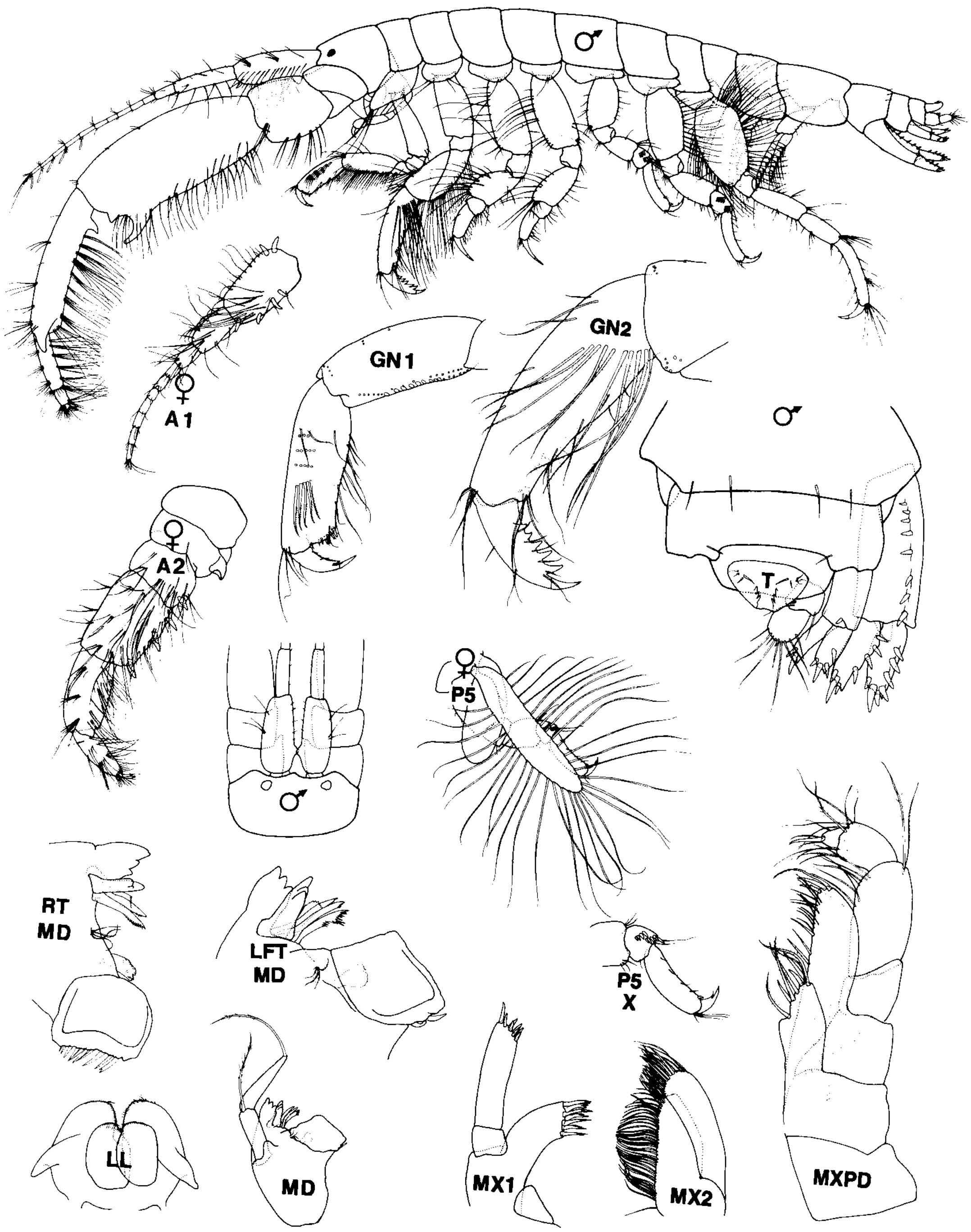


FIG. 17. ***Americorophium brevis*** **(Shoem.). Pacific Beach, WA. Male (3.5 mm); female (4.0 mm).**

---

the Aleutian Islands, Prince William Sound and SE Alaska, through B. C. southward to Washington and Oregon: ALASKA.

Aleutian Islands. N.A. Powell coll., Thin Point, Unimak I., 1969 - 2 males, 2 females, 1 im.

Southeastern Alaska. ELB Stns, 1961: A43(4), A93(2), A99(1), A159(5). ELB Stns,1980: S5B3(1), S8B2(1), S13B1(4), S16B1(1).

BRITISH COLUMBIA.
Queen Charlotte Islands. ELB Stn, 1957: H14(1).
North-central mainland coast: ELB Stns, 1964: H8(1), H12(1), H16(3), H35(17), H39(3), H46(24), H58(2), H59(3), H61(7).
Vancouver Island, north end. ELB Stn, 1959: O13(2).
Vancouver Island, south end and mainland coast. ELB Stns, 1955: P2(4), P7(4), M8(2), M11(12). ELB Stns., 1964: H40(2), H41(2), H43(9). ELB Stn., 1970: P717(1). ELB Stn., 1976: B12(2).
Rocky Point, Wickaninnish Bay, C. Lobban Stn, 1972: CL1011(3); Cobble Beach, V.I. Stn., 1972: 335(1).

WASHINGTON-OREGON.
Washington, Point Roberts. ELB Stn, 1955: M10(23).
Washington, outer coast. ELB Stns, 1966: W2(1), W6(1), W20(14), W30(5), W34(2).
Oregon, outer coast, ELB Stn., 1966: W52(12).

Diagnosis. Male (5.0 mm): Head, rostrum very shallow, broad, not exceeding broad lateral head lobes. Antenna 1, peduncular segment 1 regular, inner margin with small proximal process, lateral margin setose; flagellum slender, 11-12 segmented. Antenna 2 large, pediform; segment 3 weakly setose posteriorly; segment 4 hind margin sparsely setose, posterodistal process appearing single-toothed; segment 5 not shorter than 4, posterior margin with strong proximal tooth, 4-5 clusters of long setae, and strong distal process; flagellum not shortened, 3-4 segmented, hind margin strongly long-setose.

Gnathopod 1, dactyl with minute posterior marginal tooth and fine proximal setae, tip exceeding oblique palm. Gnathopod 2, basis little broadened; carpus large, deep, with distinct posterodistal free margin; propod stout, narrowing distally, lacking distal cusp; dactyl with 5-6 unequal posterior marginal teeth.

Peraeopods 3 & 4, basis moderately broad, anterior margin moderately lined with long setae; segment 4 slightly overhanging short segment 5, anterodistal margin strongly setose; dactyl slender, length subequal to segment 6. Peraeopod 5, basis, margins weakly setose. Peraeopod 7 not elongate; basis medium broad; posterior margins of distal segments with clusters of longish setae; dactyl medium.

Pleon plate 3, lower margin smooth, hind corner rounded. Uropod 1, outer margin of peduncle lined with 7-8 short spines; rami short, unequal, outer margins with 4-5 spines. Uropod 2, rami subequal, outer margins with 1-2 spines. Uropod 3, ramus and peduncle broadened; ramus nearly as wide as long. Telson short, broad, dorsally with 4 pairs of short hook spines.

Female (4.0 mm): Head, rostrum little differing from male. Antenna 1, peduncular segment 1 with 2 proximomedian curved spines and 3-4 ventral marginal spines. Antenna 2 much shorter and strongly dissimilar in form to that of male. Peduncular segments 4 & 5 short, stout, facially and marginally setose; hind margin of segment 4 with 3-4 stout spines; flagellum short, margins setose.

Brood lamellae medium broad, strap-like, margins lined with medium numbers (35-40) of long setae.

Taxonomic and distributional commentary. *Americorophium brevis* was originally described from Puget Sound and recorded south to San Francisco Bay and north via Vancouver Island to southeastern Alaska (Shoemaker, 1949). The present study extends the range north to Prince William Sound, northern Gulf of Alaska.

Behaviourally, animals form U-shaped tubes in soft sediments, mainly subtidally to depths of ~35m. The species shows mainly apomorphic character states, and clusters most closely with the advanced *panamense-setosus* subgroup of Central American Pacific and Atlantic neotropical warm-water estuaries (Fig. 39, p. 132). It is least similar to the relatively primitive and more estuarine and intertidal species, *A. spinicorne*.

Microcorophium, new genus
(see Fig. 18)

Corophium Latreille, Hirayama, 1986: 451 (part + key).—Barnard & Karaman, 1991:184 (part).

Type species. *Corophium sextonae miospinulosum* Hirayama, 1986 (monotypy).

Diagnosis. Body minute. Urosome segments coalesced; uropods arising from lateral notches (Type F3 of Hirayama, 1987b). Head, rostrum medium to short, sexually dimorphic. Antenna 2 pediform in male (unlike and simple in female); segment 4 with bidentate posterodistal process; segment 5 lacking conspicuous median tooth or distal process; flagellum short, 3-segmented; gland cone pronounced.

Upper lip, epistome produced. Lower lip, mandibular lobes short. Mandibular palp of advanced form, with produced medial shelf (type P5 of Hirayama, 1987b). Maxilla 1, palp relatively short. Maxilliped, inner plate short, apex oblique; outer plate narrow, columnar, inner margin sparsely setose; palp segment 2 medium long, narrow.

Gnathopod 1, propod short, stout, palm strongly oblique; dactyl strong. Gnathopod 2, merus not occluding posterodistal (free) margin of carpus; propod with few proximomedial setae; dactyl medium strong, weakly bidentate.

Peraeopods 3 & 4, basis and segment 4 slightly broadened; segment 5 very short, partly overhung by segment 4. Peraeopods 5 & 6, segments 4 & 5 not shortened, posterolateral spines medium; segments 5 & 6 not reversed(?); dactyl short. Peraeopod 7, basis narrow; dactyl short.

Pleopod peduncles relatively narrow, little broader than deep. Pleon plate 3, hind corner weakly acute. Uropod 1, peduncle slender, weakly spinose; rami linear, apical spine elongate. Uropod 2 not reduced; rami linear, margins smooth, apical spine elongate. Uropod 3, ramus stouter and longer than peduncle. Uropod 3, ramus stout, longer than peduncle, weakly setose. Telson short, broad, rounded behind.

Coxal gills short, slender, sac-like, on peraeopods 2-6. Brood plates undescribed.

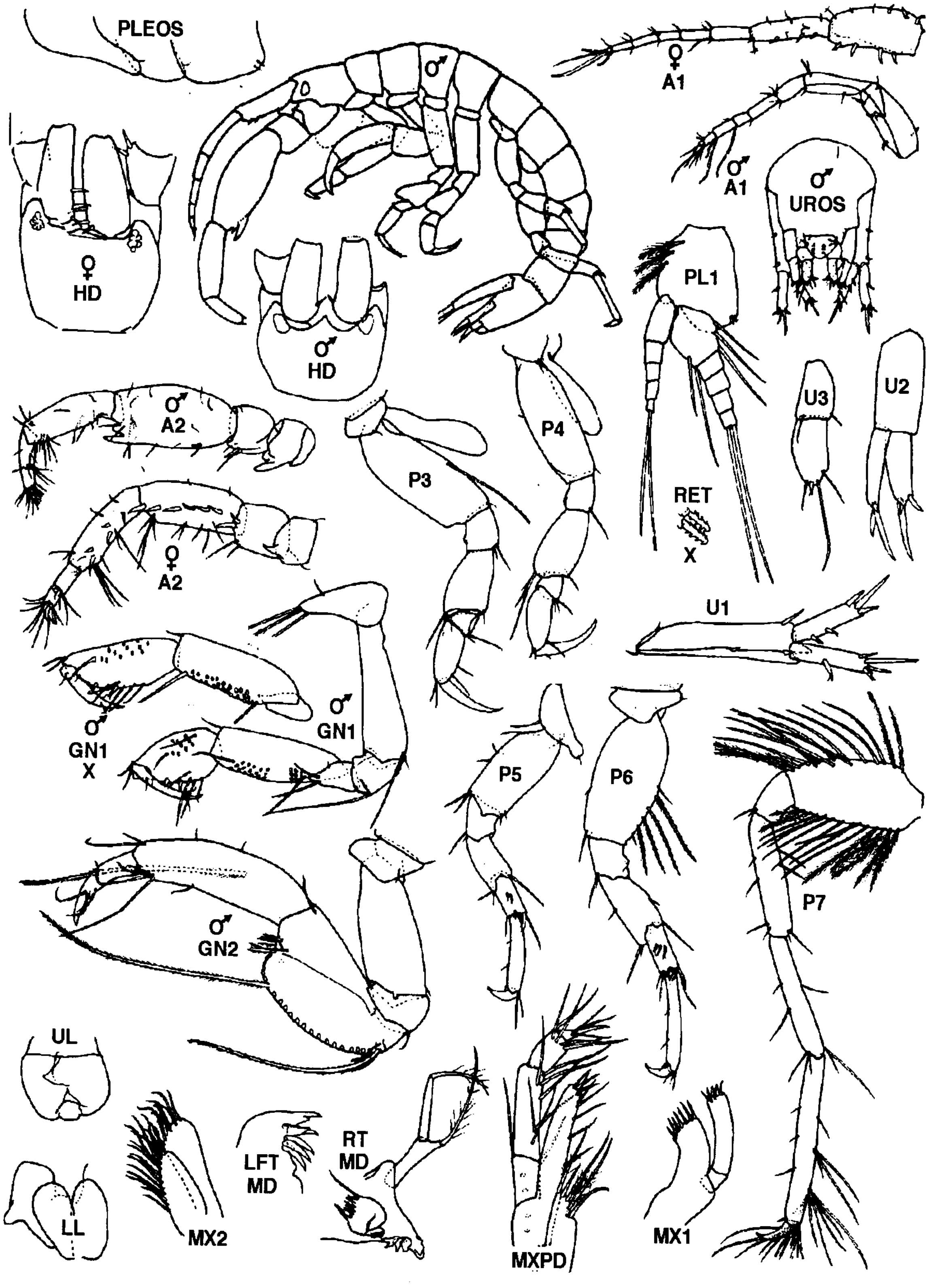


FIG. 18. *Microcorophium miospinulosum* (Hirayama). Hong Kong. Male (1.4 mm); female (1.9 mm) (after Hirayama, 1986).

Etymology: A combining form of the Greek prefix "micro", and the generic root *Corophium*., with reference to the minute size at maturity of the type species.

Distribution: Known only from the Hong Kong region of the South China Sea.

Taxonomic commentary. The type species *Microcorophium miospinulosum* was originally described as *Corophium sextonae* Crawford, 1937, subsp. *miospinulosum* Hirayama, 1986. The similarities noted by Hirayama between *miospinulosum* and *C. sextonae* would seem attributable to convergent morphology rather than close natural affinity. Thus, *C. sextonae* is a member of the genus *Monocorophium*, differing in several character states that are here considered of generic significance. In this species (as figured by Crawford, 1937 and Hurley, 1954) the epistome of the upper lip is not produced, the mandibular lobes of the lower lip are strong; the maxilliped inner plate is slender and subacute, the outer plate medium broad; gnathopod 1 is normally subchelate and the propod is slender; the dactyl of gnathopod 2 is short and tridentate; the pleopod peduncles are much broader; and in uropods 1 & 2 (male), the rami are short-spinose laterally and apically, and the apices are curved outwards and acute.

The specimens (4-5 mm) from Venice, Mediterranean Sea, figured by Myers (1982), as *Corophium sextonae* Crawford, 1937, differ somewhat in the bidentate (rather than tridentate) form of antenna 2, peduncular segment 4, and in the form and armature of the uropods.

In most character states *Microcorophium miospinulosum* must be considered a very primitive member of the corophiin subgroup having fused urosome segments. It may have evolved convergently from a *Sinocorophium*-like ancestor and is of distinctly different lineage than *Monocorophium*, sens. str. However, the form of the mandibular palp and gnathopod 1 may be considered autapomorphic within this unique genus.

Lobatocorophium, new genus
(see Fig. 19)

Corophium Latreille,1806, Hirayama, 1987a: 175 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium lobatum* Hirayama, 1987a (monotypy).

Diagnosis. Small tube-building corophiins. Urosome segments fused; uropods arising laterally (type F3A of Hirayama, 1987b). Head, rostrum medium. Antenna 1, peduncular segment 3 short. Antenna 2 (female) ordinary, segments 4 & 5 little enlarged; flagellum 2-segmented. Antenna 2 (male) undescribed, but presumably large, pediform, segments 4 & 5 with pre-amplexing processes.

Upper lip, episome unproduced. Lower lip, mandibular lobes medium. Mandibular palp advanced (type P5 of Hirayama, 1987b). Maxilla 1, palp shorter than outer plate. Maxilla 2, lobes slender. Maxilliped, inner plate short, apex subacute; outer plate columnar, apex blunt, inner margin sparsely setose; palp segment 2 elongate, slender.

Gnathopod 2, palm of propod short, oblique, greatly exceeded by simple dactyl. Gnathopod 2, merus not occluding posterodistal (free) margin of short carpus;propod relatively short, with small posterodistal cusp; dactyl short, bidentate.

Peraeopods 3 & 4, basis broad, glandular; segment 4 broadened distally, overhanging short segment 5; dactyl long. Peraeopods 5, 6, and 7 not described.

Pleon 3 strongly rounded behind. Pleopod peduncles broader than deep. Uropod 1 appearing ventral to uropod 2; peduncle very slender rami short, linear, apical spines long. Uropod 2, peduncle large, outer margin strongly arched, setulose; rami short, inner ramus slender, apex subacute, outer ramus suboval, broader than long. Uropod 3, ramus broader and longer than peduncle, outer margin spinose.

Telson small, subtriangular, bare.

Coxal gills and brood lamellae not described.

Etymology. A combining form of the Latin prefix"lobatus" and the generic root *Corophium*, with reference to the lobate form of uropod 2.

Distributional ecology. Known only from shallow sandy substrata in the southeastern Sea of Japan.

Taxonomic commentary. In species of the genera *Apocorophium* (p. 123) and *Laticorophium* (p. 125), the lateral margins of the body that "plug" (occlude) the rear of the abode are formed mainly by the lateral margins of fused urosomal segments proper. The distal margin is formed by the short outer margin of the peduncle of uropod 2, and the peduncle and ramus of uropod 3 (e.g., in *Apocorophium acutum* (Fig. 35). In *Lobatocorophium*, however, the lateral margin of the "plug" is formed entirely by the strongly arched outer margin of the peduncle of uropod 2; the distal margin is formed by the outer ramus of uropod 2, and the broad ramus of the uropod 3 pair. This unique functional morphological difference of uropod 2 provides the principal basis for separate recognition of the genus *Lobatocorphium*.

Lobatocorophium lobatum (Hirayama)
(Fig. 19)

Corophium lobatum Hirayama, 1986: 175, figs. 1-5.

Diagnosis. Female (2.3 mm): The specimen described and figured by Hirayama (loc. cit.) lacked antenna 2. The species is very probably conspicuously sexually dimorphic. However, no other material has been described, so male-female differences are yet unknown.

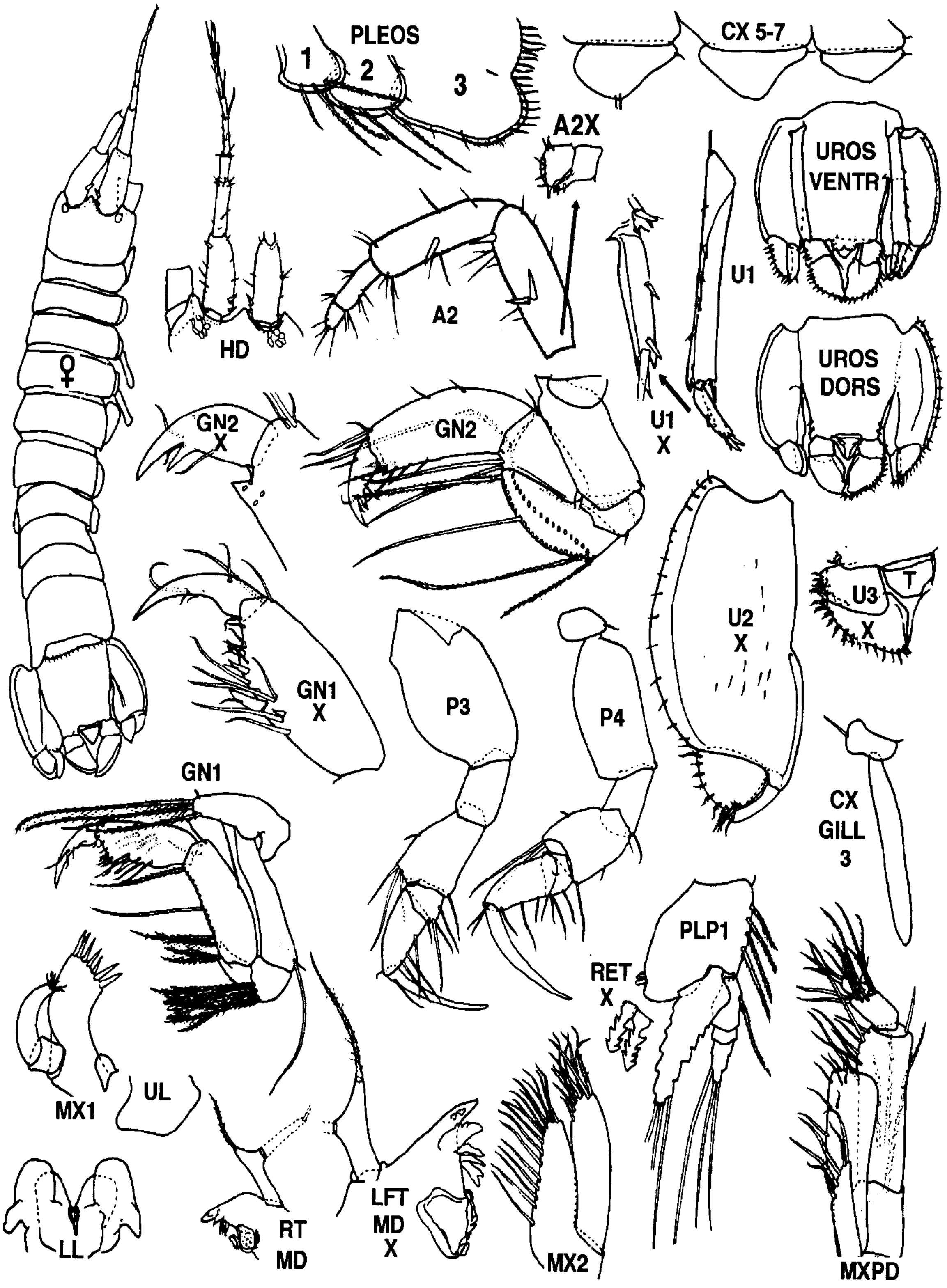


FIG. 19. ***Lobatocorophium lobatum*** **(Hirayama). Seto Inland Sea. Female (2.3 mm) (after Hirayama, 1987b).**

Crassicorophium, new genus

Corophium Latreille, 1806, Crawford, 1937: 606 (Section B, part).—Shoemaker, 1947: 47 (Section B + key, part).—Shoemaker, 1949: 66 (Section B + key, part).—Gurjanova, 1951: (part).—Just, 1970: 33 (part).—Bousfield, 1973: 198 (part).—Lincoln, 1979: 522 (part).—Hirayama, 1984: 2(+ key, part).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium crassicorne* Bruzelius, 1859 (present designation).

Species. *Crassicorophium clarencense* (Shoemaker, 1949); *C. bonelli* (Milne Edwards, 1930).

Diagnosis. Urosome segments fused. Uropods 1 & 2 arising from distinct lateral notches. Head, rostrum short, acute, slightly sexually dimorphic; inferior antennal sinus strongly regressed. Antenna 1, peduncular segment 1 variously inflated and medially spinose (female); segment 3 short. Antenna 2 sexually dimorphic; gland cone medium; peduncular segment 4 (male), posterodistal process weakly bidentate, thickened and strongly spinose (female); segment 5 with weak median and distal processes; flagellum short, with apical spines.

Upper Lip, epistome produced. Lower lip, mandibular lobes weak to medium. Mandibular palp, proximal segment distally produced (type P5 of Hirayama, 1987b); spine row with several (4-5) slender blades Maxilla 1, palp slender, slightly exceeding outer plate. Maxilliped, inner plate with 4 strong setae; outer plate large; palp segment 2 medium.

Gnathopod 1, dactyl weakly bidentate, exceeding oblique palm. Gnathopod 2, merus fused with medium-long carpus except for short posterodistal portion; propod narrowing, with minute palm and posterodistal cusp; dactyl strong, weakly bidentate, finely crenulate behind.

Peraeopods 3 & 4 short; based broad, glandular; segment 4 moderately broadened distally, partly overhanging short segment 5; dactyls elongate. Peraeopods 5 & 6, medium; bases unequal in size, setose behind; segment 5 short, with 2 poster-olateral clusters of short hook spines; segment 6 and dactyls reversed. Peraeopod 7 moderately long; basis regular; segments 4 & 5 subequal in length; dactyl short.

Pleon plate 3, hind corner sharply rounded Pleopod peduncles narrow basally, broadened distally. Uropod 1, peduncle medium, outer margin proximally setose; rami subequal, nearly straight, apices acute, slightly (or not) curved outwards, one apical spine elongate. Uropod 2, rami straight, subequal, as long as peduncle. Uropod 3 little broadened; ramus medium, longer than unmodified peduncle. Telson short, wider than long, apex rounded.

Coxal gills slender sac-like, on peraeopods 3-6; brood plates elongate, strap-like, marginal setae numerous (30-40).

Etymology. Combining the Latin prefix "crassus" - thick, and the generic root *Corophium,* with reference to the very thick or incrassate antenna 2 of the female.

Distribution. Component species are holarctic in shallow shelf water, to depths of ~50 m.

Taxonomic commentary. The genus *Crassicorophium* is superficially similar overall to *Monocorophium,* but differs in character states of the mouthparts, gnathopods, and uropods that strongly suggest a separate immediate ancestry. Although not revealed by the phenogram (p. 130), primitive features of *Crassicorophium* (e.g., of urosome) suggest a natural affinity with *Medicorophium, Sinocorophium,* and the western Pacific complex of primitive genera rather than with the modern North Atlantic assemblage represented by *Americorophium* and *Monocorophium.*.

Crassicorophium crassicorne (Bruzelius)
(Figs. 20, 21)

Corophium crassicorne Bruzelius, 1859: 15, fig. 2.—Sars, 1895a: 615, pl. 220.—Stebbing, 1906: 690, figs. 116-118.—Crawford, 1937: 607, figs. 4 a-f.—Shoemaker, 1947: 53, fig. 4.—Gurjanova, 1951: 976, fig. 679.—Bousfield, 1973: 201, pl . LXI.2.—Otte, 1976: 11, fig. 8.—Austin, 1985: 615.—Staude, 1987: 349 (key), 386.—Barnard & Karaman, 1991: 185.—Ishimaru, 1994: 35.

Material Examined. About 335 specimens in 23 lots, mostly in subtidal mixed sediments, from the Bering Sea and Aleutians Is. through SE Alaska, Queen Charlottes, and the north-central B. C. coast to the Strait of Georgia.

