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DEDICATION

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

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

From our Readers . .

The first issue of our new journal has been in your hands since January, and the response from readers has been generally encouraging. Although the number of paid subscriptions is to date a bit below initial projections, requests from international libraries and from individual researchers continue to arrive at a steady rate. Excerpts from a few letters are provided below.

We have noted some subscriber concern with mechanical errors in the printed material, and with our proposed system of refereeing submitted papers. The first issue did contain an excessive number of mechanical oversights, attributable in part to computer "glitches", and in part to production inexperience on the part of the managing editor. Although nearly all of these errors are obvious misprints, a list of the errata pertaining to subject matter, particularly in paper No. 2, is provided below (see p. 70). We apologize for these oversights, and trust that you will find this second issue to be mechanically much more acceptable.

With respect to referee scrutiny, the scientific content of submitted papers is examined by a minimum of two qualified referees, one of whom is to be provided by the submitting author(s), and the other by a member of our advisory board. In addition, papers are scrutinized both scientifically and editorially by one or more members of the editorial staff. Members of both advisory and editorial boards of AMPHIPACIFICA serve as referees for other research journals. Moreover, standards of new information content, illustration, and format appear to meet levels deemed acceptable in other refereed scientific journals. Encouragingly, readers have not yet commented negatively on the quality of the scientific content, a sign that the present review system appears to be accomplishing its primary task.

Roy Kropp (Batelle, CA) noted some of the mechanical "glitches" above but wrote: "Yesterday I received my copy of the first issue of 'Amphipacifica'. Boy, was I pleased! I have to admit that I was a bit nervous that it would be published 'on time' and was concerned that it would look more like a 'typed' journal (as one sometimes sees with some symposium proceedings). I shouldn't have worried. Not only will this first issue be very useful (the Jarrett & Bousfield article has already changed the way I have to think about certain west coast 'bugs'), but it is a quality production! Good job to all the people who put this together — I am already looking forward to the next issue."

Tom Bowman (Smithsonian Institution, Washington) states: "It was a pleasant surprise to receive a copy of the first number of AMPHIPACIFICA, full of good papers on Amphipoda". John C. Markham (Arch Cape Marine Lab, Oregon) commented: "it looks like a highly valuable contribution to an essential field that was not being served well". Several Canadian readers, including Geoff Eales (Editor, Canadian Journal of Zoology, Winnipeg), and Dale R. Calder (Royal Ontario Museum, Toronto) had positive commentary

on the format, and on the rôle of a new journal of systematic biology at this time. Some readers valued particularly the informative tribute to the late Jerry Barnard.

As readers may surmise, this new publishing enterprise continues to be a learning experience, and a very time-consuming one, since all its pre-printing phases are carried out essentially by volunteer workers. We are gradually implementing a full range of services provided by publishing programs adapted for APPLE-MAC computer systems. As our proof-reading system becomes further "tightened" and polished, we expect a steady improvement in the finished product. Again, we welcome your readership and support, and hope that you will consider AMPHIPACIFICA as a potential publication outlet for your own larger papers in aquatic biosystematics.

In this issue we delve further into the systematics and biogeography of major components of the North American Pacific amphipod fauna. In developing phyletic relationships within pleustinid amphipods, the authors have described and utilized new, readily visible, and perhaps subfamily-endemic taxonomic characters. These include the morphology and sexual dimorphism of the enlarged rostrum, and slope of the elongated "step-down" margin at the posterior angle of the gnathopod propods. This margin accommodates regularly grouped clusters of raptorial spines against which prey organisms are presumably impaled by the closing dactyl. Character state differences in this raptorial mechanism presumably reflect differences in feeding strategies, apparently even at generic level. Image-editing computer programs have been utilized to enhance comparison of character states illustrated in the earlier literature, with those of present, more detailed formats. Unexpected morphological findings within males of regional phoxocephalid subfamilies have included: (1) a remarkable diversity of vibration-sensory organelles (calceoli) and their location on antennal peduncles and flagella; and (2) a surprising range in complexity of copulatory devices located on the hindmost pair of thoracic legs. These latter mechanisms appear functionally convergent with those of somewhat different form, long known in males of a fossorially similar, but phyletically distant amphipod family, the Pontoporeiidae.

We are also undertaking complimentary exchange advertising with organizations involved in systematic biology, biodiversity, and environmental preservation. In this issue we advertise two journals, edited by Dr. D. E. McAllister, "GLOBAL BIODIVERSITY" (p. 70), and "SEA WIND", Bulletin of the Ocean Voice International (p. 150). On the following page we outline a new book by Don McAllister and Alejandro Ansula, on the care and protection of coral reefs, a need that is paramount to the health of marine environments on a global scale. We thank Dr. McAllister for his excellent introduction to our new journal in a recent issue of SEA WIND, and to the editors of the Journal of Crustacean Biology, the Canadian Journal of Zoology, and the Bulletin of the Canadian Society of Zoologists for similar courtesies.

About our Artist



Susan Laurie-Bourque is a free-lance illustrator and biologist, with extensive experience in botanical, zoological, archaeol-ogical, and general art work. Utilizing research facilities at the Canadian Museum of Nature in Ottawa, and with contract support through the Royal Ontario Museum in Toronto she has, during the past ten years, completed several hundred full plate illustrations of amphipods, isopods and other crustacenas that are basic to the present publication series. Her talents in water colours and acrylics encompass mammals, bird, fishes, and many other natural history subjects. Her studio address is: 3-159 Rue St. Etienne, Hull, Quebec, Canada J8X 1K7.

ANNOUNCEMENT - TAXONOMISTS WORKING GROUP.

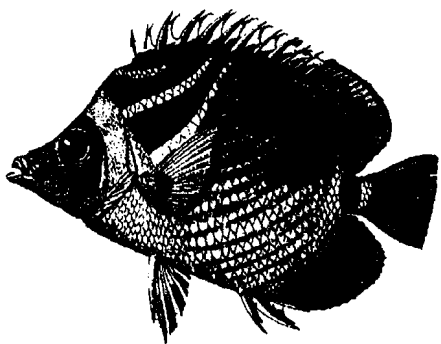
On January 21, 1994, persons interested in the formation of a new society for co-ordinating the collection and identification of aquatic biological specimens, with special emphasis on biotas of western Canada and the northwestern United States, met at the Royal British Columbia Museum, Victoria, B. C. The group is not yet formally named, but would function in association with several other regional and national aquatic biological agencies such AAC, AFS, ASLO, ANEP, APB, AWWA, NABS, PERS, and SCAMIT. Interim officers have circulated the minutes of the meeting and symposium panel discussion, a preliminary "Directory of Taxonomists", and a survey form to potential members. For further information, please contact: Linde LOOY, Fraser Environmental Services, #16 - 9324 128th Street, Surrey, B. C. Canada V3V 6A4 . Telephone and fax (604) 588-9738.

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Filipino editions will be available in 1994 from the Haribon Foundation for the Conservation of Natural Resources, 340 Villamor Street, Pinaglaganan, San Juan, Metro Manila, Philippines.

THE AMPHIPOD SUPERFAMILY LEUCOTHOIDEA ON THE PACIFIC COAST OF NORTH AMERICA. FAMILY PLEUSTIDAE: SUBFAMILY PLEUSTINAE. SYSTEMATICS AND BIOGEOGRAPHY.

By E. L. Bousfield¹ and E. A. Hendrycks²

ABSTRACT

Members of the subfamily Pleustinae Bousfield & Hendrycks, 1994 (family Pleustidae) are thick-bodied, carinated, and strongly rostrate, micro-carnivorous, benthic gammaridean amphipods that are endemic to North Pacific and Holarctic coastal shelf waters. The genus *Pleustes* Bate 1858, to which the 15 previously known world species and subspecies had been assigned, is herein subdivided into two genera, *Pleustes* with two subgenera *Pleustes* (*Pleustes*) Bate, and *Pleustes* (*Catapleustes*), new subgenus, and *Thorlaksonius*, new genus. In this systematic treatment, 12 species are newly described and keyed, all previous subspecies are rediagnosed and elevated to full species status, and the resulting 24 species and variations are reallocated to genus and subgenus, as follows:

(1) *Pleustes* (*Pleustes*) *acutirostris*, new species; *P. (P.) gurjanovae*, new species; *P. (P.) lawrencianus*, new species; *P. (P.) obtusirostris* Gurjanova, 1938; *P. (P.) sibiricus* Gurjanova, 1972; and *P. (P.) tuberculatus* Bate, 1858. "*Pleustes*" *occidentalis* (Stimpson, 1864) is considered a *nomen nudum*. Nomenclatural resolution of variation within the widespread holarctic species *Pleustes* (*Pleustes*) *panoplus* (Kroyer, 1838), which occurs mainly outside the present study region, awaits further investigation.

(2) *Pleustes* (*Catapleustes*) *constantinus*, new species; *P. (C.) victoriae*, new species; *P. (C.) angulatus* Shoemaker, 1955; *P. (C.) japonensis* Gurjanova, 1972; and *P. (C.) paradoxus* Gurjanova, 1972.

(3) *Thorlaksonius amchikanus*, new species; *T. borealis*, new species; *T. brevirostris*, new species; *T. carinatus*, new species; *T. grandirostris*, new species; *T. subcarinatus*, new species; and *T. truncatus*, new species. Rediagnosed species include the North American Pacific *Thorlaksonius depressus* (Alderman, 1936), *T. platypus* (Barnard & Given, 1960), and the Asiatic Pacific species *T. incarinatus* (Gurjanova, 1938), *T. obesirostris* (Bulycheva, 1952), and *Thorlaksonius* sp., originally treated by Nagata (1965) as a species of *Pleustes*, *sens. lat.*

Pleustinid amphipods probably originated in coastal waters of the boreal North Pacific region. From there the more advanced genus *Pleustes* has spread into colder and deeper waters of the high arctic and northern North Atlantic marine regions where it appears to be actively in the process of speciation.

INTRODUCTION

The gammaridean amphipod subfamily Pleustinae was established by Bousfield and Hendrycks (1994) to encompass a set of some 15 previously known, and about 12 undescribed, species and variants of heavy bodied, carinated, and strongly rostrate holarctic members of family Pleustidae. The purpose of this study is to describe, at the level of genus, subgenus, and species, the morphological, distributional, and ecological features of this fauna with special reference to those members occurring in North American Pacific coastal marine waters.

Previous studies on this fauna in the North Pacific region are quite limited. In North American waters, the first pleustinid record was that of Stimpson's enigmatic species, *Amphithonotus occidentalis* (1864), included by Stebbing (1906) as a species of *Pleustes*. Alderman (1936) described

and figured *Pleustes depressus* from central California, later listed by Barnard (1975), Austin (1985), and Staude (1987) from Washington to California. Barnard & Given (1960) described and figured *Pleustes platypa* from central California, and Barnard (1969b) amplified the regional morphological variability and distribution of the species. Shoemaker (1955) figured *Pleustes angulatus* from the Pt. Barrow region of Alaska. More recently O'Clair (1977) listed *Pleustes* sp. from the *Laminaria* community at Amchitka I., and Slaterry and Oliver (1987) provided notes on the ecology, life history and ecto-commensals of "*Pleustes tuberculatus*" from the Bering Sea coast of Alaska.

In the northwestern Pacific region, systematic work on pleustinids was somewhat more extensive. Although a number of variants of *Pleustes panoplus* (Kr.), had long been known from western arctic regions of Russia, Gurjanova (1938) first described *Pleustes cataphractus obtusirostris*, *P. c. typicus*,

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

² Canadian Museum of Nature, Ottawa, Ontario, Canada. K1P 6P4

and *P. incarinatus* from its far-eastern (Pacific) waters. Further records from the Okhotsk and Japan Sea regions were included in the larger compendium of Gurjanova (1951), to which Bulycheva (1952) added *Pleustes obesirostris* from Peter-the-Great Bay. In her further major revisionary study, Gurjanova (1972) amplified descriptions and summarized all pleustid records from Soviet far-eastern seas. She included the new subspecies *Pleustes panoplus sibiricus*, *Pleustes cataphractus japonensis*, the nominate subspecies *P. c. cataphractus* (Stimpson, 1853), and *Pleustes angulatus paradoxus*. Further regional distributional and ecological records were given by Tzvetkova and Kudrjaschov (1985). From coastal marine waters of Japan, Nagata (1960, 1965) recorded and figured *Pleustes panoplus*, to which records from Tomioka and Shijiki Bays were added by Hirayama (1988). All previous work on the systematics of the genus *Pleustes* (*sens. lat.*) had been updated and summarized by Barnard & Karaman (1991), a solid reference base on which the present study was brought to completion.

ACKNOWLEDGEMENTS

The present North American pleustinid material, comprising some 12 species in 3 genera and subgenera, was accumulated mainly as a result of NMNS field expeditions in the North American Pacific region, from southeastern Alaska to northern California, during the period 1955-1980. Pertinent station lists are detailed elsewhere (Bousfield, 1958, 1963, 1968; Bousfield & McAllister, 1963; and Bousfield & Jarrett, 1981). Other material, now in the research collections of the Canadian Museum of Nature, Ottawa, was provided mainly by C. E. O'Clair, Auke Bay, Alaska, C. P. Staude, Friday Harbor, Washington, and P. N. Slattery, Moss Landing, California. Full acknowledgement of assistance provided by institutions and colleagues in the field work and for provision of pleustid study material has been provided elsewhere (Bousfield & Hendrycks, 1994) and is again gratefully expressed here. The authors especially value the help of artist Susan Laurie-Bourque, Hull, Que., in preparing the line illustrations, and Marjorie Bousfield, Montreal, Que., in translating some of the pertinent Russian literature. We thank Drs. C.-t. Shih, K. E. Conlan, and Diana Laubitz, CMN, for their commentary on earlier drafts of the text, and C. P. Staude, FHL, and P. Lambert, Royal British Columbia Museum, for all phases of editorial assistance in this issue.

SYSTEMATICS

An updated overview of gammaridean amphipod family Pleustidae and its subfamily composition has been provided recently by the authors (Bousfield and Hendrycks, 1994). The present study provides a detailed revision of the nominate subfamily Pleustinae, based mainly on material from the North American Pacific coastal marine region, and on new insights applied to the pertinent taxonomic literature.

PLEUSTINAE, Bousfield & Hendrycks, 1994 (Figs. 1, 2)

Pleustidae Stebbing, 1906: 310 (partim).—Gurjanova, 1951: 336 (part);—Gurjanova, 1972: 635 (part).—Barnard, 1969a: 421 (partim).—Barnard & Karaman, 1991: 644 (partim).
Pleustinae Bousfield & Hendrycks, 1994: 39.

Type Genus. *Pleustes* (*Pleustes*) Bate, 1858: 362.

Genera and Subgenera: *Pleustes* (*Catapleustes*), new subgenus; *Thorlaksonius*, new genus.

Diagnosis: Body stout, broadest at pereon segment 5. Pereon, pleon and urosome variously carinate or toothed mid-dorsally and dorso-laterally. Urosome segment 2 dorsally occluded (or nearly so) by segments 1 & 3. Rostrum strongly developed, often sexually dimorphic (larger in male). Eyes large, roundish, protruding from head surface. Anterior head lobe acute; inferior antennal sinus shallow. Antennae medium, slender. Antenna 1 slightly longer than antenna 2; peduncular segments 2 and 3 short. Accessory flagellum lacking.

Mouthparts modified. Upper lip, median notch shallow, lobes slightly asymmetrical. Lower lip, inner lobes small, deep, outer lobes large, oblique, not widely separated. Mandible, molar very small, conical, apex pilose; spine-row long, blades numerous (14-30+), thick, pectinate; left lacinia 7-8 dentate, right lacinia lacking; incisor irregularly 8-dentate; palp not elongate, stout, segment 3 often with basal cluster of "A" setae, or none. Maxilla 1, outer plate with 9 apical spines; inner plate small, with 1 subapical seta; palp segment 1 with prominent setose lateral wing; apex of segment 2, oblique, spinose. Maxilla 2, inner plate broadened, short, inner basal submarginal plumose seta(e) often present. Maxilliped, outer plate narrow, basically columnar (outer margin may be slightly convex), inner margin setose, apex rounded, spinose; inner plate short, broad, with stout apical and inner marginal spines; palp stout, apex of segment 3 rounded, slightly extending beyond base of dactyl, armed with pectinate spines; dactyl slender.

Coxal plates 1-4 very deep, broad, covering leg bases, often medially ribbed; hind cusps small or lacking; coxa 1 hatchet-shaped, covering lower head, but excavated beneath the eye; coxa 4 with posterior process. Gnathopods large, powerfully subchelate, subequal, not sexually dimorphic; basis slender, anterior margin setose; merus with acute postero-distal process; carpus short, hind lobe narrow, deep; propod, palm smoothly convex, lacking median tooth, posterior angle with well-developed "step-down" margin bearing 3(4) groups of stout spines; outer "s.-d." marginal spines often extend along palmar margin, distally largest; inner marginal spines few (3-5), subequal; hind margin short, bare.

Pereopods 3 and 4 slender, anterior margin of basis setose, segment 4 longest, 5 shortest, dactyls medium short. Pereopods 5-7 homopodous, stouter, and dactyls longer, than in pereopods 3-4; coxae acute behind, laterally ridged;

bases slightly narrowed, vertically ribbed; basis of peraeopod 7 with proximal posterior tooth or cusp; segment 4 usually strongly overhanging segment 5 behind.

Pleon plates broad, deep, hind corners acute or produced, hind margins smooth or with basal cusp. Pleopods strong, rami subequal, peduncles long, marginally setose. Uropods 1-2, rami long, serially spinose marginally, apices acute; uropod 1, rami subequal, peduncle lacking distal ecdysial spine. Uropods 2 & 3, outer ramus markedly shorter than inner ramus. Uropod 3, inner ramus more than twice length of peduncle. Telson short, broad, keeled proximally, penicillate setae distal, apex subtruncate.

Coxal gills large, laminar or plate-like, smaller or pallet-like on peraeopods 2 & 6. Brood plates broad, normal.

Distributional Ecology: To date, members of this subfamily have been recorded only from high-salinity, summer-cold waters of the North Pacific, North Atlantic, and Arctic seas. Shallow-water species are associated with rocky coastlines where they frequently cling to large kelps and benthic algae, or to sponges and other colonial invertebrates. Many are beautifully maculated, in all colours from nearly pure white to almost black. Some mimic the shells of mitrellid snails (Carter & Behrens, 1980). The thick, heavily armoured bodies and slow rate of ecdysis (of larger instars of arctic species) render them attractive substrata for temporary settlement of barnacles and other fouling organisms (Slattery & Oliver, 1987).

Taxonomic commentary: The Pleustinae is a moderately advanced but very distinctive subfamily group. Apomorphic character states occur commonly in the mouthparts (vestigial mandibular molar, small columnar outer plate of the maxilliped), gnathopods (powerfully subchelate, smooth-palmed, with short, deeply lobate carpus), and peraeopods (modified coxae and bases of peraeopods 5-7). These are shared mainly with the Parapleustinae, Pleusirinae, and other advanced pleustid subfamilies (see Bousfield & Hendrycks, 1994). However, the strongly rostrate head and carinated body, weakly modified upper and lower lips, and strong spine-teeth of the inner plate of the maxillipeds are considered plesiomorphic with respect to other subfamilies. The sexually dimorphic rostrum and the dorso-laterally bicarinate urosome are apomorphies unique to the Pleustinae. However, these character states appear remarkably congruent with corresponding features of the enigmatic leucothoidean family Lafystiidae (Bousfield, 1987).

With subfamily Pleustinae, members of the *Pleustes panoplus* group of species are demonstrably more similar to the *Pleustes angulatus* group, than to members of the *P. platypus-depressus* group. The principal differences are summarized in the following key (p. 9), and in the dorsal body outlines (Fig. 1). Hence the decision here to recognize, formally, the first two taxonomic groups as the subgenera *Pleustes* and *Catapleustes* within genus *Pleustes* (pp. 8 and 28), and the last group as a distinct full genus of its own, *Thorlaksonius* (p. 38).

Table I. Genera, Subgenera and Species of Pleustinae

<i>Pleustes (Pleustes) panoplus</i> (Kroyer)	Holarctic;
and variants	North Atlantic
<i>P. (P.) acutirostris</i> , new species	Can. Arctic
<i>P. (P.) tuberculatus</i> Bate, 1858	Arctic
<i>P. (P.) sibiricus</i> Gurjanova, 1972	Siberian Sea
<i>P. (P.) gurjanovae</i> , new species	Siberian Arctic
<i>P. (P.) lawrencianus</i> , new species & var.	Bering Sea
<i>P. (P.) obtusirostris</i> Gurjanova, 1938	Okhotsk, Japan
<i>P. (P.) occidentalis</i> (Stimpson, 1864) *	Eastern Pacific
<i>Pleustes (Catapleustes) victoriae</i> , n. sp.	BC
<i>P. (C.) constantinus</i> , new species & var.	Bering Sea-BC
<i>P. (C.) angulatus</i> Shoemaker, 1955	Arctic Alaska
<i>P. (C.) japonensis</i> Gurjanova, 1972	Japan - Bering?
<i>P. (C.) paradoxus</i> Gurjanova, 1972	Okhotsk Sea
<i>Thorlaksonius amchitkanus</i> , new species	Bering Sea
<i>T. incarinatus</i> (Gurjanova, 1938)	Okhotsk - Japan
<i>T. platypus</i> (Barnard & Given, 1960)	California
<i>T. borealis</i> , new species	SE Alaska - BC
<i>T. brevisrostris</i> , new species	SE Alaska - OR
<i>T. subcarinatus</i> , new species	SE Alaska - BC
<i>T. depressus</i> (Alderman, 1936)	California
<i>T. grandirostris</i> , new species	BC - Oregon
<i>T. obesirostris</i> (Bulycheva, 1952)	Japan Sea
<i>Thorlaksonius</i> species (Nagata, 1960-65)	Coasts of Japan
<i>T. carinatus</i> , new species	SE Alaska - BC
<i>T. truncatus</i> , new species & var.	BC

* *nomen nudum*

TAXONOMIC FEATURES OF PLEUSTINIDS

In previous taxonomic treatments of pleustinid amphipods, characters of the external body surface and of the gnathopods have been utilized most frequently. These features tend to vary somewhat within species and populations, and between sexes and instars, but limits of variation for each can be established. Character states of peraeopods, uropods and telson have been less consistently employed, and those of the mouthparts, coxal gills and pleopods utilized little or not at all. Thus, for pragmatic reasons, and until a geographically broader series of specimens can be examined for each species, conspicuous external features are employed mainly here also.

The terminology of principal taxonomic features of the Pleustinae are illustrated in Figs. 1 & 2. With respect to external body features (Figs. 1, 2A), protruberances (teeth, tubercles, carinations) of the upper body surface (peraeon, pleon, and urosome) are localized longitudinally in a mid-dorsal carina, and paired dorso-lateral carinae and mid-lateral ridges or carinae. In members of subgenus *Catapleustes*, the lateral carinae of coxae 5-7 may extend wing-like from the body surface, and inferior lateral tubercles (carinae) may be present just above the mid-lateral ridge.

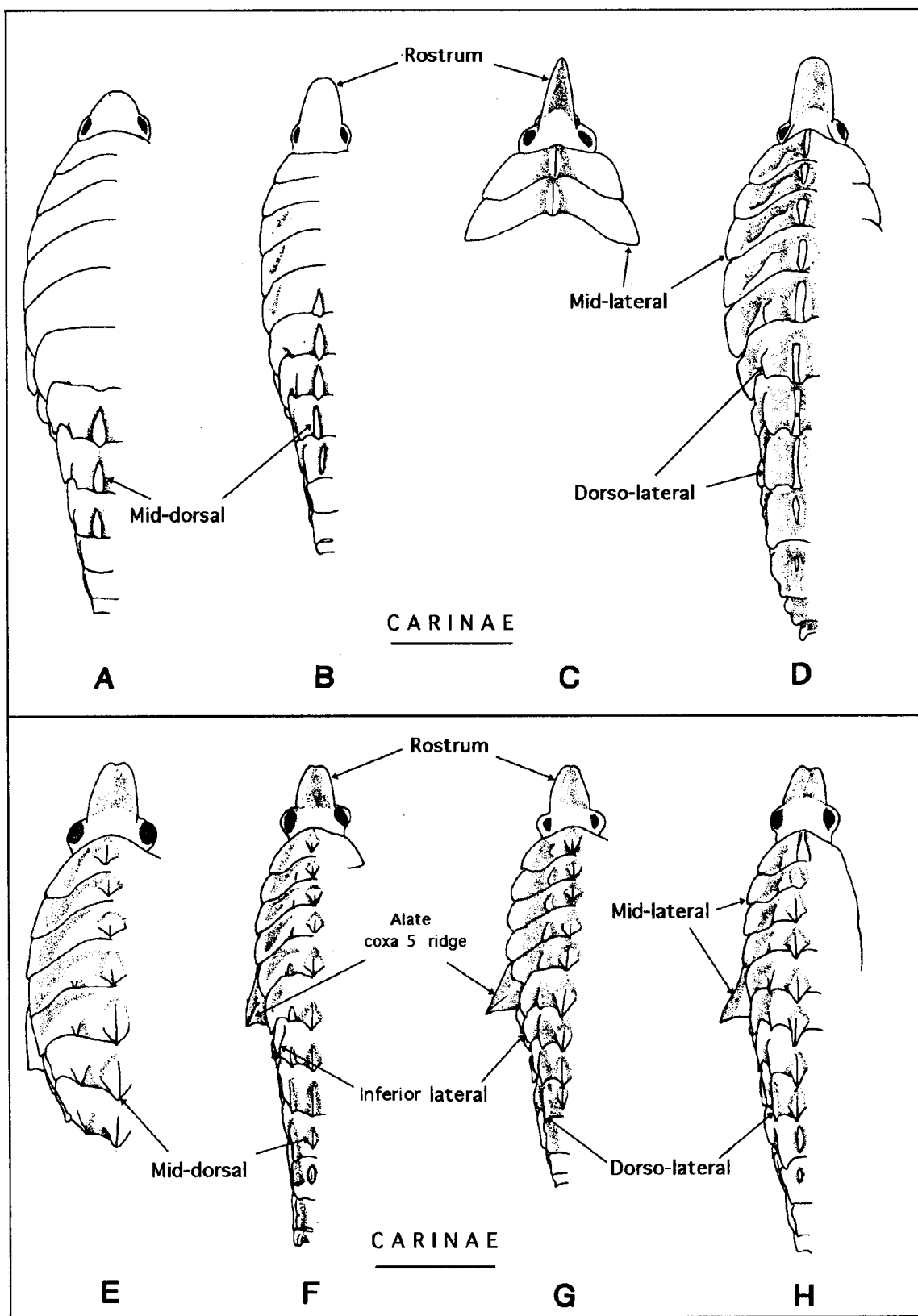


FIG. 1. Dorsal View of *Thorlaksonius* spp. A-B; *Pleustes* (*Pleustes*) spp. C-D; *Pleustes* (*Catapleustes*) spp. E-H.