KEY TO SPECIES OF *CRASSICOROPHIUM*

1. Uropod 1, outer margin of peduncle spinose; uropod 2, margins of peduncle bare . . *C. bonelli* (p. 105)

—Uropod 1, outer margin of peduncle proximally setose; uropod 2, peduncular margins spinose . . . . . . 2.

2. Antenna 2 (female), peduncular segment 4 very thick, incrassate, heavily spinose posteriorly; antenna 2 (male), segment 5 with distinct median tooth . . . . *C. crassicorne* (p. 102)

—Antenna 2 (female), peduncular segment 4 normally stout and spinose; antenna 2 (male), segment 5, median tooth inconspicuous or lacking . . . . *C. clarencense* (p. 105)

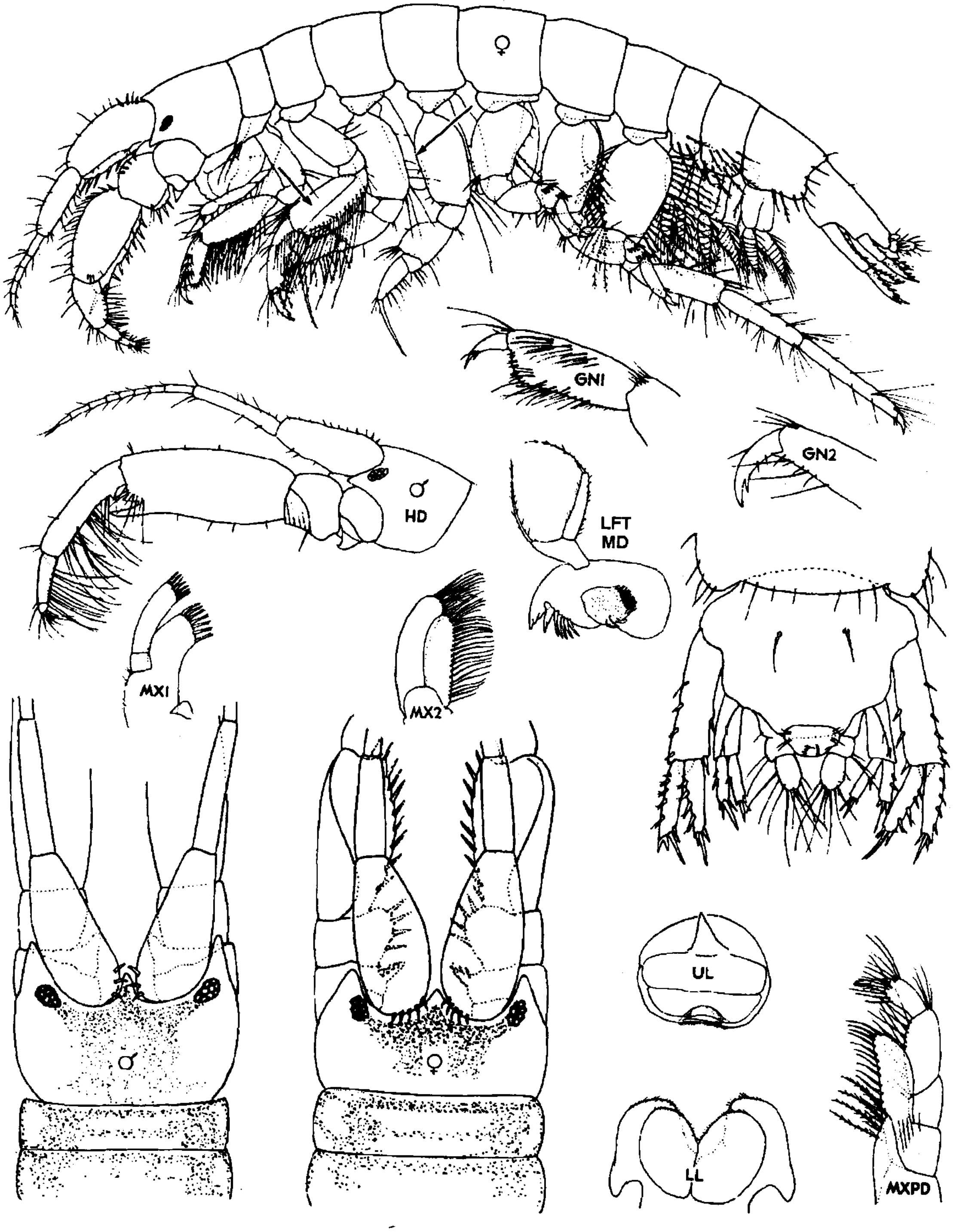


FIG. 20. ***Crassicorophium crassicorne*** **(Bruz.). Massachusetts Bay. Male (3.5 mm); female (3.5 mm) (after Bousfield, 1973).**

ALASKA.

Bering Sea Region. P. Slattery Stns, St. Lawrence I., 1980-92 specimens.

Aleutian Islands. C.E.O'Clair Stns, St. Makarius Bay. 1969-1972 - 7 specimens.

Unimak Island. N.A.Powell Stn., Izembek Lagoon., 1969 - 1 specimen.

BRITISH COLUMBIA.

Queen Charlotte Islands. ELB Stns, 1957: H3(14), H8b(12). North-central mainland coast. ELB Stn, 1964: H50(1).

C. Levings Stns, Swanson Bay, 45-62 m, 1973: S1B,025-029(120). C. Levings Stns, 52-67 m, 1975: 002-012(66).

Vancouver Island, north end. ELB Stn, 1959: V3 (Hope I.) - 9 spmns, incl. male (3.5 mm)(**fig'd**); female ov (4.0 mm) (**fig'd**), CMN Cat. No. NMCC1992-0735.

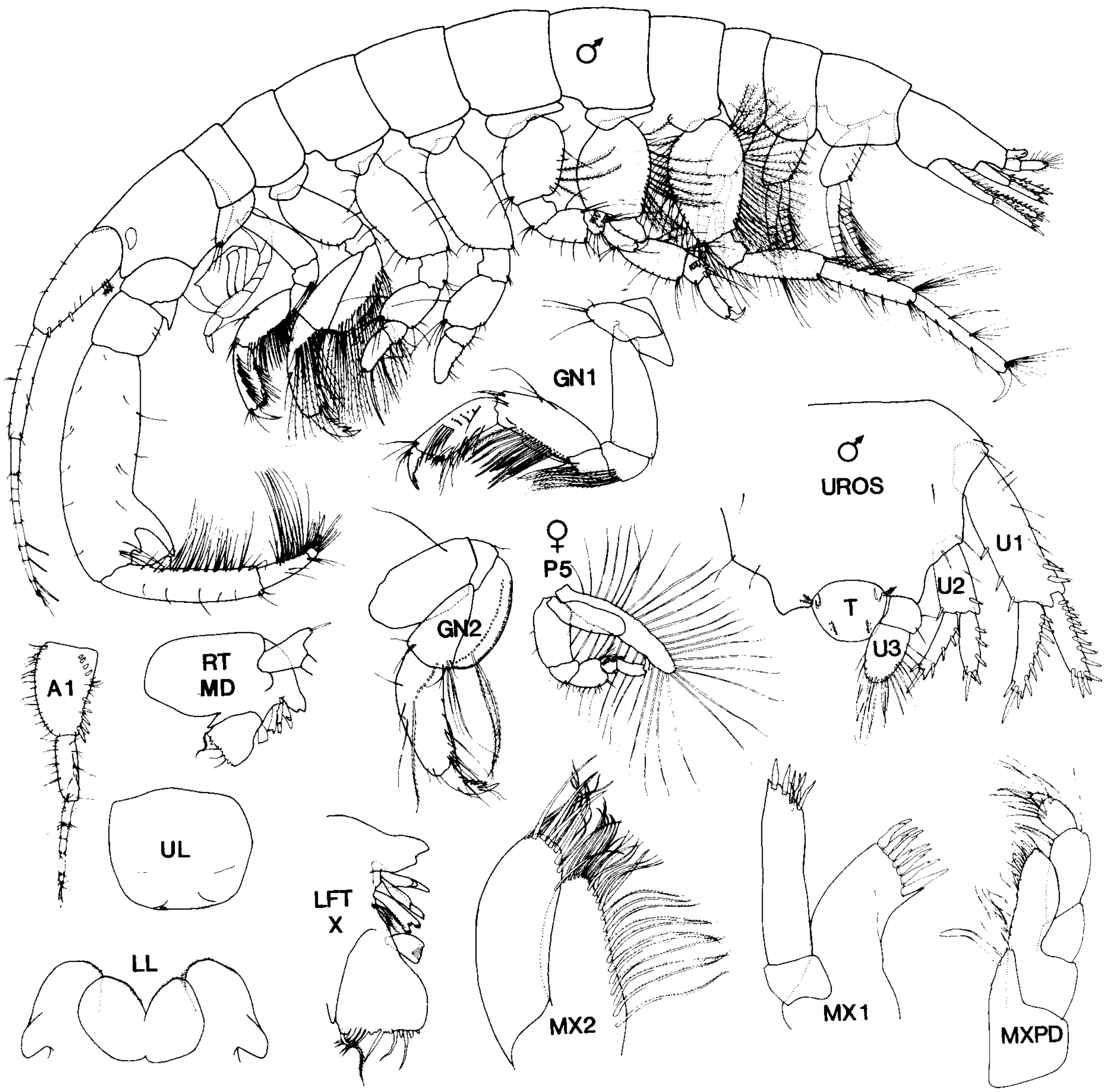


Fig. 21. ***Crassicorophium crassicorne*** **(Bruz.). Hope I., B. C. Male (3.5 mm); female (4.0 mm).**

Vancouver I., south end. ELB Stn, 1975: P5A(1). K. Conlan Stns, 1977. French Creek - 10 specimens; Saanich Inlet - 1 specimen.

Diagnosis. Male (3.5-4.0 mm): Pleosome segment 3 dorsally smooth. Urosome with distinct lateral notches; uropod 1 inserted entirely laterally. Head, rostrum short, recessed posterior to lateral head lobes. Antenna 1, peduncular segment 1 broadened proximally, with short proximal marginal spines; segment 2 slender; segment 3 short; flagellum slender, 7-8 segmented. Antenna 2 strongly pediform; peduncular segment 5 shorter than 4, with proximal median tooth and distal process, posterior margin strongly setose; flagellum 2(3)-segmented, posterior margin strongly setose.

Gnathopod 1, dactyl tip little exceeding oblique palm. Gnathopod 2, basis short, not broadened; carpus medium, with short posterodistal free margin; propod narrowing, with distinct posterodistal cusp; dactyl with single small posterior marginal tooth.

Peraeopods 3 & 4, bases broad, anterior margin weakly setose; segment 4 broad and overhanging small segment 5, anterior margin (of 4) nearly bare; dactyls large, nearly straight, longer than segment 6. Peraeopods 5 & 6, bases varieously setose posteriorly. Peraeopod 7 medium; basis medium broad; distal segments marginally setose; dactyl short.

Uropod 1, peduncular outer margin distally spinose, proximally with a few setae; rami medium, each with 4-7 outer marginal spines. Uropod 2 medium; rami with 1-2 outer marginal spines, outer ramus shorter. Uropod 3, peduncle short, not broadened or lobate; ramus longer than broad, apical setae elongate. Telson short, broad, with 3 posterodorsal pairs of small hook spines.

Female (3.3-4.0 mm): Rostrum short, less strongly recessed than in male. Antenna 1, peduncular segment 1 strongly broadened, with 4-5 proximal marginal spines.. Antenna 2, peduncular segments 3 & 4 shorter, deeper, and more marginally spinose than in male, with strong flange-like posterodistal process; segment 5 very short, deep, posterior margin lined with medium setae; flagellum subequal in length to segment 5, distally with short setae.

Brood lamellae strong, strap-like, with numerous (35-40) long marginal setae.

Taxonomic commentary. Specimens from the North American Pacific region differ little from those of the North American Atlantic region. However, the material from Japanese and Korean coastal waters, identified as *Corophium crassicorne* by Hirayama (1984) and Kim (1991), respectively, shows several differences, especially in the antennae and gnathopods (Fig. 20, 21) from North Atlantic material and merit further comparison.

Distribsutional Ecology. A holarctic and subarctic species, extending southwards in the North Pacific to the Sea of Japan in the west, and British Columbia and Washington in the east; on sand and coarse sand, from LW level to depths of 37 m.

Crassicorophium clarencense (Shoemaker)
(Figs. 22)

Corophium clarencense Shoemaker, 1949: 78, fig. 7.—Just, 1970: 33, figs. 17-20.—Barnard & Karaman, 1991: 185.
Corophium bonelli (M-E) forma. Shoemaker, 1920: 22.

Material examined. One lot marginally from the study region. The holotype male specimen, and four female paratypes, from Port Clarence, Grantley Harbor, Alaska (northen Bering Sea), are in collections of the CMN, Ottawa.

Diagnosis. Male (4.0 mm): Pleosome segment 3 dorsally smooth. Urosome with distinct lateral notches; uropod 1 inserted entirely laterally. Head, rostrum medium, basally narrow, tip exceeding short lateral head lobes. Antenna 1, peduncular segment 1 broadened proximally, inner margin weakly setose; segments 2 & 3 relatively short; flagellum 6-7 segmented. Antenna 2 medium strongly pediform; peduncular segment 5 little shorter than 4, with very weak proximal median tooth and distal process, posterior margin with medium setae; flagellum very short, 3-segmented, posterior margin with longish setae.

Gnathopod 1, dactyl with weak posterior tooth, tip distinctly exceeding short palm. Gnathopod 2, basis short; carpus medium short, with short posterodistal free margin; propod with distinct posterodistal cusp; dactyl slender, with a single small posterior marginal tooth and a few setae.

Peraeopods 3 & 4 not described, probably much as in *C. crassicorne*. Peraeopod 5, basis little broadened, hind margin posterodistally setose. Peraeopod 7 not described.

Uropod 1, peduncular outer margin setose proximally, spinose distally; rami medium, subequal, each with 5-6 outer marginal spines. Uropod 2 medium; rami, outer margins each with 2-4 spines. Uropod 3, peduncle short, with small setose lateral lobe; ramus longer than broad, margins with long setae. Telson broader than long, apex rounded, with 4 posterodorsal pairs of small hook spines.

Female (3.8 mm). Rostrum short, very broad. Antenna 1, peduncular segment 1 with 2-3 proximo-median spines. Antenna 2 strongly dissimilar to male; peduncular segment 4 little broadened, posterior margin with 3-4 single spines and a few setae; segment 5 slightly shorter than 4, posterior margin with 3 pairs of strong spines; flagellum weakly setose posteriorly.

Brood lamellae relatively long, strap-like, with numerous (>40) marginal setae.

Taxonomic and distributional commentary. *Crassicorophium clarencense* is an intermediate member of the genus (Fig. 41, p. 133). Specimens from the western North American Arctic region (Shoem., loc. cit.) appear slightly more advanced than those from the eastern Arctic and Arctic-Atlantic region (Fig. 22), especially in characters of the antennae, gnathopods and uropods. Although *C. clarencense* was not taken strictly in the present study region, or previously recorded there (e.g., Otte, 1976), the species would not be unexpected along the western coast of Alaska, from the Bering Strait region perhaps southward to the glacial fiords of Prince William Sound.

Crassicorophium bonelli (Milne Edwards)
(Fig. 23)

Corophium bonelli Milne Edwards, 1830: 385.—Sars, 1895a: 616, pl. 221.1.—Crawford, 1937: 608, fig. 2,H-O.—Gurjanova, 1951: 978, fig. 681.—Bousfield, 1973: 202, pl. LXII.1.—Kudrjaschov, 1979: 127.—Myers, e al. 1989: 319, fig.1.—Barnard & Karaman, 1991:185.—Ishimaru, 1994: 35.
Corophium contractum Stimpson, 1856: 383 (material from Japan, possibly identical with *C. bonelli*, fide Stebbing, 1906).
non *Corophium bonelli* Shoemaker, 1920 [= *Crassicorophium clarencense* (Shoemaker, 1949)].

Material Examined. None from within the North Pacific study region.

Diagnosis. Female (4.5-6.0 mm): Pleosome segment 3 posterodorsally smooth. Urosome with distinct lateral notches; uropod 1 inserted mainly laterally. Head, rostrum short, apex level with inferior head lobes. Antenna 1, peduncular segment 1 broadened proximally, with 3 inner marginal spines; segments 2 & 3 relatively short; flagellum short, 5-6 segmented. Antenna 2, segments 3-5 normally stout; peduncular segment 4 with 3 posterior margin pairs of medium spines; segment 5 little shorter than 4, posterior

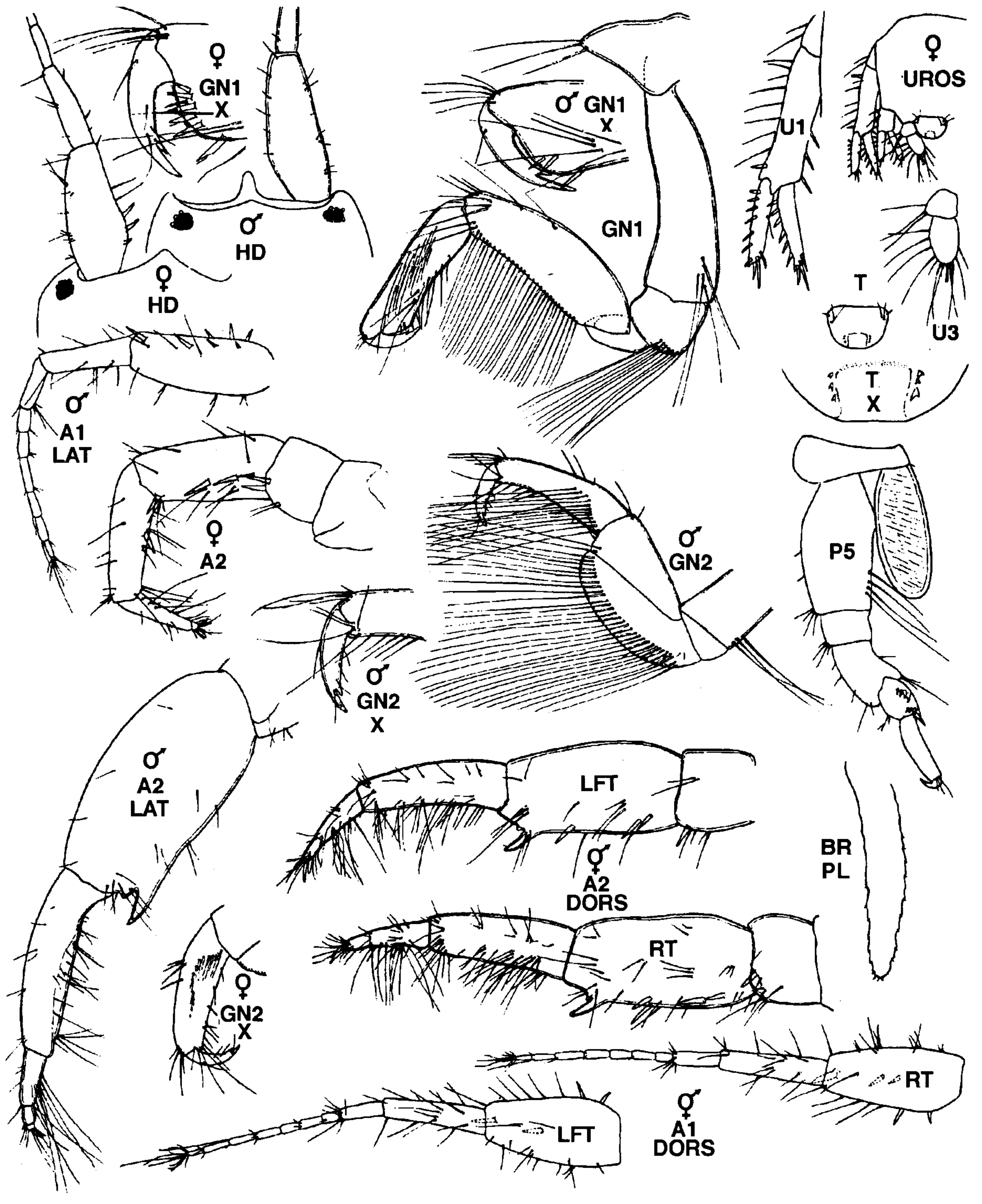


FIG. 22. *Crassicorophium clarencense* (Shoem.). North Greenland. Male (4.0 mm); female (4.0 mm) (after Just, 1970).

margin with 2 pairs of spines and several setae; flagellum medium, 3-segmented, moderately setose.

Gnathopod 1, propod slightly broadening distally; dactyl with small posterior marginal tooth, tip closing slightly beyond oblique palm. Gnathopod 2, basis stout; carpus short, posterodistal free margin lacking; propod long, with posterodistal cusp; dactyl slender, with small posterior marginal tooth.

Peraeopods 3 & 4 strong; basis broad, anterior margin weakly setose; segment 4 medium broad, partly overhanging short segment 5, anterior margin (of 4) nearly bare; dactyl slender, longer than segment 6. Peraeopod 5, hind margin of basis nearly bare. Peraeopod 7 moderately long; basis medium broad; margins of distal segments with short setae; dactyl short.

Pleon plates 1-3 weakly setose below. Uropod 1, outer

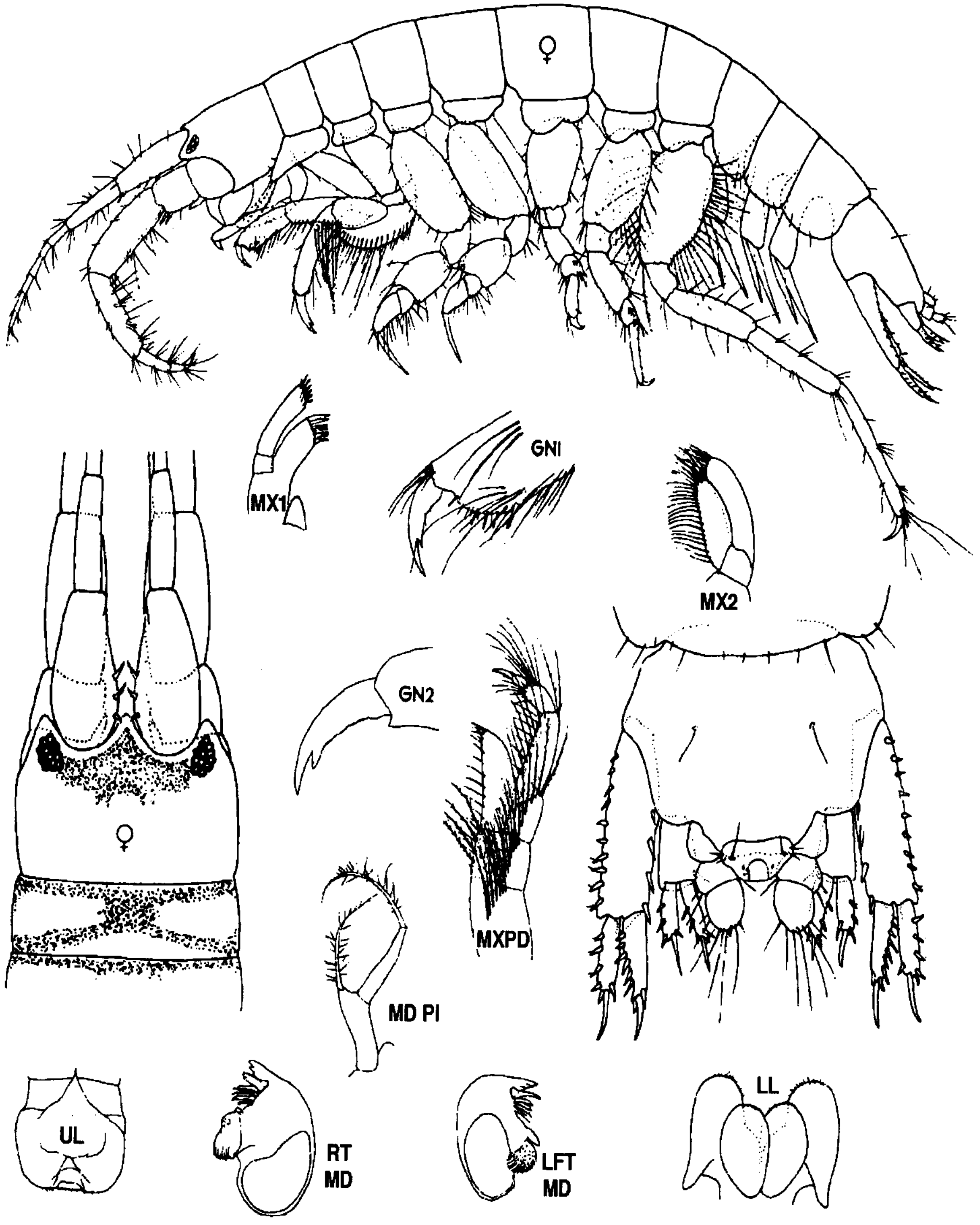


FIG. 23. ***Crassicorophium bonelli*** **(M. E.). Outer coast, Nova Scotia. Female (4.5 mm) (after Bousfield, 1973).**

margin of peduncle with short spines throughout; rami medium, subequal, each with 3-6 outer marginal spines. Uropod 2 medium; peduncular margins lacking spines; rami medium, each with 2 outer marginal pines. Uropod 3, peduncle broad, with small setose lateral lobe; ramus suborbicular, distal margin with long setae. Telson short, broad, with 4 posterodorsal pairs of small hook spines.

Brood lamellae slender, with gaps between each (Shillaker & Moore, 1987).

Adult male (3.8 mm): A presumed juvenile male (2.3 mm) from Ireland was described and illustrated by Myers et al (1989). The dactyls of gnathopods 1 & 2 conform closely

KEY TO SPECIES OF *HIRAYAMAIA*, NEW GENUS

1. Gnathopod 2, dactyl posteriorly bidentate; uropod 2, peduncular margins spinose .... *H. tridentia* (Hirayama) (Fig. 25)
—Gnathopod 2, dactyl with 1 posterior marginal tooth; uropod 2, peduncular margins bare .... 2.

2. Urosome, lateral margins convex; uropod 3, ramus suborbiculate .... *H. hongkongensis* (Hirayama)
—Urosome, lateral margins straight; uropod 3 subovate, longer than wide ...*H. mortoni* (Hirayama)(Fig. 24)

---

with those of the adult female. In antenna 2, peduncular segment 4 bears a single-toothed distal process, and segment 5 has a small proximal medial marginal process.

Taxonomic and distributional commentary. The species is widely boreal and subarctic in the North Atlantic and northwestern North Pacific Tatar Strait, northern Sea of Japan)(Kudrjaschov, 1979; Ishimaru, 1994); recorded recently from the Bering Sea coast of Alaska by O'Clair (Coyle & Mueller (1981).

The species has not previously been recorded from the present study region (e.g., in Otte, 1976; Austin, 1985) nor found in study materials here.

Distributional ecology. Gurjanova (1951) interpreted previous distributional records of *C. bonelli* as those of a cosmopolitan species, widespread in temperate and tropical waters of both hemispheres. However, records from warm-water localities are probably attributable to females of superficially similar species, especially *Monocorphium insidiosum,* as Crawford (loc. cit.) so ably demonstrated. Authentic records of *C. bonelli* are restricted to arctic-boreal and boreal subregions of the northern hemisphere. Maximum abundance is reached in the Tatar strait region, in sandy shoals which border on the lower horizon of the littoral zone, and in deep cracks in rocks which have been blocked up with sand and overgrown with *Zostera marina* (Kudryaschov, loc. cit.).

The species is mainly hermaphroditic, males being extremely rare (Myers, et al., 1989). The life cycle is semi-annual, with two generations per year (Powell & Moore, 1991).

Hirayamaia new genus
(see Figs. 24, 25)

Corophium Latreille,1806, Hirayama, 1986: 449 (part).—Barnard & Karaman, 1991: 184 (part).

Type species. *Corophium mortoni* Hirayama, 1986 (present designation).

Species. *Hirayamaia hongkongensis* (Hirayama, 1986); *H. tridentia* (Hirayama, 1986).

Diagnosis. Urosome segments fused; lateral margins straight or convex, lacking distinct notch for uropod 1 that is inserted mainly ventrally. Head, rostrum short, weakly sexually dimorphic; inferior antennal sinus strongly regressed. Antenna 1 ordinary; peduncular segment 3 short. Antenna 2 strongly sexually dimorphic; gland cone small; segment 4 (male) large, pediform, posterodistal process bidentate; segment 5 , median and distal processes weak or lacking; flagellum short, with paired terminal spines.

Upper lip, epistome produced. Lower lip, mandibular lobes medium. Mandibular palp, basal segment with distal shelf or short process (type P4 or P5 of Hirayama, 1987b); spine row with 2-3 stout blades. Maxilla 1, palp slender. Maxilliped, outer plate slender, subcolumnar; palp segment 2 medium.

Gnathopod 1, carpus narrowing distally; propod, palm oblique, exceeded by weakly bidentate dactyl. Gnathopod 2, carpus medium, with small free lower margin beyond apex of fused shallow merus; propod, palm minute, with small cusp; dactyl short, with 1-3 posterior marginal teeth.

Peraeopods 3 & 4 short; basis variously broadened, glandular; segment 4 distally overhanging short segment 5. Peraeopods 5 & 6 short, bases unequal, that of peraeopod 5 lacking posterior marginal setae; segment 5 medium short; distal cluster with longish hook spines; segment 5 and dactyl variously reversed. Peraeopod 7 medium; basis little broadened; dactyl short.

Pleon plate 3, hind corner obtuse. Pleopod peduncles broader than deep; rami short, 6-7 segmented. Uropod 1, peduncle linear, outer margin spinose; rami straight, apices acute, one apical spine elongate, outer ramus the shorter. Uropod 2 short, rami slightly curved, lateral margins bare (or nearly so), acute apices with single long spine. Uropod 3, rami short, not strongly broadened, distal margin weakly setose. Telson short, broad, rounded.

Coxal gills narrow, sac-like, on peraeopods 3-6. Brood lamellae not described.

Etymology. The genus is named in honour of Dr. Akira Hirayama, in recognition of his outstanding contributions to the systematics of corophiin amphipods.

Distribution. Component species are endemic to shallow waters of the Hong Kong region of the South China Sea.

Taxonomic commentary. Species of the genus *Hirayamaia* cluster between those of the more primitive genus *Crassicorophium,* and the more advanced genus *Monocorophium* (Fig. 40, p. 133). Although many of *Hirayamaia* character states (e. g., form of the mandibular palp, propod and dactyl of gnathopod 2, and uropod 3) appear to be

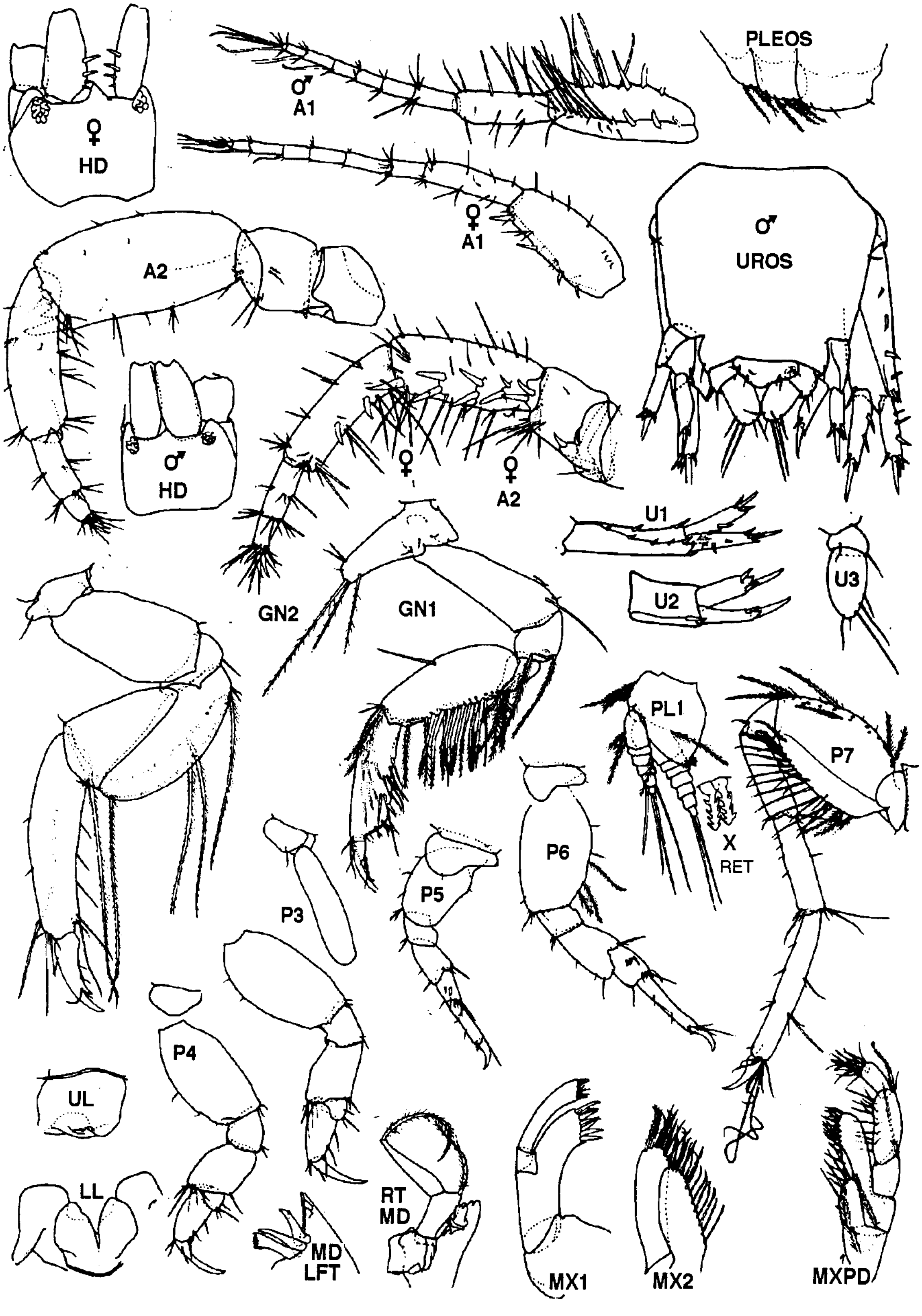


FIG. 24. *Hirayamaa mortoni* (Hirayama). Hong Kong. Male (2.3 mm); female (3.0 mm) (after Harayama, 1986).

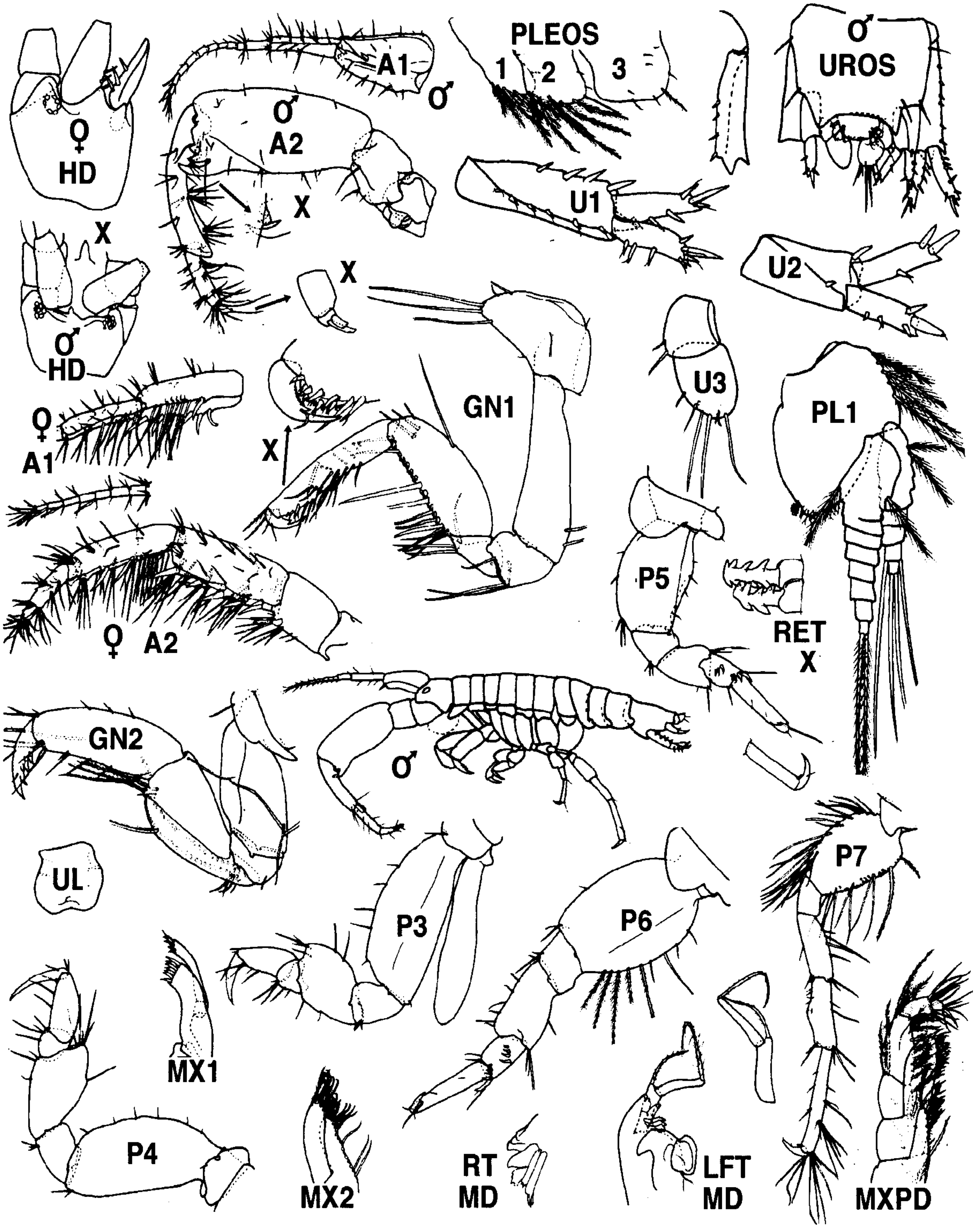


FIG. 25. ***Hirayamaia tridentia*** **(Hirayama). Hong Kong. Male (3.0 mm); female (4.8 mm) (after Hirayama, 1986).**

intermediate between the other two genera, its uniform (unnotched) lateral margin of the fused urosome segments is here considered an autapomorphy which, in combination with the advanced form of the mandibular palp, precludes direct ancestry with any other generic group treated herein.

Monocorophium, new genus

Corophium Latreille, 1806, Stebbing 1906: 685 (part).—Crawford, 1937: 606 (Section B).—Chevreux & Fage, 1925: 363 (part).—Shoemaker, 1947: 47 (Section B.1, most).—Gurjanova, 1951: 684 (part).—Bousfield, 1973: 198 (part).—Lincoln, 1979: 522 (part).—Myers, 1982:185 (part).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium insidiosum* Crawford, 1937 (present designation).

Species. *M. carlottensis*, n. sp. (p. 114); *M. steinegeri* (Gurjanova, 1951); *M. acherusicum* (Costa, 1857); *M. uenoi* (Steph-ensen, 1932); *M. tuberculatum* (Shoemaker, 1934b); *M. sextonae* (Crawford, 1937); *M. californianum* (Shoemaker, 1934a); *M. oaklandense* (Shoemaker, 1949).

Diagnosis: Urosome segments fused; uropods arising from lateral notches. Head, rostrum distinct; anterior margin sexually dimorphic. Antenna 1, segment 3 short. Antenna 2 strongly pediform, variously (or not) sexually dimorphic; segment 4 (male), with bidentate distal process; segment 5 usually with proximomedial tooth; distal process weak or lacking; gland cone short, relatively inconspicuous; flagellum short, 3-segmented, with apical paired spines.

Upper lip, epistome little (or not) produced. Lower lip, mandibular lobes strong. Mandible: spine row moderate (3-5 blades; palp of intermediate form [type P4 of Hirayama (1987b)]. Maxilliped, inner plate short to medium, apex subacute; outer plate slender, medial margin setose throughout; palp segment 2 medium to short.

Gnathopod 1 medium subchelate; dactyl denticulate behind, or tip weakly bidentate, exceeding short oblique palm. Gnathopod 2, merus not covering small anterodistal portion of carpus; dactyl short, tri- or quadridentate.

Peraeopods 3 & 4 short, bases broad (glandular); segment 4 expanded, often setose anteriorly; segment 5 short, overhung by segment 4. Peraeopods 5 & 6 short, segments 4 and 5 short, the latter with 2 clusters of short strong hook spines; segment 6 and dactyl reversed. Peraeopod 7 not elongate, basis medium broad; dactyl medium.

Pleon plate 3, hind corner rounded. Pleopod peduncles stout, wider than deep. Uropods 1 and 2, peduncle stout, widening distally; rami short, spinose laterally and apically, apices curved, acute. Uropod 3, ramus short, broad.

Telson short, wide, with dorsal hooks. Coxal gills slender, sac-like, on peraeopods 3-6. Brood lamellae relatively large, broad, margins with few setae.

Etymology. Combining the Greek prefix *mono* - one, and the generic root *Corophium*, with reference to the fused, one-segmented urosome.

Distributional ecology: Mostly tube-building species, of temperate-tropical affinities, but a few (*M. carlottensis, M. steinegeri*) are boreal and subarctic.

Taxonomic commentary. This relatively large subgroup was first recognized by Crawford (1937). At that time the complex comprised *C. insidiosum, C. tuberculatum, C. bonelli, C. sextonae, C. uenoi, C. acherusicum*, *C. crassicorne* and *C. californianum.* The group may be polyphyletic, the main subgroup arising from a *triaeonyx*-like ancestor with unfused urosome segments.

Within the genus *Monocorophium*, the *insidiosum* subgroup (above) is characterized by a strongly sexually dimorphic rostrum, type P4 mandibular palp, tri- or quadridentate dactyl of gnathopod 2, and short, broad ramus of uropod 3.

A second subgroup, of *C. californianum* and *C. oaklandense*, encompasses a pair of closely related species endemic to the Pacific coast of North America, in which antenna 2 is strongly pedamorphic in both sexes (p. 123). *C. miospinulosum,* a minute burrowing species assigned to Crawford's section B by Hirayama (1986), is here recognized as generically distinct at a more primitive level (Fig. 41, p.133).

Corophium ellisi Shoemaker, 1934b, has fused urosomal segments but otherwise conforms closely with the diagnosis of the genus *Americorophium* (see p. 90). The Indo-Pacific species *C. triaeonyx*, with urosome segments free, conforms partially with the genus *Americorophium* on the one hand, and *Monocorophium* on the other. It may prove to be a living "missing link" that transcends the otherwise sharp taxonomic distinction between genera with urosome segments separate and those with segments fused.

Monocorophium insidiosum (Crawford)
(Figs. 26, 27)

Corophium insidiosum Crawford, 1937: 615, fig. 2a-g.—Shoemaker, 1947: 53, figs. 6, 7.—Barnard, 1970: 101, fig. 54.—Bousfield, 1973: 203, fig. LXII.1.—Barnard, 1975: 338-340 (key), figs. 142, 145.—Otte, 1976: 6 (key), figs. 6, 7.—Carlton, 1979: 658.—Lincoln, 1979: 530, figs. 254d-h.—Hirayama, 1984: 14.—Austin, 1985: 615.—Barnard & Karaman, 1991:185.—Ishimaru, 1994: 35.
Corophium cylindricum Say, 1818: 287(?).

Material Examined. About 85 specimens in 25 lots:
BRITISH COLUMBIA.
Vancouver Island and southeastern mainland coast. ELB Stns, 1955: G13(10), M1(3), P7(5). ELB Stns, 1959: O6(Louis Creek lagoon) - 14 spms incl. male (5.2 mm) **(fig'd)**; female (4.8 mm) **(fig'd)**, CMN Cat. No. NMCC1992-0848. N23(2), V27(1), N18(1). ELB Stns, 1970: P701(1), P702(1), P706(7), P719(4), P721(4). ELB Stn, 1975: P26(2).
J.F.L. Hart Stn, Victoria, 1928 -1 specimen.
K. Conlan Stns, Saanich Inlet, 1975: 1104S- 4 specimens.

WASHINGTON.
Inner coast. ELB Stn, Friday Harbor, 1955: M13(1).
Outer coast. ELB Stns, 1966: W22(3); W29(13).

KEY TO SPECIES OF *MONOCOROPHIUM*

1. Antenna 2 strong, segment 4 with distal bidentate process in both male and female; peraeopod 3, basis narrower than in peraeopod 4 . . . . 2.
—Antenna 2 strong in male but smaller, lacking bidentate distal process in female; peraeopods 3 & 4, bases subequally broad . . . . 3.

2. Antenna 2, distal process of peduncular segment 5 very strong, length ~flagellar segment 1; peraeopod 7, basis narrow, width ~1/2 length; uropod 1, peduncle with few (3-5) outer marginal spines. . . . . *M. californianum* (Shoem.) (p. 123)
—Antenna 2, distal process of peduncular segment 5 short, >1/2 flagellar segment 1; peraeopod 7, basis broad, width ~ length; uropod 1, peduncle with 8-10 outer marginal spines . . . . . *M. oaklandense* (Shoem.) (p. 123)

3. Rostrum (male) weak, not projecting beyond lateral head lobes; gnathopod 2, dactyl with 2 posterior marginal teeth; uropod 2, inner ramus, outer margin spines . . . . 4.
—Rostrum (male) strong, projecting beyond lateral head lobes; gnathopod 2, dactyl with 3-4 posterior marginal teeth; uropod 2, inner ramus, outer margin bare . . . . 6.

4. Gnathopod 1, dactyl short, thick, barely overlapping palm; uropod 1 spinose, rami with 6-8 outer marginal spines . . . . *M. sextonae* (Crawf.) (p. 120)
—Gnathopod 1, dactyl slender, distinctly exceeding palm; uropod 1, rami with 4 outer marginal spines . 5.

5. Antenna 2 (both sexes), posterior margin of peduncle and flagellum strongly setose; peraeopods 3 & 4, anterior margin of segment 4 setose; North Atlantic . . . . *M. tuberculatum* (Shoem.)
—Antenna 2, posterior margin of segments weakly setose; peraeopods 3 & 4, segment 4 anterior margin nearly bare; North Atlantic, synanthropic in North Pacific . . . . *M. acherusicum* (Costa) (p. 117)

6. Rostrum (male) short, projecting slightly beyond lateral head lobes; urosome, lateral notch small, uropod 1 inserted mainly ventrally; gnathopod 1, dactyl greatly (50%) exceeding palm . *M. uenoi* (Steph.) (p. 119)
—Rostrum (male) long, tip projecting distinctly beyond lateral head lobes; urosome with distinct lateral notches, uropod 1 inserted mainly laterally; gnathopod 1, dactyl short, tip little exceeding palm. . . . . . 7.

7. Peraeopods 3 & 4, anterior margins of basis and segment 4 weakly (or not) setose; peraeopod 7 elongate, segment 6 with elongate distal setae . . . . *M. carlottensis*, n. sp. (p. 114)
—Peraeopods 3 & 4 (esp. in male), anterior margins of basis and segment 4 strongly setose; peraeopod 7 relatively short, segment 6 with short distal setae . . . . 8.

8. Pleosome segment 3 with short posterodorsal tufted process; uropod 2, outer ramus with distinct outer marginal spine . . . . *M. insidiosum* (Crawf.) (p. 111)
—Pleosome segment 3 lacking distinct tufted mid-dorsal process; uropod 2, outer ramus lacking outer marginal spine . . . . *M. steinegeri* (Gurj.) (p. 116)

Diagnosis. Male (4.0 mm). Pleosome segment 3 with low posterior median tufted process or hump. Urosome with distinct lateral notch; uropod 1 inserted mainly laterally. Head, rostrum elongate, tip distinctly exceeding lateral head lobes. Antenna 1, peduncular segment 1 with inner marginal conical process; flagellum 7-8 segmented. Antenna 2 strongly pediform; peduncular segment 5 not shorter than 4, with small proximal median tooth and distal process; flagellum 3-segmented, posterior margin strongly setose.

Gnathopod 1, dactyl tip little exceeding palm. Gnathopod 2, basis stout; carpus short, with short postero-distal free margin; propod lacking postero-distal cusp; dactyl with 3 unequal posterior marginal teeth.

Peraeopods 3 & 4, anterior margin of basis and segment 4 moderately to strongly setose; dactyls curved, shorter than segment 6. Peraeopods 5 & 6, bases setose postero-distally. Peraeopod 7 not elongate, basis medium broad; distal segments weakly setose; dactyl short.

Uropod 1, rami short, unequal, each with 3 outer marginal spines. Uropod 2 short, outer ramus with 1 outer margin spine, inner ramus bare. Uropod 3, peduncle with small setose lateral lobe. Telson broader than long, with 4 postero-dorsal pairs of small hook spines.

Female (3.8 mm). Rostrum short, not exceeding lateral head lobes. Antenna 1, peduncular segment 1 with 3-4 proximomedian spines. Antenna 2, peduncular segments short, stout; segment 4, posterior margin with 3 pairs of strong spines; flagellum weakly setose posteriorly.

Peraeopods 3 & 4, anterior margins of basis and segment 4 relatively sparsely setose.

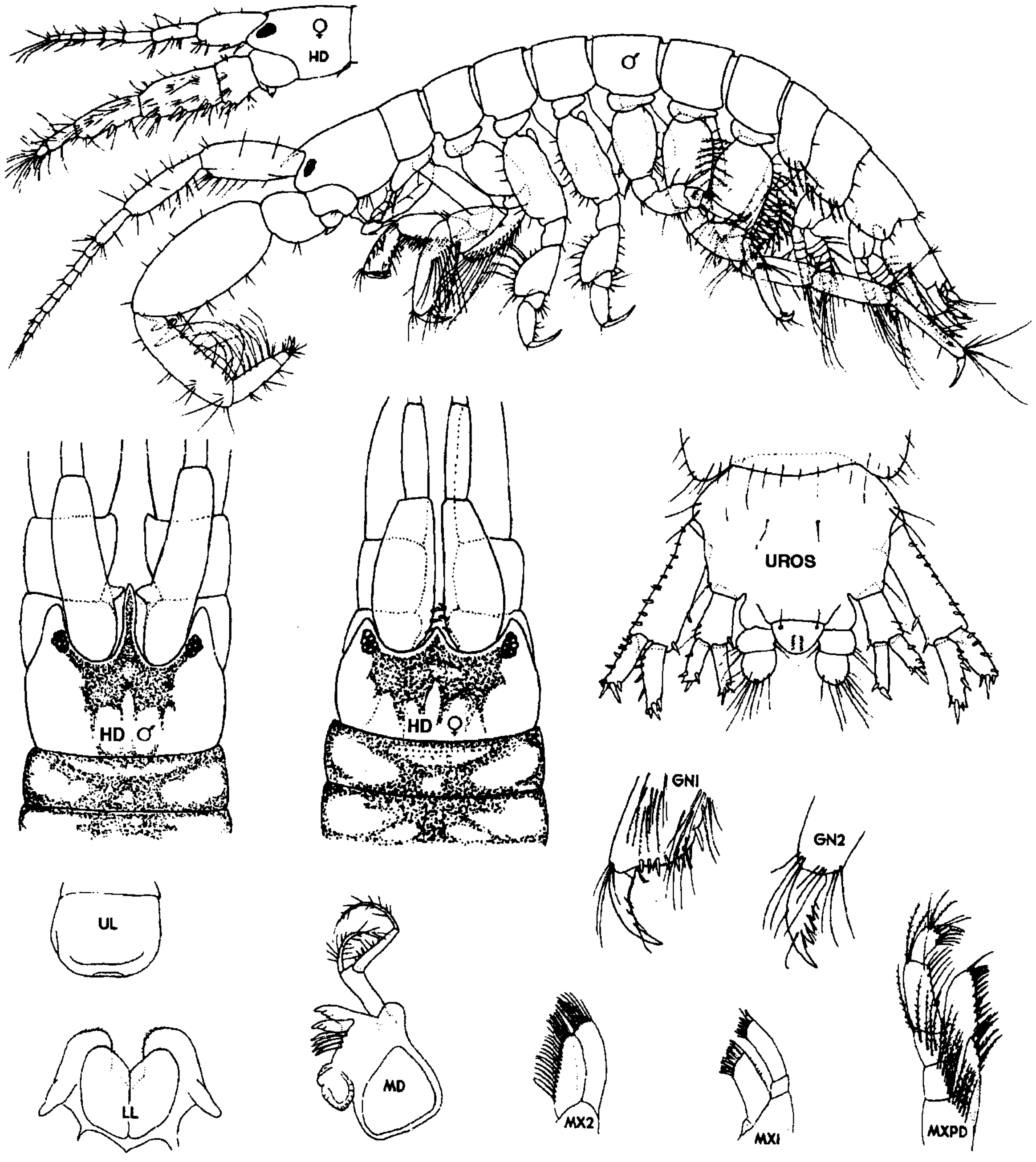


FIG. 26. *Monocorophium insidiosum* (Crawford). Southwestern Gulf of St. Lawrence Male (4.0 mm); female (4.5 mm) (after Bousfield, 1973).

Brood lamellae relatively short and slender, with few (<20) marginal setae.

Taxonomic and distributional commentary. Specimens of *Monocorophium insidiosum* from the North American Pacific region differ slightly from those of the North American Atlantic region in their slightly larger size at maturity, and generally more strongly setose appendages.

The species is considered native to the North Atlantic region from whence it has presumably been transported by commercial vessels to the North Pacific. The species has been widely recorded from the Strait of Georgia and Puget Sound, south to central California (Carlton, 1979).