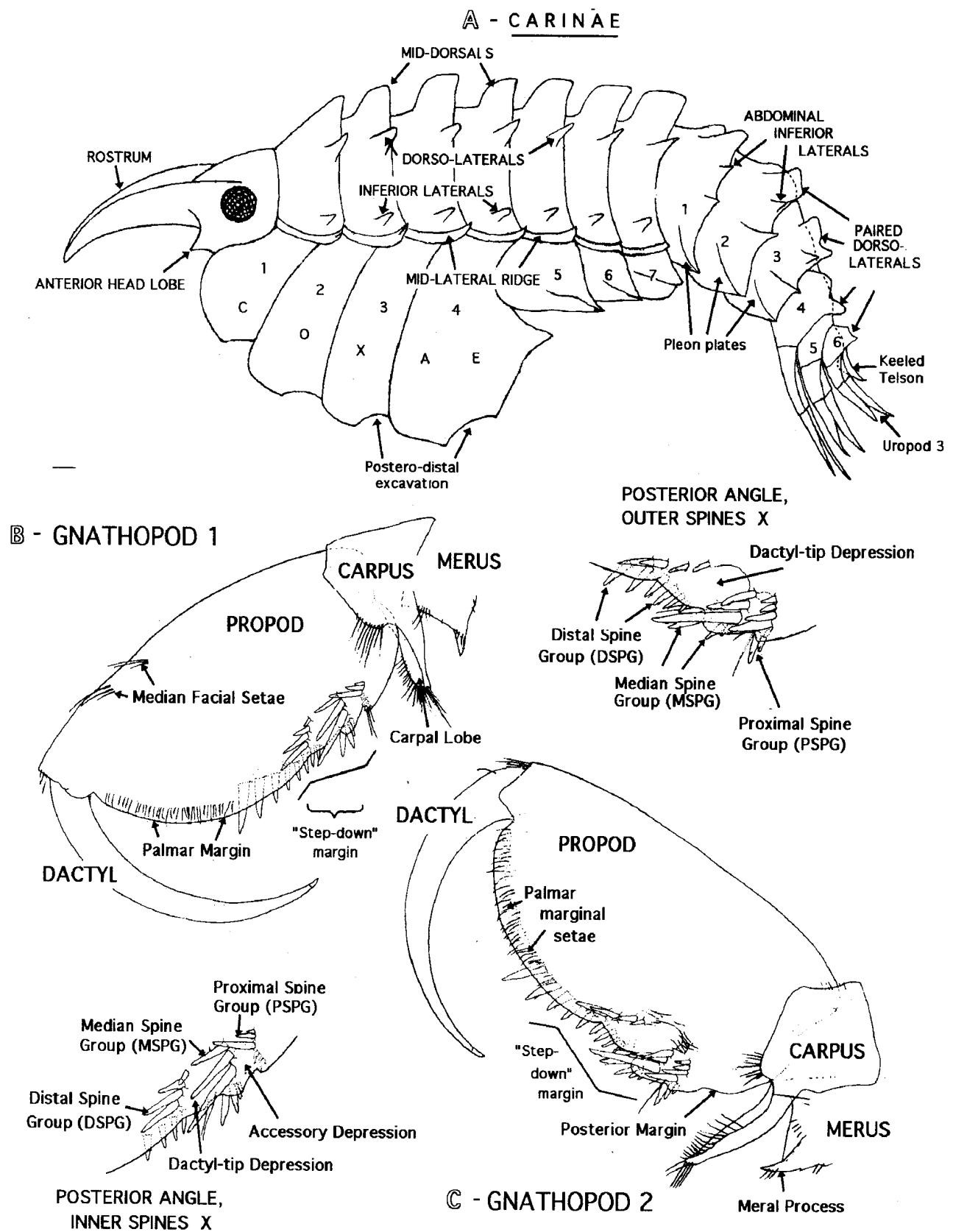


FIG. 2. MORPHOLOGICAL TERMINOLOGY OF PLEUSTINAE A. Body - Lateral View
B. Gnathopod 1 - Lateral View C. Gnathopod 2 - Lateral View

In the posterior pleon and urosomal segments 1 & 2, the mid-dorsal carinae are usually low, but the paired dorso-lateral carinae are large, often tooth-like, or elongate (ridge-like or wing-like) and variously medially incised, often deeply so. Inferior-lateral teeth may extend onto pleon segments 1-3 in *Catapleustes*. Urosome segment 2 is very short and lacks dorsal processes in all pleustinids. In subgenera of *Pleustes*, the hind margins of pleon plates 1-3 usually bear a proximal tooth or cusp.

In gammaridean amphipods, the posterior angle of the gnathopod propod demarcates the junction of the palmar margin with the posterior margin. In pleustinids, the posterior angle is armed with spines of various sizes and thicknesses which are grouped, usually in 3 clusters, on both inner and outer marginal faces of the propod. Prey organisms are presumably impaled on these spines when the dactyl is closed suddenly. These consist of a distal spine group (DSPG), a median spine group (MSPG) and a proximal spine group (PSPG) (rarely also a fourth small accessory proximal spine group). In species of *Catapleustes* and *Thorlaksonius*, the distal spine group extends along the outer margin of the palm. Its distal-most spine is the largest of the series, often much larger than the adjacent spine. The number of spines in each cluster, and the total number of major spines at the posterior angle are here considered to be taxonomic features that appear to be diagnostic of the species. Spine counts here represent a minimal number since minute, vestigial, or setose spines are not included.

In pleustinids also, the palmar angle has an elongated border of its own, here termed the "step-down" margin, that is usually sloped or angled differently to either the palmar or posterior margins. The angular change of slope between palmar and "step-down" margin may be gentle (<30°), merging equally gently with the posterior margin. In most species of *Pleustes*, however, the angle of change is often large (>45°), usually larger in gnathopod 2, and occasionally nearly at right angles to the palmar margin.

When resting, the tip of the dactyl closes into a shallow cavity or dactyl-tip depression (D-TD) on the inner face of the propod, between the DSPG and the MSPG. The pit varies in size and shape, and its proximal border may be marked by a faint semi-circular line or ring on the surface of the propod. A second smaller accessory depression occurs between the inner median and proximal spine groups.

Other noteworthy features of the distal segments of the pleustinid gnathopod include the acute postero-distal process of the merus, the very narrow carpal lobe (larger in gnathopod 2), the short posterior margin of the propod (often less than 1/2 length of palmar margin), the median anteriorly submarginal facial setae of the propod, the short closely set palmar marginal setae, and the smooth, uniformly arcuate dactyl with its very short, and weakly differentiated unguis. The anterior margin of the basis of gnathopod 1 is lined with numerous medium-long setae, the clustering and location of which appears to have species-level significance. Features of the mouthparts are equally diagnostic, but are much less useful in pragmatic identification keys.

Pleustes Bate

Pleustes Bate, 1958: 362.—Stebbing, 1906: 309.—Gurjanova, 1951: 635 (partim).—Barnard, 1969a: 425 (partim).—Gurjanova, 1972: 141 (partim).—Karaman & Barnard, 1979: 114 (partim).—Barnard & Karaman, 1991: 650 (partim).

Subgeneric content: *Pleustes* (*Pleustes*) Bate 1858: 362 (TYPE); *Pleustes* (*Catapleustes*), new subgenus (p. 28).

Diagnosis: Body carinate, toothed or ridged mid-dorsally, dorso-laterally, and mid-laterally (occasionally inferior laterally) on some or all peraeonal, pleon, and urosomal segments. Pleon 3 with prominent pair of bilobate, dorso-lateral carinae. Urosome 3, paired dorso-lateral carinae elevated, acute behind. Rostrum large, basally broad, with median dorsal depression and paired dorso-lateral ridges that are proximally supra-orbital, distally often deflexed or down-curved, tip acute or less often truncate, slightly sexually dimorphic.

Antenna 1, peduncular segment 1 large, 2 & 3 relatively long. Mouthparts distinctive. Mandible, palp segment 3 with numerous (4-12) long simple setae arising basally on outer and inner faces (baso-facial or "A" setae). Maxilla 2, inner plate with stout inner marginal seta. Maxilliped, palp segment 2 equal to or longer than 3; inner plate broadened medially.

Coxal plates 1-4 very deep, often vertically ribbed, lower hind margin often incised. Gnathopods 1 & 2, propod, angle of "step-down" margin often large (>45°), especially in gnathopod 2; distal-most group of spines at posterior angle variously (or not) extending along palmar margin; dactyl-tip depression often large, deep; accessory depression, smaller, less distinct.

Peraeopods 3-7 slender, seldom stout; segment 5 short, not strongly overhung posteriorly (<40%) by segment 4; dactyls medium to medium long. Peraeopods 5-7, coxae laterally ridged, often toothed or wing-like, usually acute and/or produced behind; bases, hind margins shallowly incised or straight, hind lobes narrowly rounded or subacute.

Pleon plates 1 & 2 (occ. 3) with acute basal posterior marginal cusps. Uropods ordinary. Telson short, little longer than wide, apex subtruncate. Coxal gills large, plate-like, little modified anteriorly.

Taxonomic commentary: The subgenera combined within genus *Pleustes* would appear, in balance, more closely similar to each other than to the genus *Thorlaksonius* (see Discussion, p. 63). Especially diagnostic are: the form of the rostrum (basally broad with lateral ridges, arising supra-orbitally, not strongly sexually dimorphic); strongly carinate and toothed peraeon, pleon and coxae 5-7; generally slender peraeopods, somewhat stronger in peraeopods 5-7 than in peraeopods 3-4; and the baso-facially setose mandibular palp, among other differences.

The present taxonomic treatment departs from previous studies in two main procedures: (1) elevation, to species and

KEY TO GENERA AND SUBGENERA OF SUBFAMILY PLEUSTINAE

1. Body carinated or ridged dorsally and/or mid-laterally on peraeon segments 1-4 and dorso-laterally on urosome segment 3; rostrum lateral ridges arise supra-orbitally; mandible, palp segment 3 with numerous (5-12) baso-facial setae 2.
- Peraeon segments 1-4 and urosome segment 3 dorsally and laterally smooth; rostrum lateral ridges arise antero-orbitally; mandible, palp segment 3 with 0-1 (rarely 3-5) baso-facial setae. *Thorlaksonius* (p. 38)
2. Coxae 1-4, lower hind margin sharply and deeply incised; peraeon segments 1-4 usually with mid-lateral carinae or teeth; gnathopod 2, propod, spines at posterior angle extending onto outer margin of palm and beyond corresponding inner marginal spines *Pleustes* (*Catapleustes*) n. subg. (p. 28)
- Coxae 1-4, lower margin continuous, nearly straight throughout; peraeon segments 1-4 rarely bearing mid-lateral teeth; gnathopod 2, propod, spines at posterior angle not extending onto outer palmar margin *Pleustes* (*Pleustes*) Bate (p. 9)

subgeneric significance, characters earlier treated as of subspecific value only, and (2) utilization of new characters and new character states (mainly of mouthparts and gnathopods) in diagnoses at all levels. The need to re-examine type material, much of which is no longer available, especially where the original species descriptions and illustrations were limited, is urgent. However, general correlations between body carination, rostral form, and other superficial features (prominently treated in the literature) can be made with detailed characters of mouthparts, gnathopods and other seemingly more reliable taxonomic characters. A phylogenetically more satisfactory arrangement of all species, previously known or newly described herein, may then be attempted (see below, p. 62).

Pleustes (*Pleustes*) Bate, new status

Pleustes Gurjanova, 1951: 435 (partim).—Barnard, 1969a: 425 (partim).—Gurjanova, 1972 (partim): 141.—Barnard & Karaman, 1991: 650.

Type Species: *Amphithoe panopla* Kroyer, 1838 (*non* *Pleustes tuberculata* Bate, 1858).

Species content: *Pleustes* (*P.*) *panoplus* (Kroyer, 1838: 270); *Pleustes* (*P.*) *occidentalis* (Stimpson, 1864: 158); *Pleustes* (*P.*) *tuberculatus* Bate, 1858: 362; Stephensen, 1938: 252; Gurjanova, 1972: 148, figs. 4B, 6; *Pleustes* (*P.*) *obtusirostris* Gurjanova, 1938: 313, fig. 38; *Pleustes* (*P.*) *sibiricus* Gurjanova, 1972: 150, figs. 7B, 8; *Pleustes* (*P.*) *lawrencianus*, new species (p. 23); *Pleustes* (*P.*) *gurjanovae*, new species (p. 22); *Pleustes* (*P.*) *acutirostris*, new species (p. 18).

LEGEND FOR FIGURES

A1	- antenna 1	MX1	- maxilla 1
A2	- antenna 2	MX2	- maxilla 2
DACT	- dactyl	MXPD	- maxilliped
EP1-3	- pleon plates 1-3	OU PL	- outer plate
GN1	- gnathopod 1	PLP	- palp
GN2	- gnathopod 2	P3-7	- peraeopods 3-7
HD	- head	RT	- right
IN PL	- inner plate	T	- telson
LFT	- left	U1-3	- uropods 1-3
LL	- lower lip	UROS	- urosome
MD	- mandible	♂	- male
		♀	- female

Diagnosis: Body large at maturity (15-28 mm). Peraeon and pleon segments moderately to strongly carinate and/or toothed dorsally and mid-laterally; peraeon segments 1-4 usually not (or weakly) carinate mid-laterally (dorso-laterally), not inferior laterally, nor strongly laterally; pleon segment 3 usually lacking acute postero-lateral cusp. Head, rostrum usually strong, slender, tip acute or occasionally truncate, dorsal median depression shallow; lateral ridges arising fully supra-orbitally, lower margin straight or slightly concave.

Mandible: blade row with numerous (20-30+) blades; palp segment 3 with numerous (11-16+) baso-facial setae. Maxilla 1, palp segment 1, lateral process strongly developed. Maxilliped, outer plate usually with 2 apical spines.

Coxal plates 1-4 facially smooth or with faint vertical mid-rib only; lower margin appearing straight or slightly curved, hind corners squarish or rounded, not excavate or incised. Coxae 5-7, usually acute, produced behind, laterally ribbed, not toothed. and setose.

Gnathopods 1 & 2, propods, distal group of postero-distal spines not extending onto outer palmar margin, and not beyond corresponding inner marginal spines; dactyl-tip depression (between distal and penultimate spine groups) usually large angle of "step-down" margin steep, (usually $>45^{\circ}$ to line of palmar margin).

Peraeopods 5-7, segments usually little stronger and dactyls not noticeably longer than in peraeopods 3-4; bases, hind margins gently rounded or straight, rarely concave, hind lobes usually rounded.

Uropods relatively short; uropod 1 not longer than pleon segment 3 and urosome segments 1-3 combined. Telson typically short, squarish, slightly broadened distally.

Distributional Ecology: Component members tend to be Arctic and Holarctic, extending southwards into the North Atlantic and North Pacific regions approximately to the limit of summer-cold shelf waters, seldom at slope or abyssal depths. This situation contrasts with that of the subgenus *Catapleustes*, the 5 known species of which tend to occur deeply subtidally in northeastern and northwestern Pacific regions, and with the 12 known species of genus *Thorlaksonius* that occur mainly shallowly subtidally on both N. American and Asiatic coasts of the North Pacific region.

Taxonomic Commentary: Within subfamily Pleustinae, members of the subgenus *Pleustes* are morphologically much more similar to members of the *Catapleustes* subgroup than to those of the *Thorlaksonius* subgroup. Hence the decision to recognize *Thorlaksonius* as a separate full genus (p. 38).

Pleustes (Pleustes) panoplus (Kroyer)

Amphithoe panopla Kröyer, 1838: 270, fig. 9.

Amphithonoptus cataphractus Stimpson, 1853: 52.

Pleustes panoplus Sars, 1895: 344, pl. 121.—Stebbing, 1906: 310.—Gurjanova, 1951: 635, fig. 433.—Barnard & Karaman, 1991: 651, fig. 115A.

Pleustes panopla J. L. Barnard, 1969a: 425, fig. 152b.

Pleustes panoplus panoplus Gurjanova, 1972: 147, fig. 4A (partim).

Diagnosis. Mature female (18-27 mm): Peraeon with mid-dorsal ridge, becoming carinated and weakly toothed on posterior 2 segments; dorso-lateral tubercles or teeth lacking on peraeon segments 1-4, trace or very weak on peraeon 5-7; lateral margins weakly carinated or ridged. Pleon segments 1-3 with low mid-dorsal carina, and with dorso-lateral tubercles or teeth on each side, strongest on pleon 2, ridge-like on

pleon 3; pleon plates 1 & 2 each with proximal posterior marginal tooth. Urosome segments 1 and 3, paired dorso-lateral ridges not strongly elevated.

Rostrum slender, arched, apex subacute, lower margin slightly concave. Eye medium, sub-ovate. Antenna 1, flagellum with 30-45 segments. Antenna 2 shorter, flagellum with 20-26 segments.

Mouthparts typical of genus. Mandibular palp segment 3 with cluster of 11-12 baso-facial setae; spine row with 25-30+ blades. Maxilliped, outer plate with 2 apical spines.

Coxa 1 regularly hatchet-shaped. Coxa 4, hind margin steeply sloped. Coxae 5-7 with shallow lateral ridge, acuminate behind. Gnathopod 1, basis, anterior margin strongly setose throughout; propod, angle of "step-down" margin medium (about 45°), dactyl-tip depression medium small; distal cluster of 3-4 short subequal spines, none enlarged. Normal or regular postero-distal spine (PDSP) formula: outer - 4:3:3; inner - 3:3:4, total of 20-21. Gnathopod 2, propod slightly deeper and shorter; PDSP formula: outer 3:3:4; inner 4:3:3, total of 20-21; total gnathopod spine count 40-42.

Peraeopods 5-7, hind margin of bases nearly straight, very slightly convex; segment 4 weakly (~30%) overhanging segment 5 posteriorly; dactyls relatively short, < 50% length of respective propods.

Uropod 2, outer ramus about 4/5 length of inner ramus. Uropod 3, inner ramus 3 X length of peduncle, and 1.7 X length of outer ramus.

Telson broadening distally, about as long as wide, apex broadly rounded

Sexual dimorphism inconspicuous. Males slightly smaller than females.

Colour: Body dark brown, whitish, or variegated with shades of brown; eye dark red (Sars, 1895; Stebbing, 1906).

Distribution: This species has been recorded widely throughout Arctic and North Atlantic regions. Figured specimens that rigorously match the type morphology have been recorded only from the eastern North Atlantic region, in coastal waters from Scandinavia to Iceland, in depths of 5-155 m.

Taxonomic Commentary: The present diagnosis is based mainly on the description and figures of Sars (1895), supplemented by notes from Stebbing (1906) and Gurjanova (1951) who examined material from the general region of the type locality, and adjacent waters. In addition, considerable morphological variation has been noted in material from various subregions throughout the holarctic range of this species. Five regional variants are treated immediately below. However, several records of *Pleustes panoplus* in previous literature can be attributed to other species, as noted elsewhere in the text. A full treatment of all records, in which pertinent material can be re-examined, is recommended by the authors.

KEY TO KNOWN SPECIES OF *PLEUSTES* (*PLEUSTES*)

1. Rostrum, apex variously pointed or acute; peraeopods 3 - 7 slender, segments 4 and 5, length > 3X respective width; urosome 3, paired dorso-lateral carinae or "wings" acutely pointed behind; maxilliped, inner plate with 5-7 apical spines 2.
 —Rostrum, apex variously blunt or truncate; peraeopods 3-4 relatively short, stout, segments 4 & 5, length < 3X respective width; urosome 3, dorso-lateral "wings" low, rounded behind; maxilliped, inner plate with 8 apical spines 6.
2. Peraeon segment 5 lacking elevated or posteriorly toothed mid-dorsal carination; gnathopods 1 & 2, spine count at posterior angle of propod high (>15) 3.
 —Peraeon segment 5 with elevated and/or posteriorly toothed mid-dorsal carination; gnathopods 1 & 2, spine count at posterior angle of propod low (<15) 5.
3. Peraeon segments 6 & 7, mid-dorsal carinae low, not elevated, lacking posterior tooth; pleosome 3, paired lateral carinae not deeply incised medially and little elevated above mid-dorsal line; gnathopod 2 propod, spine count at posterior angle totals 18-22 *P. panoplus* complex (pp.10-17)
 —Peraeon segments 6 & 7, mid-dorsal carinae elevated, each with posterior tooth; pleon segment 3, paired dorso-lateral carinations elevated well above mid-dorsal line, each with deep median notch; gnathopod 2, propod, spine count at posterior angle totals 15-19 4.
4. Rostrum, apex very slender, nearly straight; peraeon segment 5 lacking dorso-lateral tooth; coxa 1 with 2 postero-distal cusps; gnathopod 2, propod, spine count at posterior angle totals 17-18 *P. acutirostris*, n. sp. (p. 18)
 —Rostrum normally thick, apex downcurved; peraeon segment 5 with dorso-lateral tooth; coxa 1 with single postero-distal cusp; gnathopod 2, propod spine count at posterior angle totals 15-17 *P. tuberculatus* Boeck (p. 18)
5. Rostrum elongate, slender; peraeon segments 1-3 lacking dorso-lateral tooth; coxa 1 with 3 postero-distal cusps; coxa 4, hind margin vertical; gnathopod propods, spine count at posterior angle totals 14-15 *P. sibiricus* Gurjanova (p. 21)
 —Rostrum thick, strongly down-curved; peraeon segments 1-3 each with prominent dorso-lateral tooth or tubercle; coxa 1, single postero-distal tooth very small or lacking; coxa 4, hind margin oblique; gnathopod propods, spine count at posterior angle totals 10-12 *P. gurjanovae*, n. sp. (p. 22)
6. Peraeon segments 1-7 strongly carinated mid-dorsally; peraeon segments 1-4 each with trace of dorso-lateral tubercles; telson short, broad 7.
 Peraeon segments 1-7, mid-dorsal carinations low, not elevated; peraeon segments 1-4 lacking any trace of dorso-lateral tubercles; telson slender, length 1-5 X width . . . *P. obtusirostris* Gurjanova (p. 27)
7. Rostrum elongate, 2-3 X depth, apex narrowly truncate; gnathopod propods, spine count at postero-distal angle totals 18-19 *P. lawrencianus* n. sp. (p. 23)
 —Rostrum medium-short, length about twice depth, apex deeply truncate; gnathopod propods, spine count at postero-distal angle totals 16-17 *P. lawrencianus* var. (p. 23)

Pleustes (*Pleustes*) *panoplus* variants

Subsequent to the original description and illustration of "*Amphithoe*" *panopla* Kroyer 1838 from Norwegian waters, several other species, subspecies, and varieties have been identified in the literature from various holarctic, Atlantic, and Pacific regions. None of these forms has previously been treated in full taxonomic fashion, particularly in details of mouthpart morphology, so that species status and precise phyletic inter-relationships are not yet determinable (Table, p. 12). Such treatment, involving re-

examination of type and topotype material, might include several of the species and subspecies of *Pleustes* (sens. lat.) of Gurjanova (1972). That material, not readily available to us, is beyond the scope of this essentially North American Pacific regional study. However, information provided by previous authors, notably Stebbing (1906), Stephensen (1938), and Gurjanova (1938, 1951, 1972), is sufficient to establish, with reasonable degree of reliability, the generic and subgeneric status of their taxa. The correct identities of their species, however, are somewhat more problematical, and some species new to science may yet be formally recognized.

P. (Pleustes) panoplus, Variation 1
(Fig. 3)

Amphithonotus cataphractus Stimpson, 1853: 52

Pleustes cataphractus Stebbing, 1906: 310.

Pleustes panoplus Holmes, 1905: 489, fig., pl. XXIX.—
Shoemaker, 1930: 309.—Dunbar, 1954: 750?

non: *Pleustes cataphractus* Stephensen, 1938: 252, fig. 28.
—Slattery & Oliver, 1987: 360.

Pleustes cataphractus cataphractus Gurjanova, 1972: 153.

Pleustes panopla Shoemaker, 1955: fig. 14B.

Material Examined: "Prince" Stn. 13, Passamaquoddy Bay, Bay of Fundy, N. B., A. G. Huntsman, Biological Board of Canada, July 8, 1913. - 1 female br. II (16.0 mm) + slide mount, CMN Cat. No. NMCC1994-366 (selected from other material of that collection series, Acc: 51-15).

Diagnosis (Adult female, 12-16 mm): Body medium large, broad, strongly carinate dorsally and laterally (quiquecarinate); surface heavily pitted. Peraeonal segments 1-7 with median dorsal carina increasing in size and acumination posteriorly; small mid-lateral (dorso-lateral) posterior marginal teeth on peraeon segments 5-7; lateral margins (of all) sharply ridged. and posteriorly acuminate, posteriorly produced on segment 5-7; pleon segments 1-3 mid-dorsally carinate (decreasing posteriorly); pleon 1 & 2 each with paired dorsolateral teeth (very strong and acute in 2) and small lateral hind marginal teeth; pleon 3 with paired dorso-lateral ridges, slightly notched medially, hind margin smooth; urosome segments 1 and 3 with paired dorso-lateral carinae, medially notched in 1, elevated and wing-like in 3. Head, rostrum strong, concave above, distally deflexed and acute, lower margin slightly concave. Eyes rounded, bulging from sides of head. Antenna 1, flagellum 40+ segmented. Antenna 2, flagellum slightly shorter than in antenna 1, 28-segmented.

Mandibular palp, segment 3 with cluster of 10-11 basofacial setae. Maxilliped, inner plate with 6-7 apical spines and 1 subapical marginal spine.

Coxal plates 1-4 very deep, lower corners rounded, hind corners with small cusp. Gnathopod 1, basis distally expanded, anterior margin medially heavily long-setose, distally bare; propod, hind margin > 1/2 palmar margin; spine groups at posterior angle each with elongate distal-most spine. Gnathopod 2, angle of "step-down" margin steep (60-70°), D-TD large, deep, distal-most spine of each cluster about twice size of adjacent spine.

Peraeopods 5-7, coxae strongly ridged laterally, acutely produced behind; bases straight or slightly convex behind, lower hind lobes rounded; segment 4 moderately (1/3) overhanging segment 5 posteriorly; dactyls medium (<1/2 propod).

Pleon plates 2 & 3, hind corners acuminate. Uropods 1 & 2, rami slender, inner ramus longer than peduncle. Uropod 3, inner ramus not extending as far posteriorly, margins 6-7 spinose; outer ramus about 60% length of inner ramus. Telson subquadrate, truncate, hind corners rounded.

Body colouration (fresh): "Colour very variable, generally dark reddish or brown, variegated and mottled with white. Some specimens were of a uniform deep purple, others pure white. Eyes yellowish or vermillion colored, with a black dot in the middle" (Stimpson, 1853).

Distributional Ecology: North American Atlantic coast, Labrador to the Gulf of Maine, subtidally to depths of more than 100 m. Not yet recorded from the St. Lawrence estuary or Saguenay fiord.

Behaviour: Stimpson (loc. cit.) noted that the animal in motion "preserves an erect posture, like the isopods, with its tail bent up underneath. It seldom swims but makes powerful leaps by means of its well-developed caudal stylets. When disturbed it rolls itself up and remains quiescent, as if feigning death." In possessing a short urosome segment 2, members of the Pleustinae are morphologically similar to other amphipod groups such as talitroideans and oedicerotoideans with similar saltating behaviour.

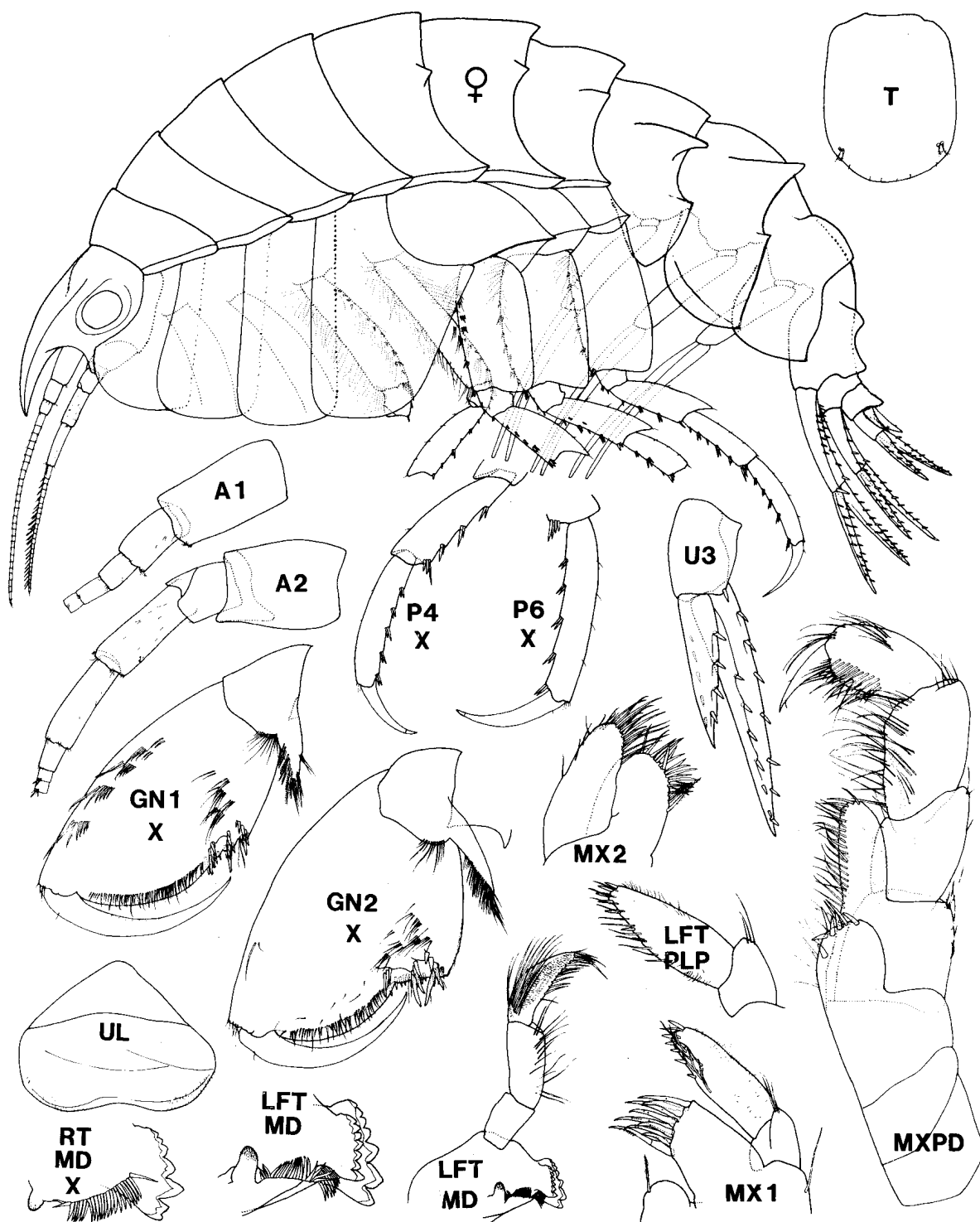
Taxonomic Commentary: Stimpson (loc. cit.) did not figure his material, but gave a reasonably accurate and complete account of its external body features. His description applies closely to the description, figures and lateral view plate of Holmes (1905) based on material from the Grand Manan (type) locality. It is also applicable to material from nearby Passamaquoddy Bay examined above (see fig. 3). The material of Shoemaker (1930), from somewhat greater depths in the southwestern Gulf of St. Lawrence, contains three specimens (ROM collections) the largest of which (a 14.5 mm male) is similar to, but less strongly toothed than, the Gulf of Maine material.