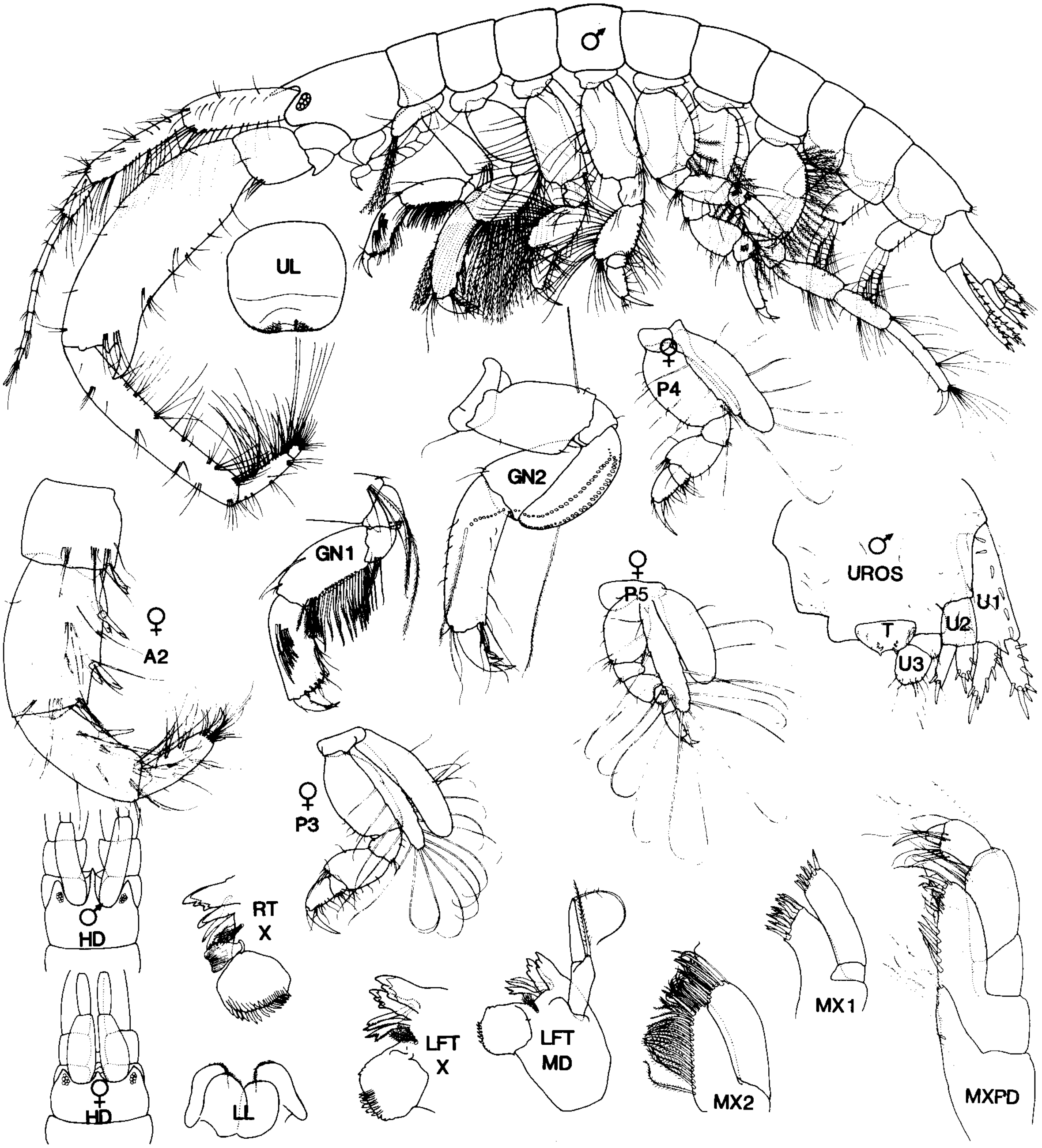


FIG. 27. ***Monocorophium insidiosum*** **(Crawford). Louis Creek lagoon, B. C.. Male (5.2 mm); female (4.8 mm).**

Taxonomic and distributional commentary. *Monocorophium insidiosum* is endemic to temperate to warm-temperate waters of the North Atlantic region (Bousfield, 1973). On the basis of distributional overlap, *M. insidiosum* may prove synonymous with *C. cylindricum* Say, 1818, for which the type material is apparently not extant. Carlton (loc. cit.) has summarized synanthropic records of *M. insidiosum* from the Pacific coast of North America, including central and northern California, Washington, and British Columbia. The latter records are encompassed by Otte (1976) and Austin (1985). The species is apparently synanthropic in Hawaii (Barnard, 1970) and Japan (Hirayama, 1984; Ishimaru, 1994).

Monocorophium carlottensis, new species
(Fig. 28)

Corophium insidiosum (Crawford) f. Staude, 1987: 351 (key), 386.—Barnard, 1975: 338-340 (key)?.—Otte, 1976: 6 (part).—Austin, 1985: 615.

Material Examined: About 290 specimens in 29 lots, mostly from tide pools and brackish waters, from Prince William Sound and S.E. Alaska, through the Queen Charlotte Islands, and north-entral coast, scarcer to S. Vancouver I., but none southwards in Washington State.

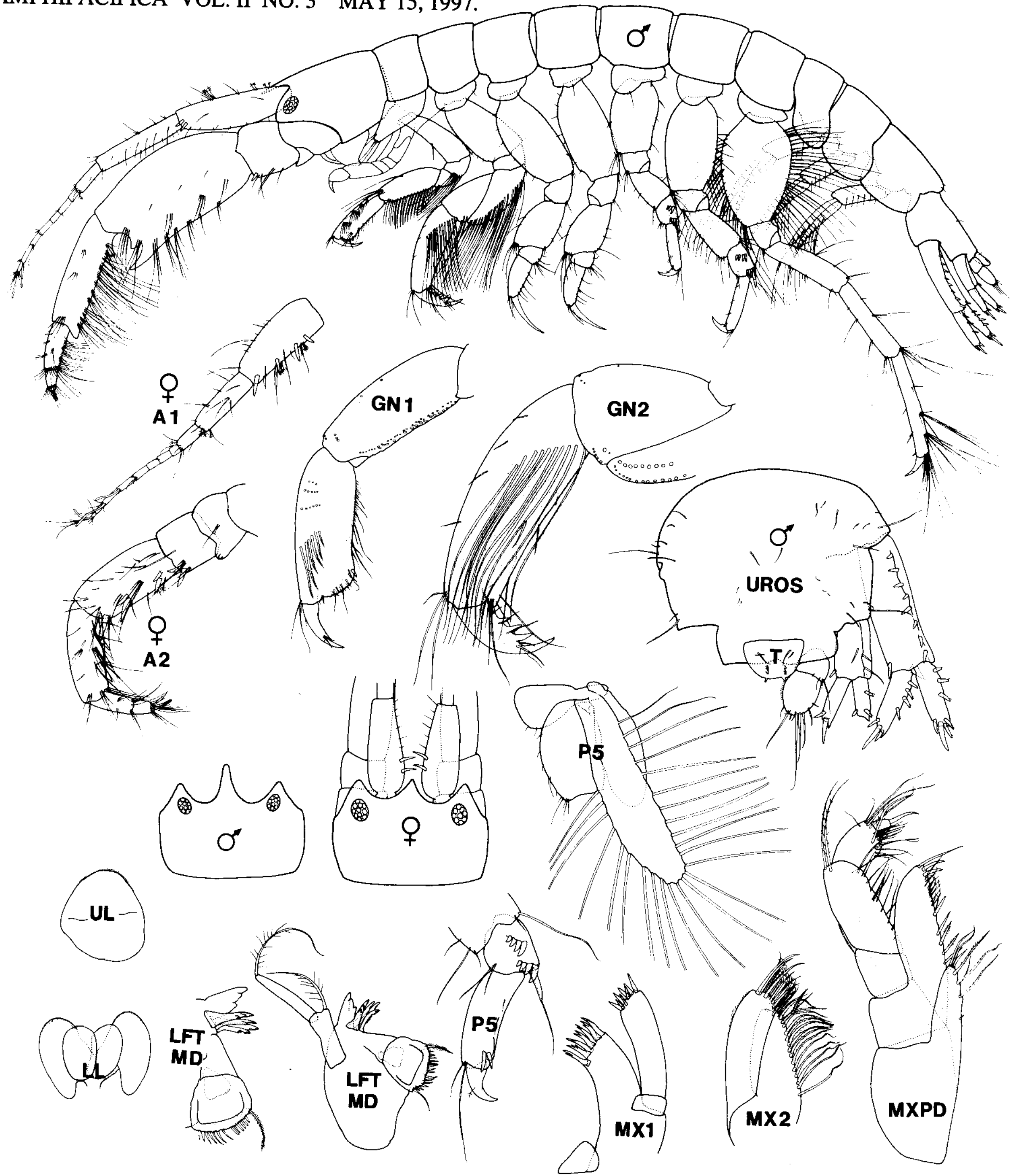


FIG. 28. *Monocorophium carlottensis*, new species. Codfish Pass, B. C. Fem. (4.2 mm). Island Bay, Q. C. I. Male (3.0 mm).

ALASKA.

Southeastern Alaska. ELB Stns, 1961: A3(2), A70(1), A86(4), A91(1), A92(2), A96(7), A105(2), A131(1).

ELB Stn. S23F1 (Taigud I, Baranof I.), 1980 - 14 females, 4 im, CMN Cat. No. NMCC1992-0985.

BRITISH COLUMBIA.

Queen Charlotte Islands. ELB Stns., 1957: H2, H2b(4), H8b(8), E5(1), E14c(10), W3a(3). J Scoggan Stn 68-155, Island Bay, 1968 - male (3.0 mm), slide mount, **allotype**, 2 males, 6 females, CMN Cat No. NMCC1992-0943.

North-central mainland coast. ELB Stns., 1964: H5(7), H6(6), H12(1), H25(3), H26(7), H30(>50), H31(3), H36(10), H39(1), H47(Codfish Bay) - female ov. (4.2 mm), slide mount, **holotype**, 50 **paratypes**, CMN Cat. No. NMCC1992-0777, H48(1), H50(4), H53(11), H59(5).

Diagnosis. Male (3.0 mm): Pleosome segment 3 with small posterior median tufted process or hump. Urosome with distinct lateral notch; uropod 1 inserted mainly laterally. Head, rostrum elongate, tip distinctly exceeding lateral head lobes. Antenna 1, peduncular segment 1 with weak inner marginal conical process; flagellum short, 7-8 segmented. Antenna 2 stoutly pediform; peduncular segment

5 shorter than 4, with prominent distal process, posterior margin with small proximal median tooth and densely lined with longish setae; flagellum very short, 3-segmented, posterior margin moderately setose.

Gnathopod 1, dactyl tip little exceeding palm. Gnathopod 2, basis medium broad; carpus short, with distinct free posterodistal margin; propod with posterodistal cusp; dactyl with 3 unequal posterior marginal teeth.

Peraeopods 3 & 4, anterior basis and segment 4 moderately broadened setose, anterior margins weakly (or not) setose; dactyls slender, longer than segment 6. Peraeopod 5, basis virtually lacking posterior marginal setae. Peraeopod 7 somewhat elongate, basis medium broad; segment 6 with 3 posterodistal clusters of long setae; dactyl short.

Pleon plates 1-3 weakly (or not) setose below. Uropod 1, rami short, subequal, each with 3 outer marginal spines. Uropod 2 short, outer ramus with 1 outer marginal spine; inner ramus bare. Uropod 3, peduncle lacking lateral lobe. Telson short, broad, with 3-4 posterodorsal pairs of small hook spines.

Female (4.2 mm): Rostrum short, broad, tip about level with apex of lateral head lobes. Antenna 1, peduncular segment 1 with 2 proximo-medial spines. Antenna 2, peduncular segments short, stout; segment 4, posterior margin with 3 pairs of medium spines; segment 5 and flagellum moderately setose posteriorly.

Peraeopods 3 & 4, anterior margins of basis and segment 4 relatively sparsely setose.

Brood lamellae broadly strap-like, with moderate numbers (~25) of marginal setae.

Etymology. The species name recognizes its regional centre of distribution in the Queen Charlotte Islands, British Columbia.

Distributional ecology. From Prince William Sound and southeastern Alaska, south to the Queen Charlotte Islands and the north-central mainland coast of B. C. On kelp, eel grass and stones, over mud and sand, mainly along surf-protected shores, from LW level to depths of 10 m, in summer water temperatures of ~10-15‰ .

Taxonomic commentary. *Monocorophium carlottensis* is a member of the *insidiosum-uenoi* group characterized by an elongate rostrum and heavy distal antennal setation in the male. It differs markedly from the Pacific regional *M. uenoi* and from the Atlantic regional *M. insidiosum* in characters of the key to species (p. 112).

The species is also similar to *M. steinegeri* but differs in its distinctly smaller size and less heavy armature of antennae and peraeopods.

The overall morphological similarity of *M. carlottensis* and *M. insidiosum* might justify sibling species designation. However, *M. carlottensis* has markedly more tightly setose antenna 2, and weakly setose peraeopods 3 & 3 (male). It is also smaller in size, and distributionally non-overlapping.

Monocorophium steinegeri (Gurjanova)
(Figs. 29)

Corophium steinegeri Gurjanova, 1951: 979, fig. 682.—Kudrjaschov, 1979: 126.—Barnard & Karaman, 1991: 186.

Material Examined. About 225 specimens in 8 lots.
ALASKA.
Aleutian Islands. N.A. Powell Stn., Unimak I., Izembek Lagoon, 1969: ~200 specimens. (male, female, **fig'd**) NMCC-1992-0749.
Southeast Alaska. ELB Stns., 1961: A19(1), A139(1).

BRITISH COLUMBIA.
Queen Charlotte Islands. ELB Stns, 1957: H4 (9 males, 3 females, 3 imm).
North-central mainland coast. ELB Stn, 1964: H25(3)

Diagnosis. Male (6.0 mm). Pleosome segment 3 with trace posterior median tufted process. Urosome with distinct lateral notch; uropod 1 inserted partly ventrally.

Peraeopods 3 & 4, anterior margin of basis and segment 4 strongly setose; dactyl curved, shorter than segment 6. Peraeopod 5, bases weakly setose posterodistally. Peraeopod 7 not elongate; basis nearly as broad as deep.

Pleopod peduncles very broad, width nearly twice length. Uropod 1, rami short, subequal, each with 4-5 outer marginal spines. Uropod 2 short, rami lacking marginal spines. Uropod 3, peduncle with small setose lateral lobe. Telson slightly broader than long.

Female (to 5.5 mm): Rostrum short, broad, not exceeding lateral head lobes. Antenna 1, peduncular segment 1 with small spined median process. Antenna 2, peduncular segments short, stout; segment 4, posterior margin with 3 pairs of strong spines; segment 5 with single median posterior pair of spines; flagellum very short, weakly setose posteriorly.

Peraeopods 3 & 4, anterior margins of basis and segment 4 relatively less strongly setose than in male.

Brood lamellae long, strap-like, with moderate numbers (25-35) of marginal setae.

Taxonomic commentary. Specimens of *Monocorophium steinegeri* from the North American Bering Sea region differ very little from specimens from the coast of Kamchatka described and figured by Gurjanova (1951). The species appears most closely related to *M. insidiosum* and *M. carlottensis.*

Distributional ecology. Eastern Kamchatka, northern Sea of Okhotsk and the Bering Sea, from LW level littorally and sublittorally on sand. Characterized by Kudrjaschov (loc. cit.) as a high-boreal Asiatic Pacific species for which the northern part of the Tatar Strait is probably the extreme southern boundary of distribution.

On the North American Pacific coast, it occurs sporadically south to the Queen Charlotte Islands.

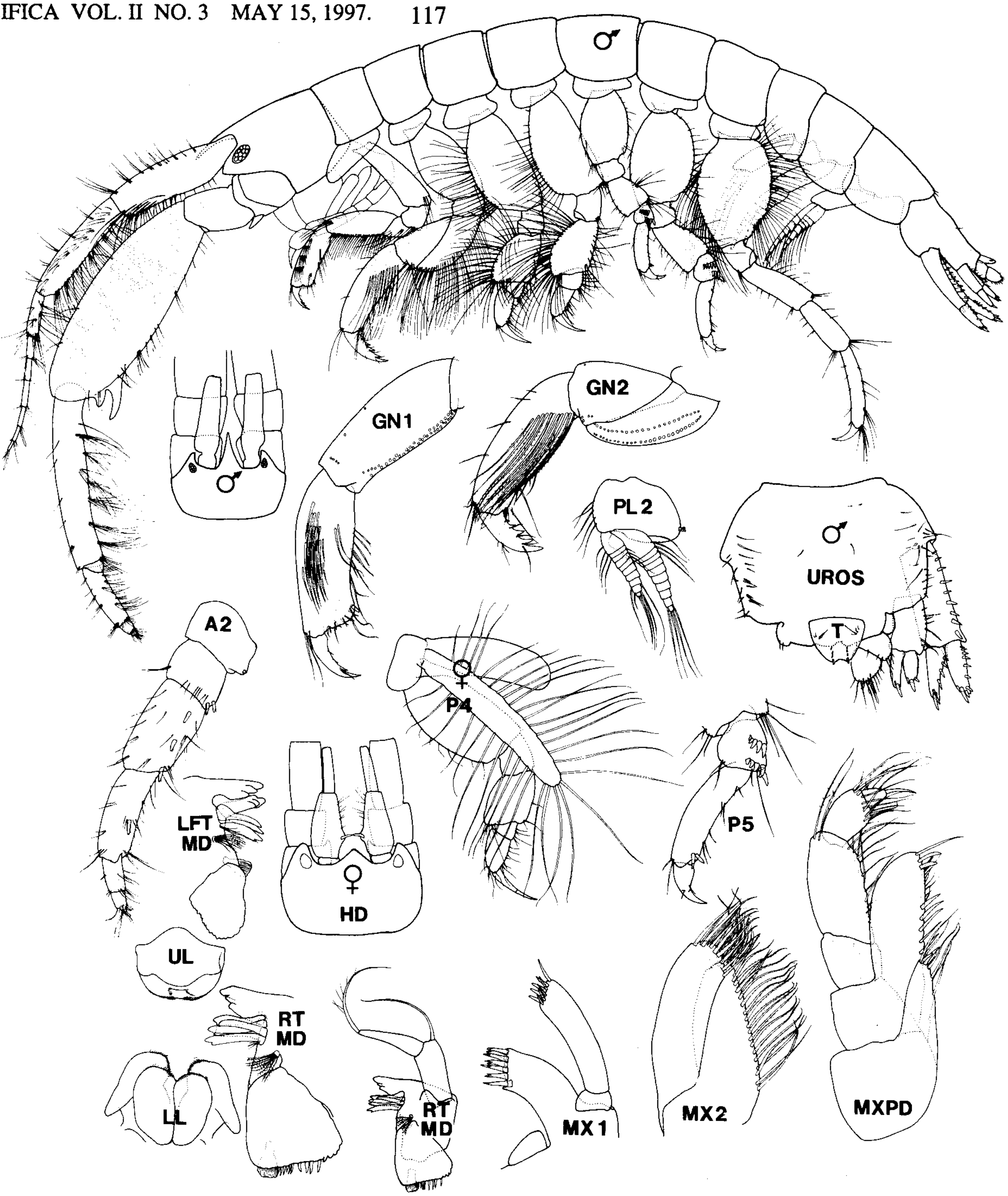


FIG. 29. ***Monocorophium steinegeri*** **(Gurjanova). Aleutian Is. Male (6.0 mm); female (6.0 mm).**

Monocorophium acherusicum (Costa)
(Figs. 30)

Corophium acherusicum Costa, 1851: 232.—Shoemaker, 1947: 53, figs. 2, 3.—Shoemaker, 1949: 76.—Bousfield, 1973: 201, Pl.LXII.2.—Barnard, 1975: 338-340 (key), figs. 143, 144, 147.—Otte, 1976: 8 (key), figs. 6, 7.—Carlton, 1979: 655 (distribution list, Alaska to California).– Hong, 1983: 135, figs. 6-8.—Hirayama, 1984: 13.—Austin, 1985: 615.—Staude, 1987: 386, fig. 18.27.—Kim, 1991: 114, fig. 26—Ishimaru, 1994: 35.

Corophium acherusicum Costa (nomen nudum) Stebbing, 1906: 692.—Barnard & Karaman, 1991: 185.

Material Examined.

BRITISH COLUMBIA.

Southern Vancouver Island and southeastern mainland.. ELB Stns., 1955: P9(3), G20(1), M1(5). ELB Stns.,1970: P709(15), P712(6). ELB Stns, 1972: P2(>50), P6(4), P6a(2), P6c(1), P18a(11). ELB Stmns., 1977: B6b(3), B7(1). JFL Carl Stn, 1938. Berkley Beach, Departure Bay - 1 spm; Ibid, 1931. Stn 2242 - 5 specimens; K. Conlan, Stns, 1977. French Creek, Stn. FC-1(2); Stn. FC-11(1); coll. unknown, 1987. Stn 87 Sepping I, Barkley Sd.- 2 specimens; D.V. Ellis Stns., 1976.: Stn. 4 (Tsable Estuary) - 4 specimens; Stn 7 (Chemainus Estuary) - 1 specimen.

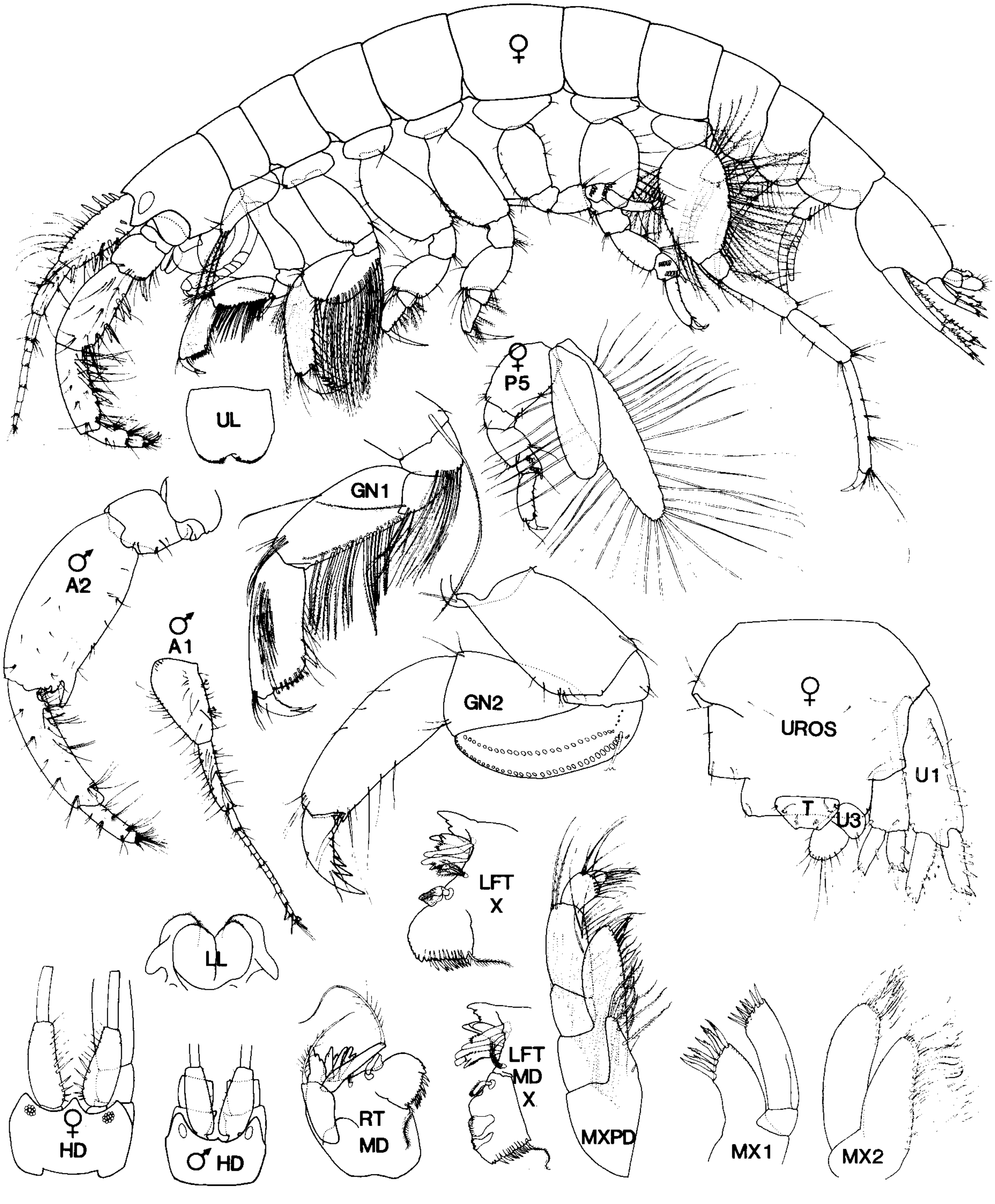


Fig. 30. ***Monocorophium acherusicum*** **(Costa). Steamboat I., WA. Male (4.0 mm); female (4.2 mm).**

WASHINGTON-OREGON:
Washington. ELB Stns, 1966: W3(15); W4(2); W8 (442); W10(42); W12(51); W13 (Steamboat I.) - 55 spmns incl. male (4.0 mm) **(fig'd)**; female ov. (4.2 mm) **(fig'd)**, CMN Cat. Nos. NMCC1992-0744+0785; W30(22); W35(many); W44(32).

Oregon. ELB Stn 1966: W64 (63).

Diagnosis. Male (4.0 mm): Pleosome segment 3 dorsally smooth. Urosome with distinct lateral notch; uropod 1 inserted mainly laterally. Head, rostrum very short, recessed posterior to lateral head lobes. Antenna 1, peduncular segment 1 smooth, bulging proximally, narrowing distally; flagellum slender, 7-9-segmented. Antenna 2 strongly pediform; peduncular segment 5 shorter than 4, with broad distal process, posterior margin with small proximal tooth but few setae; flagellum, short, weakly setose.

Gnathopod 1, propod not narrowing distally; dactyl tip little exceeding palm. Gnathopod 2, basis medium broad; carpus short, deep, with distinct postero-distal free margin; propod with distinct postero-distal cusp; dactyl with 2-3 unequal posterior marginal teeth.

Peraeopods 3 & 4, basis broad, anterior margin bare; segment 4 medium, lacking anterior marginal setae; dactyl slender, longer than segment 6. Peraeopods 5, basis small, hind margin not setose. Peraeopod 7 not elongate, basis medium broad; segment 6 not strongly setose distally; dactyl short.

Pleon plates 1-3 weakly (or not) setose below. Uropod 1, rami short, unequal, each with 4-6 outer marginal spines. Uropod 2 short, rami each with 1(2) outer marginal spine(s). Uropod 3, peduncle with small nearly bare lateral lobe. Telson short, broad, with 3-4 postero-dorsal pairs of small hook spines.

Female (3.5 mm): Rostrum short, broad, apex about level with lateral head lobes. Antenna 1, peduncular segment 1 with numerous strong median and posterior spines. Antenna 2, peduncular segments short, stout; segment 4, posterior margin with 3 -4 pairs of strong spines; segment 5, posterior margin with 2 spine groups and clusters of setae; flagellum short, with whorls of setae.