Pleustes cataphractus Slattery & Oliver, 1987, is close to, but probably specifically distinct from, Stimpson's original species from Grand Manan in the Gulf of Maine (see p. 13). Further material is needed to establish its full identity, however.

TABLE OF LOCALITIES OF *P. (P.) PANOPLUS* VAR.

TYPE	<i>P. (P.) panoplus</i> (Koyer).	- N. E. Atlantic
VAR. 1	<i>P. (P.) cataphractus</i> (Stimps)	- N. W. Atlantic
VAR. 2	<i>P. (P.) panoplus</i> Gurjanova	- Greenland Sea
VAR. 3	<i>P. (P.) panoplus</i> Shoemaker	- Can. Arctic
VAR. 4	<i>P. (P.) cataphractus</i> Slattery & Oliver	- N. Bering Sea
VAR. 5	<i>P. (P.) panoplus</i> Slattery	- N. Bering Sea

FIG. 3. *Pleustes (Pleustes) panoplus*, variation 1.
FEMALE, br. II (16.0 mm). Bay of Fundy.
(SEE PAGE 13 - OPPOSITE)



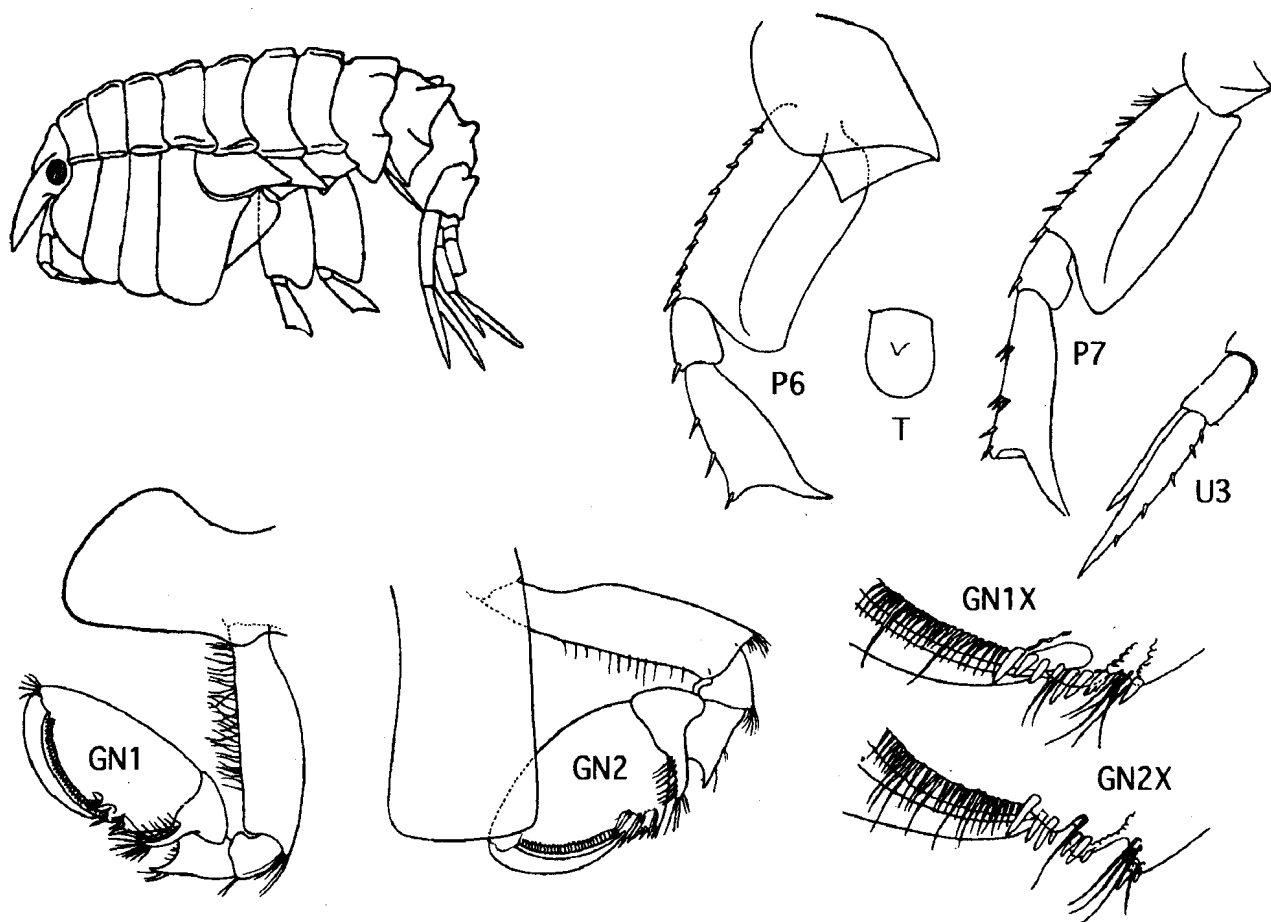


FIG. 4. *Pleustes panoplus* var. 2. (20.0 mm). Greenland Sea.
(modified from Gurjanova, 1972, figs. 4 & 5).

Pleustes (Pleustes) panoplus, variation 2
(Fig. 4)

Pleustes panoplus panoplus Gurjanova, 1972: 147, figs. 4A, 5. (partim).

Diagnosis (Female, 20 mm): Peraeon segments 1-7 with low mid-dorsal carination but lacking dorsal or dorso-lateral teeth or tubercles; lateral ridges regular, not pronounced. Pleon segments 1-3 with low mid-dorsal carination; dorso-lateral teeth distinct, but not exceptional; pleon plates 2 & 3 each with single mid-lateral hind marginal tooth.

Rostrum slender, elongate, lower margin nearly straight, apex acute. Antenna 1, flagellum not clearly shown but estimated to be about 30-35 segments.

Coxal plates 1-4 deep, narrow, gently rounded below; coxa 1 asymmetrically hatchet-shaped, hind corner lacking cusp(?); coxa 4 with sloping posterior margin. Coxae 5-7, mid-lateral ridge acutely produced behind.

Gnathopod 1, anterior margin of basis strongly setose except near antero-distal corner; propod ovate, with long palmar margin (~2X posterior margin), angle of "step-

down" margin shallow, very gently merging with posterior margin. Gnathopod 2, posterior margin very short (1/2 palmar margin); "step-down" at posterior angle gentle (about 30°); dactyl-tip concavity unpronounced; distal group of 3-4 ordinary spines, largest not greatly larger than adjacent spine.

Peraeopods 5-7, hind margins of bases variable, from gently concave (peraeopod 5) to gently convex (peraeopod 7); segment 4 postero-distal lobe with about 1/3 overhang of segment 5.

Uropod 3, length of inner ramus about 3X peduncle and 1.5 X outer ramus. Telson short, little longer than wide, very slightly broadening distally, apex broadly rounded.

Distribution: A deep-water form of the northern part of the Greenland Sea, central Barents Sea, and off Nova Zemlya, in depths of 170-360 m (Gurjanova, 1972).

Taxonomic Commentary: Gurjanova's description and illustration of *Pleustes panoplus panoplus* from the northern part of the Greenland Sea (*loc. cit.*, p. 147, figs 4A, 5) is close to, but minor features distinct from, Kroyer's *P. panoplus*, as

figured and described by Sars (1895, p. 344, pl. 141), and Gurjanova (1951 p. 636, fig.433). Her material may yet be designated as a separate full species.

Pleustes (Pleustes) panoplus variation 3.

Material: Richmond Gulf, Hudson Bay, N. W. T., Canada, F. Johansen coll., Aug. 25, 1920 - 1 male (14.5 mm) + slide mount. Royal Ontario Museum collections, Toronto?

Diagnosis. Male (14.5 mm): Peraeon segments 1-7 with medium strong lateral ridges. Peraeon segments 5 & 6 with low mid-dorsal ridges and small dorso-lateral cusps. Peraeon 4 with slight mid-dorsal ridge posteriorly but no trace of dorso-lateral cusp. Pleon segments 1 & 2 with low mid-dorsal carinae; pleon segment 1, dorso-lateral carina low; dorso-lateral process on pleon 2 subacute, not strongly elevated. Pleon segment 3, dorso-lateral ridge shallowly incised. Urosome 1, dorso-lateral ridge low, elevated barely above mid-dorsal line.

Mandibular palp with 7-9 baso-facial setae. Maxilliped, outer plate with 2 apical spines; inner plate with 8 apical and 2 sub-apical inner marginal spines.

Gnathopod 1, basis with median anterior marginal cluster of long setae; propod, angle of "step-down" margin strong (50-60°); PDSP formula: inner- 3:3:3-4.

Peraeopods 3-4, distal segments relatively short, dactyl about 40% length of segment 6. Peraeopods 5-7, bases, hind margins slightly convex, lower corners rounded; dactyls medium (< 1/2 segment 6).

Pleopod peduncles shorter than subequal rami (inner ramus slightly the shorter), outer margin strongly setose. Inner ramus basally with 5-6 slender, apically bifurcate clothespin spines. Uropod 3, inner ramus 2.5 X peduncle, 60% longer than outer ramus that bears 6-7 serial pairs of marginal spines. Telson slightly longer than wide, slightly broadening distally, apex truncate or shallowly convex.

Variations of Slattery & Oliver (1987).

Material from the southern Chukchi Sea, identified as *Pleustes panoplus* by Slattery & Oliver (1987, p. 362), was not accompanied by taxonomic information. Subsequent re-identification of this material, kindly provided by Dr. Slattery, reveals two distinct variations of the *P. pleustes* form.

Pleustes (Pleustes) panoplus variation 4
(Fig. 5)

Material: Icy Cape, Alaska, southern Chukchi Sea, trawl haul, 8 m., P. N. Slattery coll., July 23, 1984 - 1 female, br. I. (16.0 mm) + slide mount, CMN Cat. No. NMCC1994-367; 1 male (15.0 mm) + slide mount CMN Cat. No. NMCC1994-368; several other male and non-ovigerous female specimens present in this lot..

Diagnosis. Female ov. (16 mm); male (14.0 mm): Peraeon segments 1-7, mid-lateral ridge distinct, little produced posteriorly; mid-dorsal ridge very weak or lacking; peraeon

segments 6 & 7 with very low mid-dorsal carinae and minute trace of dorso-lateral cusps. Pleon segments 1 & 2, dorso-lateral processes low, not or barely extending above low mid-dorsal carinae. Pleon segment 3, and urosome segment 1, dorso-lateral ridge low, shallowly incised. Pleon 1 & 2, basal posterior marginal cusp strong. Rostrum relatively longer and narrower in male. Antenna 1, peduncular segment 2 relatively short, length <1/2 segment 1.

Maxilliped, inner plate with 7 apical spines, and 2 very unequal, subapical inner marginal spines.

Coxa 1, hind cusp small. Coxa 4 not very broad, hind slope steep (~75°). Gnathopod 1, propodus, angle of "step-down" margin medium (~30°); D-TD medium; PDSP formula: outer - 4:3:1; inner - 3:3:4-5, total of 18-19. Meral process minute. Gnathopod 2, angle of "step-down" margin medium (~30-40°); D-TD large; PDSP formula: outer - 4:3:2; inner - 3:3:4-5, total of 19-20; meral process strong.

Peraeopods 3-7, segments normal, dactyls short (40% of respective segment 6).

Telson short, broadening distally, little longer than wide, apex subtruncate.

Pleustes (Pleustes) panoplus, variation 5
(Fig. 6)

Material: Off Wainwright, Alaska, southern Chukchi Sea, otter trawl, 30 m., P. N. Slattery Stn. AHTR9, July 21, 1984 - 1 female (16.0 mm) + slide mount, CMN Cat. No. NMCC1994-369; male (17.0 mm) + slide mount, CMN Cat. No. NMCC1994-370; several other males and females.

Diagnosis. Female, br. I (20.0 mm); male (17.0 mm): Peraeon segments 1-7, mid-dorsal and mid-lateral ridges distinct, mid-dorsal carinae and dorso-lateral cusps distinct on peraeon segments 6 & 7. Pleon segments 1 & 2, mid-dorsal carinae low but distinct; dorso-lateral cusps acute, that of 2 elevated above mid-dorsal line; pleon 3 and urosome 1, dorso-lateral carinae are deeply incised and elevated above mid-line. Urosome 3, dorsal ridge strongly elevated. Pleon plates 1 & 2 each with strong hind marginal cusp. Carinae and teeth relatively larger and stronger, and rostrum, slightly longer in male. Antenna 1, segment 2 relatively long.

Maxilliped inner plate with 8 unequal apical spines, and 2 nearly subequal subapical inner marginal spines.

Coxa 1, hind cusp distinct. Coxa 4 deep, hind margin steeply sloped (70-80°). Gnathopod 1, propod distinctly shallower than that of gnathopod 2. Hind margins regular, not short, length > 1/2 palmar margin. Gnathopod 1, angle of "step-down" margin medium (~30°); D-TD medium; PDSP formula: outer - 4:3:1; inner - 3:3:3+, total of 18-19; meral process medium long. Gnathopod 2, angle of "step-down" margin large (~60°); D-TD large; PDSP formula: outer - 4:3:2+; inner - 3:3+:3+, total of 18-20; meral process strong, acute.

Peraeopods 3-7, segments slender, dactyls long (>1/2 respective segment 6).

Telson short, broadening distally, apex rounded.

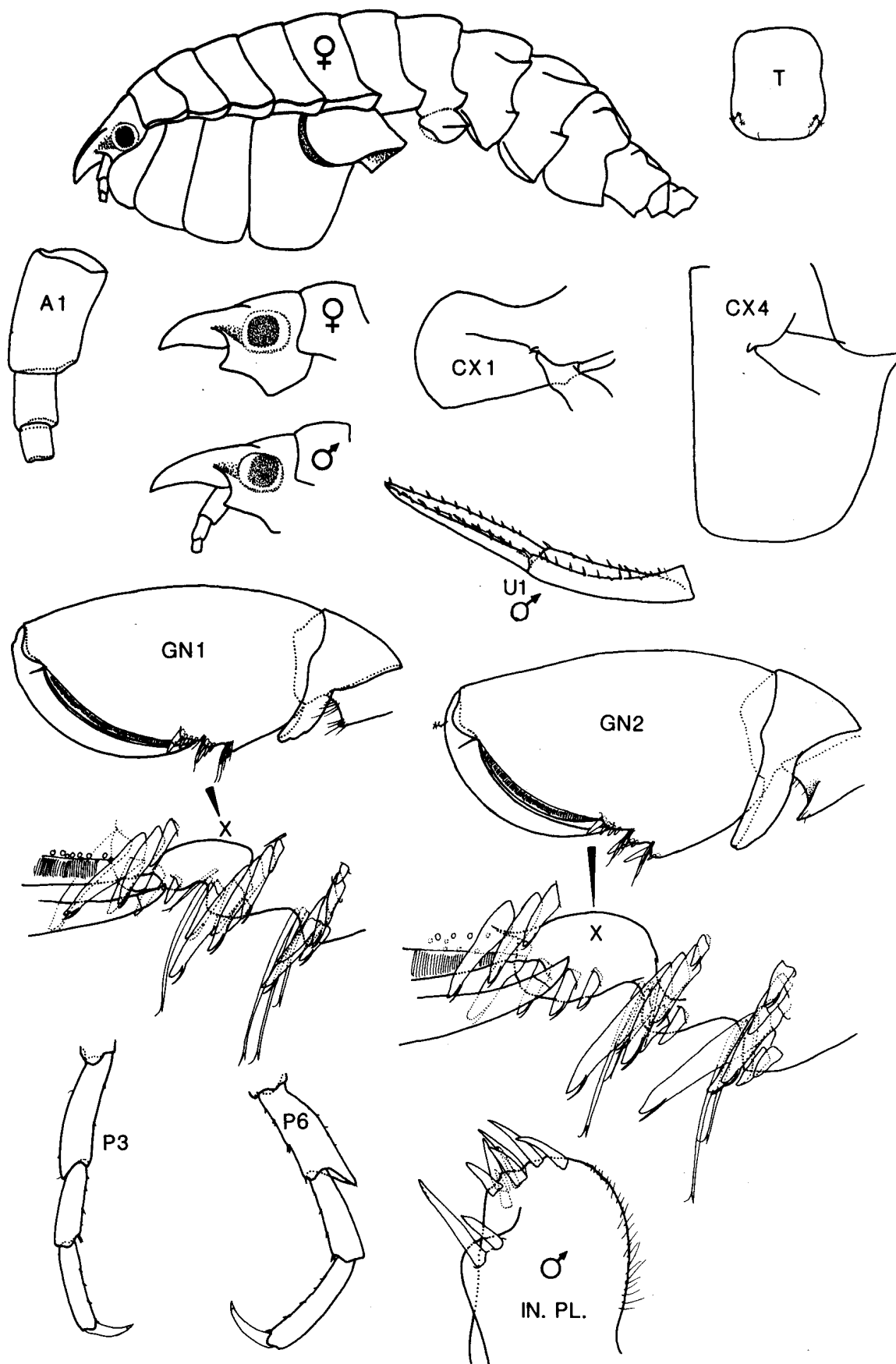


FIG. 5. *Pleustes panoplus* var. 4 ♀ (16 mm) ♂ (14 mm)
Icy Cape, Alaska.

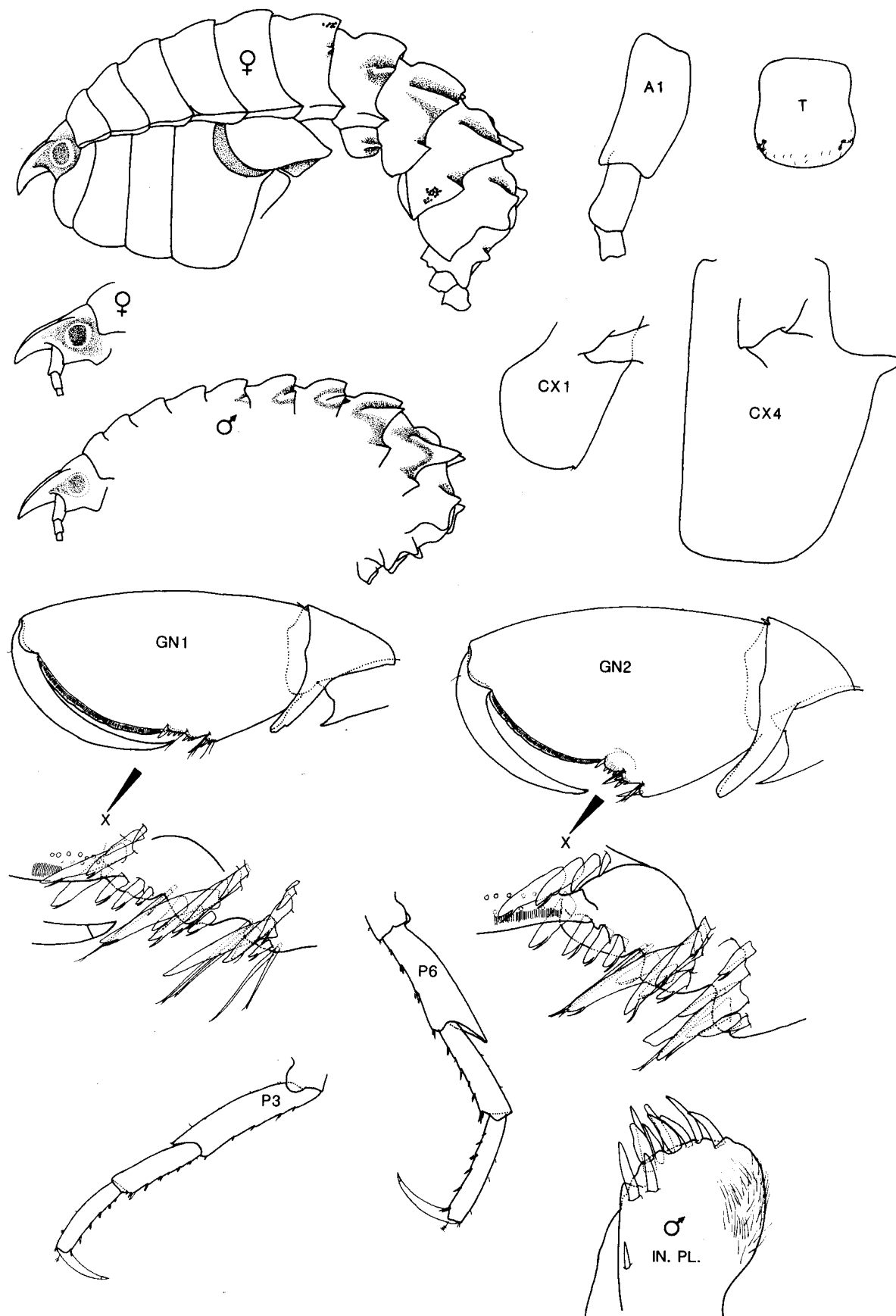


FIG. 6. *Pleustes panoplus* var. 5. ♀ (20.0 mm) ♂ (17.0 mm)
(off Wainwright, Alaska).

Pleustes acutirostris, new species
(Figs. 1B, 7)

Pleustes panoplus Shoemaker, 1955: 40 (partim)?

Material Examined: Prince of Wales Strait, N.W.T., trawl #4, J. Wacasey, Arctic Biol. Stn., 24 July, 1962 - 1 female, br. II (19.0 mm) + slide mount, HOLOTYPE, CMN Cat. No. NMNS 1994-371; *Ibid*, trawl #10, July 26, 1962 - 1 male (16.0 mm) + slide mount, female br. II, PARATYPES, CMN Cat. No. NMCC 1994-372.

Diagnosis: Female br. II (19.0 mm). Peraeon segments 1-4 with low mid-dorsal carinae; peraeon segments 5-7, carinae low, increasing in size, not produced posteriorly; mid-lateral ridges distinct, sharply produced posteriorly; segments 6 & 7 each with medium strong dorso-lateral tooth. Pleon segments 1 & 2 with unproduced ridge-like mid-dorsal carinae, lower on 2; with increasingly large and strongly acute dorso-lateral processes and short ridged posterior marginal cusps. Pleon segment 3 with very low median carina and sharply bilobate ridged dorso-lateral carina but no posterior marginal cusp; hind corners of pleon plates 2 & 3 weakly acute, not produced. Urosome 1, mid-lateral carina elevated, ridge-like, deeply incised medially. Urosome 3, dorso-lateral tooth wing-like, postero-dorsally acute.

Head, rostrum slender, nearly straight, apex narrowly acute, median depression shallow. Antenna 1 & 2 subequal; flagellum of antenna 1 with about 40 very short segments; peduncle 4 of antenna 2 extending beyond peduncle 3 of antenna 1.

Mandible, palp segment 3 with 8-10 baso-facial setae; blade row with 25-30+ blades. Maxilla 1, palp segment 1, lateral lobe with about 6 short setae; apex medially oblique, with 6 spines and sub marginal curve-tipped setae. Maxilla 2, inner margin with weak non-plumose basal seta. Maxilliped, outer plate with 3-4 slender apical spines; inner plate very short, apex with 7 apical and 2 unequal inner marginal stout spines.

Coxal plates 1-4 very large and deep, lower margins slightly convex; hind corner of 2 & 3 each minutely doubly cusped. Gnathopod 1, basis, anterior margin setose proximally and medially; propod, angle of "step-down" margin shallow (~30°), D-TD medium; normal or regular PDSP formula: outer - 4:2:2; inner - 3:4:2, total of 17-19. Gnathopod 2, angle of "step-down" margin steep (60-70°); PDSP formula: outer 3:2:2; inner 3:4:3, total of 17-18; carpal lobe with some distally pectinate setae.

Peraeopods 3-7 medium slender, dactyls medium long (~1/2 length of respective propods); segment 4 overhang (of segment 5) relatively short (<20%). Peraeopods 5-7, coxae strongly acute and produced behind; bases, hind margins slightly convex, lower hind lobes sharply rounded.

Uropods 1 & 2, inner ramus longer than peduncle. Uropod 3, length of outer ramus about 60% that of inner ramus which has 7-8 serial pairs of marginal spines. Telson nearly square, slightly broadened distally, apex subtruncate.

Coxal gills large, plate-like, smaller on peraeopod 6.

Etymology: From the Latin *acutus* - sharpened, and *rostrum* - beak, alluding to the very slender, acute tip of the rostrum.

Distribution: Western Canadian Arctic. The species may also have been included in the material of Shoemaker (1955) from the Pt. Barrow region of Alaska, but that material has not been re-examined.

Taxonomic Commentary: The slender straight rostrum, slender peraeopods, and lowgnathopod propodal spine count distinguish this species from *P. (P.) panoplus* (Kr.) and its variations.

Pleustes (Pleustes) tuberculatus Bate
(Fig. 8)

Pleustes tuberculata Bate, 1858: 362.—Sars, 1895: 344.—Stebbing, 1906: 311.—Stephensen, 1938: 253.

Pleustes panoplus tuberculatus Gurjanova, 1951: 637.—Gurjanova, 1972: 148, figs. 4B, 6. (Kara Sea).—Tzvetkova & Kudrjaschov, 1985.

Diagnosis: Peraeon segments 1-7 mid-dorsally ridged; segments 6-7 each with elevated dorsal and dorso-lateral carina or ridges, toothed weakly behind; segment 5 with weak dorsal carina and trace of dorso-lateral tooth. All peraeon segments with moderate mid-lateral ridges. Pleon segments 1-3 with low mid-dorsal carinae, but very stout, elevated or projecting dorso-lateral teeth, rounded and weakly bifid on 3; pleon plates 1 & 2 each with hind marginal cusp.

Head, rostrum regular, apex acute. Antenna 1, flagellum with about 40 segments. Antenna 2, flagellum distinctly shorter than in antenna 1, with about 20 segments.