Brood lamellae large, broadly strap-like; margins with numerous (35-40) setae.

Taxonomic and distributional commentary. Specimens of *Monocorophium acherusicum* from the North American Pacific region are similar to those of the western North Pacific (figured by Hong, 1983). However, they differ from those of the North American Atlantic region in their more heavily spinose antennae, more elongate dactyl of gnathopod 1, and more strongly dentate dactyl of gnathopod 2. At present these differences are considered only varietally or regionally significant since *M. acherusicum* is considered native to the North Atlantic region and widely synanthropic elsewhere.

Monocorophium acherusicum is more closely similar to *M. sextonae* (Crawford) and other more primitive members of the genus. However, morphological similarity with members of the genus *Crassicorophium*, especially with *C. bonelli* is here considered homoplasious (Fig. 40, p. 133).

Carlton (loc. cit.) has summarized records from the Pacific coast of North America, from Alaska to California, and Ishimaru (loc. cit.) from Japanese coastal waters where it is very probably commercially synanthropic. *M. acherusicum* is perhaps the most widely distributed species of corophiin amphipod in temperate-tropical waters of the world. Its region of endemicity is now difficult to pin-point. However, the eastern North Atlantic, from which it was originally described, seems the most probable source region.

Stebbing (loc. cit.), and Barnard & Karaman (loc. cit.) consider this species to be a nomen nudum. However, under the ICZN 50-year usage rule, the name is here considered sufficiently authentic to justify its formal recognition as a legitimate species name.

Monocorophium uenoi (Stephensen)
(Fig. 31)

Corophium uenoi Stephensen, 1932: 494, figs. 3, 4.—Barnard, 1964:130 (map).—Barnard, 1952a: 28, pls. 8,9.—Barnard, 1975: 338-340 (key), fig. 139.—Carlton, 1979: 660.—Chapman, 1988: 366.—Kim, 1991: 118, fig. 28.—Barnard & Karaman, 1991: 186.—Ishimaru, 1994: 36.

Diagnosis. Male (to 5.0 mm): Pleosome segment 3 essentially smooth dorsally. Urosome with indistinct lateral notch and slightly marginal concavity; uropod 1 inserted mainly ventrally. Head, rostrum slightly exceeding lateral head lobes. Antenna 1, peduncular segment 1 with very low inner marginal swelling; flagellum slender, 8-9 segmented. Antenna 2 strongly pediform; peduncular segment 5 not shorter than 4, with prominent distal process, posterior margin with small proximal median tooth and 5-6 clusters of longish setae; flagellum short, 3-segmented, posterior margin strongly setose.

Gnathopod 1, dactyl slender, tip greatly (50%) exceeding short palm. Gnathopod 2, basis very stout; carpus short, deep, with distinct free posterodistal margin; propod lacking posterodistal cusp; dactyl with 3 unequal posterior marginal teeth, middle tooth often strongest.

Peraeopods 3 & 4 very short, basis broad, anterior margin nearly bare; segment 4 very broad, totally overhanging short segment 5, anterior margin moderately setose; dactyls curved, shorter than segment 6. Peraeopod 5, posterior margin of basis nearly bare. Peraeopod 7 not elongate; basis medium broad; segment 6 with longish posterodistal setae; dactyl curved, subequal in length to segment 6.

Pleopod peduncles very broad, rhomboidal, width nearly twice length. Uropod 1, rami short, unequal, each with 3-4 outer marginal spines. Uropod 2 short; rami unequal, outer ramus with 1-2 outer marginal spine, inner ramus often bare. Uropod 3, peduncle with small setose lateral lobe. Telson short, broad, hook spines undescribed.

Female (4.6 mm): Rostrum very short, broad, not exceeding lateral head lobes. Antenna 1, peduncular segments more strongly setose; peduncular segment 1 with more pronounced median swelling. Antenna 2, peduncular segments moderately broad; segment 4, posterior margin with 3 pairs of strong spines; segment 5 with stout median spine and several setal clusters; flagellum short, posterior setae short.

Peraeopods 3 & 4, anterior margins of basis and segment 4 relatively sparsely setose. Brood lamellae not described.

Taxonomic and distributional commentary. *Monocorophium uenoi* is apparently endemic to the Sea of Japan and the South China Sea, from whence it has been introduced, in post-W.W. II times, with the importation of Japanese oysters and other fisheries products to San Francisco Bay and other central Californian localities (e.g., Bodega Bay) and southern California (e.g., Newport Bay) (Carleton, 1979; Chapman, 1988). The species has not yet been recorded from the present, more northerly study region.

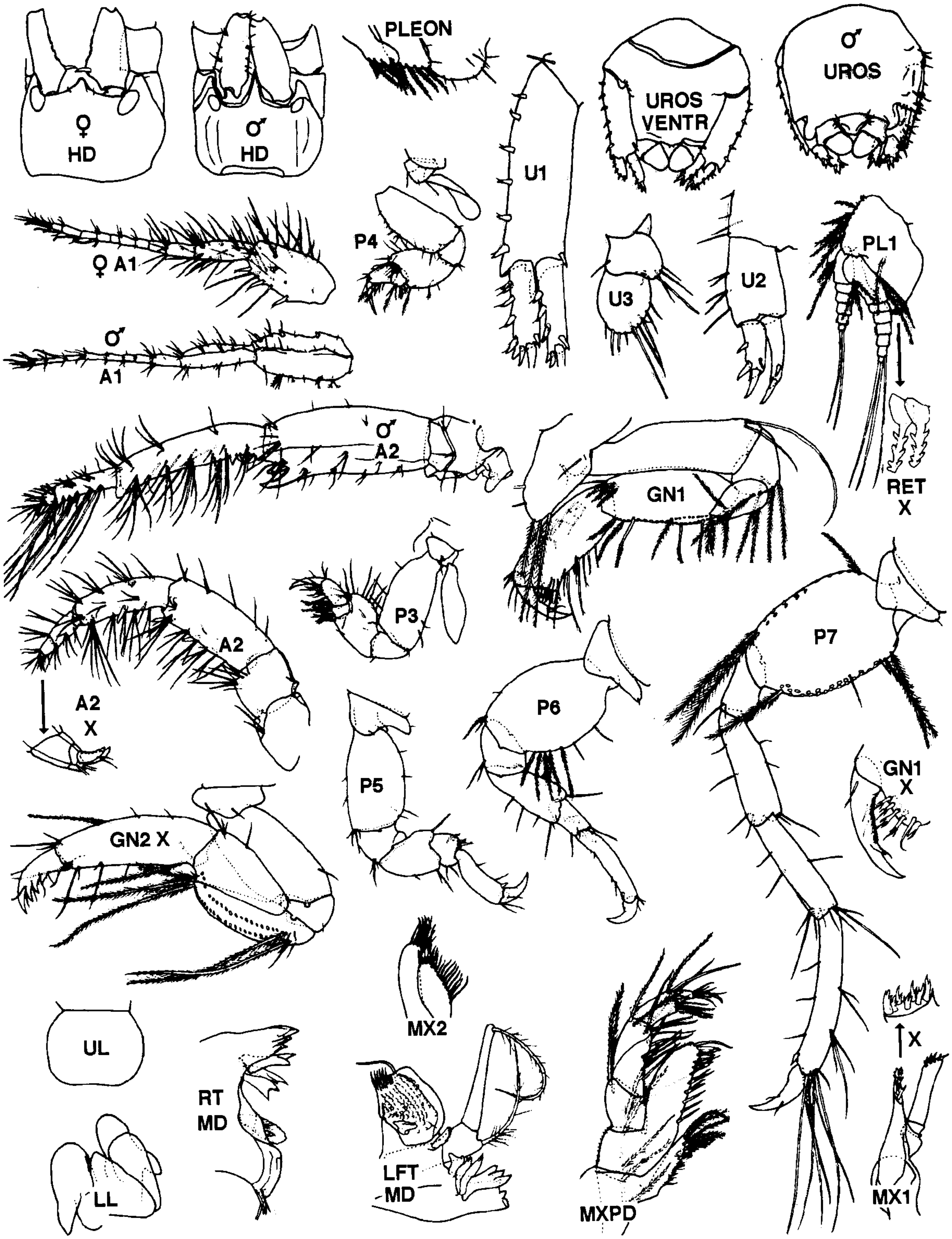


FIG. 31. *Monocorophium uenoi* (Stephensen). Hong Kong. Male (2.0 mm); female (4.6 mm) (after Hirayama, 1986).

Monocorophium sextonae (Crawford)
(Fig. 32)

Corophium sextoni Crawford, 1937: 620, figs. 3, 4.

Corophium sextonae Crawford, 1937 emend Hurley, 1954: 433, figs. 1, 2.—Hirayama, 1987b: p. 572, Fig. 3.—Barnard & Karaman, 1991: 185.—Ishimaru, 1994: 35.

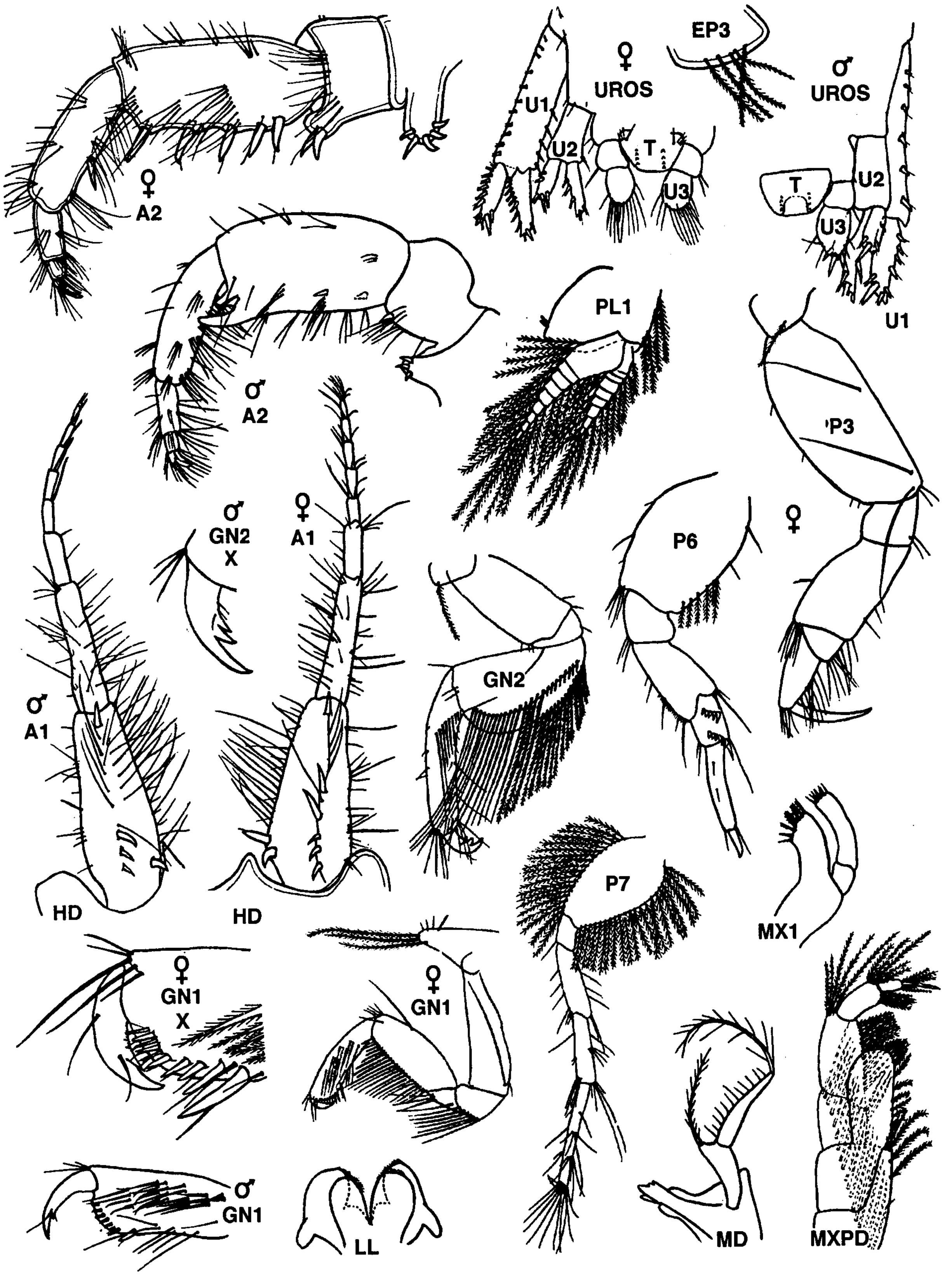


FIG. 32. ***Monocorophium sextonae*** **(Crawford). Otago, New Zealand. Male (4.0 mm); female (5.0 mm) (after Crawford, 1937; Hurley, 1954).**

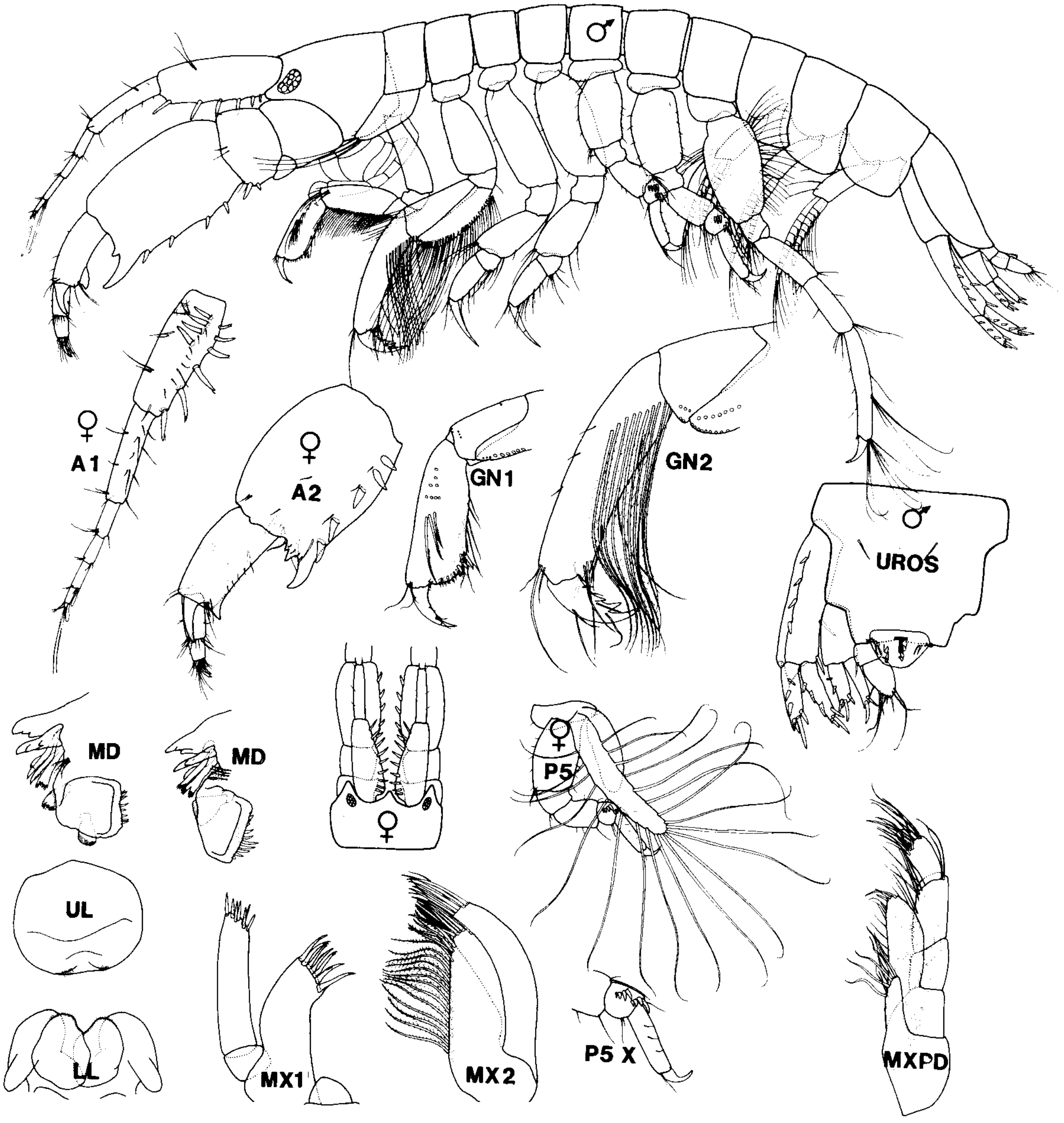


Fig. 32. ***Monocorophium californianum*** **(Shoem.). S. Vancouver I., B.C. Male (3.2 mm); female (2.8 mm).**

Taxonomic and distributional commentary.

Monocorophium sextonae is almost certainly endemic to the eastern North Atlantic and Mediterranean regions, from whence it has been spread by commerce to world-wide temperate marine waters, including those of Australia and New Zealand (Hurley, 1954), and the western North Pacific (Nagata, 1965; Ishimaru, 1994). It has not yet been recorded authentically from the eastern North Pacific region. The species exhibits numerous plesiomorphic character states, including a non-sexually dimorphic rostrum, strongly spinose antennae, closed lower margin of the fused merus and carpus, bidentate dactyl of gnathopod 2, and strongly spinose rami of uropods 1 & 2. Some facets of morphological similarity between *Monocorophium sextonae* and *Crassicorophium bonelli* may not be entirely homoplasious.

Monocorophium californianum (Shoemaker)
(Fig. 33)

Corophium californianum Shoemaker, 1934a: 359, fig. 2.—Shoemaker, 1949: 76.—Barnard, 1975: 338 (key).—Otte, 1976: 11, fig. 9.—Austin, 1985: 615.—Barnard & Karaman, 1991: 185.

Material Examined.
BRITISH COLUMBIA .
Southern Vancouver island. Dobrachy Seatech Stn W2B, off McCauley Point, Victoria, August, 1976 - 1 male (3.2mm) **(fig'd)**, CMN Cat. No. NMCC1992-0938; ELB Stn P714, 1970 - 1 female ov (2.8 mm), **(fig'd)**, CMN Cat. No. NMCC1997-0948.

Diagnosis. Male (3.2 mm): Pleon segment 3 smooth dorsally . Urosome with distinct lateral notches; uropod 1 inserted laterally. Head, rostrum short, broad, tip not exceeding lateral head lobes. Antenna 1, peduncular segment 1 with strong inner marginal and posterior marginal spines; peduncular segment 2 distinctly smaller than 1; segment 3 short, flagellum very short, 4-segmented. Antenna 2 strongly pediform; segment 4 very thick, lower margin with short spines; peduncular segment 5 very short, with large curved distal process and stout posterodistal tooth; flagellum very short, 4-segmented, margins weakly setose.

Gnathopod 1, propod slightly broadening distally, dactyl tip little exceeding palm. Gnathopod 2, basis medium; carpus medium long, with small posterodistal free margin; propod with small posterodistal cusp; dactyl with 2 unequal posterior marginal teeth.

Peraeopods 3 & 4 slightly dissimilar; basis of peraeopod 3 distinctly less broadened than that of peraeopod 4, anterior margins bare; segment 4 little broadened, partly overhanging short segment 5; dactyls slender, slightly longer than segment 6. Peraeopods 5 & 6, hind margin of basis with few setae. Peraeopod 7 not elongate, basis medium; segment 6 with 2 posterodistal clusters of long setae; dactyl short.

Uropod 1, rami short, unequal, each with 3 outer marginal spines. Uropod 2 stout, outer ramus with 2 outer marginal spines, inner ramus bare. Uropod 3, peduncle small, lacking lateral lobe, ramus narrowing distally. Telson short, broad, with 4 posterodorsal pairs of small hook spines.

Female (2.8 mm): Rostrum short. Antennae 1 & 2 similar to those of male but slightly less robust.

Brood lamellae relatively large, strap-like, with few (~20) long marginal setae.

Distributional ecology. Endemic to the North American Pacific coast, from Central California (Monterey Bay) to southern British Columbia, on sandy bottoms to depths of 100 m.

Taxonomic commentary. *Monocorophium californianum* and *M. oaklandense* form a natural subgroup within the genus, distinguished by the very stout, not sexually dimorphic antenna 2, and plesiomorphic condition of the gnathopods (Fig. 41, p. 133).

Monocorophium oaklandense (Shoemaker)
(Fig. 34)

Corophium oaklandense Shoekaker, 1949: 60, fig. 8.—Barnard, 1975: 338 (key), fig. 140.—Otte, 1976:11, fig. 9.—Austin, 1985: 615.—Barnard & Karaman, 1991: 185.

Material examined: None from study region. *Monocorophium oaklandense* is known only from experimental test blocks set out in San Francisco Bay. Otte (loc. cit.) considered this species a possible introduction to coastal waters of British Columbia.

Taxonomic and distributional commentary. *Monocorophium oaklandense* is similar to *M. californianum* in having stout, not sexually dimorphic antennae, and gnathopods of plesiomorphic form. However, the former differs from *M. californianum* in its less spinose, more setose peduncular segment 1, and longer flagellum, of antenna 1; less strongly produced segment 5 of antenna 2; tri-dentate dactyl of gnathopod 2; broader basis of peraeopod 7; marginally spinose inner ramus of uropod 2; and broader ramus of uropod 3.

M. oaklandense is apparently unknown outside the San Francisco Bay region of the Pacific coast of North America. However, it was not recorded in the present more northerly study region.

Apocorophium, new genus
(see Fig. 35)

Corophium Latreille, Crawford, 1937: 623 (Section C+ key).—Shoemaker, 1947: 47 (Section C).—Shoemaker, 1949: 66 (Section C).—Barnard, 1973: 17 (part).—Bousfield, 1973: 198 (part).—Otte, 1976: 4 (part).—Lincoln, 1979: 522 (part).—Myers, 1982: 185 (part).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1994: 35 (part).

Type species. *Corophium acutum* Chevreux, 1908 (present designation).

Species. *Apocorophium simile* (Shoemaker, 1934b). *A. lacustre* (Vanhoffen, 1911). *A. louisianum* (Shoemaker, 1934b).

Diagnosis. Urosome segments fused; uropods arising ventrally on urosome. Head, rostrum distinct, interior antennal sinus large, recessed. Antenna 1, peduncular segment 3 short. Antenna 2 short-pediform, sexually unlike (except in *simile*); distal process of segment 4 bidentate; segment 5, median tooth and distal process variously developed; flagellum short, 3-segmented; gland cone short (except in *A. louisianum*).

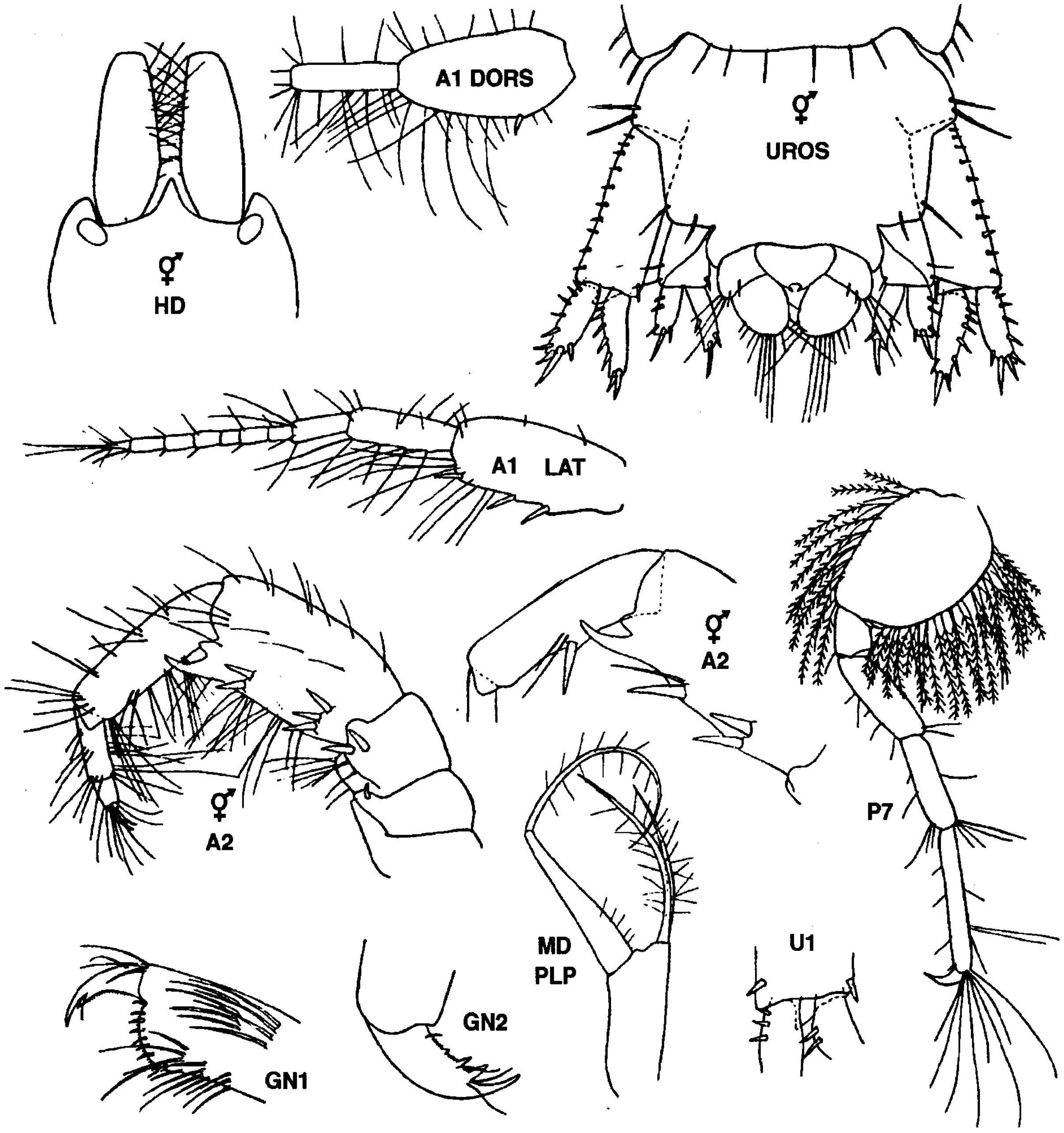


Fig. 34. ***Monocorophium oaklandense*** **(Shoem.). San Fancisco Bay. Hermaphr. ov. (5.0 mm) (after Shoemaker, 1949).**

Upper lip, epistome not produced. Lower lip, mandibular lobes strong. Mandibular palp of moderately advanced form (type P4 of Hirayama, 1987b). Maxilla 1, palp short, not exceeding outer plate. Maxilla 2, inner plate slender. Maxilliped, inner plate short; outer plate slender, inner margin setose distally; palp segment 2 short.

Gnathopod 1, dactyl with weak posteriorly marginal tooth, tip little exceeding palm. Gnathopod 2, merus not occluding posterodistal (free) margin of short carpus (~ 1/2 propod); dactyl short, tri- or quadridentate.