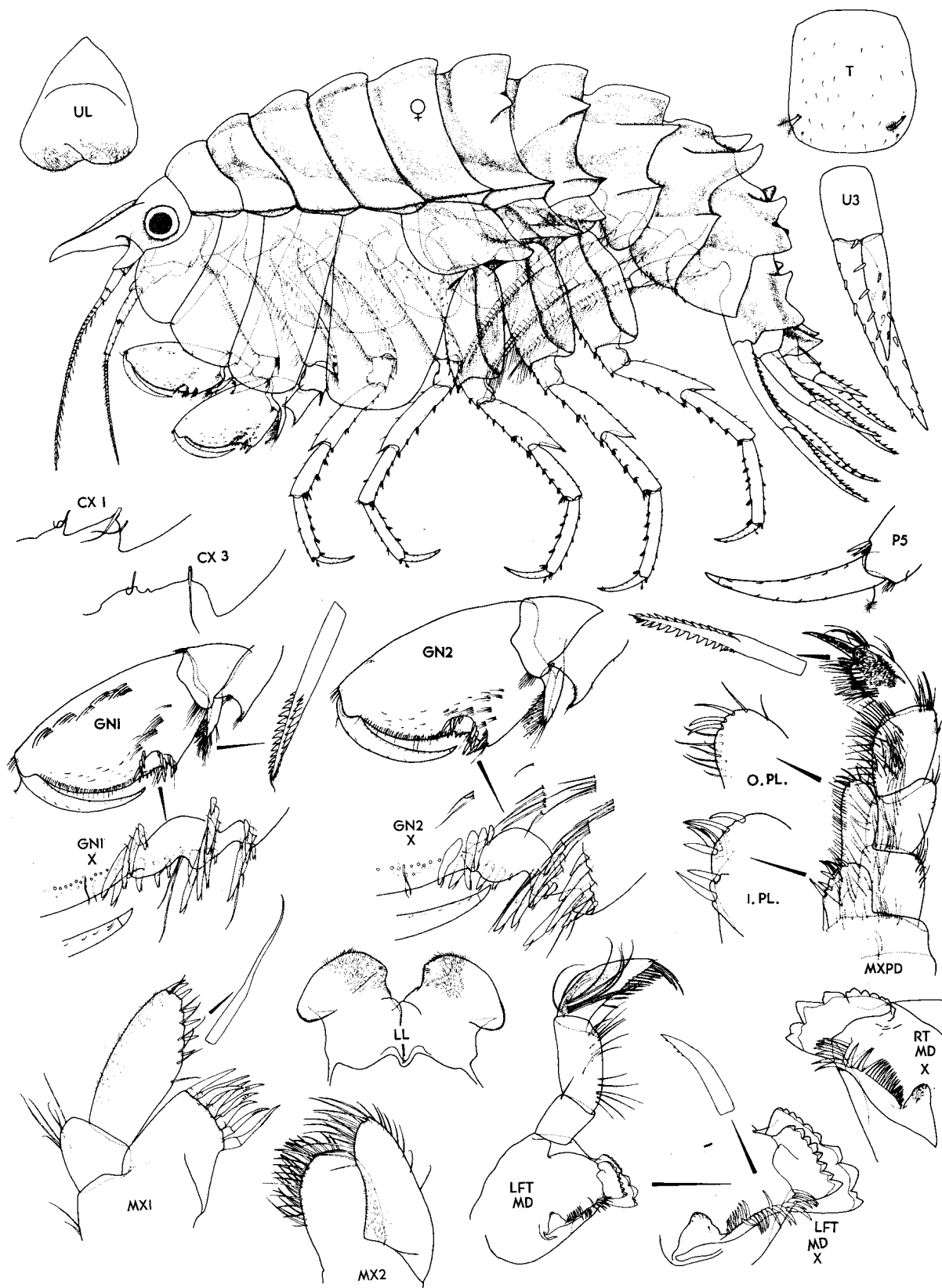
Mouthparts not described.

Coxae 1-4 deep, narrow, not ridged medially, gently rounded below; coxa 1 with single hind marginal cusp; coxa 4 narrow, rectangular, hind margin almost perpendicular, sub-parallel to anterior margin. Coxae 5-7, lateral ridges prolonged and acute posteriorly.

Gnathopod 1, anterior margin of basis with single proximo-medial cluster of long setae; propod ovate, much less deep than in gnathopod 2; angle of "step-down" margin very shallow (<20°); D-TD very small; PDSP formula: outer - 3:2:1(?); inner - 3:3:4, total of 16-17. Gnathopod 2, propod deepest about mid point, angle of "step-down" margin very steep (nearly right-angled), D-TD very pronounced, with distal cluster of 4 spines, one of which is much (3X) longer than the adjacent spine; PDSP formula, total of 14; meral process very strong.

Peraeopods 5-7, hind margin of basis distinctly convex; segment 4, postero-distal process pronounced, overhanging about 40% length of segment 5.

FIG. 7. *Pleustes (Pleustes) acutirostris*, new species
FEMALE ov. (19.0 mm).
(SEE PAGE 19 - OPPOSITE)



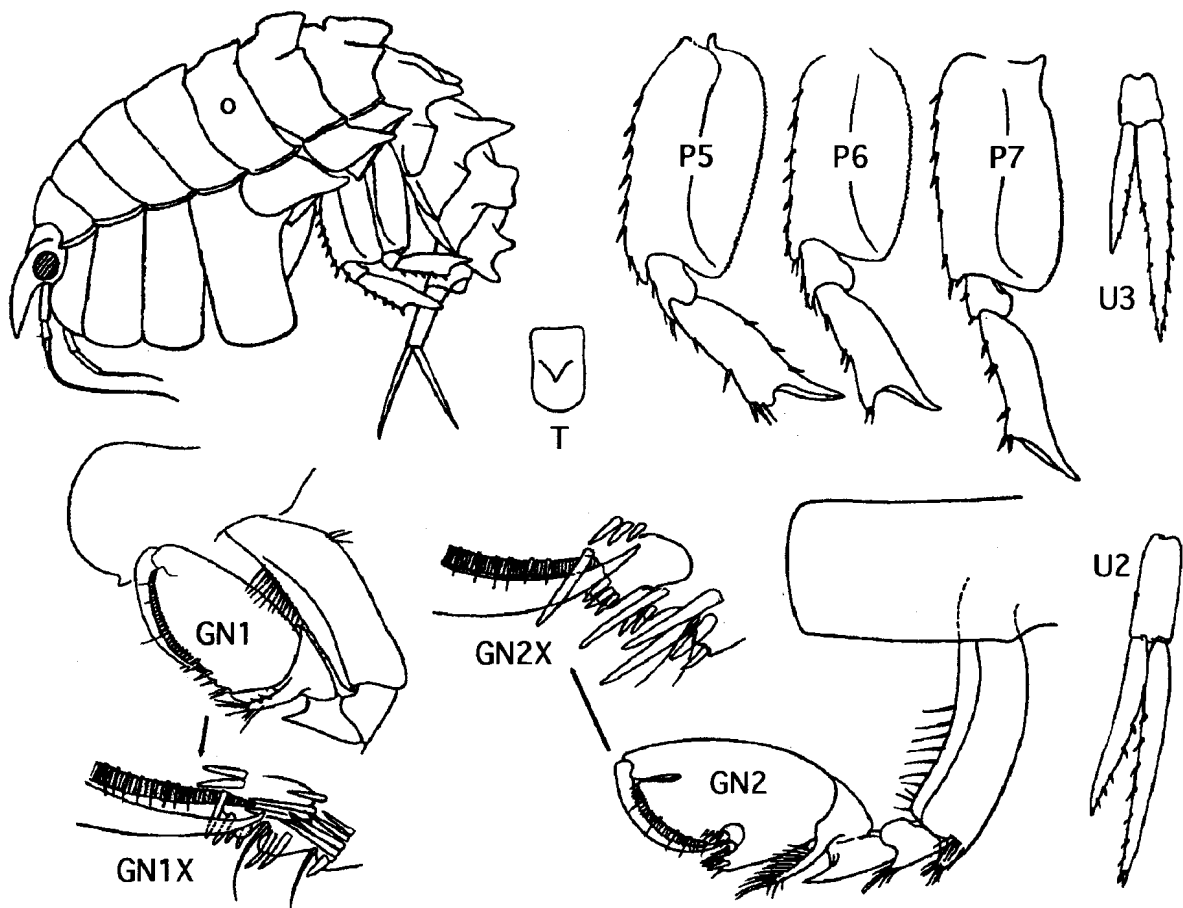


FIG. 8. *Pleustes tuberculatus* (Bate) ♀ ov. (18.0 mm) Kara Sea
(modified from Gurjanova, 1972, figs. 4, 6)

Uropod 2, rami markedly unequal. Uropod 3, inner ramus elongate, more than 4 times length of peduncle and twice length of the inner ramus. Telson sub-rectangular, longer than wide, apex rounded.

Distributional Ecology: Greenland Sea, Barents Sea, Kara Sea, and East Siberia to Sea of Japan, in depths of 25 - 200m. The species is mentioned by Tzvetkova & Kudrjaschov (1985) as a subspecies of *panoplus* east of Nova Zemlya to the Sea of Japan.

Taxonomic Commentary: Bate's original Latin diagnosis of *Pleustes tuberculata* (1858, p. 362) has been translated by Stephensen (1938, *loc. cit.*) as follows (parentheses of present authors): "All the mesosome (peraeon) and the two anterior metasome (abdominal) segments have each a medio-dorsal tubercle (carinata or tooth). The 3 posterior mesosome (peraeon) and all the metasome (abdominal) segments are laterally (i.e. dorso-laterally) tuberculate. The side plates (coxarum) of all the mesosome segments and of the two anterior metasome segments with the hind margin tuberculate (toothed). The 3 posterior peraeopoda with 1st joint (the coxa) tuberculate. Uropod 3 has the inner ramus rather long." The meaning of the third sentence is somewhat

ambiguous. However, in the context of Bate's generic diagnosis of the anterior coxae (*loc. cit.*), the third sentence may be interpreted to mean "the lateral ridge of all peraeon segments and the lateral margin of the first two pleon segments toothed behind".

There seems little doubt that Bate's original description is best applicable to the subgenus *Pleustes*, as defined herewith (p. 9). His description does not fit the very strongly processiferous segments and distally emarginated coxae characterizing subgenus *Catapleustes*. The dorsal and mid-lateral body carination is much too strong to fit the genus *Thorlaksonius*. Moreover, although Bate did not provide locality data for his material, subsequent authors (e.g Sars, 1895; Stebbing, 1906) refer to *P. tuberculatus* as a species of the Arctic Ocean wherein species of *Catapleustes* are rare, and *Thorlaksonius* are totally lacking.

However, the precise species identification of *P. (P.) tuberculatus* Bate yet remains uncertain. Gurjanova (1972, p. 148, figs 4B, 6) has assigned the name *tuberculatus* to a species from the Kara Sea region having weakly toothed peraeonal and mid-dorsal pleonal segments and an abrupt "stepdown" margin at the postero-distal angle of the propod of gnathopod 2. This form is herewith accepted as most probably identical with Bate's original species.

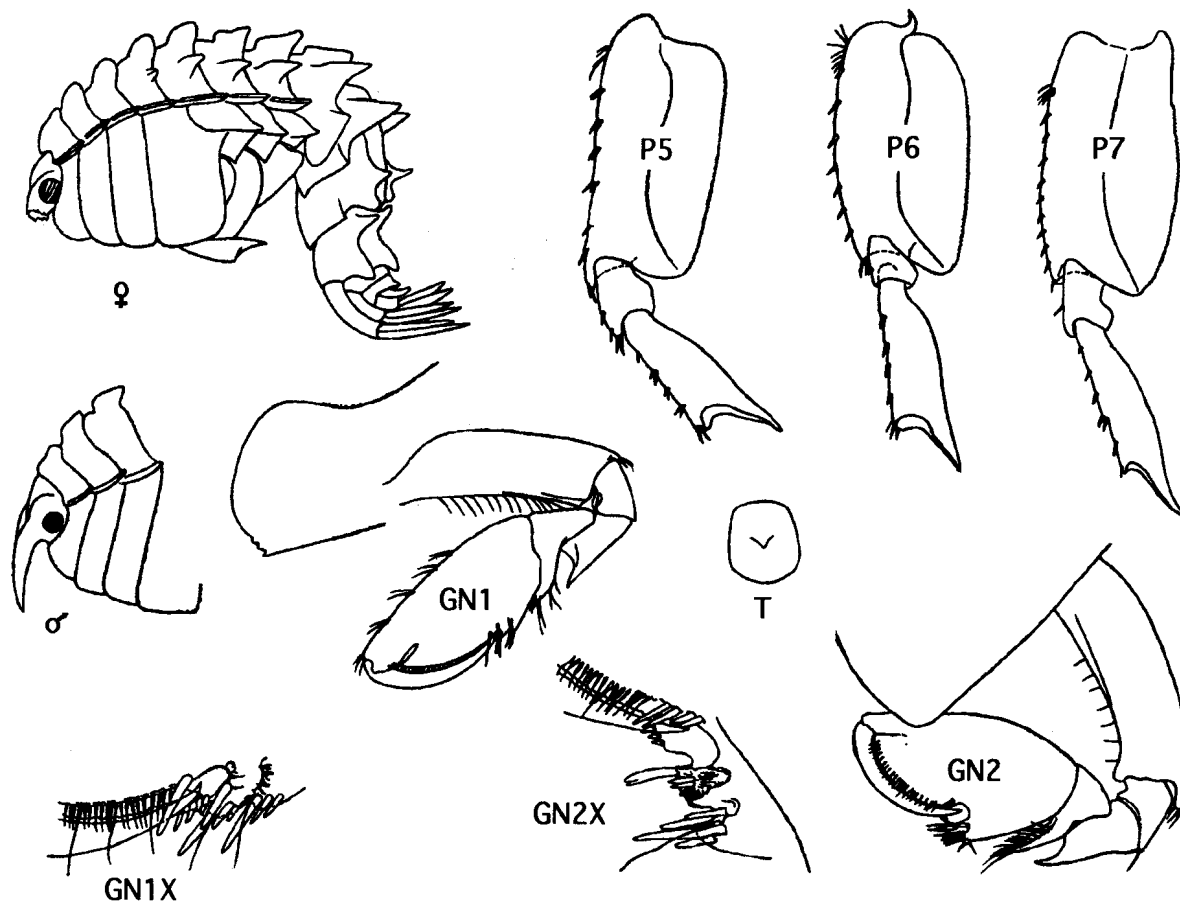


FIG. 9. *Pleustes (Pleustes) sibiricus* Gurjanova ♀ (28.0 mm) ♂ (20.0 mm)
New Siberian Islands. (modified from Gurjanova, 1972, figs. 7, 8)

Pleustes (Pleustes) sibiricus Gurjanova, new status
(Fig. 9)

Pleustes panoplus sibiricus Gurjanova, 1972: 150, figs. 7B, 8.—Barnard & Karaman, 1991: 651.

Diagnosis (Female 20-28 mm): Peraeon segments 1-7 carinated and strongly toothed mid-dorsally, and strongly ridged mid-laterally. Peraeon segments 3-7 with prominent dorso-lateral tubercles or teeth (lacking on peraeon segments 1-3), posteriorly becoming strongly elevated. Pleon segments 1-3 with strongly toothed and elevated mid-dorsal and paired dorso-lateral carinae; pleon plates 2 & 3 each with posterior marginal tooth. Urosome segment 1, dorso-lateral carina long, deeply excavated. Urosome 3, dorso-lateral carina small, acute.

Rostrum long, slender, slightly down-curved, apex acute. Eyes relatively large, rounded. Antennae and mouthparts not described.

Coxal plates 1-4 deep, broad, lacking strong mid-rib; coxa 1, hind margin nearly straight, postero-distally with 2-3 small cusps; coxa 4 sub-rectangular, hind margin sub-parallel to anterior margin. Coxae 5-7 each with strong mid-

lateral ridge, toothed behind. Gnathopod 1, anterior margin of basis armed medio-distally with relatively short setae; propod relatively slender and less deep than that of gnathopod 2; angle of "step-down" margin shallow ($<30^\circ$), D-TP small; PDSP formula: outer - 3:3:2; inner 1:1:1(?), total of 11-12. Gnathopod 2, propod deep, angle of "step-down" margin abrupt ($\sim 70^\circ$), dactyl-tip depression large; distal group of four spines ordinary, not enlarged; PDSP formula: outer - 3:3:2; inner - 4:3:3, total of 18; meral process elongate.

Peraeopods 5-7, hind margin of basis gently convex; segment 4 posterior overhanging about 1/3 the length of segment 5; dactyls not described (presumably elongate).

Uropod 1, rami little longer than peduncle. Uropods 2 & 3, outer ramus little shorter than inner ramus. Telson little longer than wide, broadening distally, apex rounded.

Distribution: An arctic species of New Siberian and Laptev Seas, taken subtidally from the shore-line to depths of 35 m.

Taxonomic Commentary: Gurjanova's lateral view figure (1972) of the body, and detailed figures of the gnathopods and posterior peraeopods of *Pleustes panoplus sibiricus* are clearly those of subgenus *Pleustes*.

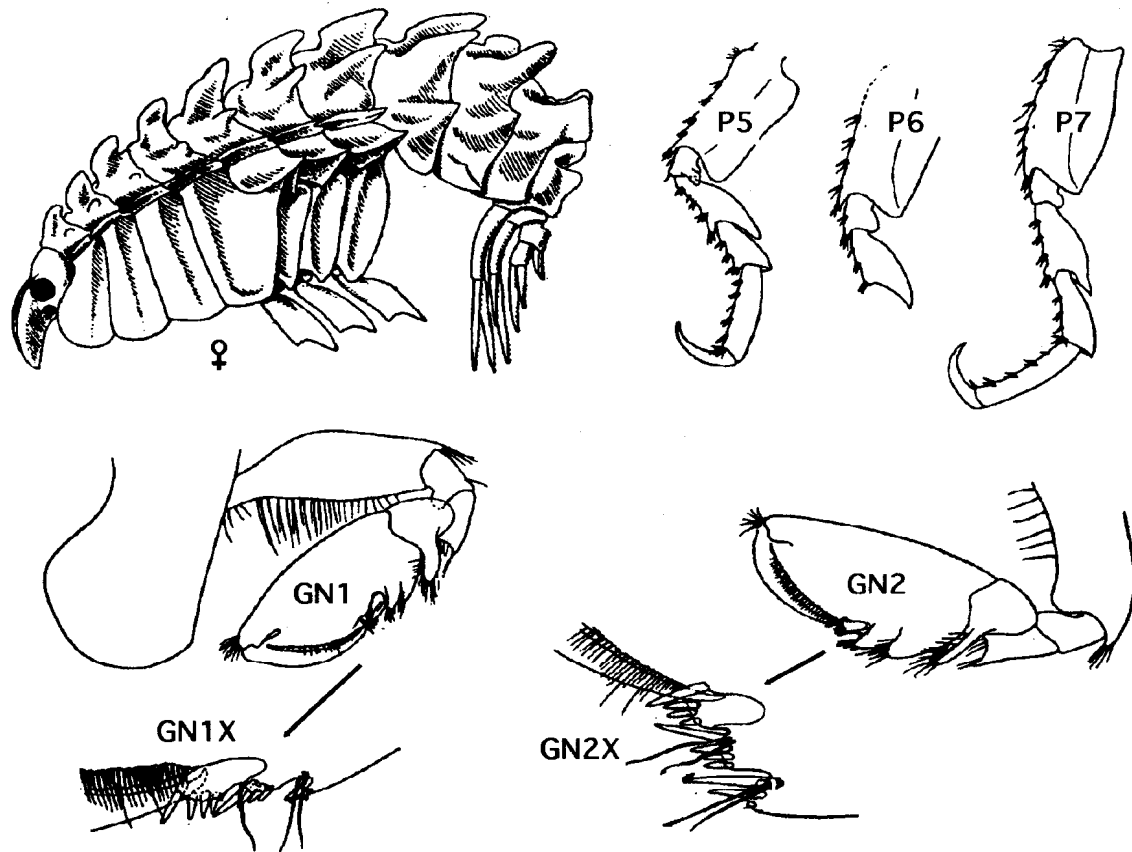


FIG. 10. *Pleustes (Pleustes) gurjanovae* new species. ♀ (23.0 mm).
Dezhneva Basin (modified from Gurjanova, 1972, figs. 7 & 9)

Pleustes (Pleustes) gurjanovae, new species
(Fig. 10)

Pleustes cataphractus cataphractus Gurjanova, 1972: 153,
Figs. 7A, 9.—Barnard & Karaman, 1991: 650.

Diagnosis. Female (23.0 mm): Peraeon segments 1-7 strongly carinated and processiferous mid-dorsally, dorso-laterally, and with strong mid-lateral ridges that are acutely produced posteriorly. Pleon segments 1-3 with strongly elevated mid-dorsal and dorso-lateral processes; pleon plates 1 & 2 each with posterior marginal tooth. Urosome 1, dorso-lateral process elevated, shallowly incised.

Rostrum large, deep, deflexed distally and slightly concave below, apex acute. Mouthparts and antennae not described.

Coxal plates 1-4 deep, with median ridge, lower margins gently convex. Coxa 1 asymmetrically hatchet-shaped, postero-distal cusp very small or lacking. Coxa 4, hind margin sloped, not vertical. Coxae 5-7 with projecting mid-lateral ridges, acuminate behind. Gnathopod 1, anterior margin of basis strongly setose except distally; propod distinctly smaller and less deep than in gnathopod 2; angle of "step-down" margin very gentle ($<20^\circ$), D-TD medium; PDSP formula: outer -3:2:1; inner -1:1:1(?), total of 9-10. Gnathopod 2, angle of "step-down" margin abrupt (about 60°), dactyl-tip depression distinct; distal-most spine of

distal spine cluster is enlarged, nearly twice length of adjacent spine; PDSP formula: outer -3:3:2; inner -1:1:1(?), total of 11; meral process medium.

Peraeopods 5-7, hind margin of bases varying from slightly concave (in peraeopod 5) to slightly convex (in peraeopod 7); distal segments medium, not slender; segment 4, postero-distal "overhang" is about 40% of the length of segment 5; dactyls strong, stout, length of each $> 1/2$ respective propod.

Uropods 1 & 2, inner ramus longer than peduncle. Uropod 3, inner ramus about 3 X peduncle, and 1.6 X outer ramus. Telson sub-rectangular, hind margin rounded.

Distribution: Gurjanova (*loc. cit.*) gives several records from the Arctic coast of Russia, from the Barents Sea, Kara Sea, East Siberian Sea, via the Sea of Okhotsk, and the Bering Sea to the Kurile Islands and northern Sea of Japan, in depths of 0 - 200 m.

Taxonomic Commentary: This is the most strongly carinated and tuberculated species of the subgenus *Pleustes* yet described. It differs markedly from Stimpson's "*cataphractus*" variation of *P. panoplus* (Kr.) in character states provided in the key to species. The authors take pleasure, therefore, in naming this very distinctive species in honour of the late Eupraxie F. Gurjanova, who first described and figured it.

Pleustes (Pleustes) lawrencianus, new species

(Figs. 1A, 11, 12)

Pleustes panoplus tuberculatus Slattery & Oliver, 1987.

Material Examined: Off South-east Cape, St. Lawrence I., Bering Sea, Alaska, 8 m., P. Slattery coll., 6 June, 198 - 1 female, br I (17.0 mm) + slide mount, HOLOTYPE, CMN Cat. No. NMCC1994-373. Off Cape Thompson, southern Chukchi Sea, 6 m., P. Slattery, July, 1984 - 1 male (25.0 mm), CMN Cat. No. NMCC1994-374. Off North Pt., Little Diomed I., Bering Sea, Alaska, P. Slattery coll., 15 July, 1984 - 1 female (27.0 mm) + slide mount, PARATYPE (fig'd); *Ibid.* - 3 post-br. III females, ~100 immatures, CMN Cat. No. NMCC1994-375.

Diagnosis. Female, br. I (17.0 mm): Peraeon segments 1-4 each with medium-tall flange-like posteriorly unproduced carinate and very low dorso-lateral tubercle; peraeon segments 5-7 with increasingly large and posteriorly slightly produced mid-dorsal carinae, dorso-lateral posterior marginal teeth, and acutely produced lateral ridges. Pleon segments 1 & 2 with elevated, ridge-like mid-dorsal carinae, high on pleon 1, low on pleon 2, with increasingly large and strongly acute dorso-lateral processes and short, ridged, posterior marginal cusps. Pleon segment 3 with acute mid-dorsal tooth and oblique, weakly incised dorso-lateral carina, but no posterior marginal cusp; hind corners of pleon plates 2 & 3 acuminate, lower margins spinose. Urosome 1, dorso-lateral carina low, weakly notched; urosome 3, dorso-lateral tooth forming an elevated ridge.

Head, rostrum long, medium deep, straight, apex narrowly truncate, median depression shallow. Antennae 1 & 2 subequal in length; flagellum of antenna 1 with about 30 short segments; peduncle 4 of antenna 2 extending well past peduncle 3 of antenna 1; flagellum 25-segmented.

Mandible, palp segment 3 with 15+ long baso-facial setae; blade row with 26-30+ blades. Maxilla 1, palp segment 1, lateral lobe with 3-4 very short setae; apex sharply rounded and medially oblique, with 8 spines and 8 sub-marginal curved setae. Maxilla 2, inner plate broad, basal inner marginal seta long, stout, plumose. Maxilliped, outer plate with 2 stout apical spines; inner plate with 8 apical and 2 subequal inner marginal stout spines.

Coxal plates 1-4 large, deep, each with prominent vertical midrib; lower margins rounded, hind cusp minute. Gnathopod 2, propod distinctly larger and deeper than in gnathopod 1. Gnathopod 1, basis with median anterior marginal setae; propod, angle of "step-down" margin very gentle ($<10^\circ$), D-TD medium; PDSP formula: outer - 4:2:1(?), inner - 3:3:3, total of 17-18. Gnathopod 2, propod, angle of "step-down" margin steep ($\sim 60^\circ$), D-TD and accessory D-TD well demarcated; PDSP formula: outer - 4:2:2; inner - 3:3:4 (+2?), total of 20; meral process finely acute.

Peraeopods 3-7 relatively short, segments heavy, spinose. Peraeopods 3 & 4 distinctly shorter than peraeopods 5-7, dactyls short ($\sim 1/3$ respective propods). Peraeopods 5-7, coxae strongly ridged and acute posteriorly; bases subequal,

with gently convex hind margins and broadly rounded lower hind lobes; segment 4 postero-distally overhanging segment 5 by about 30%.

Uropods 1 & 2, inner ramus shorter than (or equal to) peduncle. Uropod 3, inner ramus relatively broad, with 6-7 serial pairs of marginal spines. Telson nearly square, slightly broadened distally, apex subtruncate.

Coxal gills large, plate-like, very slightly smaller on peraeopods 2 and 6.

Etymology: The species name alludes to the geographical type locality, near St. Lawrence Island, Bering Sea.

Distributional Ecology: Northern Bering Sea region: coast of Alaska to St. Lawrence Island. It is the only known species of the subgenus to penetrate N. American Pacific coastal waters.

Taxonomic Commentary: This species differs rather markedly from *Pleustes tuberculatus*, as figured and redescribed by Gurjanova (1972). The heavy, strongly toothed body, relatively short heavy peraeopods, and long, narrowly truncate rostrum are diagnostic of *P. (P.) lawrencianus*. It (and varietal form below) appears most closely similar to *P. (P.) obtusirostris* Gurjanova from the western Pacific coastal marine region (p. 27). Some larger (and presumably older) specimens were fouled lightly on peraeonal segments and leg bases by newly settled spat (larvae) of acorn barnacles (*Balanus* sp.) (Fig. 12). In these pleustininid specimens, some evidence of sexual dimorphism can be noted in the rostrum (longer, tip more broadly truncate in males) and in the mid-dorsal and dorso-lateral carinae (larger and more strongly elevated in males). A small mid-ventral sternal process was noted on peraeon segment 3 of one male specimen (Fig. 12).

Pleustes (Pleustes) lawrencianus, variation 1.

(Fig. 13)

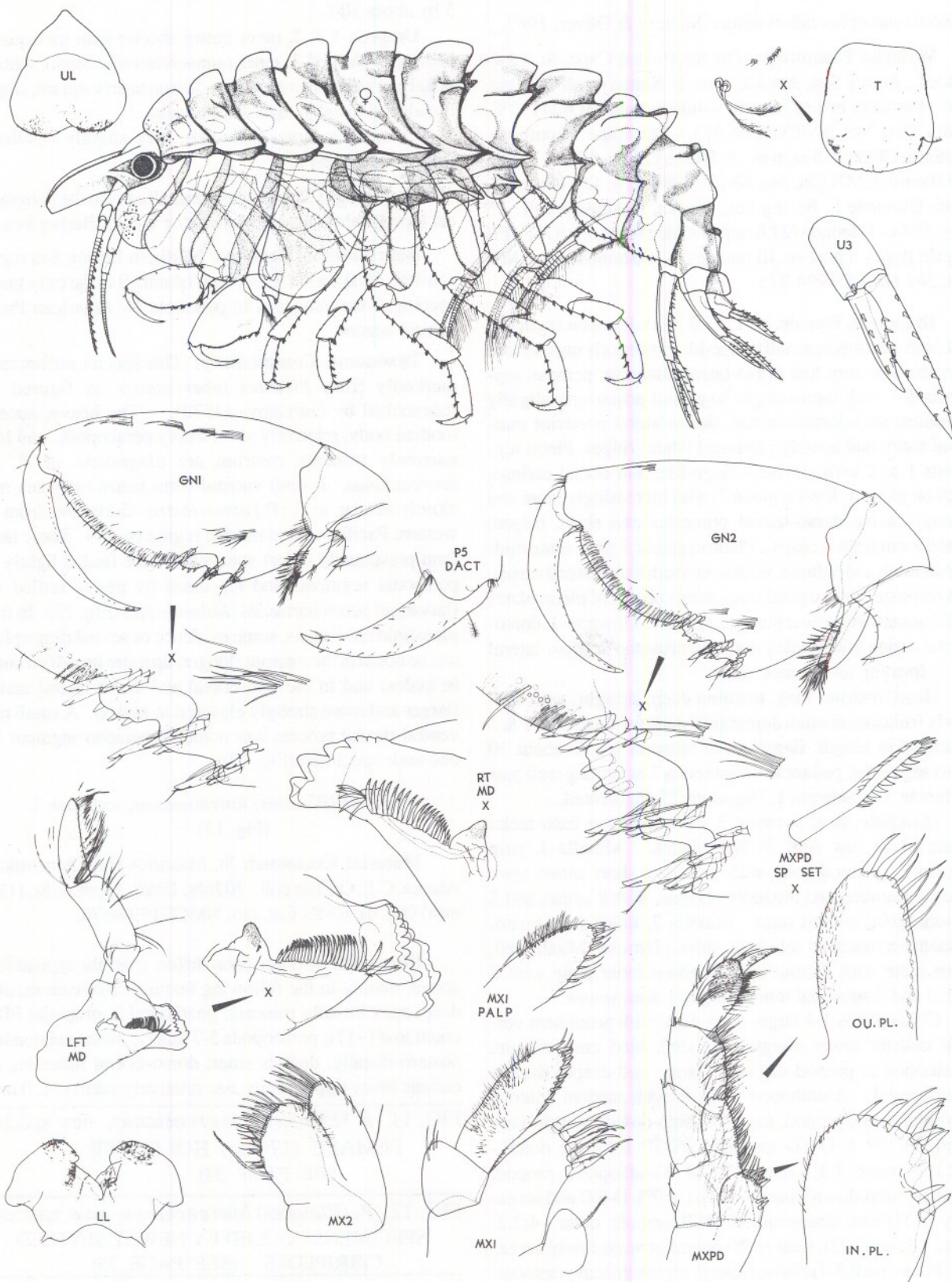
Material Examined: St. Makarius Bay, Amchitka I., Alaska, C.E. O'Clair coll., 20 July, 1968 - 1 female br. I (11.0 mm) (fig'd), CMN Cat. No. NMCC1994-376.

Diagnosis: This variation differs from the typical form above, mainly in the following features: Rostrum medium deep, apex broadly truncate; gnathopod 2, propodal PDSP count low (~ 17); peraeopods 5-7 heavy, bases subquadrate postero-distally, dactyls stout; dorso-lateral tubercles and carinae blunt-tipped; body size relatively small (11.0 mm).

FIG. 11. *P. (Pleustes) lawrencianus*, new species
FEMALE (17 mm) HOLOTYPE
(SEE PAGE 24)

FIG. 12. *P. (Pleustes) lawrencianus*, new species
SPECIMENS FOULED BY NEWLY SETTLED
CIRRIPEDS (SEE PAGE 25)

FIG. 13. *P. (Pleustes) lawrencianus*, variation 1
FEMALE br. II. (11.0 mm).
(SEE PAGE 26)



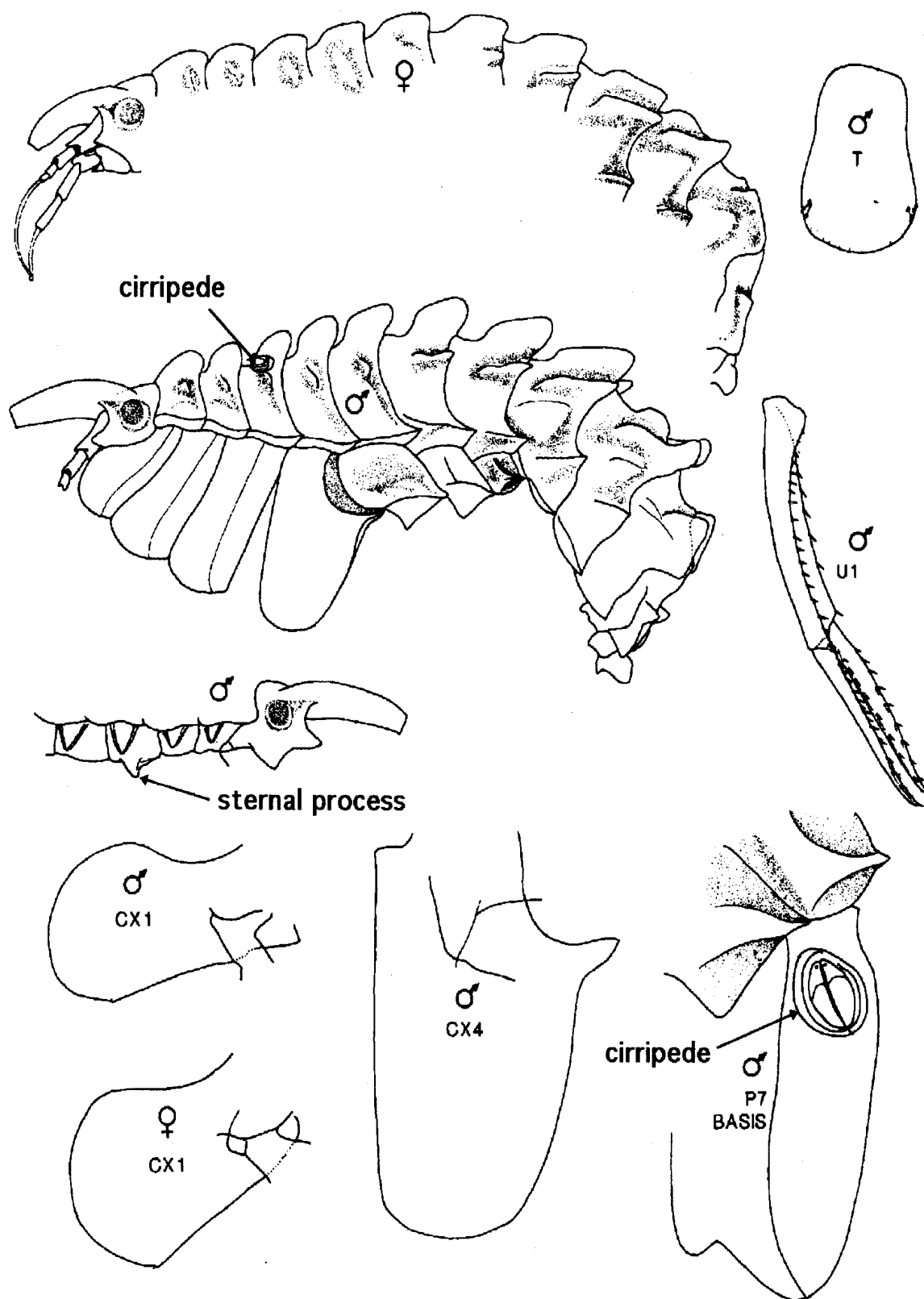
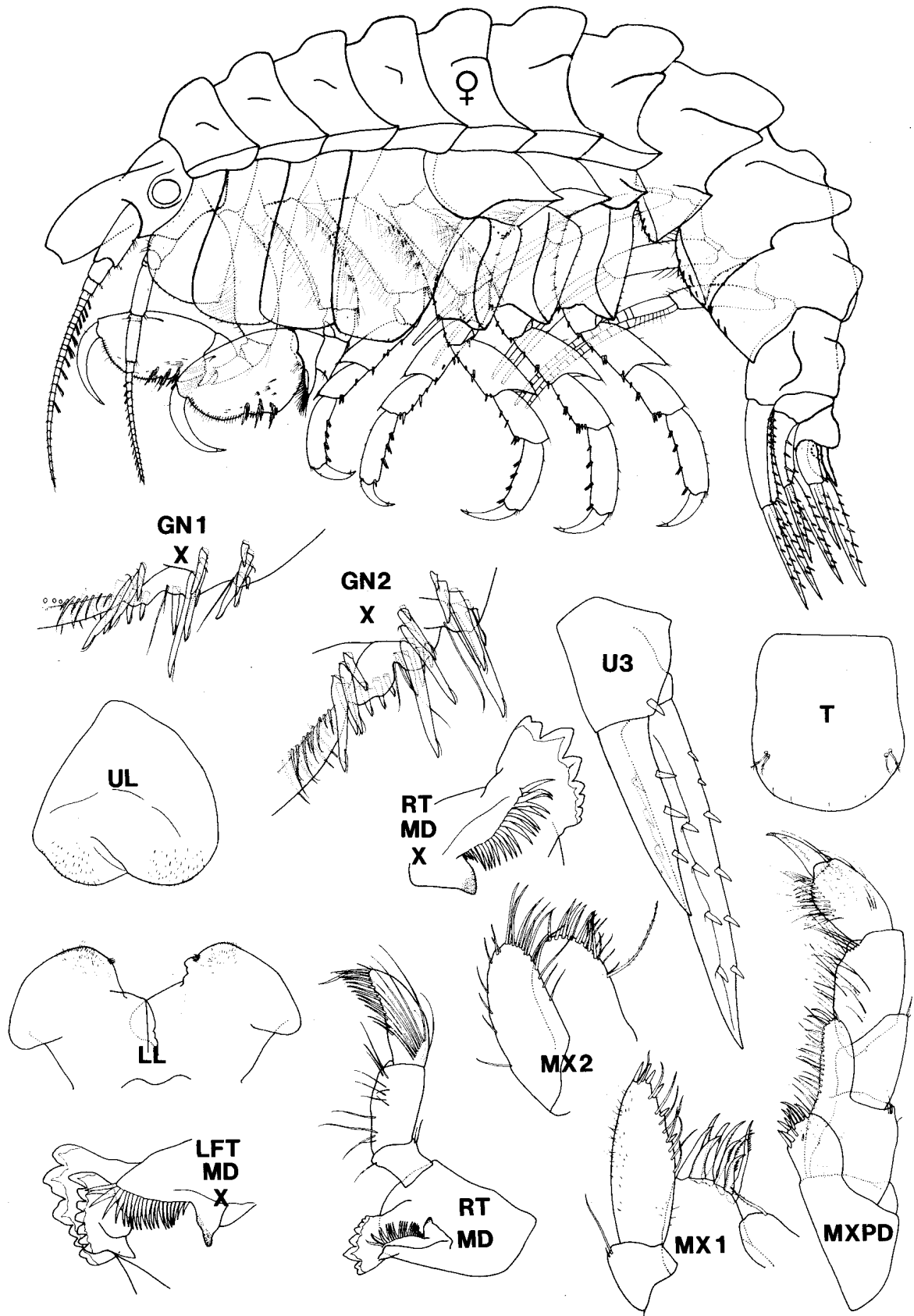


FIG. 12. *Pleustes lawrencianus* n. sp. ♂, ♀. Diomed Pt., Alaska
(newly settled cirripedes on plates)



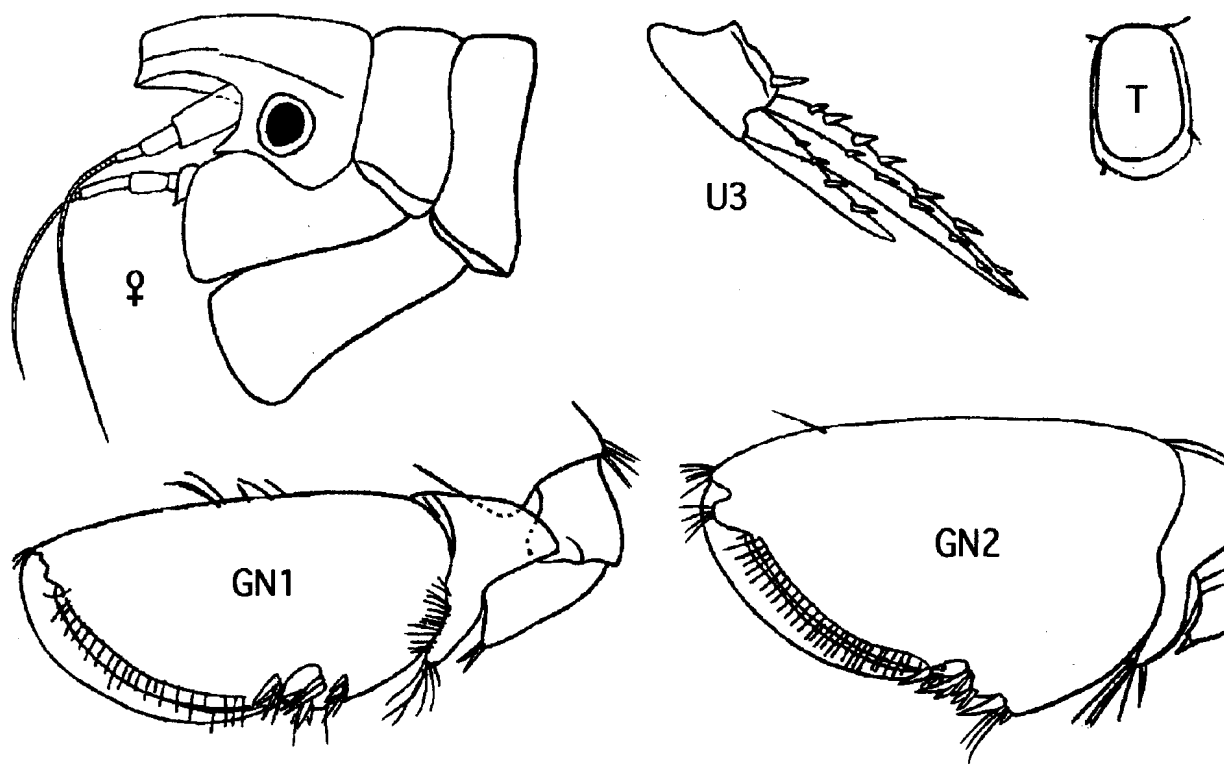


FIG. 14. *Pleustes (Pleustes) obtusirostris* Gurjanova. ♀ (16.0 mm). Japan & Okhotsk Seas (modified from Gurjanova, 1951, fig. 435).

Pleustes (Pleustes) obtusirostris Gurjanova, new status
(Fig. 14)

Pleustes cataphractus obtusirostris Gurjanova, 1938: 313, Fig. 38.—Gurjanova, 1951: 638, Fig. 435.—Gurjanova, 1972: 143.—Kudrjaschov, 1972: 102—Tzvetkova & Kudrjaschov, 1985: 4.—Barnard & Karaman, 1991: 650.

Diagnosis: Peraeon and pleon segments mid-laterally ridged but not unusually strongly carinate or toothed dorsally or dorso-laterally. Rostrum short, slightly down-curved towards sharply truncate apex. Antenna 1 distinctly longer than antenna 2, precise number of flagellar segments not discernible but probably > 30.

Gnathopod 1, propod distinctly smaller and more slender than in gnathopod 2. Gnathopod 1, propod, angle of "step-down" margin gentle (~30°), D-TD small; PDSP formula: outer-undeterminable; inner-3:3:3(?). Gnathopod 2, propod, angle of "step-down" margin ~45°, D-TD distinct; PDSP formula: outer undeterminable; inner-2:4:2(?). Meral pr-cess ordinary.

Uropod 3, inner ramus with 5-6 pairs of marginal spines, length >2X peduncle, and nearly 2X length of inner ramus. Telson markedly longer than wide, slightly broadening distally, apex rounded.

Distribution: Recorded from the Okhotsk and Japan Seas, in depths from 0 - 80 m, on coralline algae.

Taxonomic Commentary: Gurjanova (1951, *loc. cit.*) has redescribed and refigured material described originally (1938) from depths of 0-80 m. in Siaukhu and Sudzukhe Bays in the Sea of Japan. Regretably, the original description of the species is limited, identity of the propods is reversed, and provides little information pertaining to the mouthparts and pereopods. However, her figures clearly show that the lateral rostral margin dorsally overlaps the eye margin, a factor that places the species in the genus *Pleustes* (*sens. lat.*) and not in the genus *Thorlaksonius* where a truncate rostrum also occurs in some species (p. 38). The figures show also that the lower margins of coxae 1-2 are rounded (not incised), and that the anterior peraeon lacks dorsal and lateral carinae or tubercles, character states that place the species in subgenus *Pleustes* rather than in subgenus *Catapleustes*. Moreover, at the postero-distal angle of gnathopod 2, the marginal "step-down" angle is large, the dactyl-tip depression is distinct, and the postero-distal cluster of spines does not extend along the outer palmar margin, character states that also rule out possible placement in the subgenus *Catapleustes*.

In view of the dearth of species-critical detail in the previous descriptions, this species could not be included confidently in the phenetic analysis and construction of a phenogram of morphological relationships (pp. 63-64). A detailed study of further material, and comparison with Gurjanova's original type specimen, is a necessary prelude to establishing the true relationship of this enigmatic form.

Pleustes (Catapleustes), new subgenus

Pleustes (partim) Gurjanova, 1951: 635.—Gurjanova, 1972: 131.—Barnard and Karaman, 1991: 650.

Type species: *Pleustes angulatus angulatus* Shoemaker, 1955: 40, fig. 14B.

Component Species:

P. (C.) japonensis Gurjanova, 1972: 154, figs 10, 11.

P. (C.) paradoxus Gurjanova 1972: 156, figs. 13, 14

P. (C.) victoriae, new species (p. 28)

P. (C.) constantinus, new species (p. 32).

Diagnosis: Body carinated (toothed) mid-dorsally on all segments of peraeon and pleon; weakly to strongly dorso-laterally on peraeon segments 1-7, pleon segments 1-3, and urosome segments 1 & 3; medium to strongly ridged or toothed laterally on peraeon segments 1-7, and toothed behind on pleon segments 1, 2, & usually 3, often toothed inferior laterally on peraeon and pleon segments. Head, rostrum large, long, basally broad, with deep median depression; apex narrowing, subtruncate, distally deflexed, lower margin concave. Antennae medium, flagella 20-40 segmented.

Mandible: blade row with relatively few (<20) blades; palp segment 3 with relatively few (4-6) baso-facial setae. Maxilla 1, segment 1, lateral process moderately developed, weakly setose. Maxilla 2, plates small, with inner marginal basal plumose seta. Maxilliped, palp segment 3 with well developed medio-distal pectinate spines.

Coxal plates 1-4, lower margin appearing angular, lower hind margin deeply incised or scalloped, outer face with distinct vertical rib; coxa 4 usually also with 2 posterior horizontal ridges. Coxa 5 with strongly developed, wing-like, lateral process.

Gnathopods 1 & 2, distal-most group of postero-distal spines of propod extending submarginally along outer palmar face and beyond corresponding group of 4 inner marginal spines; distal-most outer spine variously (20 - 50%+) larger than adjacent spine; dactyl-tip depression (D-TD) small, shallow; angle of "step-down" margin shallow (usually < 30°), hind margin appearing nearly continuous with palmar margin; meral process weak to medium.

Peraeopods 3-7 generally slender. Peraeopods 5-7 typically more robust, and dactyls markedly longer than in peraeopods 3-4; coxae strongly horizontally ribbed, rounded or acute behind; hind margins of bases straight or shallowly incised, lower hind lobes sub-acute, proximal tooth of peraeopod 7 strong.

Uropods 1-2 relatively long; inner ramus usually longer than respective peduncle. Uropod 1 often longer than pleon segment 3 and urosome segments 1-3 combined.

Telson short-rectangular, slightly broadening distally, apex subtruncate.

Coxal gills large, plate-like.

Etymology: A combining form of the Greek prefix "kata" of Stimpson's species name "*cataphractus*" and the generic root "*Pleustes*", referring to the sharply incised lower margins of the anterior coxal plates of this subgenus, not found in subgenus *Pleustes*.

Taxonomic commentary: Although closely similar to subgenus *Pleustes* in most character states, subgenus *Catapleustes* embodies some character states of the genus *Thorlaksonius* (see commentary in *Pleustes*). These latter encompass the distal outer palmar spines of the gnathopod propod that extend along the outer palmar margin, the gentle angle of the "step-down" propodal margin, as well as the generally weak dactyl-tip depression, the weakly setose mandibular palp, the relatively few mandibular blades, and relatively short uropod 3.

Pleustes (Catapleustes) victoriae, new species
(Figs. 1E, 1F, 15, 16C)

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands: ELB Stn. H8b, Delkatla Slough, near Masset, Aug., 1957 - 2 subadult males.

Northern Vancouver Island: ELB Stn. V18, Kelsey Bay, wharf, LW, July, 1959 - 2 females (1 slide mount), 5 im. (dried spms); ELB Stn. V17, Boat Bay., LW, July, 1959 - 1 female (br. I), 1 im.

Southern Vancouver Island: Off Victoria, outer harbour, B. C., C. Low coll., 8 June, 1981 - Female, br. II (7.3 mm) + slide mount, HOLOTYPE, CMN Cat. No. NMCC1994-362. Malcolm Pt., N.W. tip Malcolm I. (50.1°N, 127.1°W), surface tow, E. Black, C. Low coll., 11 Sept., 1980 - Male (6.3 mm) + slide mount, ALLOTYPE, CMN Cat. No. NMCC1994-363; *Ibid* - 2 males, 6 females, CMN Cat. No. NMCC1994-380. Greens Creek Delta, Hawk Inlet, B.C., E. Black coll., 1981 - 1 im.; unstated locality, Victoria area, B. C., E. Black coll., 1981 - 4 females, 2 males.

Diagnosis: A generally plesiomorphic member of the subgenus having relatively weakly developed dorsal and dorso-lateral tubercles and weak peraeonal and coxal lateral processes.

Female, br. II (7.3 mm): Mid-dorsal tubercles directed vertically and slightly posteriorly, short and acute on peraeon 1-4 (1 not noticeably larger than 2), higher and more broadly ridge-like on peraeon segments 5-7, broadly carinate on pleon 1, and progressively lower, unevenly ridge-like on pleon 2 & 3; dorso-lateral tubercles faint on peraeon 1-4, small, acute posteriorly on peraeon 5-7, ridged and posteriorly acute on pleon 1 & 2 and protruding little above mid-dorsal line on pleon 2, ridge-like and mid-dorsally excavate on pleon 3 and urosome 1, and wing-like, acute above on urosome 3; mid-lateral ridges extending narrowly from sides of peraeon 1-7, sharply acute behind, short-ridged and cusped on hind margin of pleon 1 & 2, indistinct on pleon 3.

Head very broad; eyes large, protruding half-diameter

KEY TO SPECIES OF *PLEUSTES* (*CATAPLEUSTES*)

1. Peraeon segments 1-7, mid-lateral ridges variously shelf-like, rounded or acute behind, not produced outwards as tooth-like processes; inferior lateral tubercles lacking; gnathopods 1 & 2, submarginal palmar spines few (3-6), extending not more than one-third along outer face of palm; distal spine usually distinctly larger (about 50% longer) than adjacent spine 2.
 —Peraeon segments 1-7, mid-lateral ridges of peraeon segments 1-7 strongly produced outwards, tooth like; inferior lateral tubercles present on peraeon segments 1-7 and pleon 1-3; gnathopods 1 & 2, submarginal palmar spines numerous (8-12), extending at least half way along outer face of palm; distal palmar spine about 20% longer than adjacent spine 4.
2. Peraeon segments 1-4 with distinct dorso-lateral tubercles, each as tall as broadbasally; peraeon segments 1-7 with elevated mid-dorsal carinations, carinae about as broad as tall *P. (C.) japonensis* Gurjanova (p. 34)
 —Peraeon segments 1-4, dorso-lateral tubercles weak or faint, low peraeon segments 1-7 with narrow vertically directed mid-dorsal teeth, apices acute 3.
3. Mid-dorsal tooth of peraeon 1 not larger than on peraeon 2; coxa 5, lateral wing weak, extending outwards less than half its length; pleon 3 lacking distinct posterior marginal cusp; antenna 1, flagellum 30+ segmented *P. (C.) victoriae*, n. sp. (p. 28)
 —Mid-dorsal tooth of peraeon 1 taller and broader than in peraeon 2; coxa 5, lateral wing strongly developed, extending outwards more than half its length; pleon 3 with distinct hind marginal cusp; antenna 1, flagellum short, with 22-25 segments *P. (C.) constantinus*, n. sp. (p. 32)
4. Coxal plates 2-5 each with small antero-proximal tubercle; head with distinct mid-lateral ridge; peraeopods 5-7, basis lower hind corner sharply rounded *P. (C.) paradoxus* Gurjanova (p. 36)
 —Coxal plates 2-5 lacking antero-proximal tubercles; head lacking distinct median ridge; peraeopods 5-7, basis, lower hind corner subacute *P. (C.) angulatus* Shoemaker (p. 35)

from lateral surface; rostrum large, slightly longer than its basal width and longer than head, distally down-curved, apex narrowly subtruncate. Antenna 1 the longer, flagellum about 30-segmented, not basally conjoint; antenna 2, peduncle 4 not reaching end of peduncle of antenna 1, flagellum about 22-segmented, not basally conjoint.

Coxae 1-4 broad, medium deep, lower margins relatively shallowly incised behind; coxa 1 not totally covering anterior head lobe, medial rib weakly developed; coxa 4, median and horizontal ribs indistinct, hind lobe strong, acute, covering about 40% of lower margin of coxa 5. Coxa 5, lateral wing medium strong.

Mouthparts regular. Mandible, apex of molar relatively broad but non-tritulative; spine row with 15-17 thick blades; left lacinia 7-dentate; palp segments 2 & 3 subequal in length, segment 3 with 4-5 baso-facial setae. Maxilla 1, palp segment 1 with single outer marginal seta; palp segment 2 broad, with 6 apical and inner marginal spines. Maxilla 2, plates short, basal inner marginal plumose seta medium strong. Maxilliped, inner plate with 4-5 apical, and 2 subequal subapical inner marginal spines; outer plate columnar, with 3-4 slender apical spines; palp not exceptionally powerful, segment 3 with row of subapical pectinate spines.

Gnathopods 1 & 2, propods subovate, subequal, 2 deeper. Gnathopod 1, basis with small anterior marginal cluster of setae medially; propod with 3 clusters of median facial submarginal setae; angle of "step-down" margin shallow (<20°); D-TD very weak; distal group of 6 spines, three of

which extend onto outer palmar margin; PDSP formula: outer - 6:3:3; inner - 3-4:3:3, total of 21-22. Gnathopod 2, propod, angle of "step-down" margin shallow (20-30°); D-TD barely discernible; PDSP formula: outer - 5(6):3:3; inner - 3:3:4, total of 21-22, and a small group of 1-2 accessory proximal spines; meral process short.

Peraeopods 3-4 as stout as, but shorter than, peraeopods 5-7; dactyls short. Peraeopods 5-7 subequal in length; bases with median ridge, hind margins slightly concave, hind corners squarish; segment 4 overhang shallow, about 20% length of segment 5; dactyls long, about half length of respective segment 6.

Pleon plates 2 & 3, hind corners acuminate, not produced. Uropods 1 & 2, inner ramus slender, distinctly longer than peduncle. Uropod 3, inner ramus nearly twice length of outer ramus, margins with 8 serial pairs of spines.

Telson slightly broadening distally, longer than wide, apex subtruncate. Coxal gills on peraeopods 2-6 large, laminar.