Peraeopods 3 & 4, basis broadened, glandular; segment 4 moderately broadened distally, overhanging short segment 5. Peraeopods 5 & 6, segment 4 short; segment 5 short, posterodistal hook spines short, stout; segment 6 and dactyls reversed; basis of peraeopod 6, hind margin setose. Peraeopod 7 not markedly elongate; dactyl short.

Pleon plate 3, hind corner obtuse or rounded. Pleopod peduncles very broad distally. Uropods 1 & 2, peduncles stout, broad; rami short, subequal, spinose on outer margin and apically, apex acute, curved outwards. Uropod 3, ramus short, broad, apex rounded, setose. Telson regular, with dorsal hook spines, apex rounded.

REVISED KEY TO SPECIES OF *APOCOROPHIUM*

1. Antenna 2 essentially similar in male and female .... *A. simile* (Shoem.)
—Sexes more or less unlike .... 2.

2. Antenna 2 (male), segment 5 with strong medial tooth .... *A. acutum* (Chevreux).
—Antenna 2 (male) lacking medial process .... 3.

3. Antenna 1 (male), peduncle 1 strongly setose anteriorly, with no basal process .. *A. lacustre* (Vanhoffen)
—Antenna 1 (male), peduncle 1 weakly setose but strong basal process .... *A. louisianum* (Shoemaker)

Coxal gills slender, sac-like, on peraeopods 3-6, small on peraeopod 6. Brood lamellae short, slender, margins regularly setose.

Etymology. Combining the Greek prefix "*apo*" - advanced, and the generic root "*Corophium*", with reference to the overall apomorphic character states of member species.

Distributional ecology: Small to medium-sized species living in open-ended abodes, usually colonial, cemented to hydroids, wharf piling, oysters, and other solid substrata. Occurring mainly in coastal summer-warm marine and brackish waters of the Atlantic and Mediterranean regions; widely synanthropic in the western North Pacific and the Southern Hemisphere, including Australia and New Zealand (Hurley, 1954).

Taxonomic commentary. Crawford (loc. cit.) first recognized and keyed this group as a distinct taxonomic assemblage. However, neither he nor Shoemaker (1947, 1949) gave it formal taxonomic recognition. The genus *Apocorophium* may be a polymorphic assemblage of two or three separate lineages. Thus, the type species *A. acutum* has evolved from Atlantic regional ancestors (*Monocorophium* subgroup) in concert with, but differing from, other Atlantic apocorophiids in having strongly sexually dimorphic antenna 2, with medially and distally processiferous peduncular segment 5.

The Pacific species, *Corophium baconi*, superficially seems to belong here. It differs in having a processiferous epistome on the upper lip, more advanced mandibular palp (Type P5 of Hirayama, 1987), bidentate dactyl of gnathopod 2, laterally notched urosome, much reduced uropod 2, strongly lobate peduncle of uropod 3, and may have evolved independently from a Pacific-endemic ancestral form (below).

Laticorophium, new genus

Corophium Latreille 1806, Shoemaker, 1934a: 356 (part).—Crawford, 1937: 623 (Section C, part).– Shoemaker, 1949: 66 (Section C, part).—Otte, 1976: 2 (+ key, part).—Hirayama, 1986: 449 (part).—Barnard & Karaman, 1991: 184 (part).—Ishimaru, 1991: 35 (part).

Type species. *Corophium baconi* Shoemaker, 1934a (monotypy).

Diagnosis. Urosome segments fused, lateral margins notched. Uropods inserted ventrally. Head, rostrum short, little sexually dimorphic; inferior antennal sinus strongly regressed. Antenna 1, peduncular segments 1 & 2 long, 3 short. Antenna 2 markedly sexually dimorphic, strongly pediform (male); gland cone short; peduncular segment 4, posterodistal process bifid; segment 5 with strong medial and distal processes; flagellum short, with apical spines.

Upper lip, epistome produced anteriorly. Lower lip, mandibular lobes medium. Mandibular palp, basal segment with notched shelf (type P4 of Hirayama, 1987b); blades few (2-3), stout. Maxilla 1, palp slender, slightly exceeding outer plate. Maxilliped, inner and outer plates short; palp segment 2 short.

Gnathopod 1, dactyl bifid, tip exceeding short, oblique palm.. Gnathopod 2, carpus short, deep, posterodistal setose free margin not occluded by short merus; propod lacking palm; dactyl short, typically bidentate.

Peraeopods 3 & 4 short; basis broad, glandular; segment 4 broadened distally, slightly overhanging short segment 5. Peraeopods 5 & 6 short, similar in form but bases markedly unequal in size; segment 5 short, with 2 posterolateral clusters of short hook spines; segment 6 and dactyl reversed. Peraeopod 7 not elongate; basis medium broad; dactyl short.

Pleon plate 3, hind corner rounded. Pleopod bases strongly broader than deep, proximo-medial margin strongly convex; rami short. Uropod 1, peduncle stout, outer ramus the shorter, outer margins spinose, apices acute, curved outwards. Uropod 2 relatively small, outer margin of rami setose. Uropod 3; peduncle with distinct lateral lobe; ramus short, broad, subtriangular. Telson not broader than long, apex rounded.

Coxal gills narrow, sac-like, on peraeopods 3-6. Brood lamellae linear, margins moderately setose (<20), on peraeopods 3-5.

Etymology. A combining form of the Latin prefix "latus" - broad, and the generic root *Corophium*, with reference to the very broad, short urosome.

Distributional ecology. Endemic to the North American Pacific coast; probably synanthropic in the Sea of Japan.

Taxonomic commentary. Crawford (1937) placed *Corophium baconi* in Section C, which contained *Corophium acutum* and related species having urosome segments

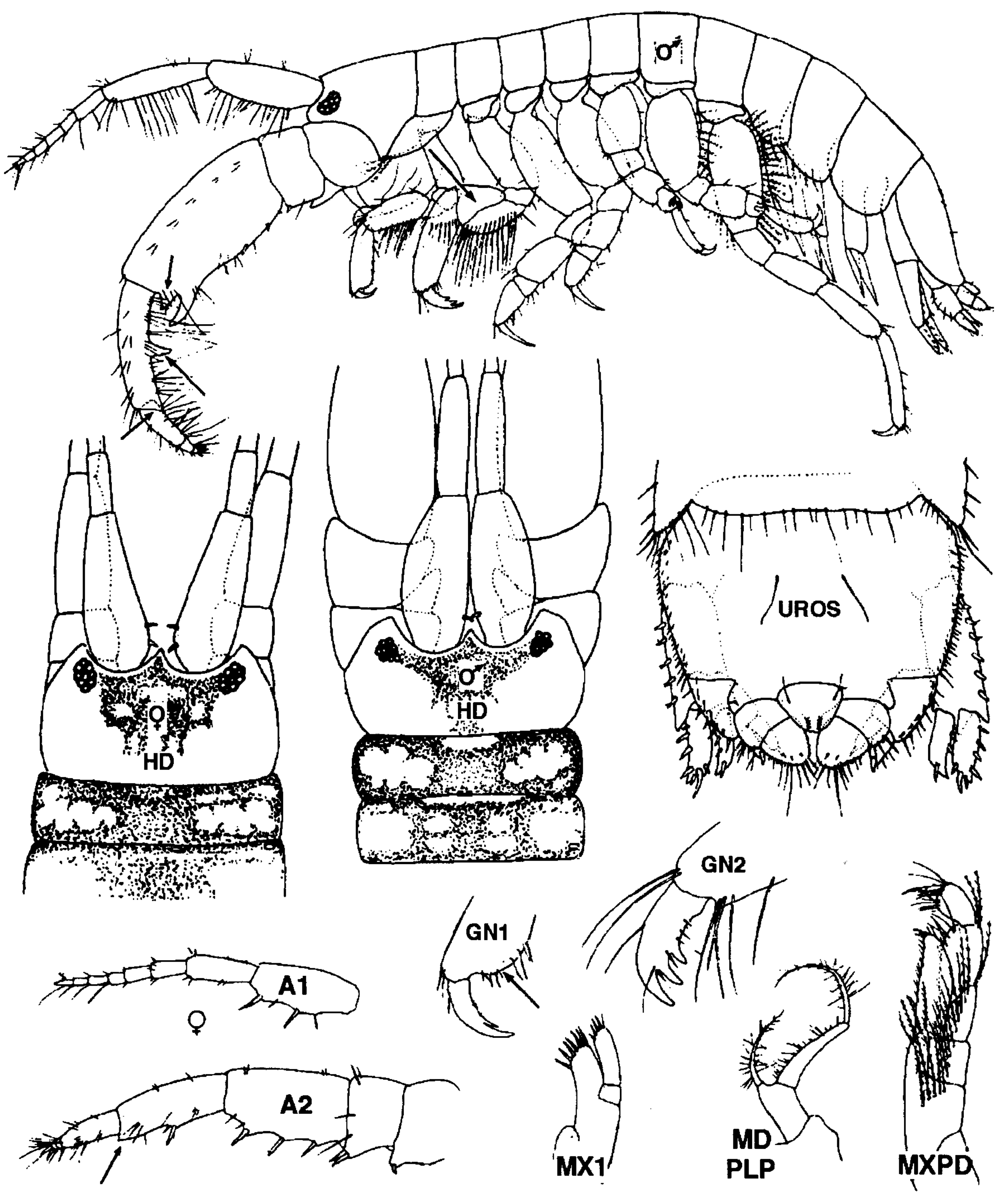


FIG. 35. *Apocorophium acutum* (Chevreux). Woods Hole region. Male 2.3 mm); female (2.0 mm) (after Bousfield, 1973).

fused, and uropods arising ventrally. This decision was accepted by Shoemaker (1949), Otte (1976), and Hirayama (1986). However, as noted above and in the phenogram (Fig. 40, p. 133), *L. baconi* is generically distinctive in its strongly processiferous epistome of the upper lip, the columnar form of the maxillipedal outer plate, the bidentate dactyl of gnathopod 2, and the short broad, laterally notched urosome.

Laticorophium baconi (Shoemaker)
(Figs. 36, 37)

Corophium baconi Shoemaker, 1934a: 356-359, fig. 1.—Shoemaker, 1949: 82, fig. 5g, h.—Barnard, 1970: 101, fig. 53.—Otte, 1976: 11, fig. 8.—Hirayama, 1986: 472, figs. 12-14.—Barnard & Karaman, 1991: 185.—Ishimaru, 1994: 35.

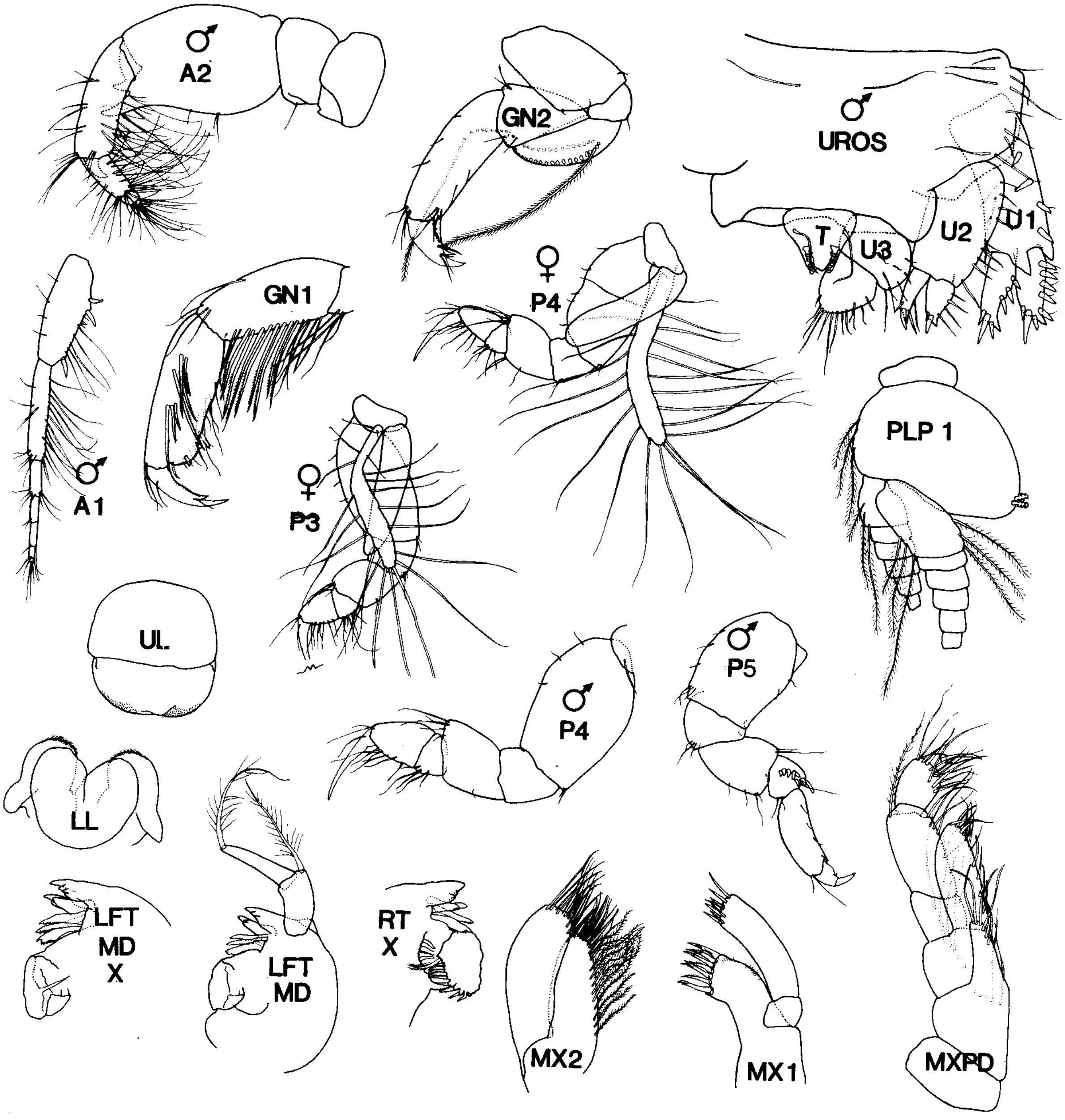


FIG. 36. ***Laticorophium baconi*** **(Shoem.). Goose I., B. C. Male (4.0 mm). Pidwell Reef, B. C. Female 4.0 mm).**

Material Examined. 36 specimens in 15 lots, as follows:
ALASKA.
Aleutian Islands. Unimak I., N. A. Powell, Stn, IzeMbek lagoon., 1969 - 2 males, 4 imm (damaged).

BRITISH COLUMBIA.
Queen Charlotte Islands. FRB survey, JWS Stn 106 (Hecate Strait), 1965 -1 im.
North-central mainland coast. ELB Stns, 1964. H34 (Pidwell Reef) - 1 female (**fig'd** spmn), CMN Cat. No. NMCC1942-0948.(3), H50 (Goose I. anchorage) - male (4.0 mm) (**fig'd** spmn), 1 male, 1 female, CMN Cat. No. NMCC1992-0872.
Vancouver Island. North end. ELB Stn B29a (Gooding Cove), 1975 - 2 females.
South end and southeastern mainland coast. ELB Stn H44 (off Brady's Beach), 1964 - 1 female; ELB Stns, 1970: P714 (7), P719(4); ELB Stn, 1975: P14(1); ELB Stn, 1976, EB2 (Burrard Inlet) - 2 im; ELB Stns, 1977: B16(2), B19b(1), B21b(1); ELB. Stn, 1978, V6 (Burrard Inlet) - 1 female.

WASHINGTON.
Juan de Fuca Strait. ELB Stn, 1966: W35(1).

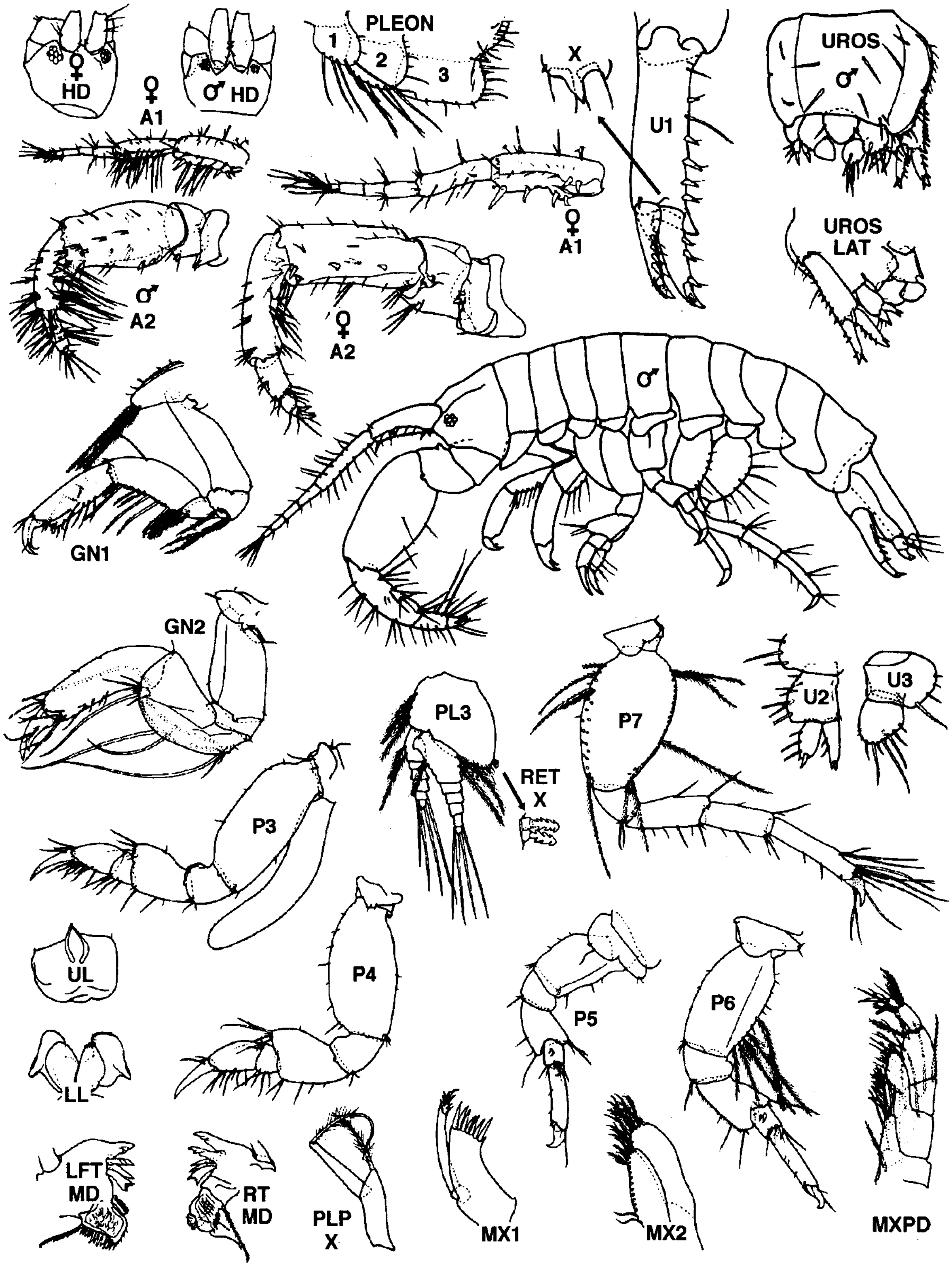


FIG. 37. ***Laticorophium baconi*** **(Shoem.). Hong Kong. Male (3.4 mm); female (3.2 mm) (after Hirayama, 1986).**

Diagnosis. Male (3.4 mm): Pleosome segment 3 with slight posterior marginal elevation. Urosome short, broad, with convex lateral margin, entire except for slight notch posterior to ventral insertion of uropod 1. Head, rostrum short, basally broad, tip not exceeding lateral head lobes. Antenna 1 slender; peduncular segment 1 with 2 proximomedial and 3-4 posterior marginal spines; segments 1 & 2 strongly setose posteriorly; segment 3 short; flagellum 3-segmented. Antenna 2 short, strongly pediform; segment 4 deep, nearly smooth below; peduncular segment 5 shorter than 4, with distinct distal median tooth and strong curved distal process; flagellum medium, 3-segmented; posterior margin of segment 5 and flagellum strongly setose.

Gnathopod 1, propod margins subparallel; dactyl with small posterior marginal tooth, tip distinctly exceeding short palm. Gnathopod 2, basis stout; carpus short, with distinct posterodistal free margin; propod strong, lacking palm or posterodistal cusp; dactyl with a single posterior marginal tooth and a few setae.

Peraeopods 3 & 4, bases broad (3 slightly narrower than 4), anterior margin nearly bare; segment 4 distally medium broad, strongly overhanging short segment 5, anterior margin (of 4) nearly bare; dactyl slender, subequal in length to segment 6. Peraeopod 5, posterior margin of basis nearly bare. Peraeopod 7 not elongate; basis medium broad; segment 6 with 2 distal clusters of long setae; dactyl short.

Pleon plates 1 & 2 with long marginal setae; pleon plate 3 setose behind. Uropod 1, rami short, unequal, each with 2-4 outer marginal spines. Uropod 2 small; outer ramus with 3-4, and inner ramus with 1-2, slender outer marginal spines. Uropod 3, peduncle broad, with distinct setose lateral lobe; ramus short, narrowing and rounded apically. Telson little broader than long, narrowing distally, with 4 posterodorsal pairs of small hook spines.

Female (3.2 mm): Rostrum and antenna 1 much as in male. Antenna 2 dissimilar to that of male; peduncular segments 3 & 4 with short posterior marginal spines; segment 5 shorter than 4, margins weakly setose; margin of segment 5 with 3 pairs of strong spines; flagellum short, with medium setae.

Brood lamellae relatively short and slender, with few (~20) marginal setae.

Taxonomic and distributional commentary. Specimens from the North American Pacific region (Fig. 36) differ little from those of the Asiatic North Pacific region (Fig. 37), confirming the high probability that the latter are synanthropic in the western Pacific. However, as the writers did not examine material of the latter, further study is recommended.

Laticorophium baconi is unlike all other North American Pacific corophiins in its unique combination of plesiomorphic and apomorphic character states. (Fig. 40, p. 133). Plesiomorphic character states include the processiferous epistome and weakly toothed form of the dactyl of gnathopod 2. Advanced character states include the form of the mandibular palp (type P5), short maxillipedal palp segment 2, and ventral insertion of uropod 1. Although the phenetic similarity of *L. baconi* is closest to the advanced *Monocorophium-Apocorophium* North Atlantic complex of species (Fig. 40, p. 133), its phyletic affinities may lie with the more primitive arctic and western North Pacific genera (viz, *Crassicorophium* and *Hirayamia* respectively).

DISCUSSION AND CONCLUSIONS

The genus *Corophium* Latreille sens. lat. has long posed a difficult taxonomic and classificatory problem within superfamily Corophioidea. Considerable morphological diversity is encompassed within the 60+ species previously assigned to this generic concept. Such diversity exceeds tolerable species group limits within almost any other gammaridean amphipod species complex of comparable size, as well as some less speciose generic groups. For instance, fusion of urosome segments is elsewhere considered a character state of significance at the family level (e.g., Kuriidae, Thaumatelsonidae) or even in superfamily classification (e.g., Ampeliscoidea) (Barnard, 1969a; Barnard & Karman, 1991).

The present study of North American Pacific corophiins treats barely 20% of the known world species, and only one that is new to science. However, in attempting to deal realistically with the systematics of even this relatively limited but diverse assemblage of species, the need for critical assessment of character states other than those previously employed (e.g., form of the rostrum, antennae and urosome) became apparent. Hirayama (1987b) had proposed hypothetical phylogenies based on the form of the mandibular palp (where described), and proposed new categories of urosome and uropod arrangement based on newly discovered Asiatic North Pacific taxa. However, as detailed in the systematic section (above), morphological correlations of potential generic significance soon became apparent in most other appendages. These included the structure of the gnathopods, especially the armature of the dactyls and degree of fusion of merus and carpus of gnathopod 2, the shortening and broadening of segments of peraeopods 3-6 (associated with development of silk glands and "spinning" apparatus), broadening of pleopod peduncles, and modifications of uropods 1-3.

The present revision has also been greatly aided by a series of revisionary studies on the sister corophiid subfamily Siphonoecetinae, by Jean Just (1983, 1984,1988). His classification is essentially phyletic and reflects apparent changes in life style from free-burrowing (primitive) to abode-building (advanced). However, unlike siphonoecetins, free-burrowing corophiins occur mainly on pure sediments with little macro-particulate detritus. Furthermore, domicolous corophiins live mainly in fixed abodes on hard substrata, or on shell-modified soft substrata, usually in large colonies. If animals relocate elsewhere, they cannot transport the abode with them but must crawl or swim freely to a new location, and there construct a new abode, or evict another tenant from an existing tube (Shillaker & Moore, 1983, etc.?). As in the Siphonoecetinae, however, increasing adaptation within the Corophiinae from a burrowing to a domicolous life style is reflected in corresponding morphological changes. Thus, peraeopods apparently become less fossorial and/or ambulatory but more specialized for secretion of cementing silk and/or clinging to the tube walls. Moreover, in various ways the

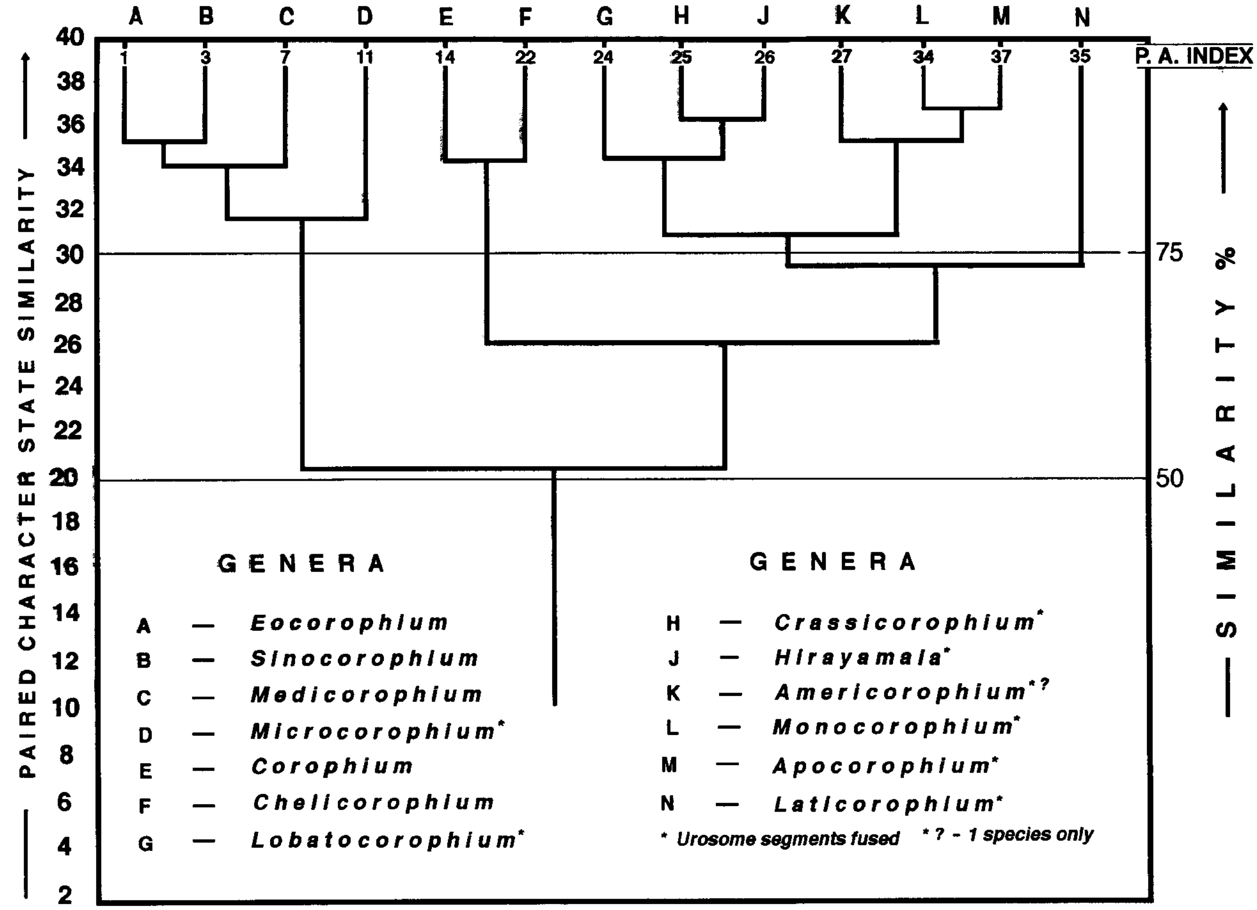


FIG. 38. PHENOGRAM: GENERA OF COROPHIINAE

urosome becomes more efficiently modified for "plugging" the rear entrance of the tube when the animal is active at the other end. Facilitating the corophiin "fixed" life style, the double opening of the abode presumably permits the animal to continuously filter food particles borne by directionally changing tidal currents.