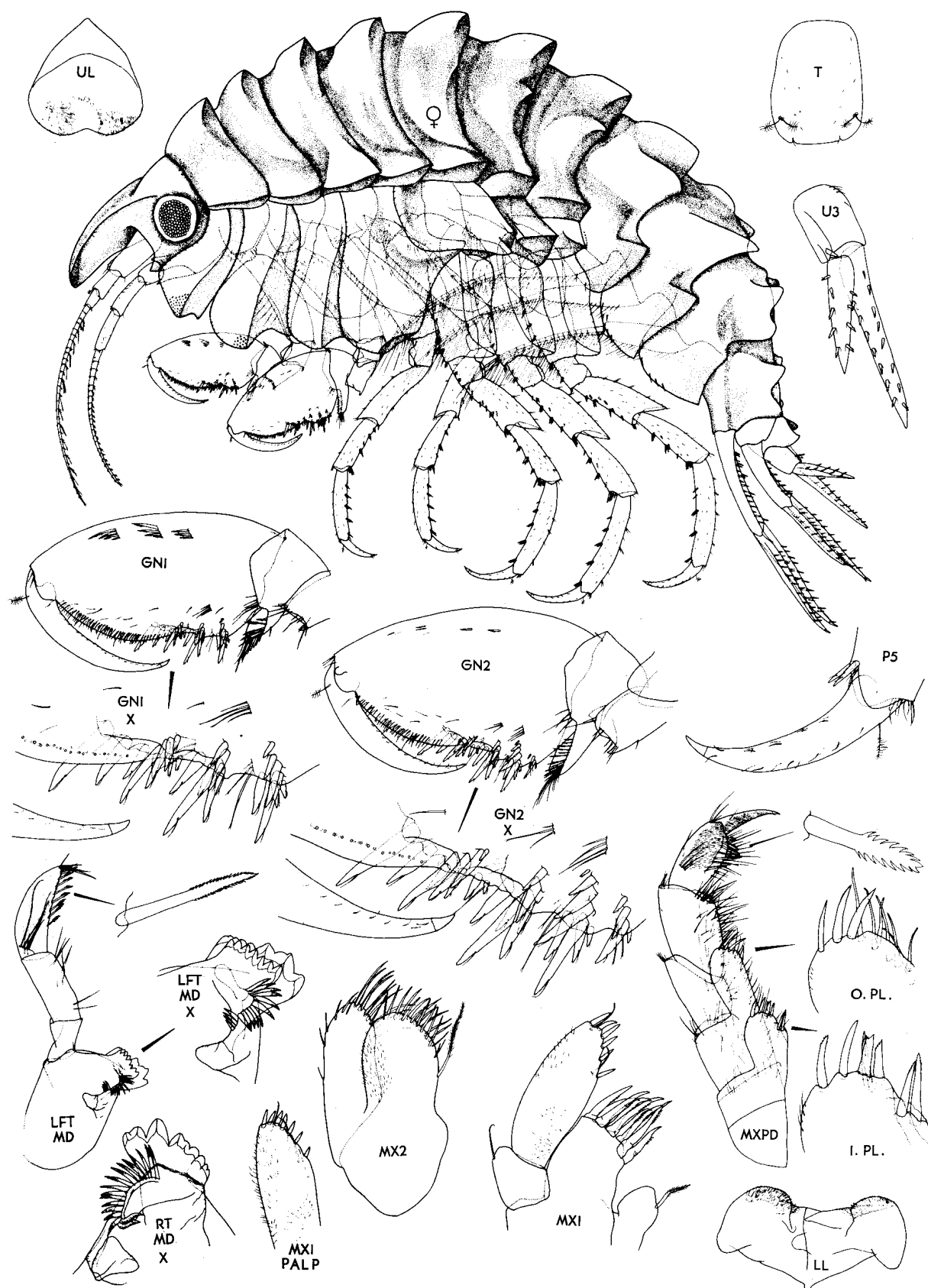
Body colouration: orange (*vide* E. Black).

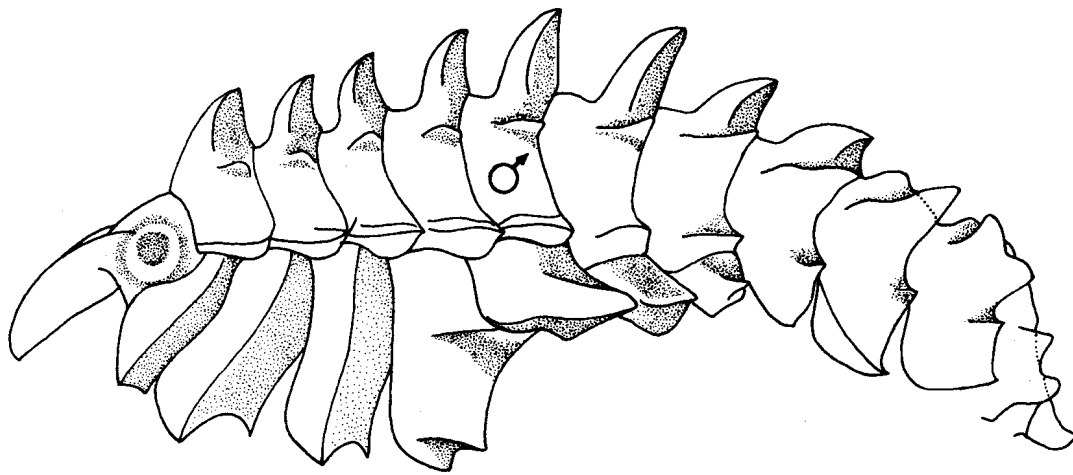
FIG. 15. *Pleustes (Catapleustes) victoriae*, n. sp.

FEMALE ov. (7.3 mm) HOLOTYPE; MALE (6.3 mm) ALLOTYPE. (SEE PAGE 30)

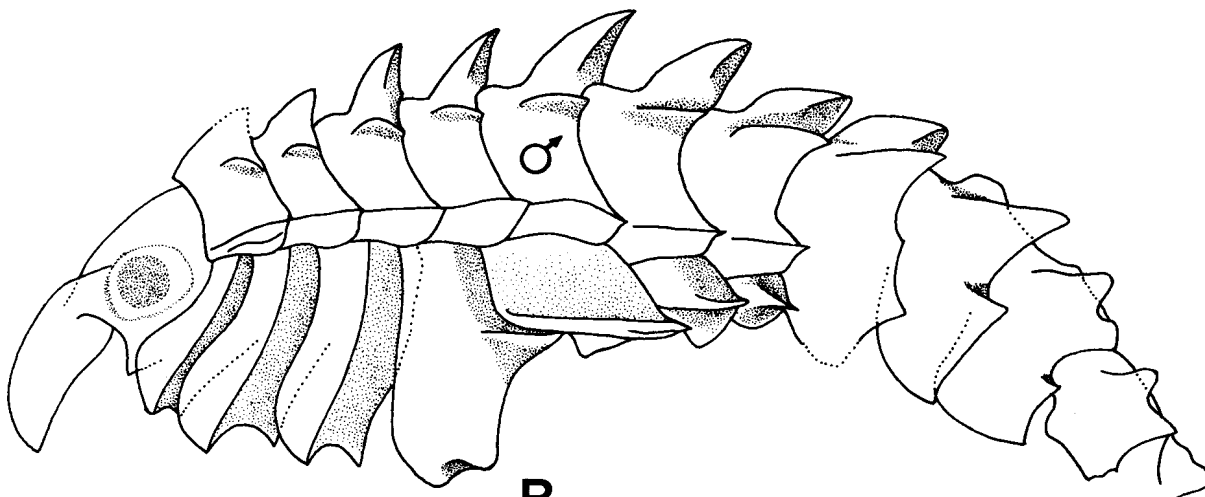
FIG. 16. *Pleustes (Catapleustes)* spp. - lateral views.

A. - *P. (C.) constantinus*, n. sp.; B. - *P. (C.) constantinus* var.; C. - *P. (C.) victoriae*, n. sp. (SEE PAGE 31)

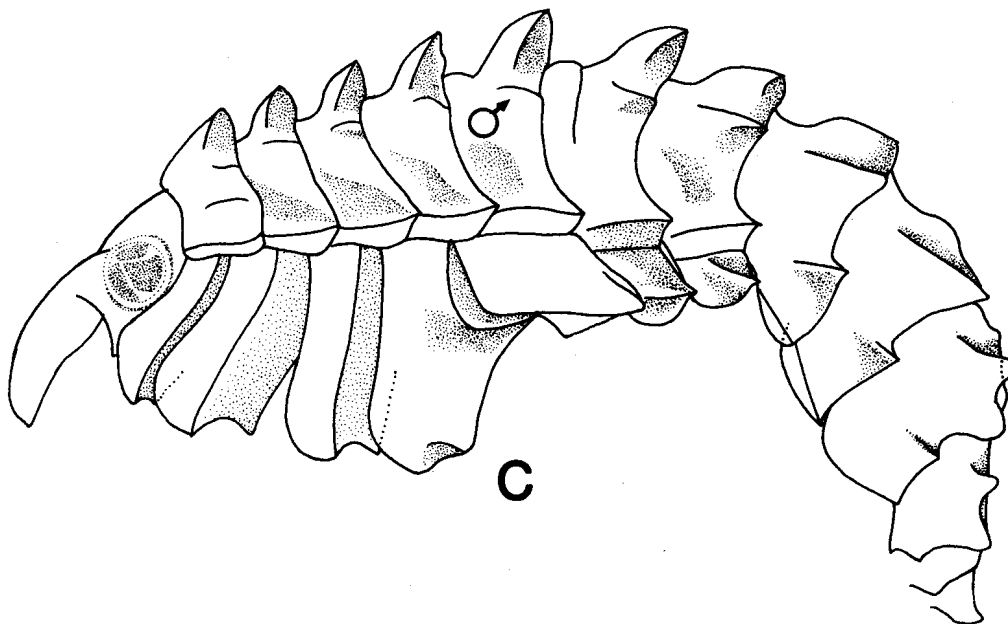




A



B



C

Pleustes (Catapleustes) constantinus, new species
(Figs. 1G, 16A, 17)

Material Examined: Constantine Harbor, Amchitka I., Alaska, from plankton pump samples, off dock, P. Slattery coll., 21 Sept., 1969 - 1 male (8.0 mm) + slide mount, HOLOTYPE, CMN Cat. No. NMCC1994-364; *Ibid.* - 3 males, PARATYPES, CMN Cat. No. NMCC1994-379.

Diagnosis: An advanced member of the *victoriae* subgroup having relatively strongly developed dorsal and dorso-lateral tubercles and strong lateral coxal processes.

Male (8.0 mm): Mid-dorsal tubercles directed vertically and slightly posteriorly, tips acute, medium strong (height greater than basal width) on peraeon 1-4, very strong on peraeon 5 & 6, successively decreasing and basally broadening on peraeon 7 and pleon 1, unevenly ridge-like on pleon segments 2 & 3; dorso-lateral tubercles rounded, low, on peraeon 1-4, increasingly strong, tooth-like on peraeon 5-7, strongly elevated on pleon 1 & 2 (above mid-dorsal line) broadly ridge-like and dorsally incised on pleon 3 and urosome 1 small & postero-dorsally toothed on urosome 3; mid-lateral ridge extending broadly (more than half segment length) from sides of peraeon 1-7, hind corners acuminate; coxae 5-7 acute and produced behind. Pleon plates 1-3, hind margin with basal cusp; inferior lateral tubercles lacking.

Head broad; eyes large, protruding nearly half-diameter from facial surface; rostrum very large, longer than its basal width and about 40% longer than head, apex narrowing, subtruncate, distally slightly downcurved. Antennae subequal, Antenna 1 slightly longer than antenna 2, flagellum about 22-segmented; antenna 2, flagellum with about 16 segments, basally conjoint.

Coxae 1-3 relatively narrow (> 2X width), median rib strong, lower margin deeply incised, hind corner acuminate; coxa 1 covering anterior head lobe; coxa 4, horizontal ribs distinct, hind process produced, covering nearly half lower margin of coxa 5. Coxa 5, lateral wing very strong, projecting outwards nearly equal to its length, apex sharply acute; coxae 6 & 7 laterally ridged and toothed behind.

Mouthparts reduced. Mandible, palp segment 3 with 6-7 inner marginal pectinate setae and 5 (3+2) baso-facial setae; blade row with 15-17 blades. Maxilliped, palp segment 3 with 3 stout medio-distal saw-tooth spines set close to base of dactyl; outer plate with 2 strong apical spines; inner plate with 5-6 longish apical spines and 2 stouter inner marginal spines.

Gnathopods strongly developed. Gnathopod 1, basis with a few short slender spines distally on anterior margin; propod, distal group of postero-distal spines relatively long, extending dactylward about half their length beyond palmar margin; angle of "step-down" margin very shallow, almost continuous with palmar margin; D-TD inconspicuous; PDSP formula: outer - 6:3:2; inner - 3-4:3:3, total of 20-21. Gnathopod 2, propod with 3 clusters of postero-distal spines; distal group of 6 lateral spines extending submarginally

about 1/4 palmar margin, distal spine about 50% longer than the adjacent spine; angle of "step-down" margin shallow (~20°); D-TD very weak; PDSP formula: outer - 6:3:3; inner - 3:3:3, total of 21; meral process short, acute.

Peraeopods 5-7, hind lobes of bases shallowly concave behind, proximally very broadly rounded in peraeopods 5 & 6, strongly toothed and nearly square on peraeopod 7; segment 4 overhanging segment 5 by about 30% of its length; dactyls slightly more than half length of respective propods.

Pleon plates 2 & 3, lower margins nearly bare, with 1-2 short stout spines only, hind corners acuminate, slightly produced. Uropod 3, inner ramus slender, about 2 1/2 X length of peduncle, margins 6-spinose; inner ramus, margins 3-spinose.

Telson short, rectangular, broadening distally, apex gently convex, hind corners very broadly rounding. Coxal gills large, plate-like, smaller on peraeopod 6.

Adult Female: Unknown.

Etymology: The name "*constantinus*" alludes to the type locality of the species at Constantine Harbor, Aleutian Islands, Alaska.

Taxonomic Commentary: A closely similar variant of the Aleutian species was obtained at several stations along the mainland coast of British Columbia as follows:

Pleustes (Catapleustes) constantinus, variation 1
(Fig. 1H; 16B)

Material Examined: ELB Stn. H26, Cox Point, mouth of Rivers Inlet, B. C., 30 m. dredge, July 19, 1964 - 1 male (7.5 mm.) + slide mount, (fig. 1d), CMN Cat. No. NMCC1994-365. ELB Stn. H5, Hinks I., B.C., LW level, July, 1964 - 2 males, 6 subadult specimens. Unnamed locality near Victoria, B. C., E. Black SCUBA Stn. B10 506 009, 1981 - 1 imm male + slide mount. CMN collections.

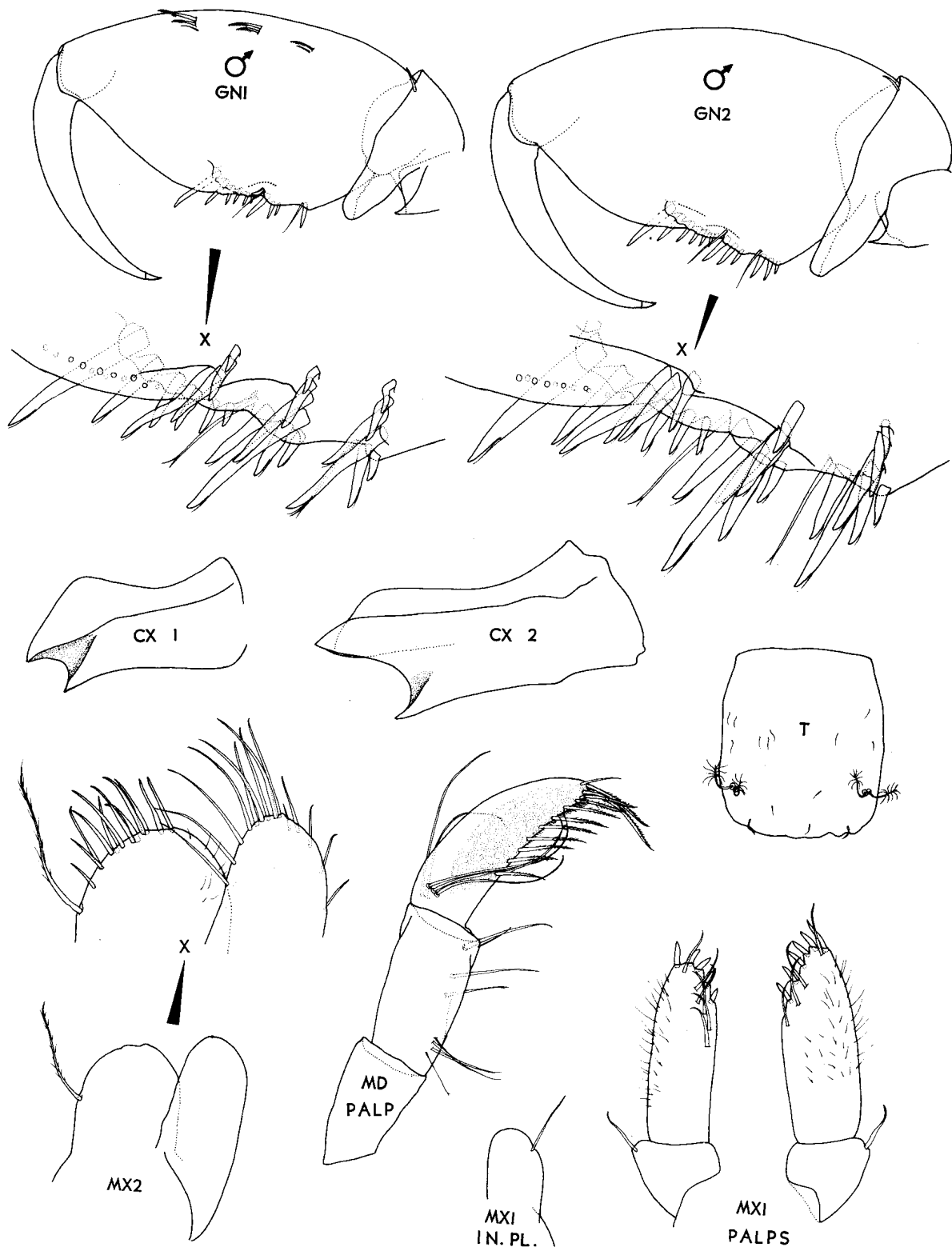
Diagnosis: Male (7.5 mm). This variant is similar to *P. (C.) constantinus*, having strongly elevated dorso-lateral and dorsal tuberculations on peraeon and pleon, and strong outward projection of the lateral process of coxa 5. It differs in the following character states:

Head, rostrum relatively deep, and more strongly deflexed distally. Mid-dorsal carinae more narrow, and bent more strongly posteriorly than in the species type.

Mandible, segment 3 with 11-12 inner marginal pectinate setae and 4 (2 + 2) baso-facial setae. Maxilliped, palp segment 3 elongate, with 5 stout medio-distal saw-tooth spines; outer plate with 2 stout apical spines; inner plate with 5-6 stout apical spines and 3 inner marginal spines.

FIG. 17. *Pleustes constantinus*, new species.

MALE ov. (8.0 mm) HOLOTYPE ;
(SEE PAGE 33 - OPPOSITE).



Coxae 1 not quite covering anterior head lobe, lateral rib strong, lower margin with narrow, deep, posterior excavation; coxa 2, lower margin, anterior portion smoothly convex, posterior excavation deep, semi-circular. Coxae 5-7 more sharply acute posteriorly.

Gnathopods 1 & 2, propod, 5 postero-distal spines extend submarginally along 1/3 palmar margin, distal spine slightly (20%) longer than adjacent spine; basis (of gnathopod 1) with medium-length setae, clustered centrally along anterior margin; basis (of gnathopod 2) with several short setae along antero-distal margin; PDSP counts as in the *C. constantinus* type.

Peraeopods 5-6, hind margin of basis nearly straight, proximal corner sharply rounding; peraeopod 7, hind margin with shallow excavations above and below sub-median "hump", proximal corner raised and subacute; dactyls elongate, about 60% length of corresponding propods.

Female: Unknown.

Extralimital Species of *Pleustes* (*Catapleustes*)

Previously treated in literature accounts of Soviet far-eastern and N. American western arctic pleustids are various forms that appear referable to subgenus *Catapleustes* of genus *Pleustes*. These include the highly ornamented species of *Pleustes* and varieties of *P. panoplus* described and figured by Gurjanova (1938, 1951, 1972) mainly from the sea of Japan and Kamchatka regions, and by Shoemaker (1955) from Pt. Barrow, Alaska. Full description and analysis of mouthparts, gnathopods, coxal gills, etc., are yet required for precise classification of all those forms. However, as outlined in the subgeneric summary (p. 28), the taxa diagnosed below appear to be valid full species that are referable to the present concept of *Catapleustes*.

Gurjanova (1951, p. 637, fig. 434) redescribed and refigured, as *Pleustes cataphractus*, a medium large (20 mm) species from moderate depths (27-30 m.) in the seas of Japan and Okhotsk. In its strongly ornamented peraeon and gently sloped "stepdown" of the posterior angles of the propods of both gnathopods, it differs markedly from Stimpson's original *cataphractus* from the N. American Atlantic coast. The scalloped lower margins of coxae 1-4, and horizontally ribbed outer surface of coxa 4, are features of subgenus *Catapleustes*. Although Shoemaker (1955, p. 40) likened this Gurjanova "variety" to his own "*angulata*", as indicated in the key to species (p. 29), a distinctly different species may be represented here. Similar material was found by Tzvetkova and Kudrjaschov (1985) in S. Sakhalin Bay.

Taxonomic and Distributional Commentary: As indicated in the phenetic analysis (p. 66) and key to species, the subgenus *Catapleustes* appears divisible into two major morphological subgroups, viz. the *C. angulatus* (TYPE) subgroup, and the *C. victoriae* subgroup. The former is more strongly dorsally and laterally carinate and tuberculate, and

generally more advanced phyletically. Within the *victoriae* subgroup, the species *japonensis* is considered slightly more advanced than *constantinus* or *victoriae*.

Pleustes (*Catapleustes*) *japonensis* Gurjanova, new status (Fig. 18)

Pleustes cataphractus japonensis Gurjanova, 1972: 154, figs. 10, 11.

Pleustes cataphractus Tzvetkova & Kudrjaschov, 1985: 2.

Diagnosis. Female (20 mm): Peraeon segments 1-7 each with strong mid-dorsal carinae, dorso-lateral tooth-like processes, and strong mid-lateral carinae, but inferior lateral tubercles lacking. Pleon segments 1 & 2 with small, low mid-dorsal carinae but strong dorso-lateral processes, bifid on pleon 2. Pleon 3 and urosome 1 each with strong paired bifid dorso-lateral carinae. Urosome 3 with single-toothed pair of dorso-lateral carinae. Pleon plates 1-3 each basally with posterior marginal tooth, hind corners acute, produced.

Head, rostrum very large, arcuate, concave between raised lateral margins, lower margin concave, apex acute. Eyes large, round. Antenna 1, flagellum with about 30 short segments. Antenna 2 shorter, flagellum with about 25 segments.

Mouthparts not described.

Coxae 1-4 ribbed medially but lacking proximal tubercles, hind corners conspicuously excavate (weakly in coxa 4). Coxae 5 with strong lateral tooth; coxae 6-7 laterally ribbed and toothed behind.

Gnathopods 1 & 2, propods subequal, slightly less deep in gnathopod 1, hind margin in gnathopod 2 very short and nearly vertical. Gnathopod 2, dactyl-tip depression of propod (at posterior angle) shallow but distinct; some 3-5 spines of distal group extend onto palmar margin, distal spine about 30% larger than adjacent spine. Gnathopod 1, propod PDSP formula: outer - 7:3:3; inner - undeterminable. Gnathopod 2, PDSP formula: outer - 7:3:3; inner - undeterminable.

Peraeopods 5-7, bases ribbed medially, hind margins straight, lower hind corners squared; distal segments relatively stout; postero-distal lobe of segment 4 overhanging about 30-40% of segment 5; dactyls strong, each 50-60% length of respective propod.

Uropod 3 rami relatively short, weakly spined, length of inner ramus only 2X peduncle and nearly twice outer ramus. Telson, length about 1.3X width, slightly narrowing distally, apex rounded.

Distributional Ecology: The species figured by Gurjanova (1972) is known from Peter-the-Great Bay and Possjet Bay in the Sea of Japan, from the lower intertidal zone to depths of 80 m. Specimens from a single station, 0.7-1 m in depth, off the west coast of S. Sakhalin, examined by Tzvetkova and Kudrjaschov (1985), are tentatively attributed to this form.

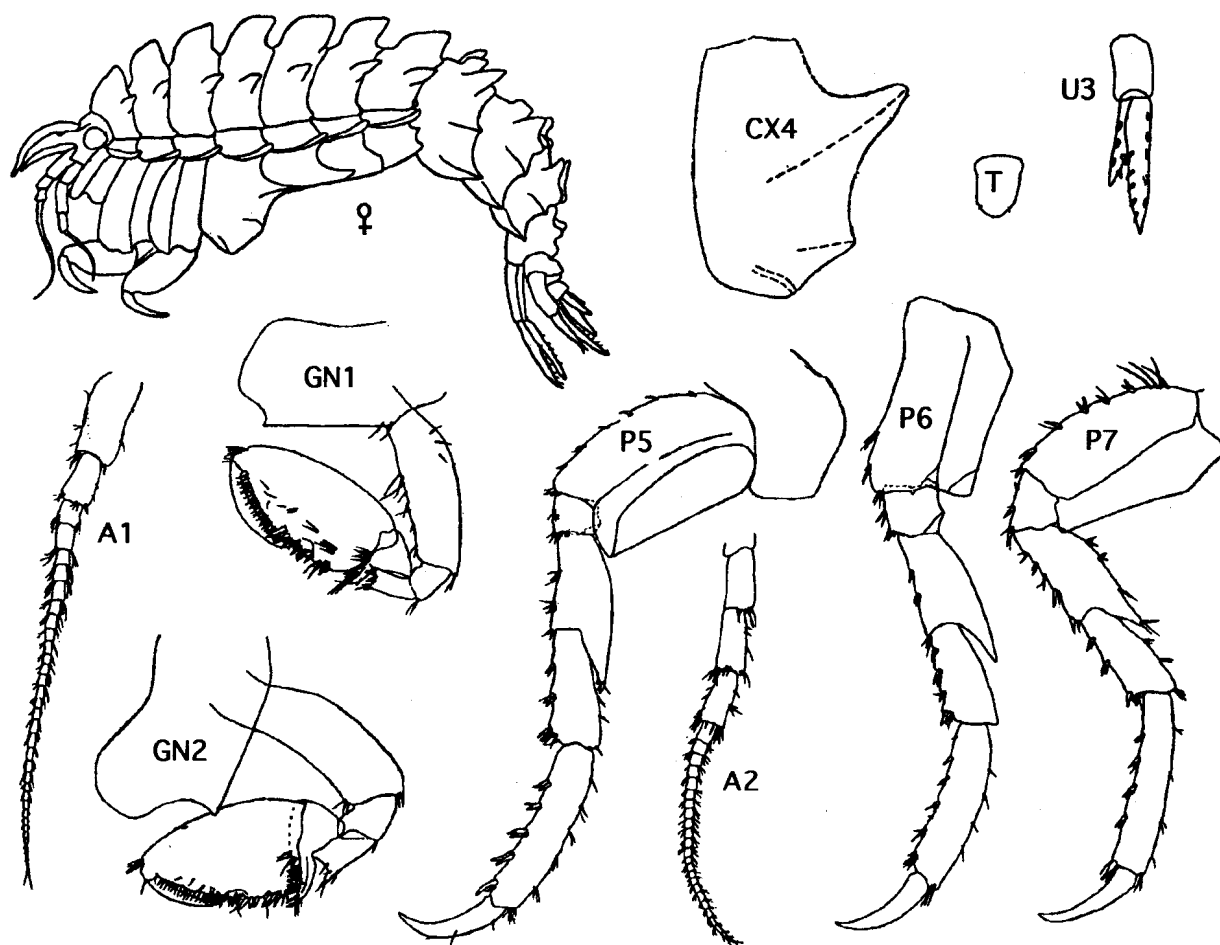


FIG. 18. *Pleustes (Catapleustes) japonensis* Gurjanova, new status ♀ (20.0 mm).
(modified from Gurjanova, 1972, figs. 10, 11). Japan Sea.

Taxonomic Commentary: Gurjanova (*loc. cit.*) described, under the name *P. cataphractus japonensis*, a medium-sized (20 mm), strongly carinated and tuberculate species from Peter-the-Great Bay in the northwestern Sea of Japan. Although details of the mouthparts and degree of lateral extension of coxa 5 have not been treated, this taxon is clearly a member of the *Catapleustes* subgenus of *Pleustes*, and clearly distinct from all other species known to date. Diagnostic features, as outlined in the key to known species, are the broadly shelved and laterally directed peraeonal margins, the broad, high, mid-dorsal carinations, and the strong dorso-lateral tubercles on peraeon segments 1-7, the strong mid-lateral hind cusps on pleon plates 1-3, and straight hind margin of the bases of peraeopods 5-7. The taxon is here elevated to full species status within subgenus *Catapleustes*.

Gurjanova (1972) has also included in the synonymy of *japonensis* material that she had previously described and illustrated as *P. cataphractus* (1938), and *P. cataphractus typicus* (1951). However, in the 1951 paper, her illustration of the presumably same 20 mm female differs in some features, especially in abdominal carination and gnathopod propodal PDSP counts, that might be considered specifically

significant, but which we attribute to less careful execution of the early figures. However, formal recognition of other taxa in Gurjanova's material (1951) must await detailed comparison with other regional species, and with the type of *P. (C.) japonensis*.

***Pleustes (Catapleustes) angulatus* Shoemaker, new status (Fig. 19B)**

Pleustes panopla angulata Shoemaker, 1955: 40, fig. 14B.
Pleustes angulatus angulatus Gurjanova, 1972: 155, fig. 12.
—Barnard & Karaman, 1991: 650, fig. 115 (part).

Diagnosis: Male (10.0 mm). Peraeon segments 1-7 and pleon segments 1-2 each with strong dorsal and dorso-lateral acute processes or teeth, tips directed posteriorly, and low inferior lateral tubercles or teeth. Peraeon segments 1-7, mid-lateral carinae subulate. Pleon segments 1 and urosome segment 3 with strong bifid dorso-lateral carinae. Urosome 3 with small tooth-like dorsolateral carinae. Pleon plates 1-3 each basally with a strong posterior margin tooth or cusp.

Head with mid-dorsal ridge. Rostrum deep, elongate (length 1.5X head), nearly straight, apex acute. Eye medium-large, round. Antennae subequal. Antenna 1, flagellum with about 22 segments. Antenna 2, flagellum with 16-18 segments.

Coxal plates 1-4 medially ribbed, lacking proximal low tubercles, hind corners strongly excavate. Coxae 5-7, median ridge produced laterally as strong tooth, hind margins of coxae 6 & 7 rounded.

Gnathopods 1 & 2, propod spination not shown in detail. Propods large, subovate, that of gnathopod 1 slightly more slender than in gnathopod 2; angle of "step-down" margin of both propods is gentle (~30°) although appearing slightly greater in gnathopod 2; about 6 distal spines extend onto outer palmar margin of both propods; meral process moderately produced in both gnathopods.

Peraeopods 3-4 & 5-7, distal segments relatively short, stout, dactyls medium strong. Peraeopods 5-7, bases with slightly concave hind margins and squared hind corners; segment 4 overhanging segment 5 behind by nearly 50%.

Uropod 2, inner ramus distinctly longer than outer ramus, and longer than peduncle. Uropod 3, outer ramus appearing relatively thick and about half length of inner ramus. Telson not described in detail.

Distributional Ecology: *P. (C.) angulatus* is known from 2 specimens, to 7 m. depth, off Pt. Barrow, Alaska.

Taxonomic Commentary: Despite the lack of information concerning mouthparts and gnathopods, the external morphology of *P. (C.) angulatus* is here regarded as distinctive at the full species level. Differences of external body ornamentation and of gnathopod palmar armature, have been detailed in the key to species (p. 29) and in the treatment of *P. (C.) paradoxus* (below). In *P. (C.) angulatus*, the flagellum of antenna 1 has only 22 segments (vs. 30+ in *paradoxus*) the lateral process of coxa 7 is shorter, and the distal segments (4-6) of the peraeopods are relatively short and stout.

Shoemaker (*loc. cit.*) supported the contention of Sars (1895), that the spine groups arising from what is termed here the "step-down" margin, are posterior, rather than palmar, marginal in origin.

Pleustes (Catapleustes) paradoxus Gurjanova, new status (Fig. 19A)

Pleustes angulatus paradoxus Gurjanova, 1972: 156, Figs. 13, 14.—Barnard & Karaman, 1991: 650.

Diagnosis. Male (16.0 mm): Peraeon segments 1-7 and pleon segments 1-2, each with high, arched, acute mid-dorsal and dorso-lateral tooth-like processes, and inferior lateral tubercles or small teeth. Median carinae of peraeon segments 1-7 form tooth-like projections. Pleon segment 3 and urosome segment 1 each with strongly bicusperate lateral carinae. Urosome segment 3 with pair of wing-like dorso-lateral carinae. Pleon plates 1-3 each basally with strong

posterior marginal tooth.

Head with strong mid-dorsal ridge. Rostrum large, deep, strongly arched, lateral margins dorsally elevated, lower margin concave, apex subacute. Eye medium, round. Antenna 1, flagellum with 35-40 small segments (estimated). Antenna 2, flagellum slightly shorter, flagellum of 20-25 short segments (estimated).

Mouthparts undescribed.

Coxal plates 1-4 strongly ribbed medially, lower hind corner strongly excavate, processes acute; coxae 2-4 each proximally with low rounded protruberance. Coxa 5 deep, broad, with low facial protruberance anteriorly, strong wing-like mid-lateral ridge, and acutely produced hind margin. Coxae 6-7 rounded behind, median ridge extending laterally as very strong acute tooth.

Gnathopod 1, basis with proximal and distal groups of anterior marginal setae; propod more slender and with smaller "step-down" posterior angle (~20°) than in gnathopod 2 (~60°); dactyl-tip depression shallow but distinct; distal row of 11 spines at posterior angle extend about 2/3 length of outer palmar margin, distal spine only slightly larger than adjacent spine; propodal PDSP formula: outer - 9:3:2; inner - 2:2:2, total of 20. Gnathopod 2, distal row of 10 spines extending more than half way along outer palmar margin; propodal PDSP formula: outer - 8:2:4; inner - 3:1:0(?), total of 18(?); meral process strong.

Peraeopods 5-7, bases broadest proximally, medially ribbed, hind margins varying from slightly concave (peraeopod 5), to slightly convex (peraeopod 7), lower hind corners squarish; segment 4 slender, postero-distal process relatively short (distal segments and dactyls not shown).

Uropods and telson indistinctly shown. Uropods 1 & 2, rami appearing slender, inner ramus longer than peduncle. Uropod 3, rami long, slender, length of inner ramus about 1.5X outer ramus. Telson not shown dorsally.

Distributional Ecology: Type lot from Kasatka Bay, southeastern Iturup Ids, Okhotsk Sea, 414 m. in depth.

Taxonomic Commentary: As noted above, *P. (C.) paradoxus* is grossly similar to *C. angulatus* in form and armature of peraeonal mid-dorsal, dorso-lateral, and mid-lateral processes or carinae, and inferior lateral tubercles. Gurjanova (*loc. cit.*, fig. 14) appears to have reversed labels on her enlargements of palmar margins of gnathopods 1 & 2, corrected here in fig. 19A, and in the text (above). In gnathopods of *paradoxus*, the outer palmar spines are much stouter, and extend 1/2 to 2/3 the length of the palmar margins, rather than ~ 1/3, as in *angulatus*. Moreover, the coxal plates of *paradoxus* are much more deeply and sharply incised postero-distally, and bear small proximal facial "knobs", lacking in *angulatus*. With respect to the form of the bases of peraeopods 5-7 of both species, the hind lobes are broad, with nearly straight hind margins and sharply squared lower hind corners, although the hind lobe of peraeopod 7 is illustrated as rounded by Gurjanova (above).

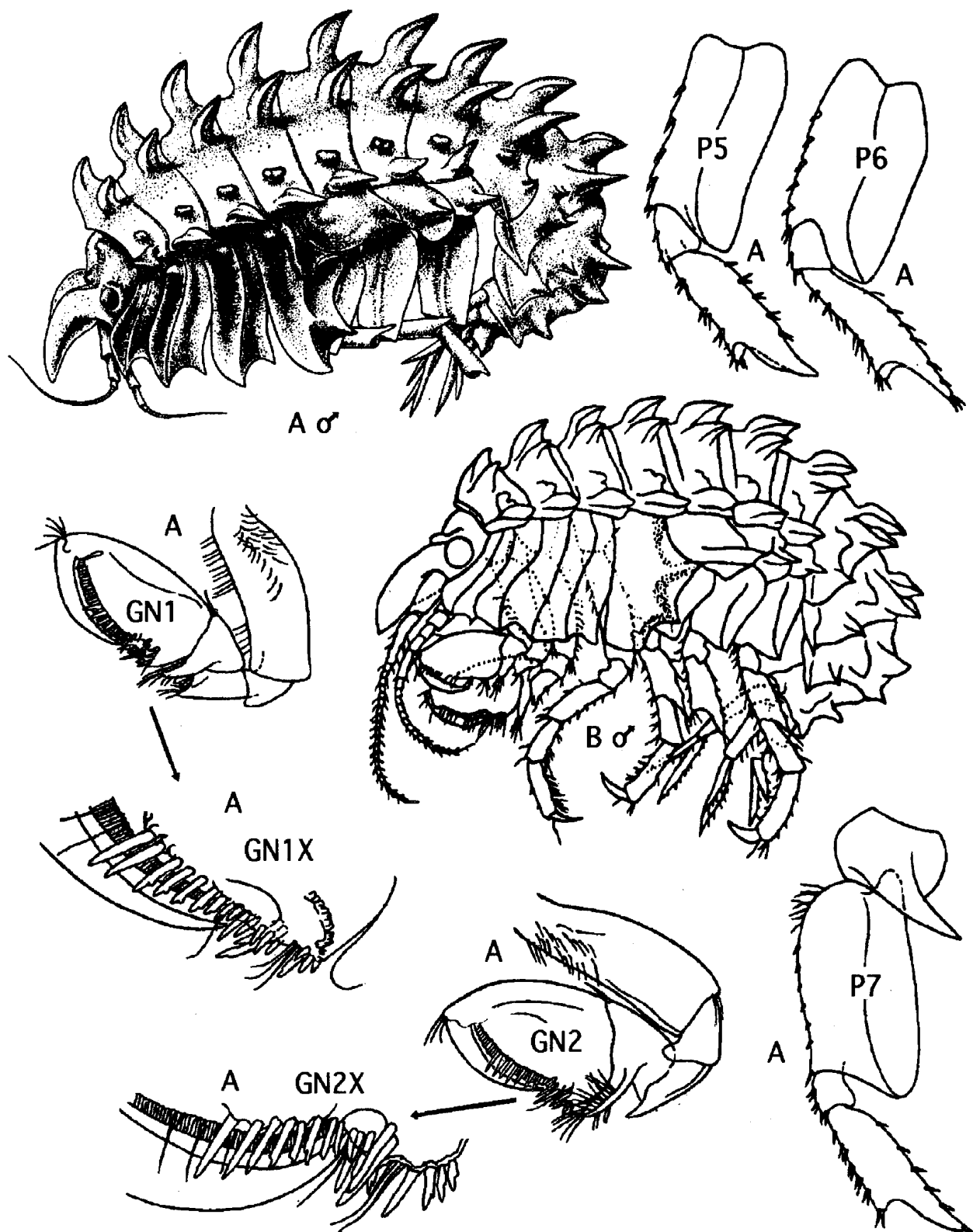


FIG. 19A. *Pleustes (Catapleustes) paradoxus* Gurjanova. ♂ (16.0 mm)
Iturup I. (modified from Gurjanova, 1972)

FIG. 19B *Pleustes (Catapleustes) angulatus* Shoemaker, ♂ (10.0 mm).
Pt. Barrow, Alaska. (modified from Shoemaker, 1955, fig. 14B)

Thorlaksonius, new genus

Pleustes (partim): Gurjanova, 1951: 435.—Barnard, 1969a: 425.—Gurjanova, 1972: 141—Barnard & Karaman, 1991: 650.

Type species: *Thorlaksonius brevirostris*, new species (present designation).

Other Species: *Thorlaksonius incarinatus* (Gurjanova, 1938); *T. amchitkanus*, new species; *T. borealis*, new species; *T. obesirostris* (Bulycheva, 1952); *T. depressus* (Alderman, 1936); *T. platypus* (Barnard & Given, 1960); *T. subcarinatus*, new species; *T. carinatus*, new species; *T. truncatus*, new species; *Thorlaksonius* sp. (Nagata, 1960, 1965).

Diagnosis: Body small to medium in size, broad, heavy. Carinae relatively weak, variably on pleon and posterior peraeon, weak or lacking on urosome. Peraeon segments 1-4 totally lacking mid-dorsal, dorso-lateral, and mid-lateral teeth or carinae. Head, rostrum deep, blunt (apex deflexed, rounded, or truncate, seldom acute), mid-dorsally flat or slightly humped (not depressed), lateral ridges arising antero-orbitally; trending (often conspicuously) to sexual dimorphism (longer and more slender in males). Antenna 1, peduncular segments 2 & 3 very short.

Coxae 1-4 large, deep, facially smooth or with slight mid-rib; lower margin nearly straight, never scalloped or incised behind; hind corner squarish. Coxae 5-6 with weak lateral ridge, acute posteriorly; coxa 7 variably ridged and toothed.

Mouthparts apomorphic. Mandible: palp segment 3 with 0-1 (rarely 3-5) baso-facial setae; spine row short (15-20 blades). Maxilla 1, palp segment 1, lateral shelf prominent, often strongly setose. Maxilla 2, inner plate, basal plumose seta very weak, usually lacking. Maxilliped, palp stout; outer plate small, slender, apex 2-4 spinose; inner plate with 6-9 apical and 2-3 subapical inner marginal spines.

Gnathopod 1, propod slightly more slender than 2; postero-distal spines in 3 groups, distal group extending submarginally along palmar margin (4-12 spines), distal spine often conspicuously enlarged; inner marginal spines few (3-4), subequal; angle of palmar "step-down" margin gentle, not abrupt (<45°); D-TD shallow, small; carpal hind lobes slender, well-developed; meral process strong.

Peraeopods 3 & 4 generally more slender and dactyls shorter than in peraeopods 5-7. Peraeopods 5-7, segments relatively short and stout; bases weakly ridged laterally, postero-distally rounded, hind margin convex (usually) or nearly straight; segment 4 usually strongly overhanging segment 5 behind.

Pleon plates 1-3, basal hind marginal cusps very weak or lacking. Urosome 1, lateral ridge low, shallowly incised, occasionally raised and prominent. Uropods 1 & 2, rami slender, serially spinose, inner ramus longer than peduncle. Uropod 3, inner ramus short, ~ 60% length of outer ramus, tips not exceeding rami of uropod 2. Telson relatively long,

length up to 1.5 times width, slightly narrowing or little broadened distally.

Coxal gills often unequal in size; gill on peraeopod 2 often sublinear, gill on peraeopod 6 usually smaller than on peraeopod 5.

Etymology: The genus is named in honour of Dr. Neil F. Thorlakson, Bellevue, Washington who, with his wife, Pat, and family, has long been an active outdoorsman and supporter of biological research and resource conservation in the North American Pacific region.

Taxonomic and Biogeographical Commentary: As outlined in the key (p. 9), members of this genus are distinguished mainly by the dorso-ventral depth of the rostrum, the relatively weak dorsal body carinae, and the spinose palmar margins of the gnathopods. In addition, the mouthparts are relatively specialized. Many of the species are strikingly pigmented with disruptive patterns or warning colouration. Males are smaller and more slender, the rostrum typically much larger (longer), the eyes relatively larger, and the antennae relatively longer than in corresponding mature females.

The genus is boreal amphi-Pacific in distribution, with three-fourths of the known species endemic to the North America Pacific coastal marine region. They range southward mainly in shallow water, apparently to the limit of macro-algal substrata, and northward into the Bering Sea; not yet found in the Chukchi Sea or western arctic localities.

The species cluster into 3 major phyletic subgroups (p. 64), representatives of all three occurring along both Asiatic and North American coasts.

Thorlaksonius amchitkanus, new species
(Fig. 20)

Material Examined: Cyril Cove, Amchitka I., Alaska, subtidal BCF dive buoys, C.E.O'Clair coll., 26 June, 1972. - 1 female ov. (13.0 mm).+ slide mount, HOLOTYPE, CMN Cat. No. NMCC1994-351.

Diagnosis. Female ov. (13.0 mm): Body short, very deep, medium-large. Peraeon totally lacking dorso-lateral and mid-lateral carinae or teeth; pleon segments 1-3 lacking lateral carinae, teeth, and/or posterior cusps; mid-dorsal carinae low, ridge-like, posteriorly rounded on peraeon segments 6 & 7 and pleon segments 1 & 2, not elevated on pleon 3; small dorso-lateral tooth on pleon 2; medium, ridge-like dorso-lateral ridges on pleon 3 and urosome 1; urosome 3 with short, paired, dorso-lateral "wings". Head, rostrum slender, slightly longer than head, lower margin straight, apex slightly down-curved, acute. Antenna 1 slightly the longer, flagellum with 35-40 very short segments; antenna 2, peduncle 4 not reaching distal margin of peduncle 3 of antenna 1.

KEY TO SPECIES OF *THORLAKSONIUS* (FEMALES AND SUBADULTS)

1. Pleon segment 3 and urosome segment 1 each with strong dorso-lateral carinae, elevated above level of mid-dorsal carina; gnathopod propods, distal-most palmar spine not enlarged, <50% longer than adjacent spine 2.
- Pleon segment 3 and urosome segment 1 with low or inconspicuous dorso-lateral carinae, not elevated above level of mid-dorsal carina; gnathopod propods, distal-most palmar spine enlarged, length > 2X adjacent spine (except in *T. borealis*) 5.
2. Rostrum elongate, slender, apex subacute; peraeon segments 5-7 lacking mid-dorsal and dorso-lateral carination or teeth; coxa 7 not laterally ridged, rounded behind 3.
- Rostrum short, deep, apex truncate or bluntly rounded; peraeon segments 5-7 with conspicuous mid-dorsal and dorso-lateral carinae or teeth; coxa 7 sharply ridged laterally and toothed behind 4.
3. Rostrum very long, about 50% longer than head; gnathopod propods each with 8 palmar outer marginal spines; uropod 3, inner ramus elongate, more than 2.5 X length peduncle . *T. incarinatus* Gurj. (p. 40)
- Rostrum shorter, slightly longer than dorsal head margin; gnathopod propods with 4-5 spines along outer palmar margin; uropod 3, inner ramus about 2X length of peduncle ... *T. amchikanus*, n. sp. (p. 38)
4. Rostrum, apex truncate; antenna 1, flagellum 35-40 segmented *T. truncatus*, n. sp. (p. 59)
- Rostrum, apex rounded; antenna 1, flagellum 25-30 segmented *T. carinatus*, n. sp. (p. 57)
5. Rostrum elongate, "duck-bill"-shaped, apex not deflexed, lower margin convex 6.
- Rostrum short, apex strongly deflexed, lower margin straight or nearly so 8.
6. Coxa 5 with lateral ridge, toothed behind; gnathopod propods, distal palmar spine not enlarged, < 50% longer than adjacent spine *T. borealis*, n. sp. (p. 42)
- Coxa 5 lacking lateral ridge, rounded behind; gnathopod propods, distal palmar spine enlarged, length < 2X adjacent spine. 7.
7. Antenna 1, flagellum with 16- 20-segments; peraeon segments 6-7, and pleon segments 1 & 2, mid-dorsal carinae not toothed behind *T. grandirostris*, n. sp. (p. 54)
- Antenna 1, flagellum with 25-30 segments; peraeon segments 6 & 7, and pleon segments 1 & 2, carinae distinctly toothed behind ... *T. platypus* (Barnard & Given), (p. 47)
8. Coxa 7, not laterally ridged or toothed behind 9.
- Coxa 7 laterally ridged and toothed behind 10.
9. Antenna 2, flagellum with 16-18 segments; pleon plate 3, hind corner acute, not produced; mandible, palp segment 3 lacking facial setae. *T. brevirostris*, n. sp. (p. 49)
- Antenna 2, flagellum with ~25 segments; pleon plate 3 strongly produced behind; mandibular palp segment 3 with numerous short facial setae *T. obesirostris* Bulycheva (p. 45)
10. Mid-dorsal carinae of peraeon segments 6-7 and pleon segments 1-2 strongly toothed behind; gnathopods 1 & 2, propod slender, length 2X depth *Thorlaksonius* sp. (Nagata, 1965) (p. 56)
- Mid-dorsal carinae low, not toothed behind; gnathopod 2 propod relatively short, length about 1/2 depth 11.
11. Peraeon segments 6-7 with dorso-lateral teeth; rostrum short, blunt, lower margin straight; antenna 1, flagellum with 22 segments *T. subcarinatus*, n. sp. (p. 52)
- Peraeon segments 6-7 lacking dorso-lateral teeth; rostrum large, lower margin convex, apex rounded; antenna 1, flagellum with 15 segments *T. depressus* (Alderman) (p. 47)

Coxae 1-4 very deep, narrow; 2 & 3 with faint median rib, lower margins slightly convex, corners sharply rounded; coxa 1 not covering anterior head lobe, medial rib faint; coxa 4, hind lobe acute, extending half-way along lower margin of coxa 5. Coxae 5-7 short, deep, rounded behind, lacking postero-lateral ridges.

Mouthparts plesiomorphic. Mandible, blade row short, with 14-16 blades; molar relatively large, thumb-like, apex subacute; palp segment 3 with about 5 baso-facial setae, inner margin of segment 2 moderately strongly (18-20) setose. Maxilla 1, palp little broadened, apical spines and setae extend along medially oblique margin nearly to mid-point; segment 1, lateral process small, 1-setose. Maxilla 2, inner plate broadened, inner margin lacking plumose seta. Maxilliped, palp large, strong; inner plate tall, inner margin richly setose, apex with 2-3 long spines; inner plate relatively large, apex rounded, with 7-9 spines of various sizes (inner-most short, stout) and 2 subapical marginal spines.

Gnathopods 1 & 2, propods subequal in size, 1 more slender, and inner face with 5 clusters of superior submarginal setae; carpal lobe relatively short. Gnathopod 1, basis, anterior margin lined with numerous short setae; angle of "step-down" margin ~ 30°; PDSP formula: outer - 8:3:3; inner - 4:3:4, total of 25; meral cusp small. Gnathopod 2, propod, angle of "step-down" margin similar, D-TD short, shallow; PDSP formula: outer - 8:3:4; inner - 3:4:5, total of 27; postero-distal spines extending submarginally less than one-third of palm, distal spine about 30% longer than adjacent spine; meral process medium strong.

Peraeopods 5-7, distal segments short, stout, powerful; bases enlarging posteriorly, hind margins straight; proximal cusp of basis of peraeopod 7 sharply acute; segment 4 posteriorly overhanging segment 5 by about 60-70% of its length; dactyls stout, powerful, about twice as large as those of peraeopods 3 & 4.

Pleon plates 1 & 2, hind margin sinuous, hind corner acute, produced in 2. Pleon plate 3, hind margin straight, hind corner squarish; lower margins finely spinose. Uropods 1 & 2, margins spinose, inner ramus little or not longer than peduncle, tips extending scarcely beyond tip of uropod 3. Uropod 3, inner ramus short, barely twice length of peduncle, only 50% longer than inner ramus, margins 6-7 spinose.

Telson short, broadest subapically, apex broadly rounded. Coxal gills pallet-like on peraeopods 2-3, plate-like on 4-6.

Etymology: The name "*amchitkanus*" alludes to the type locality of the species, in the outer islands of the Aleutian chain, Alaska.

Distributional Ecology: Known only from the type locality. The low body carinations and heavy structure of the posterior (clinging) peraeopods suggests that the species inhabits wave- and surf-exposed localities.

Taxonomic commentary: Although this species bears a few apomorphic specializations of the peraeopods, uropods, and telson, the overall body form and armature, and structure of the gnathopods and mouthparts is distinctly the most

plesiomorphic of known N. American forms (see discussion analysis, p. 62). Its phyletically nearest relative appears to be *T. incarinatus* Gurjanova, a species occurring in subarctic-boreal seas of the north-western Pacific region.

Thorlaksonius incarinatus (Gurjanova)

(Fig. 21)

Pleustes incarinatus Gurjanova 1938: 314, fig. 29 (English summary: 396).—Gurjanova, 1951: 641, fig. 437.—Gurjanova, 1955: 186, Pl. XXXII, fig. 7.—Gurjanova, 1972: 142, 143.

Diagnosis: Gurjanova (*loc. cit.*) has provided a reasonably complete and accurate description of external body features and details of gnathopods, uropod 3, and telson of this relatively small (7.0 mm) species. The diagnostic features are as follows:

Peraeon segments 1-7, mid-dorsal carinae feebly developed (on peraeon 6 & 7) or lacking, dorso-lateral teeth or carinae lacking; pleon segments with low mid-dorsal carinae and strong, ridge-like, medially indented, dorso-lateral carinae; pleon plates, hind marginal cusps lacking. Urosome 1 with strong paired dorso-lateral ridge.

Head, rostrum slender, elongate (about twice length of head), lower margin nearly straight, apex subacute. Eyes round, black. Antenna 1 slightly longer than antenna 2; flagellum of about 20 segments.

Coxae 1-4 deep, narrow, rounded below. Coxae 5-7 with weak lateral ridges and posterior teeth. Gnathopods 1 & 2 somewhat dissimilar in form; gnathopod 1, propod elongate, parallel-sided, inner surface with 5 clusters of anterior submarginal setae; angle of "step-down" margin shallow (~15°); PDSP formula: outer - 8:5:3; inner - 1:2:1(?), total of 20; distal group spread 1/3 along the outer margin, outer spine stout; posterior margin very short. Gnathopod 2, propod somewhat shorter and deeper, angle of "step-down" margin nearly 45°; PDSP formula: outer - 8:5:3; inner - 1:2:2(?), total of 21; distal group extending along one-third of palmar margin, distal spine largest and heaviest; meral lobe large, acute.

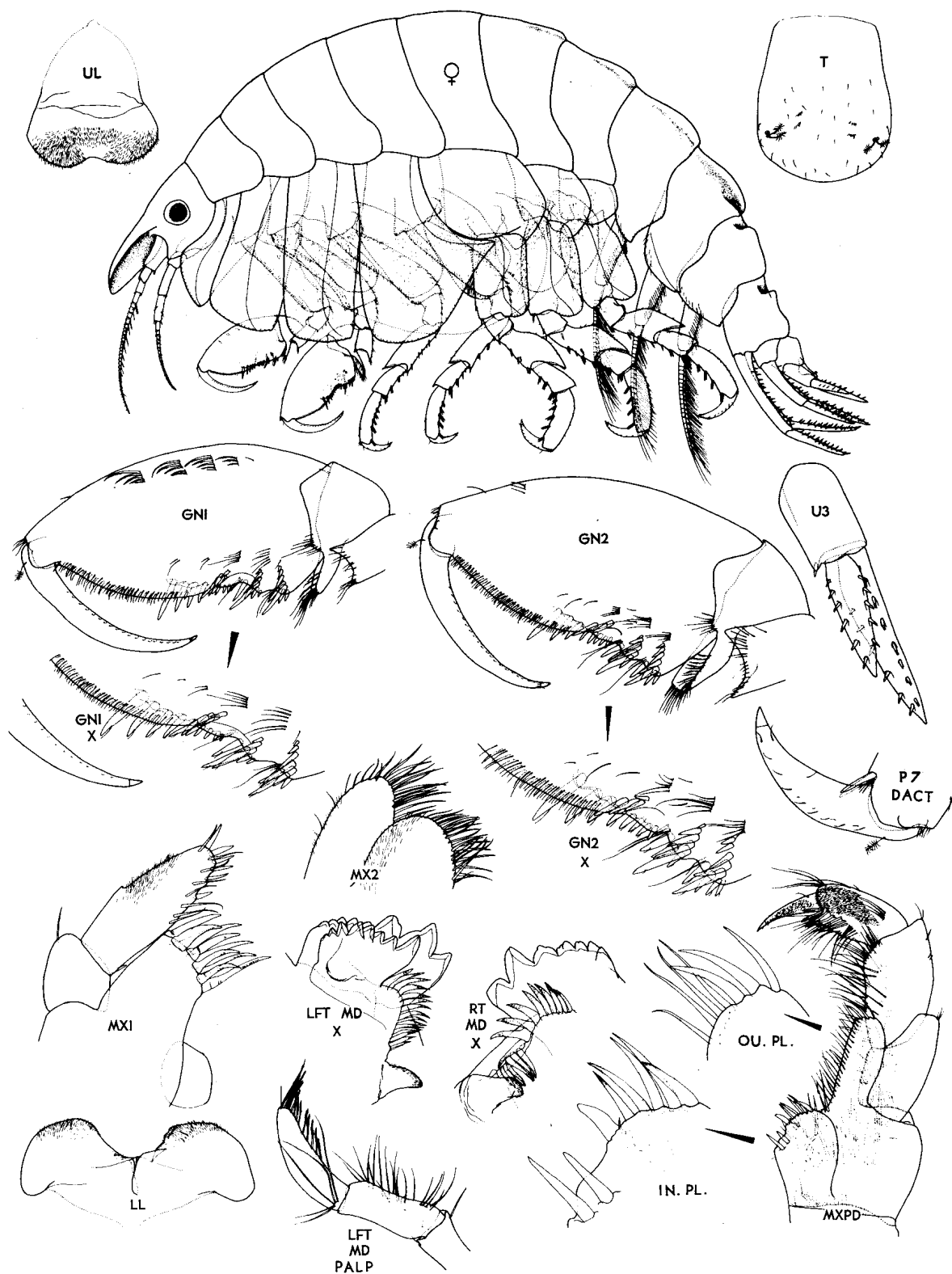
Peraeopods 5-7, bases broad, hind margins nearly straight; segments 4 & 5 relatively short, broad, with moderate overhang of segment 5; dactyls strong (< 50% length of segment 6).