The distant ancestry of corophiin amphipods is undoubtedly shared with most other members of family Isaeidae. However, their direct ancestry is more problematical. The genus *Corophium* sens. lat. (= subfamily Corophiinae) has been widely considered a monophyletic concept because of the unique form of the mandibular palp, the filtering apparatus of the gnathopods and other autapomorphies of all member species. They are also closer to siphonoecetins than to other potential isaeid outgroups because of many shared synapomorphies, several of which are outlined by Just (1983). Common features include: lack of accessory flagellum; pediform antenna 2; basically 2-segmented mandibular palp; lack of gill plate on peraeopod 2; small separated coxal plates 1-4; and dissimilar gnathopods 1 & 2.

Generic relationships within subfamily Corophiinae

Morphological similarities of corophiin genera are indicated by the phenetic analysis summarized in Fig. 38 (above). Corresponding characters and character states of the cluster analysis are provided in Table I (p. 131).

Three main subgroupings may be considered here: (1) A cluster of 4 primitive genera to the left (P. A. Indices of 1-11) that differs from the other subgroupings at the 50% similarity level; (2) a cluster of 7 advanced genera to the right (P. A. Indices of 24-35); and (3) a cluster pair of intermediate genera in the centre-left (P. A. Indices of 14-22) that differs from the advanced cluster at the 65% similarity level.

With respect to (1), character states of mouthparts, gnathopods, peraeopods and uropods are unspecialized and plesiomorphic. Only in *Microcorophium* are urosome segments fused. Three genera are endemic to the Asiatic North Pacific, one genus (*Medicorophium*) to the Mediterranean region, and one species of *Sinocorophium* (*S. alienense*) is considered synanthropic in the eastern North Pacific.

Within cluster (2) are three subclusters, viz: on the left, a relatively primitive subgroup of *Lobatocorophium, Crassicorophium,* and *Harayamaia*, each with autapomorphic features, but having gnathopod 2 plesiomorphic in form. On the centre right are 2 speciose genera, with variously advanced character states, especially of the gnathopods and peraeopods 4-6, and of probable close common ancestry. Member species are presumably the most specialized in construction of cemented abodes, and in mate-guarding reproductive behaviour. The condition of the urosome and appendages grades from the generally unfused condition in *Americorophium,* through fusion and various degrees of ventral inser-

TABLE I. CHARACTERS & CHARACTER STATES OF GENERA OF COROPHIINAE

CHARACTERS	CHARACTER STATE		
	Plesiomorphic 0	**Intermediate 1**	**Apomorphic 2**
1. Inferior antennal process	Produced	Vertical	Regressed
2. Antenna 1 (female), peduncle 1 , posterior spines	None	1 - 2	3+
3. Antenna 2 (male), peduncle 2 , gland cone	elongate, acute	medium	very short
4. A2, peduncle 4, posterodistal process	single tooth		double tooth
5. A2, peduncle 5, proximal posterior tooth	lacking	small	strong
6. Antenna 2 (female), peduncle 4, marginal spines	none	2-3 spines	4+ spines
7. Antenna 2 (female)	sim. to male; ped. 4 process simple	sim. to male; ped. 4 process bifid	hermaphroditic; simple reduced process
8. Mandibular palp	segment 3 continuous with fused segments 1 & 2	segment 3 angled inner seta on flat shelf	segment 3 oblique setal process strong
9. Lower lip, mandibular lobes	weak		distinct
10. Maxilliped, palp segment 2	Elongate; L ~=2X segment 1		Short; L ~= segment 1
11. Gnathopod 1; form of subhela	palm vertical, dactyl short		palm oblique, dactyl well exceeding palm
12. Gnathopod 2; form of dactyl	simple	1-2 posterior teeth	3-5+ posterior teeth
13. Peraeopods 3 & 4; segment 4	slender	slightly broadened	stout, distally broad
14. Peraeopods 3 & 4; segment 5	slender, normal		very short, overhung by segment 4
15. Peraeopod 6, segment 5	length subequal to segment 4		very short << seg. 4
16. Peraeopod 6, segment 5 posterodistal spines	elongate, => 1/2 segment 5		very short, <1/4 segment 5
17. Peraeopod 7, segment 4	Elongate; L ~=Basis	Medium; L~=3/4 Basis	Short; L = 1/2 Basis
18. Pleon plate 3, hind corne	Acute, produced	Squared	Rounded
19. Urosome	Segments separate, uropods 1 & 2 inserted laterally	Segments 1-3 fused uropods inserted laterally	Segments 1-3 fused uropod 1 inserted ventrally

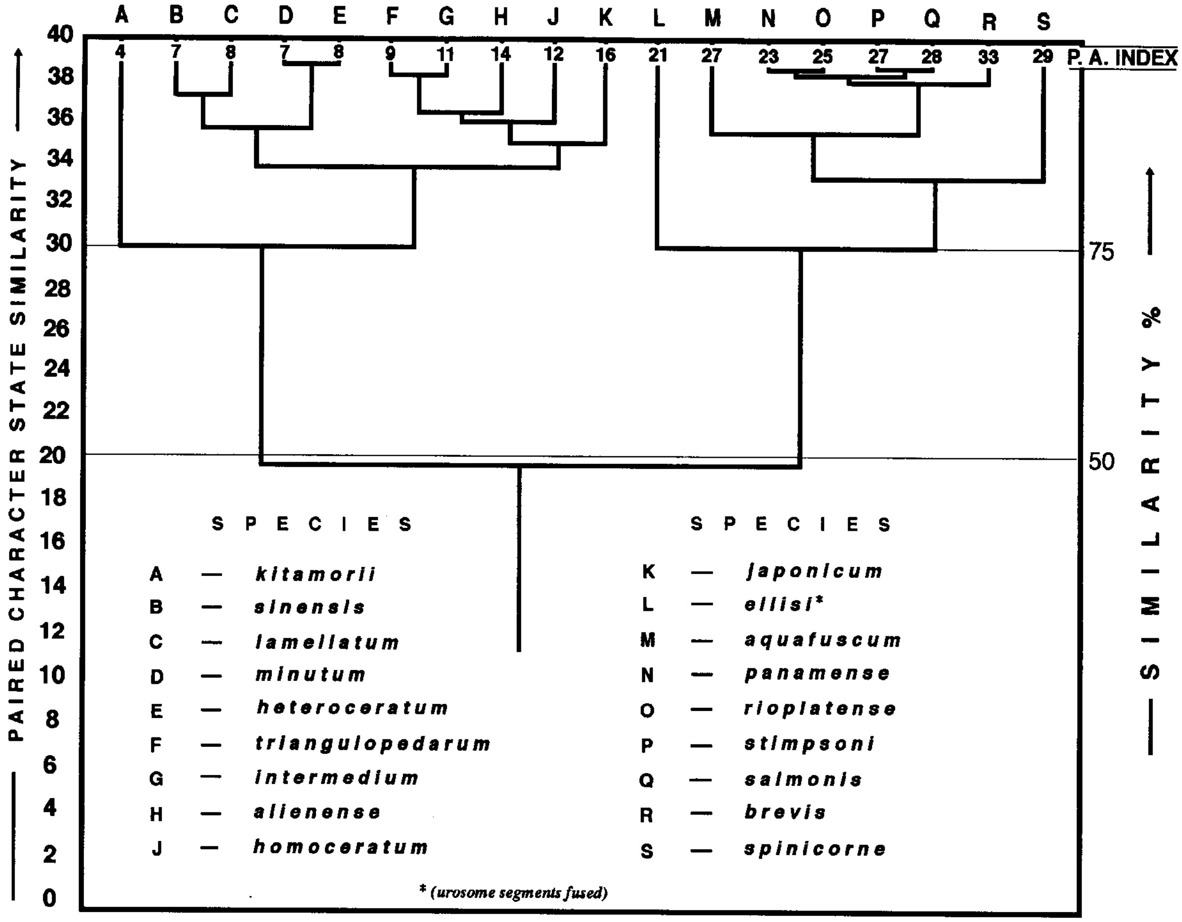


FIG. 39. PHENOGRAM: NORTH PACIFIC AND NEOTROPICAL SPECIES OF COROPHIINAE HAVING UROSOME SEGMENTS UNFUSED.

tion of uropod 1 within *Monocorophium*, to the fully fused, and fully ventral insertion of uropod 1 in *Apocorophium*. On the extreme right is the monotypic, North Pacific genus *Laticorophium*, having similarly advanced character states but plesiomorphic gnathopods and probably of differing close ancestry. The centre-left generic pair of *Corophium* and *Chelicorophium* (3) encompasses mostly littoral, mainly burrowing species, having unfused urosome segments and plesiomorphic mouthparts, but exhibiting variously advanced condition of antennae, gnathopod 2, peraeopods and uropods.

The species groupings of Crawford (1937) and Shoemaker (1947, 1949), based on the degree of fusion of urosomal segments and ventral insertion of uropod 1, are generally supported at generic level in this analysis. Differences are attributable to relatively recent discoveries of several new morphotypes, especially in the Asiatic Pacific region, and by the classificatory significance attributed to other character states by Hirayama (1987b) and the present authors.

Analysis of North Pacific corophiins with unfused urosomes.

The phenogram of corophiins with unfused urosomes (Fig. 39. p. 133) reveals two main subgroupings: (1) a complex of several primitive, largely Asiatic North Pacific species on the left (P.-A. indices of 4-16), and (2) an assemblage of relatively advanced, largely North American Pacific species on the right (P.-A. Indices of 21-33).

With respect to (1), *kitamori* is isolated from the other nine species at the 75% level, and is placed within its own genus, *Eocorophium;* the others are encompassed within *Sinocorophium*, new genus. Species of *Sinocorophium* cluster into two closely similar species subgroups, viz., a primitive complex of 4 sexually dimorphic species to the left, including the generic type species *S. sinensis* (Zhang), and a more advanced subgroup of 5 non sexually dimorphic species to the right. As noted above, the Mediterranean-endemic genus *Medicorophium* is more closely similar to the former, and the western European nominate genus *Corophium* more probably had a common ancestor with the latter.

A subgrouping of species within the relatively advanced complex (2) occurs at comparable similarity levels. Thus, the large western Atlantic estuarine species *Americorophium ellisi* (to the left) is somewhat isolated from other neotropical and eastern Pacific congeners to the right, both in plesiomorphic features (e.g., 3-segmented mandibular palp and simple, posteriorly setose dactyl of gnathopod 2), and apomorphic character states (fused urosome segments; shortened processiferous antenna 1). Within the advanced

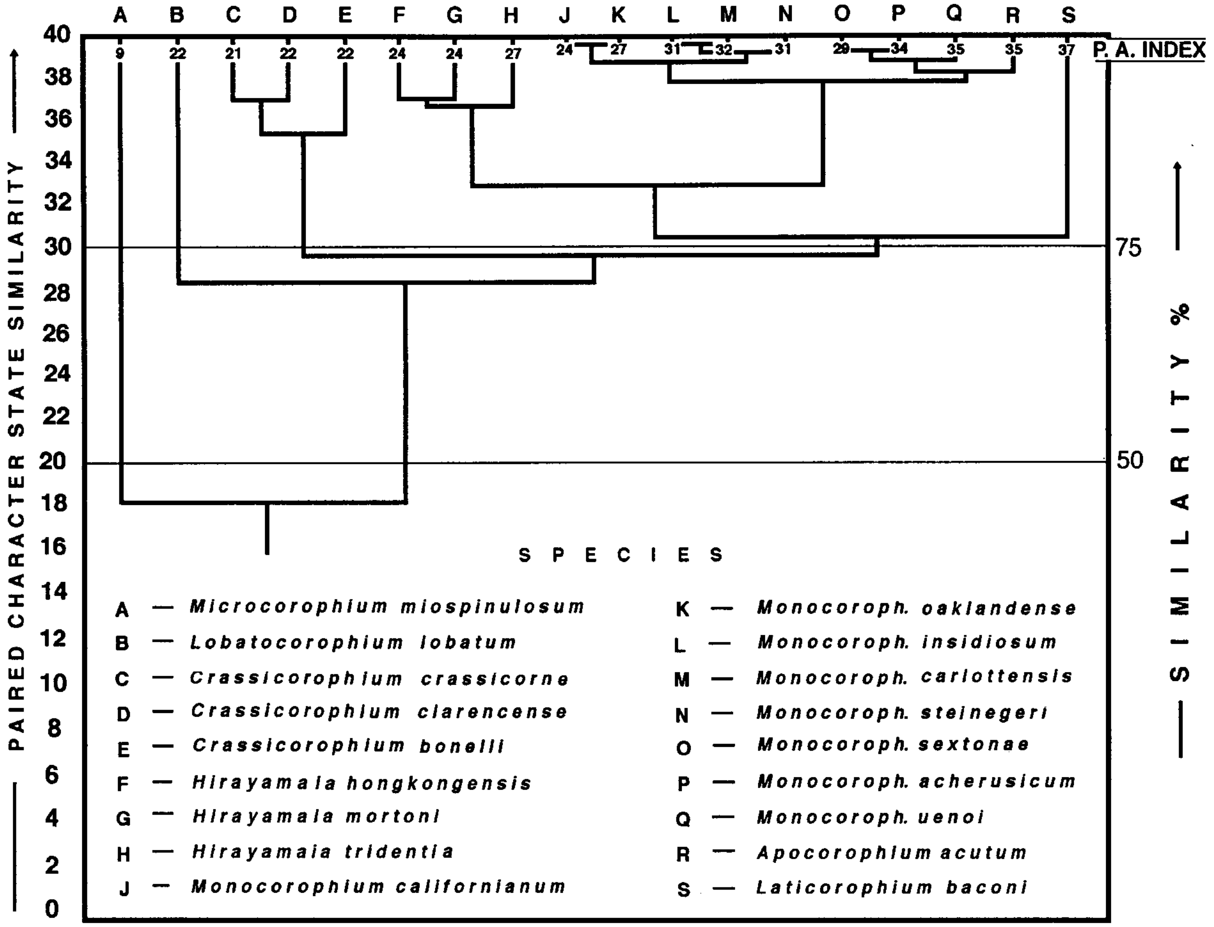


FIG. 40. PHENOGRAM: NORTH PACIFIC SPECIES OF COROPHIINAE HAVING UROSOME SEGMENTS FUSED (COALESCED).

Americorophium subgrouping to the right, three of the Pacific species cluster closely with the other sexually dimorphic Panamanian and Argentinian species. The Pacific species, *A. spinicorne*, and the Atlantic species, *A. aquafuscum*, are similar to each other in having heavily setose, not sexually dimorphic antenna 2, and several plesiomorphic features including a 3-segmented mandibular palp in *A. aquafuscum*. Such internal disparity of higher level character states might justify further generic subdivision, especially in the case of *A. ellisi*. However, more complete description of the mouthparts, coxal gills, brood lamellae, pleopods and other character states, not treated in the original description, is first recommended. The tropical North American Pacific species, *A. setosum* Shoemaker, 1949, appears most closely similar to *A. panamense* in character states described to date. However, the original account did not treat mouthparts and several other analytically critical taxonomic features, so the species has been omitted from the present analysis.

Analysis of North Pacific corophiins with fused urosome.

Three major subgroupings are revealed in the pertinent phgenogram (Fig. 40, above): (1) A primitive monotypic genus *Microcorophium* on the extreme left (P.A. Index of 9); (2) three advanced and closely similar subgroups on the right (P.-A. Indices of 29 to 37)(at and below the 75% similarity level); and (3) three intermediate subgroups on the centre left (P.-A. Indices of 21 - 27).

With respect to (1), in nearly all major character states, *Microcorophium miospinulosum* is remote from other North Pacific subgroups having fused urosomal segments (<50% morphological similarity), but is most closely similar to the primitive western North Pacific genus *Sinocorophium* (Fig. 38) that has unfused urosomal segments. Such a morphological anomaly suggests that fusion of urosome segments may be a convergent feature and therefore not reliable as a primary cladistic character state within the Corophiinae.

Within the intermediate subgroup (3), *Lobatocorophium* is distinctive in the unique form of its urosomal "plug". The genus is most closely similar to the similarly western Pacific-endemic genus *Hirayamaia* (below). The genus *Crassicorophium* encompasses three arctic and subarctic species that demonstrate generally intermediate character states and a trend to intersexual and parthenogenetic reproduction. The most advanced species, *C. bonelli*, may merit separate subgeneric recognition. The genus *Hirayamaia* embraces three western Pacific species, slightly more closely similar in generic-level character states, particularly in the partly ventral insertion of uropod 1. *H. tridentia* may prove subgenerically distinctive in its relatively advanced form of peduncular segment 5 of antenna 2, and propod and dactyl of gnathopod 2.

In the morphologically most advanced major subgroup (2) uropod 1 arises partially to fully ventrally on the fused urosome. The genus *Monocorophium* encompasses several closely similar species in which uropod 1 arises mainly laterally. These may be clustered within 3 further subgroups: a *californianum-oaklandense* pair on the left, having sexually similar antenna 2 and plesiomorphic form of gnathopod 1; a largely North Pacific endemic *insidiosum-carlottensis-steinegeri* complex in the centre, and an *acherusicum-sextonae-uenoi* assemblage on the right. The latter overlaps morphologically with members of the genus *Apocorophium* in which uropod 1 arises fully ventrally on the urosome. On the extreme right is the distinctive, monotypic North Pacific genus *Laticorophium.* As noted above (p.125), the latter shows mostly advanced character states, but also relatively plesiomorphic features of the antennal gland cone, mandibular palp, gnathopod 2, and a unique notching of the urosome lateral margin.

Systematics of other corophioidean subgroups.

Other corophioideans with superficially similar cylindrical body form and possible close common ancestors to corophiins, previously assigned to family Corophiidae by Bousfield (1982), also listed by Just (1983), include: (1) *Janice* Griffiths, 1976, and *Ritaumius* Ledoyer, 1978b. However, these genera have an elongate antenna 1 with accessory flagellum; sternal processes; subequal gnathopods (gnathopod 1 slightly dominant), and peraeopods 5-7 subsimilar in form; (2) *Kamaka* Derzhavin, 1923 and *Gaviota* Barnard, 1962 *(=Ampelisciphotis* Pirlot, 1938). However, both genera exhibit isaeid synapomorphies that rule out direct ancestry to corophiins, as well as to siphonoecetins.

On the other hand, a few antiboreal and tropical isaeid genera embrace character states that appear, at least superficially, corophiin or ancestrally corophiin in form. Such features include an elongate, lobate, and setose merus of dominant gnathopod 2. The three genera, *Paracorophium* Stebbing, 1899, *Chaetocorophium* Karaman, 1979b, and *Stenocorophium* Karaman, 1979, have been assigned to family Corophiidae by most previous authors (e.g., Barnard, 1969a, Karaman, 1979a). However, because their combination of defining character states includes an elongate antenna 1, basically 3-segmented mandibular palp; deep overlapping coxal plates; fused urosome segments 1 & 2; and primarily biramous uropod 3, none can be directly ancestral to corophiins, or (more improbably) to the sister-group siphonoecetins. In our view, those genera are more realistically placed in a specialized subfamily (Paracorophiinae) within family Isaeidae.

Biogeographic and behavioural analysis.

The distribution of genera and species of Corophiinae in the North Pacific region is summarized in Table II, (p. 135). Some 34 species are included, all but one (*C. carlottensis*, n. sp.) previously recorded from the region. Although Otte (1976) included *C. clarencense* (Shoemaker) in his treatment of corophiins of British Columbia, the species had been previously recorded only from the extreme northern Bering Sea and North Greenland (Shoemaker, 1920; Just, 1970), and marginally within the present biogeographical analysis.

The North American Pacific corophiin fauna encompasses 16 species in 5 genera, of which 4 species and 1 genus are almost certainly regionally synanthropic. The Asiatic North Pacific fauna is somewhat more diverse and encompasses 20(21?) species in 6 genera, of which 5 species and 1 genus are considered regionally synanthropic.

The North Pacific corophiinids exhibit very high regional endemicity, amounting to ~75%of the total fauna. Thus, species of four Asiatic-endemic genera (*Eocorophium, Sinocorophium, Microcorophium,* and *Lobatocorophium*) do not occur naturally along North American shores and, in fact, nowhere else. Conversely, the genus *Americorophium* is largely endemic to the Pacific coast of North and Central America\ and sparsely in the tropical and warm-temperate western Atlantic, somewhat resembling that of the *Bemlos* clade of the Aorinae (Myers, 1988). With respect to thermal affinities, primitive burrowing species occur only along warm-temperate and temperate coastlines of both continents; none reaches subarctic or arctic shores. However, a few specialized members of the polymorphic advanced tube-building genus *Monocorophium* (e.g., *M. clarencense, M. crassicorne. M. bonelli,* and *M. steinegeri*) are essentially arctic and arctic-boreal in distribution. More advanced species of *Monocorophium*, and known species of the *Apocorophium* complex, are restricted to temperate and warm-temperate waters.

Synanthropic species encompass almost exclusively colonial tube-builder species of the advanced genera *Monocorophium* and *Apocorophium.* Except for *Sinocorophium alienense,* believed to have become established in San Francisco Bay through shipments of clams and oysters from the Orient (Chapman, 1988), North Pacific burrowing species are otherwise not synanthropic. Similarly, European endemic burrowing species of the genera *Corophium, Medicorophium* and *Chelicorophium* occur nowhere else synanthropically. *Corophium volutator* occurs both in northwestern European waters, and in the Gulf of Maine region of North America, but this distribution is considered naturally amphi-Atlantic (Bousfield, 1973).

Corophiins and Siphonoecetins: compartive biology.

The world distributions of corophiin and siphonoecetin amphipods appear to be mutually exclusive, or nearly so. Thus corophiins are dominant in boreal and temperate regions of the Northern Hemisphere (10 genera vs. only 1 genus of Siphonoecetinae). About 6 species of *Siphonoecetes* overlap with corophiins in the North Atlantic. Corophiins are dominant in the North Pacific along both North American and Asiatic coasts, whereas siphonoecetins, except for a few bubocorophiids in Japan and some concholestids on the Central American coast, are virtually absent. Unlike siphon-

TABLE II. DISTRIBUTION OF GENERA AND SPECIES OF COROPHIINAE IN THE NORTH PACIFIC REGION (* synanthropic record).

GENUS	BIOGEOGRAPHIC ZONE									
	1	1A	2	3	4	5	6	7	8	9
1. ***Eocorophium*, n. g.**										
E. kitamori (Nagata)	X	X								
2. ***Sinocorophium*, n. g.**										
S. japonica (Hirayama)		X								
S. sinensis (Zhang)	X	X								
S. lamellatum (Hirayama)	X	X								
S. heteroceratum (Yu)	X									
S. intermedium (Ngoc)	X									
S. homeoceratum (Yu)	X									
S. minutum (Ngoc)	X									
S. orientale (Schellenberg)	X									
S. triangulopedarum (Hir)	X									
S. alienense (Chapman)	?							X*		
3. ***Microcorophium*, n. g.**										
M. miospinulosum (Hirayama)	X									
4. ***Lobatocorophium*, n. g.**										
L. lobatum (Hirayama)		X								
5. ***Hirayamaia* n. g.**										
H. hongkongensis (Hirayama)	X									
H. mortoni (Hirayama)	X									
H. tridentium (Hirayama)	X									
6. ***Apocorophium*, n. g.**										
A. acutum (Chevreux)		X*								
7. Crassicorophium, n. g.										
C. bonelli (M. E.)			X	X	?					
C. crassicorne (Bruz.)	x?	X	X	X	X	X	X	X		
8. ***Monocorophium*, n. g.**										
M. steinegeri (Gurjanova)			X	X	X	X	?			
M. carlottensis n. sp.				x	X	X				
M. acherusicum (Costa)	X*	X*	X*		?	X*	X*	X*	X*	
M. insidiosum (Crawford)	x*	X*					X*	X*	x*	X*
M. uenoi (Stephensen)	X	X	x?						X*	X*
M. sextonae (Crawford)		X*								
M. californianum (Shoemaker)							x	X	X	x
M. oaklandensis (Shoemaker)									X	
9. Laticorophium, n. g.										
L. baconi (Shoemaker)	X*			?	X	X	X	X	X	x
10. ***Americorophium*, n. g.**										
A. brevis (Shoemaker)			?	x	X	X	X	X	X	
A. spinicorne (Stimpson)					X	X	X	X	X	
A. salmonis (Stimpson)						X	X	X		
A. stimpsoni (Shoemaker)							x?	X		

BIOGEOGRAPHIC ZONES: 1. East & South China Seas; **1A.** SE Sea of Japan; **2.** Sea of Okhotsk & NE Sea of Japan; **3.** Bering Sea & Aleutians; **4.** Southeastern Alaska; 5. Northern B. C.; **6.** Southern B. C.; **7.** Wash.-Oregon; **8.** Northern & Central California; **9.** Southern & Baja California. (+ - excl. *H. monospinum* Shen, 1955) oecetins, a few corophiins (*Crassicorophium* spp.) have penetrated arctic waters.

By contrast in the southern hemisphere, especially in tropical regions, siphonoecetins, particularly concholestids are dominant. Except for a few commercially introduced species, corophiins are rare. However, both groups are rare or lacking in waters around South America and Antarctica.

As noted initially (pp. 70-71), the two groups contrast in behaviour and life style. Thus, all siphonoecetinids are tubicolous. Most are detritivores, but possibly also feed on settling larval stages or meiofauna. The bases of peraeopods 3 & 4 are much broadened and house silk-secreting glands. The silk is used to cement relatively large objects rather than sediment grains to form an abode, or to glue houses of other animals (esp. females) to that of the male. Simple mud tubes are never encountered. The tubes usually have only one entrance. Animals show minimal behavioural response to guard the rear, and no development of the urosome to form a "plug". When feeding currents change, siphonoecetins simply reverse direction of the entire movable house. Peraeopods 5, 6, 7 are similar to those of corophiins in having prehensile hooked dactyls that are adapted to clinging to the inside of the tube.

In sipohoneocetins, antenna 2 is powerful, ambulatory and, paired, used as legs in slow forward crawling, and dragging the isolated moveable abodes, similar to those functions in cerapid ischyrocerids, and many small pagurid decapods. Antenna 2 is also used in a "backwards jumping" behaviour peculiar to many advanced subgroups of siphonoecetins. However, it does not appear to be used in mate guarding or amplexus. Gnathopods 1 & 2 are used in manipulating building materials and/or the abodes of other animals.

In corophiins, only the most advanced members are ful-ly tubicolous. All species are believed to be filter-feeding detritivores but *Microcorophium* may be a micro-carnivore. The bases of peraeopods 3 & 4 are little broadened in strictly burrowing species, but are moderately to strongly so in silk-secreting (abode-building) species. Peraeopods 5 & 6 are short, variously adapted by means of hook spines of segment 5, and by short, curved dactyls that are reversed for clinging to the inside of the tube. However, peraeopod 7 remains elongate and the dactyl ambulatory, not hook-like.

Domicolous corophiids live in fixed abodes, often forming mats of tightly packed tubes, which may be glued to each other. The tubes have two openings. Animals show a strong flipping behaviour within the tube to guard the rear entrance against intruders or to change feeding direction as tidal currents reverse. Advanced species (with fused urosome) block the rear entrance with the modified urosome and uropods. In burrowing corophiins that excavate tubes within the substratum, antenna 2 is equipped with paired apical hook spines and is used in ambulation. However, in males, this appendage apparently functions also in mate guarding and/or amplexus (Conlan, 1991). Primitive corophiins use antenna 2 in burrowing and facilitating first entry into the substratum, and may secondarily line the tube with silk.

REFERENCES

Austin, W. C., 1985. An annotated checklist of marine invertebrates of the cold temperate northeast Pacific.Khoyatan Marine Laboratory, Cowichan Bay, B. C., Vols. I-III, 682 pp.

Aldrich, F. A., 1961. Seasonal variations in the benthic invertebrate fauna of the San Joaquin River estuary of California, with emphasis oin the amphipod, *Corophium spinicorne* Stimpson. Proc. Nat. Sci. Philadelphia 113-2): 21-28. 2 figs.

Barnard, J. L., 1952. Some Amphipoda from central California. Wasmann Journal Biology 10: 9-36, 9 pls.

————., 1954. Marine Amphipoda of Oregon. Oregon State Monographs, Studies in Zoology 8: 1-103.

————., 1958. Index to the families, genera, and spe cies of thw gammaridean Amphipoda (Crustacea). Occ. Pap. Allan Hancock Foundation Publications 19:1-145.

————, 1962. Benthic Marine Amphipoda of southern California: families Aoridae, Photidae, Ischyroceridae, Corophiidae, Podoceridae. Pacific Naturalist 3: 1-72, 32 figs.

————., 1964. Marine amphipods of Bahia de San Quintin, Baja California. Pacific Naturalist 4: 55-139, 21 figs., 17 charts, 3 tables.

————., 1969a. The families and genera of marine gammaridean Amphipoda. Bull. U. S. Nat. Mus. 271: 1-535, 173 figs.

————., 1969b. Gammaridean Amphipoda of the rocky intertidal of California: Monterey Bay to La Jolla. Bull. U. S. Nat'l Mus. 258: 1-230, 65 figs.

————, 1970. Sublittoral Gammaridea (Amphipoda) of the Hawaiian Islands. Smiths. Contr. Zool. No. 34: 286 pp., 180 figs.

————, 1973. Revision of Corophiidae and related families (Amphipoda). Smiths. Contr. Zool. No. 151: 1-27, 1 fig.

————, 1975. Amphipoda. Pp. 313-366, pls. 70-85. **In:** R. I. Smith & J. T. Carlton (eds.). Light's Manual: Intertidal Invertebrates of the Central California coast, 3rd edition. 716 pp. Univ. California Press, Berkeley.

————., & C. M. Barnard, 1983. Freshwater Amphipoda of the World. Vols. I & II. Hayfield Associates, Mt. Vernon, VA., 830 pp., 50 figs.

————, & G. S. Karaman, 1991. The Families and Genera of Marine Gammaridean Amphipoda (Except Marine Gammaroids). Rec. Austral. Mus., Suppl. 13, Parts 1 & 2, 866 pages, 133 figs.

Bousfield, E. L., 1958. Ecological Investigations on seashore invertebrates of the Pacific coast of Canada. Natl. Mus. Canada Bull. 147: 104-115.

————, 1963. Studies on littoral marine invertebrates of the Pacific coast of Canada, 1964. I. Station List. Nat'l Mus. Can. Bull. 185:72-89.

————, 1968. Investigations on seashore invertebrates of the Pacific coast of Canada, 1957 and 1959. I. Station List. Nat'l Mus. Can. Bull. 185:72-89.

——————, 1973. Shallow-water gammaridean Amphipoda of New England. Cornell University Press, Ithaca, N. Y. 312 pp., 69 pls., 13 figs.

——————, 1982. Amphipoda, Gammaridea. In: S. B. Parker [ed.]. Synopsis and Classification of Living Organisms. McGraw-Hill, N. Y. Vol 2.: 255-285.

——————, 1983. An updated phyletic classification and palaeohistory of the Amphipoda. Crust. Issues, Balkema, Rotterdam 1: 257-277.

——————, & A. Chevrier, 1996. The amphipod family Oedicerotidae on the Pacific coast of North America. Part 1. The *Monoculodes* and *Synchelidium* generic complexes: systematics and distributional ecology. Amphipacifica II (2): 75-148, 42 figs.

——————, and N. E. Jarrett, 1981. Station lists of marine biological expeditions of the National Museum of Natural Sciences in the North American Pacific coastal region, 1966 to 1980. Syllogeus, No. 34: 1-66, 13 figs., 7 tables.

——————, & D. E. McAllister, 1962. Station list of the National Museum Marine biological expedition to southeastern Alaska and Prince William Sound. Natl. Mus. Canada Bull. 183: 76-103.

——————, & C.-t. Shih, 1994. The phyletic classification of amphipod crustaceans: problems in resolution. Amphipacifica, I(3): 76-134.

Bradley, J. C., 1908. Notes on two amphipods of the genus *Corophium* from the Pacific coast. Univ. Calif. Publ. Zool. 4: 227-252, figs.

Bruzelius, R. M., 1859. Bidrag till kannedomen om skandinaviens Amphipoda Gammaridea. Kongl. Svensk Vetensk. Akad. Handl., new series, 3: 104 pp., 4 pls.

Cadien, D. B., 1991. List of the marine amphipod fauna of the temperate and boreal northeastern Pacific Ocean, including literature records of occurrence between Bahia San Quintin, Baja California, and the south side of the Aleutian Islands, incorporating nomenclatural changes listed in Barnard & Karaman, 1991. SCAMIT technical publication, Sept. 1991, 21 pp. Los Angeles, California.

Carausu, S., 1943. Amphipodes de Roumanie I. Gammarides de type Caspien. Monogr. Inst. Rech. Pisc. Romaniei 1: 293 pp., 20 figs, .85 plates.

Carausu, S., E. Dobreanu, & C. Manolache, 1955. Amphipoda forme salmastre si de apa dulce. Faune Republ. Populare Romine. Crustacea, Vol. IV (4): 409 pp., 368 figs.

Carlton, J. T., 1979. History, biogeography and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. PhD thesis, University of California, Davis. 904 pp.

——————., 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanography and Marine Biology Annual Review 23: 313-371, 1 fig.

Chapman, J. W., 1988. Introduced Northeast Pacific Amphipods. J. Crust. Biol. 8 (3): 362-382, Figs 3-5.

Chevreux, E., 1908. Sur trois nouveaux amphipodes du Mediterraneens appartenant au genre *Corophium* Latreille. Bull. Soc. Zool. Franc 33: 69-75, 6 figs.

Chevreux, E., & L. Fage, 1925. Amphipodes. Faune de France 9: 488 pp., 438 figs.

Conlan, K. E., 1983. The amphipod superfamily Corophioidea in the northeastern Pacific region. 3. Family Isaeidae: systematics and distributional ecologyt. Publ. Nat. Sci., Nat'l Mus. Nat. Sci., Canada 4: 1-75, 36 figs.

——————, 1991. Precopulatory mating behaviour and sexual dimorphism in the amphipod Crustacea. Hydrobiologica 223: 255-282.

Costa, A. 1851. Pp. 44-77, fig. 2 **In**: Gugl. Hope's Catalogo dei Crostacei Italiani e di Molti Altri del mediterranea, Napoli: Azzolino. 1851-1853. Faune del regno di Napoli and Catlaogo de' Crostacei del Regno di Napoli.

Coyle, K. O., & G. J. Mueller, 1981. New records of Alaskan marine Crustacea, with descriptions of two new gammaridean Amphipoda. Sarsia 66: 7-18, 5 figs.

Crawford, G. I., 1937. A review of the amphipod genus *Corophium* , with notes on the British species. Jour. Mar. Biol. Assoc. U. K. 21: 589-630, 4 figs.

Dana, J. D., 1849. Synopsis of the genera of Gammaracea. Amer. Jour. Sci. Arts, ser. 2, 8: 135-140.

Della-Valle, A., 1893. Gammarini del Golfo di Napoli. Fauna und Flora des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Monographie 20: 1-948, 61 pls.

Derzhavin, A. N., 1923. Bemerkung uber Crustacea Malacostraca der unteren Petschora. Russ. Hydrobiol. Jour. 2: 11-115. [with German summary].

Fabricius, J. C., 1779. Reise na h Norwegen mit Bemerkungen aus der Naturhistorie und Oekonomie, Hamburg: Carl Ernst Bohn.

Giambiagi, D., 1929. Un nuevo anfipodo de agua dulce del genero *Corophium*.. Anales del Museo Nacional de Historia Natural 34: 137-143, 3 figs.

Griffiths, C. L., 1976. The Amphipoda of southern Africa. Part. 1. The Gammaridea and Caprellidea of southern Mocambique. Ann. S. Afr. Mus. 60: 265-306, figs. 4-11.

Gurjanova, E. F., 1951. Bokoplavy morej SSSR i sopredel'-nykh vod (Amphipoda-Gammaridea). Akad. Nauk, SSSR. Opredel. po Faune SSSR 41: 1029 pp., 705 figs.

——————. ?

Heard, R. W., & W. B. Sikora, 1972. A new species of *Corophium* Latreille, 1806 (Crustacea: Amphipoda) from Georgia brackish waters with some ecological notes. Proc. Biol. Soc. Washington 84: 467-476, 3 figs.

Hirayama, A., 1984. Taxonomic Studies on the shallow water gammaridean Amphipoda of West Kyushu, Japan. II. Corophiidae. Publ. Seto Biol. Lab. 29(1/3): 1-92, figs. 43-100.

——————, 1986. Marine Gammaridean Amphipoda (Crustacea) from Hong Kong. I. The family Corophiidae, genus *Corophium*. Proc. Second Intern. Mar. Biol. Workshop. Marine Flora and Fauna of Hong Kong and Southern China. Hong Kong, 1986. E. B. Morton. Hong Kong

Univ. Press. 449-485.

————, 1987a. Two peculiar species of corophiid amphipods (Crustacea) from the Seto Inland Sea, Japan. Zool. Sci.: 175-181:175-181, 5 figs..

————, 1987b. Notes on the evolutionary systematics of the genus *Corophium.* Zool. Sci. 4: 569-574., 3 figs.

Hong, J. S., 1983. Amphipods from experimental plates in Deukryang Bay. Korean Jour. Zool. 26(2):135-153, 8 figs.

Hurley, D. E., 1954. Studies on the New Zealand amphipod fauna No. 7. The family Corophiidae, including a new species of *Paracorophium.* Trans. Roy. Soc. New Zealand 82: 431-460, 7 figs.

Irie, H., 1958. Ecological study on important species of epibenthic amphipods. Bull. Rez. Coloniz. Tsushima Cur rent, 135-145. (In Japanese).

Ishimaru S., 1994. A catalogue opf Gammaridean and Ingolfiellidean Amphipoda recorded from the vicinity of Japan. Report Sado Mar. Biol. Sta., Niigata Univ. No. 24, 86 pp.

Just, J., 1970. Amphipoda from Jorgen Brunland Fjord, North Greenland. Medd. om Groenland 184(6): 39 pp., 20 figs.

——., 1983. Siphonoecetinae, subfam. n. (Crustacea, Amphipoda, Corophiidae) 1: Classification. Steenstrupia 9 (6): 355-117.

——., 1988. Siphonoecetinae (Corophiidae) 6: A survey of phylogeny, distribution, and biology. Studies on Am phipoda. Crustaceana Suppl. 13: 193-208, 6 figs.

Karaman, G. S., 1979a. *Stenocorophium bowmani,* a new genus and species of family Corophiidae from the Palau Islands (Crustacea: Amphipoda). Proc.. Biol. Soc. Wash. 92(3): 580-588, 5 figs.

Karaman, G. S., 1979b. Revision of the genus *Paracorophium* Stebb. with description of *P.chelatum,* n. sp. and genus *Chaetocorophium,* n. gen. (fam. Corophiidae). (Contribution to the knowledge of the Amphipoda 100). Glas. Republ. Zavoda Zas. Prirode Prirodn. Muzeja Titograd 12: 87-100.

Kim, B., 1991. New Records of Corophiidae from Korea. Korean Jour. Zool. 24: 110-154, figs. 1-30.

Kudrjaschov, V. A., 1979. Faune i ecologiya raznonogikh rakoobraznykh litorali severnoi chasti Tatarskogo Proliva. Issledovaniya Pelagicheskix i Donnykh Organizmov Dal' nevostochnykh Morei 15: 123-137, 3 figs.

Latreille, P. A., 1806. Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimus explicata 1: 302 pp. Paris & Argentia: Amand Koenig.

Ledoyer, M., 1982. Crustacés Amphipodes gammariens: Familles des Acanthonotozomatidae à Gammaridae. Faune de Madagascar 59 (1): 598 pp, 226 figs.

Lincoln, R J., 1979. British Marine Amphipoda: Gammaridea, 658 pp., 280 figs., 3 pls. London: British Museum (Natural History).

Martynov, A. V., 1924. On some Interesting Malacostraca from Fresh-waters of European Russia. Russ. Gidrobiol. Zhurn. 3: 210-216. (Russian, English summary).

Milne Edwards, H., 1830. Extrait des recherches pour servir a l'histoire naturelles des crustaces amphipodes. Ann. Sci. Natur. 20: 353-399, pls. 1-11.

Miloslawskaja, N., 1931. Nachtrag zur Amphipodenfauna des Schwarzen Meeres. Trav. Sta. Biol. Karadagh 4: 59-51, 1 fig.

Myers, A. A., 1981. Amphipod Crustacea 1. Family Aoridae. Memoirs of the Hourglass Cruises. 5(5): 1-73.

—————, 1982. Family Corophiidae. In: S. Ruffo [ed.] The amphipods of the Mediterranean, Part I. Gammaridea (Acanthonotozomatidae to Gammaridae). Mem. Inst. Oceanogr. 13: 185-208, figs. 74-105.

—————, 1988. A cladistic and biogeographic analysis of the Aorinae subfam. nov. Crustaceana, Suppl. 13: 167-192.

—————, D. McGrath, & P. Cunningham, 1989. Apresumed male of the parthenogenetic amphipod *Corophium bonnelli* (Milne Edwards). Jour. Mar. Biol. Assoc. U.K. 69: 319-321, 1 fig.

Nagata, K., 1965. Studies on marine gammaridean Amphipoda of the Seto Inland Sea. I. Publ. Seto Mar. Biol. Lab. 13(4): 316-318, fig 39.

Nayar, 1950. Description of a new species of amphipod of the genus *Corophium* from Adyar, Madras, India. Jour. Wash. Acad. Sci. 40: 225-228, 1 fig.

Ngoc, D. T., 1965. New amphipods from Viet Nam. Tap San Sinh Vat-Dia Hoc 4: 146-152, 4 figs.

Nishimira, S., 1965. The zoogeographical aspects of the Japan Sea. Part I. Publ. Seto Mar. Biol. Lab. XIII(1): 35-79, figs.

O'Clair, C. E., 1977. Marine Invertebrates in rocky intertidal communities. The Environment of Amchitka Island, Alaska. Tech Information Center. NOAA, Auk Bay, Alaska. Ch. 18: 395-449.

Otte, G., 1976. A laboratory key for the identification of *Corophium* species of British Columbia. Tech. Report No. 519. Pacific Environmental Inst., West Vancouver, B. C. 19 pp., 9 figs.

Pallas, P. S., 1776. Reise durch versehiedene Provinzen des Russischen Reichs, St. Petersburg, Kaiserlichen Academie der Wissenschaften 3: 709.

Powell, R., & P. G. Moore, 1991. The breeding cycle of females of seven species of amphipods (Crustacea) from the Clyde Sea area. J. Nat. Hist. 25: 435-479.

Ricketts, E. F., & J. Calvin, 1968. Between Pacific Tides. Fourth ed., revised J. Hedgpeth. StanfordUniv. Press. 614 pp., 302 figs.

Sars, G. O., 1895a. Amphipoda. An account of the Crustacea of Norway with short descriptions and figures of all the species of Norway. Christiania & Copenhagen 1: 711 pp., 240 pl. + 8 suppl. pl.

Sars, G. O., 1895b. Contributions to the knowledge of the carcinological fauna of the Caspian Sea. Part III. Amphipoda. Third article. Gammaridae (concluded). (Corophidae). Bull. l'Acad. Imper. Sci. St. Petersbourg (5)

3: 275-314, pls., 17-24.

Say, T., 1818. An account of the Crustacea of the United States. Jour. Acad. Nat. Sci. Philadelphia 1: 374-401.

Schellenberg, A., 1928. Report on the Amphipoda. Zoological Results of the Cambridge Expedition to the Suez Canal, 1924. Trans. Zool. Soc. London 22: 633-692, figs. 198-209.

Shen, C. J., 1955. On some marine crustaceans from the coastal water of Fenghsien, Kiangsu Province. Acta Zool. Sinica 7: 75-100, 66 figs.

Schieke, U., 1978. Neue Amphipoda (Crustacea) vom Golf von Neapel (Italia). Boll. Mus. Civ. di Storia Naturale, Verona 5: 335-368, 11 figs.

Shillaker, R. O., & P. G. Moore, 1987. The biology of brooding in the amphipods *Lembos websteri* Bate, and *Corophium bonnelli* Milne-Edwards. Jour. Exper. Mar. Biol. & Ecol. 110: 113-132.

Shoemaker, C. R., 1920. The amphipods of the Canadian Arctic Expedition, 1913-1918. Report of the Canadian Arctic Expedition, 1913-1918, 7E: 30 pp., 6 figs, with appendix.

———————, 1934a. Two new species of *Corophium* from the west coast of America. Jour. Wash. Acad. Sci. 24: 356-360, 2 figs.

———————, 1934b. The amphipod genus *Corophium* on the east coast of America. Proc. Biol.Soc.Washington 47: 23-32.

———————, 1941. A new genus and a new species of Amphipoda from the Pacific coast of North America Proc. Biol Soc. Washington 54: 183-186.

———————, 1943. A new amphipod of the genus *Corophium* from Florida. Charleston Museum Leaflet 18: 6 pp., 1 fig.

———————, 1947. Further notes on the amphipod genus *Corophium* from the east coast of America. Jour. Wash. Acad. Sci. 37: 47-63, 12 figs.

———————, 1949. The amphipod genus *Corophium* on the west coast of America. Jour. Wash. Acad. Sci. 39: 68-82, 8 figs.

———————, 1955. Amphipoda collected at the Arctic Laboratory, Office of Naval Research, Point Barrow Alaska, by G. E. MacGinitie. Smiths. Misc. Coll. 128 (1): 1-78, 20 figs.

Sneath, P. H. A., & R. R. Sokal, 1973. Numerical Taxonomy. W. H. Freeman & Co., San Francisco. 573 pp.

Sowinsky, V. K., 1898. Vysshiia rakoobraznyia (Malacostraca) Bosfora, po materialam sobrannym d-rom A. A. Ostroumovym v 1892 i 93 gg. I. Amphipoda i Isopoda. Zap. Kievsk.Obshch. Estestv. 15: 447-518, pls. 8-13.

Staude, C. P. 1987. Amphipoda: Gammaridea. In: E. N. Kozloff, Marine Invertebrates of the Pacific Northwest. Univ. Wash. Press., Seattle. pp. 354 - 386, 80 figs.

Stebbing, T. R. R., 1899. Revision of Amphipoda. Ann. Mag. Nat. Hist., ser. 7, 3: 350.

———————, 1904. Gregarious Crustacea from Ceylon. Spolia Zeylanica 2(5) : 29 pp., 2 pl.

———————, 1906. Amphipoda I. Gammaridea. Das Tierreich 21: 806 pp., 127 figs.

Stephensen, K., 1915. Isopoda, Tanaidacea, Cumacea, Amphipoda (Excl. Hyperiidea). Report Danish Oceanographic Expeditions, 1908-10 to Mediterranean and adjacent Seas. 2. Biology, D, 1: 53 pp., 33 figs.

———————, 1932. Some new amphipods from Japan. Annotat. Zool. Japan 13: 487-501, 5 figs.

Stimpson, W., 1856. Descriptions of some new marine Invertebrata from the Chinese and Japanese Seas. Proc. Acad. Nat. Sci. Philadelphia 7: 375-384.

———————, 1857. The Crustacea and Echinodermata of the Pacific shores of North America. Jour. Boston Soc. Nat. Hist. 6: 1-92 [reprint], pls. 18-23.

Stock, J. H. , 1952. Some notes on the taxonomy, the distribution, and the ecology of four species of the amphipod genus *Corophium* (Crustacea: Malacostraca). Beaufortia 21: 10 pp., 15 figs.

———————, 1960. *Corophium volutator* forma *orientalis* Schellenberg, 1928, raised to specific rank. Crustaceana 1: 188-192, 2 figs.

Vanhoffen, E., 1911. Beitrage zur Kenntnis der Brackwasserfaune im Frischen Haff. Sitzungberichte Gesellschaft Naturforschung Freunde, Berlin 1911 (9):399-405, 4 figs.

Welitchovsky, V. , 1914. Description d'un amphipode d'eau douce nouveau. *Cyrtophium spongicola* n. sp. Faune du District de Walouyki du Gouvernment de Woronege (Russie), Kharkov, 12: 1-13, + unnumbered plates.

Yu, S. C., 1938. Descriptions of two new amphipod Crustacea from Tang (Vietnam). Bull. Fan. Mem. Inst. Biol., Zool. Ser. 8: 83-103.

Zhang, W., 1974. A new species of the genus *Corophium* (Crustacea, Amphipoda, Gammaridea) from the southern coast of Shangtung peninsula, North China. Stud. Mar. Sinica 9: 139-146, 2 figs.

LEGEND FOR FIGURES

A1	**- antenna 1**	**MX2**	**- maxilla 2**
A2	**- antenna 2**	**MXPD**	**- maxilliped**
AC FL	**- accessory flag.**	**O. P.**	**- outer plate**
BR PL	**- brood plate**	**P3-7**	**- peraeopods 3-7**
CX	**- coxa**	**PL1-3**	**- pleopods 1-3**
DACT	**- dactyl**	**PLEON**	**- pleon segment**
DORS	**- dorsal view**	**PLEOS**	**- pleosome**
EP	**- epimeral plate**	**PLP**	**- palp**
GN1	**- gnathopod 1**	**RET**	**- retinacula**
GN2	**- gnathopod 2**	**RT**	**- right**
HD	**- head**	**SET**	**- seta**
I. P.	**- inner plate**	**SP**	**- spine**
LAT	**- lateral view**	**T**	**- telson**
LFT	**- left**	**U1-3**	**- uropods 1-3**
LL	**- lower lip**	**UL**	**- upper lip**
MD	**- mandible**	**UROS**	**- urosome**
MLR	**- molar**	**VENTR**	**- ventral view**
MX1	**- maxilla 1**	**X**	**- magnified**

Printing Errata in Amphipacifica Vol II(2).

I. Paper No 1. The amphipod superfamily Hadzioidea on the Pacific Coast of North America: Family Melitidae. Part I. The *Melita* group: systematics and distributional ecology.
by N. E. Jarrett & E. L. Bousfield.

p. 10, col. 2, line 46, read: *Desdimelita*, n. g. (p. 40).

p. 11, col. 1, line 18, read: *Desdimelita*, n. g. (p. 40).

p. 27, col. 2, line12, read: N. American Pacific.

p. 30, col. 1, bottom, read: *kodiakensis* (p. 32).

II. Paper No 2. The amphipod family Oedicerotidae on the Pacific Coast of North America. Part I. The *Monoculodes* and *Synchelidium* generic complexes.
by E L. Bousfield & Andree Chevrier.

p. 87, col. 2, line 16, read: British Columbia.

line 44, read: *Monoculodes castalskii.*

p. 106, col. 2, line 12, read: . . in the key, are here. .

p. 122. **Type species.** *Synchelidium spinipes* Mills, 1962 is an invalid name, a printing lapsus for *Synchelidum shoemakeri* Mills, 1962.

p. 140. Fig. 40, read: *M. castalskii* .

Outline manuscripts (with completed station lists and plates) of North Pacific amphipod taxa, available on request from the Managing Editor.

1. Melitidae. Part II (includes *Maera, Ceradocus*).

2. Oedicerotidae. Part II (includes *Bathymedon, West-woodilla*).

3. Hyalidae (includes *Parallorchestes, Hyale*, several new genera).

4. Hyalellidae (*Allorchestes*); Najnidae (*Najna*).

5. Pardaliscoidea, Synopioidea.

6. Lysianassoidea (*Orchomene-Orchomenella* group).

7. Ischyroceridae (*Ischyrocerus*).

8. Cyamidae (*Cyamus*).

9. Melphidippoidea (Melphidippidae, Megaluropidae).

10. Pleustidae. Part IV. (Pleusymtinae, Neopleustinae).

11. Pleustidae. Part V. (Stenopleustinae & Miscellaneous subfamilies).

12. Anisogammaridae (*Anisogammarus*).

13. Pontoporeioidea (*Pontoporeia, Monoporeia, Diporeia, Priscillina*).