Uropods 1 & 2, rami longer than respective peduncles, tips extending beyond tips of uropod 3. Uropod 3, rami relatively long and slender; inner ramus slender, with 8 pairs of marginal spines, length nearly 3X peduncle and 1.6X outer ramus. Telson narrowing distally, length 1.3X width, apex squared.

Body colouration: All body segments marked by strong vertical striping.

FIG. 20. *Thorlaksonius amchitkanus*, new

species. FEMALE ov. (13.0 mm) HOLOTYPE
(SEE PAGE 41 - OPPOSITE)



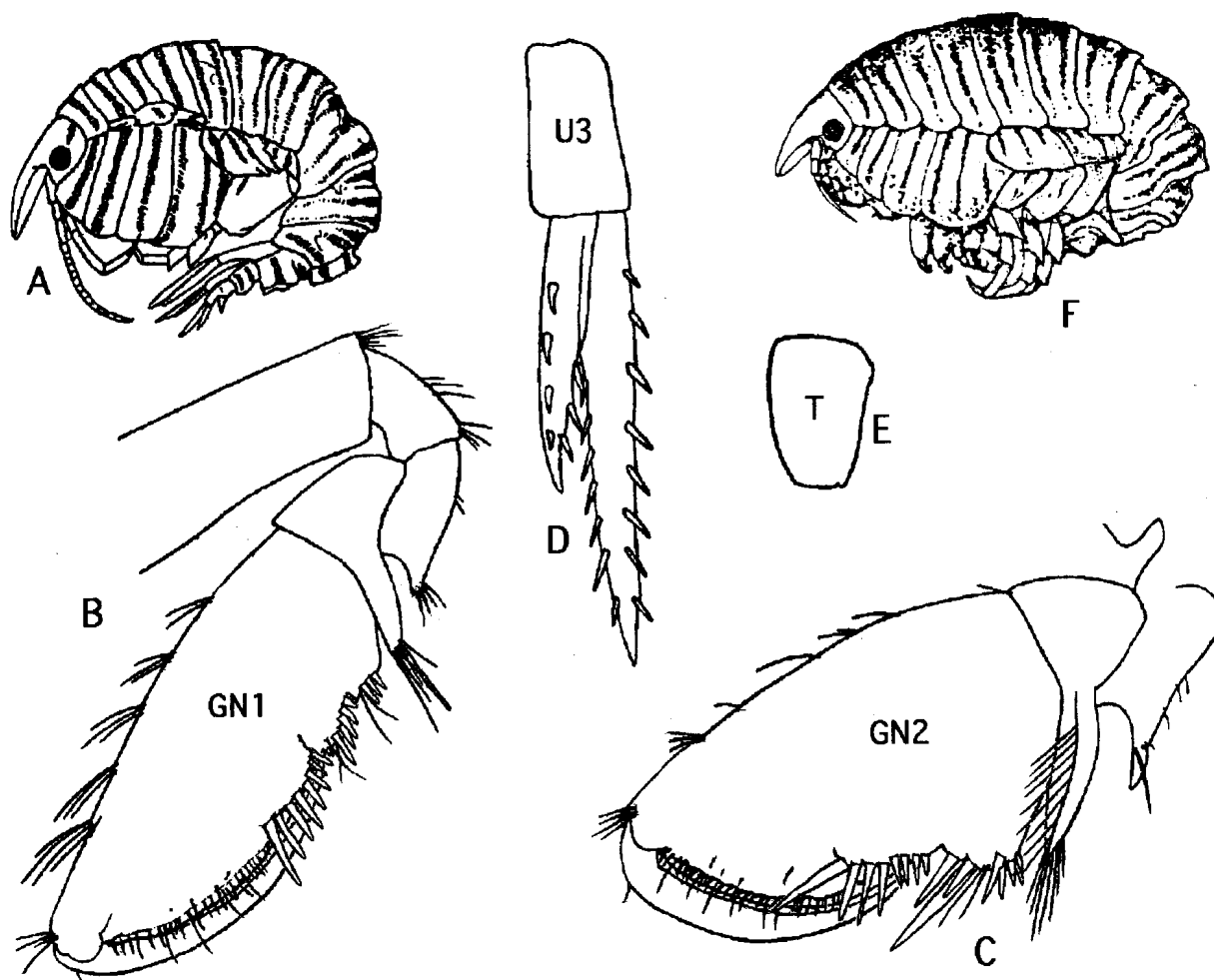


FIG. 21. *Thorlaksonius incarinatus* (Gurjanova, 1972) ♀ (7.0 mm). Okhotsk Sea.
A-E - after Gurjanova, 1972 F - after Gurjanova, 1955.

Distribution: Seas of Okhotsk and Japan, in depths of 16 to 80 m., associated with the *Desmarestia* algal zone.

Taxonomic commentary: This species bears plesiomorphic character states similar to those of its Aleutian counterpart, *T. amchitkanus* (p. 38). The close phyletic relationship (phenogram, p. 62) suggests that character states of the mouthparts, etc., not diagnosed by Gurjanova (*loc. cit.*), may be similar to those of *T. amchitkanus*.

The original descriptions and figures of this long-rostrate species regrettably provide little detail concerning the mouthparts. Presumably these bear plesiomorphic features similar to those of the closely related beringian species, *T. amchitkanus*. The lateral view figures of Gurjanova (1955, 1972) differ slightly in the size of the rostra, size and form of coxal plates, and degree of dorsal carination. Allocation of formal taxonomic significance to such differences may be justified but must await re-examination of the original material.

Thorlaksonius borealis, new species
(Figs. 22 & 23)

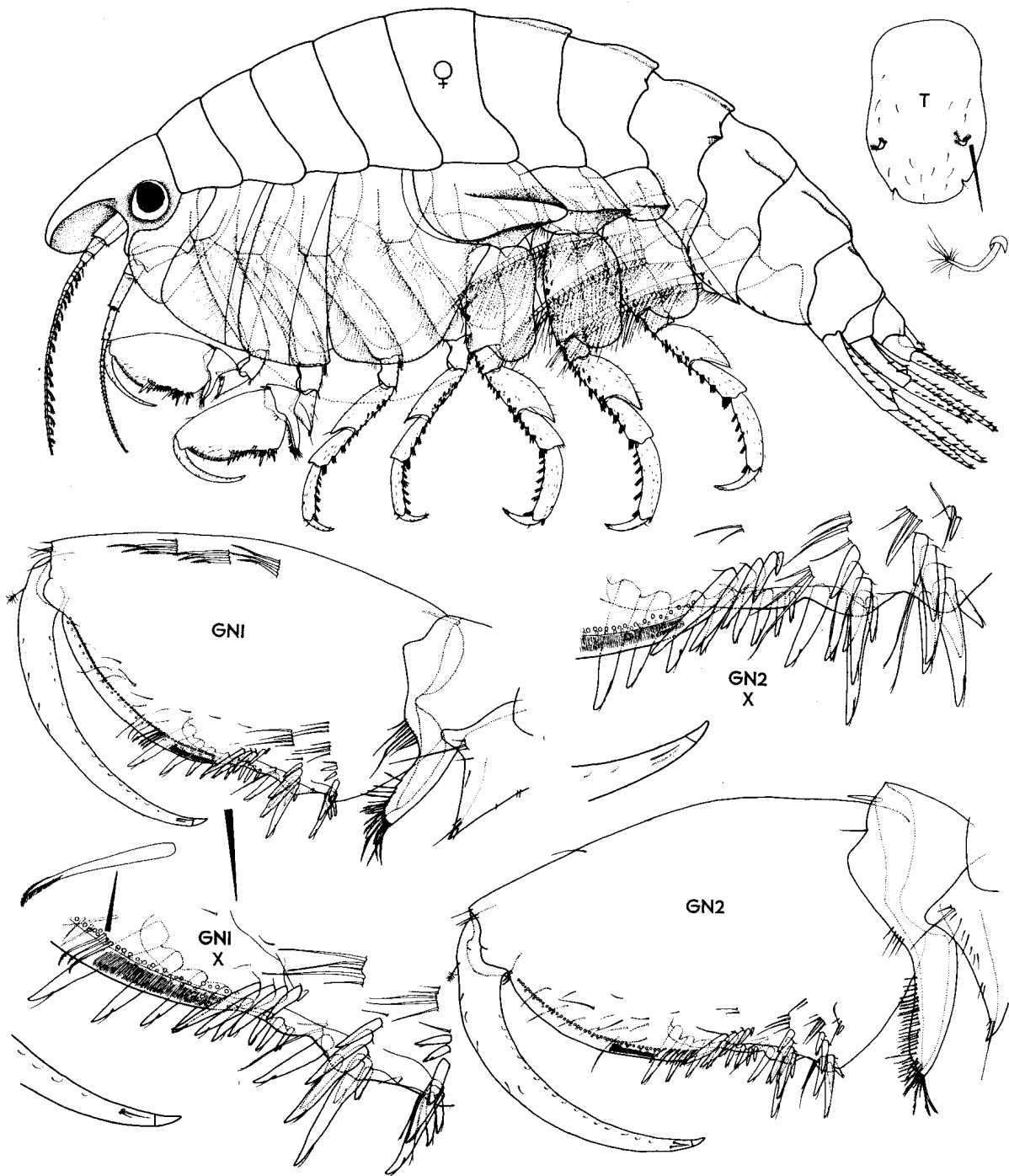
Pleustes platypa Barnard & Given, 1960: 42, Table I (partim)?—Barnard, 1969b: 207 (Table of variation - partim)?

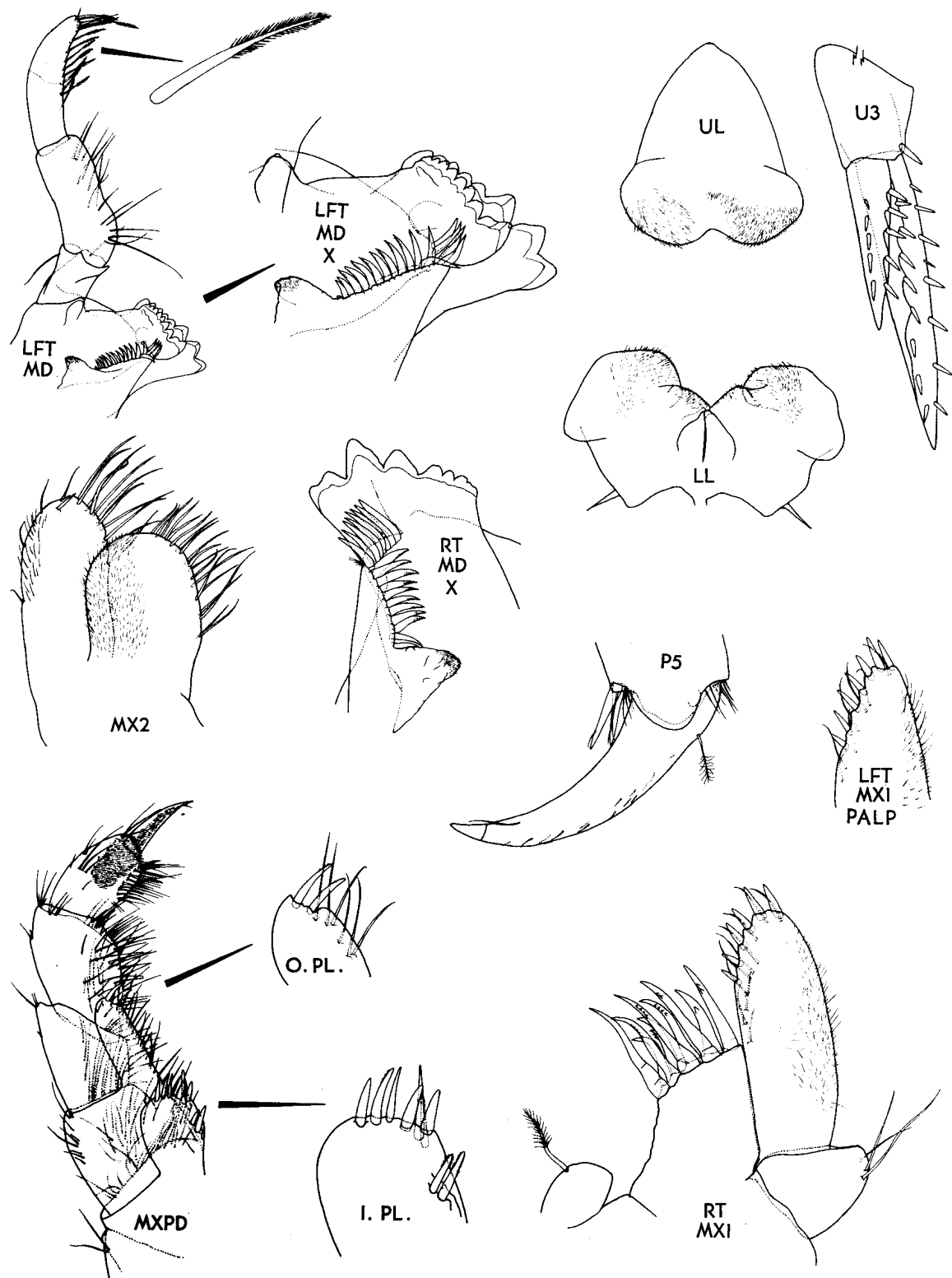
Material Examined: 28 specimens at 10 localities, southeastern Alaska to Oregon.

S. E. ALASKA: ELB & DEM Stns., 1961: Prince William Sound: A96 (1 male); A151 (1 female); Alexander Archipelago, Stn. A175 (1 female).

BRITISH COLUMBIA: North-central coast, ELB Stns. H5 (2 males, 1 female), H33 (1 female), H30 (1 female). Vancouver I. ELB Stn. B27 (1 male). ELB Stn. P710, Cape Beale, 19 July, 1970 - 1 female (11.0 mm) + slide mount, HOLOTYPE, CMN Cat. No. NMCC1994-361; 2 other

FIGS. 22 & 23. *Thorlaksonius borealis*, new species. FEMALE ov. (11.0 mm) HOLOTYPE
(SEE PAGES 43, 44).





females. Deer I., B. C., C. Low, E. Black coll., 10 m., 1980 - 15 im. specimens.

OREGON: ELB Stn. W60, Otter Rocks, Bedrock and algae, LW, Aug. 14, 1966 - 1 Female br. II + slide mount. CMN.

Diagnosis: Female ov. (11.0 mm). Peraeon segments 1-5 totally lacking mid-dorsal, dorso-lateral, and mid-lateral teeth or carinae; mid-dorsal carina very low, ridge-like on peraeon segments 6 & 7 and pleon segments 1-2; dorso-lateral teeth small posteriorly on peraeon 7 and pleon 1; medium, ridge-like dorso-lateral carinae on pleon 3 and urosome 1; lateral ridges, posterior teeth and cusps totally lacking on peraeon 1-7 and pleon 1-3.

Head, rostrum large, "duck-bill" shaped, slightly longer than deep, about equal in length to head, apex bluntly rounded, not deflexed. Antennae subequal; flagellum of antenna 1 with about 35 short segments. Antenna 2, peduncular segment 4 extending beyond peduncular segment 3 of antenna 1; flagellum of 26-28 short segments.

Mouthparts ordinary. Mandible, left and right sides with 18-20 blades; molar broadly triangular, apex blunt; palp segment 3 lacking baso-facial seta(e); inner margin of segment 2 strongly setose. Maxilla 1, palp not broadened, both left and right sides with 6-7 apical spines extending along medially oblique margin; lateral lobe of segment 1 with 3-4 longish setae. Maxilla 2, inner plate broad, inner margin lacking plumose seta. Maxilliped, outer plate relatively tall, reaching distal end of palp segment 1, apex with 2 curved spines; inner plate short, apex with 6 unequal spines, innermost not basally stout.

Coxae 1-4 deep, broad, outer face of 2 & 3 with fine mid-rib, lower margin gently convex, hind corner nearly square; coxa 1 nearly covering anterior head lobe; coxa 4 moderately produced behind, length equal to about half width of coxa; coxae 5-7 each with strongly developed, slightly oblique, postero-lateral ridge, posteriorly acute in coxae 6 & 7, strongly produced in coxa 5; coxa 5 relatively shallow, length nearly twice depth.

Gnathopod 1 slightly less deep than gnathopod 2. Gnathopod 2, angle of "step-down" margin gentle (30°), D-TD shallow, small; PDSP formula: outer - 8:3:2; inner - 4:4:5, total of 26; distal group extending submarginally about one-fourth of palm, distal spine about 30% longer than adjacent spine; posterior margin nearly equal in length to palmar margin; meral process medium, acute. Gnathopod 2, angle of "step-down" margin greater (~45°); PDSP formula: outer - 8:4:2; inner - 4:4:4, total of 26; meral process large.

Peraeopods 5-7, bases large, increasing posteriorly, hind margin of peraeopod 5 slightly concave, of peraeopods 6 & 7 straight or slightly convex, hind lobes of all broadly rounded below; proximal cusp of basis of peraeopod 7 prominent, triangular; segment 4 posteriorly overhanging segment 5 by about half its length; dactyl stout, distinctly longer and heavier than those of peraeopods 3 & 4.

Pleon plates 2 & 3, hind corners acuminate, slightly produced, lower margins weakly spinose. Uropods 1 & 2

elongate, inner ramus distinctly longer than peduncle, tips extending well beyond tip of uropod 3. Uropod 3, inner ramus stout, about 2.5 times length of peduncle, margins 8-spinose.

Telson relatively long, slightly expanded medio-distally, at level of penicillate setae, narrowing to broadly rounded apex. Coxal gills very large, narrowest on peraeopod 2, smallest on peraeopod 6.

Male (~7.5 mm): Smaller and more slender, and rostrum relatively longer, than in female. Antenna 1, flagellum with 26 segments; aesthetascs numerous. Peraeopods 5-7, dactyls very long, >> than 1/2 length of weakly spinose segment 6. Uropods 1 & 2 slender, inner ramus > peduncle.

Etymology: From the Greek root "*boreo*", meaning northern, alluding to the northerly distribution of the species on the North American Pacific coast.

Taxonomic commentary: *Thorlaksonius borealis* is isolated phylogenetically from its nearest relatives, but "bridges" character states differences between all three major subgroups (p. 63). Its morphology approximates form 1 (Table I of Barnard & Given, 1960), and possibly also one of the variants listed by Barnard (1969b) in "Velero" material from the Point Conception region of California. This species entrains a number of plesiomorphic character states of the antennae, peraeopods, uropods and telson, but the mouthparts and coxal plates are relatively apomorphic. The species superficially resembles the *platypus-depressus* subgroup but the abdomen, especially pleon 3 and urosome, bears moderately well developed dorso-lateral ridges, reminiscent of those of the primitive *amchitkanus* subgroup on the one hand, and the advanced *truncatus* group on the other.

Distributional ecology: Prince William Sound and Southeastern Alaska, through British Columbia to Oregon, mainly along surf-exposed, cold water, high salinity bedrock and algal shores.

Thorlaksonius obesirostris (Bulycheva)
(Figs. 24, 25)

Pleustes obesirostris Bulycheva, 1952: 215, fig. 16.—Gurjanova, 1972: 159, fig. 15.—Barnard & Karaman, 1991: 651.

Diagnosis: Body (7-10 mm). Mid-dorsal, dorso-lateral and mid-lateral teeth or carinae lacking on peraeon segments 1-7, weakly developed on pleon 1-3. Rostrum short, thick, deeper than long, apex blunt, deflexed, lateral margin not reaching eye. Eyes rather large, round, yellow-brown or bright cinnamon (in alcohol). Antenna 1, flagellum 14-15 segmented (part broken off?). Antenna 2, peduncular segment 4 slightly longer than 5; flagellum 21-22 segmented.

Mouthparts originally undescribed (figures of Bulycheva are small and species-diagnostic character states are not clear). Mandibular palp segment 3 bears a posterior marginal and facial brush of short setae (Gurjanova, fig. 15).

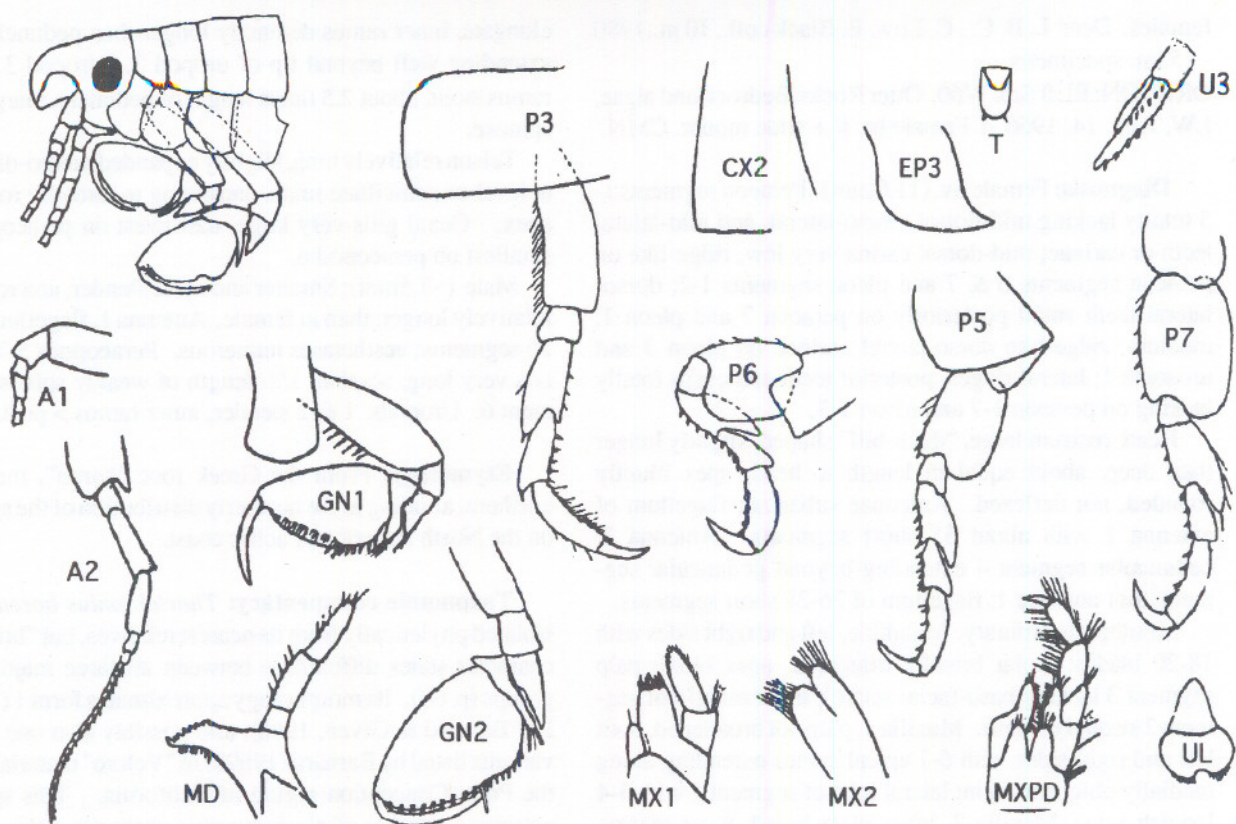


Fig. 24. *Thorlaksonius obesiostrois* Bulycheva, 1952 ♀ (9 mm). Japan Sea.
Peter the- Great Bay (modified from Bulycheva, 1952).

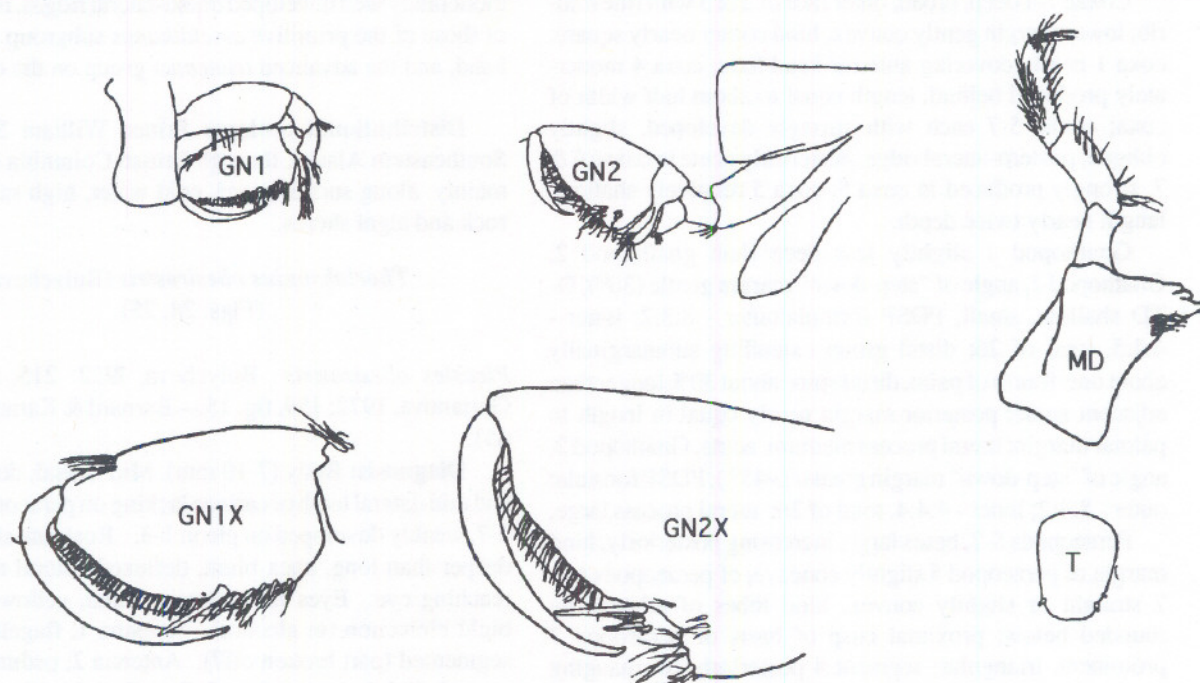


FIG. 25. *Thorlaksonius obesiostrois* Bulycheva, 1952. Syntype ♀ (~10.0 mm).
Japan Sea. (modified from Gurjanova, 1972, fig. 15).

Gnathopod 1, anterior marginal setae of basis located centrally; propod oval, palmar margin about 3/4 of its total length, with one stout cluster of antero-medial facial setae; distal spine group (DSPG) not extending onto palmar margin, distal-most spine very large, more than twice length of adjacent spine; angle of "step-down" margin very gentle; PDSP formula: outer - 2:3:2; inner - 0(?):3:1(?), total of 11(?). Gnathopod 2, propod similar but larger (inner facial setae not shown); angle of "step-down" margin sharp (45°); D-TD distinct; PDSP formula: outer - 4:1:1; inner - 1:1:1(?), total of 9; DSPG not extending onto palmar margin, distal spine more than twice length of adjacent spine(s).

Coxa 1 weakly hatchet-shaped. Coxa 2, lower hind border squarish. Peraeopods typical of the genus, hind margins of distal segments spinose.

Pleon plate 3, hind corner acute, produced. Uropod 3, outer ramus nearly twice length of inner ramus, and more than twice length of short peduncle. Telson longer than wide, narrowing slightly to rounded apex.

Distributional Ecology: Common in Peter-the-Great Bay (USSR coast, Sea of Japan), on reefs and in mature *Sargassum* and *Zostera*, at depths of 1-16 m. Tzvetkova & Kudrjaschov (1985) describe the species as abundant in the rocky shore kelp bed community and among fronds of *Sargassum*. The species occurs widely in the Seas of Japan and Okhotsk, and off the Kurile Islands and south Sakhalin.

Taxonomic commentary: The diagnosis (above) utilizes taxonomically critical information provided in the text accounts of Bulycheva (1952) and Gurjanova (1972), and is supplemented by the present authors' interpretation of figures. The armature of gnathopod propod posterior angle, setation of mandibular palp segment 3, and number of flagellar segments of antenna 1 relative to those of antenna 2, are anomalous to those character states in all other members of the genus *Thorlaksonius*. To clarify the accuracy and pertinency of these character states, detailed study of further material seems desirable.

Thorlaksonius depressus (Alderman)
(Fig. 26)

Pleustes depressus Alderman, 1936: 56, figs. 14-18.—Barnard, 1954: 9.

Pleustes depressa J. L. Barnard, 1969b: 206, fig. 58c, Table (part).—Barnard, 1975 (Light's Manual): 348 (key), 362 (list).—Carter & Behrens, 1980: 376, fig. 1.—Staude, 1987: 379, fig. 18.65, Key.

Diagnosis: The following diagnosis is based on species-level character states provided in the taxonomic description and figures of Alderman (1936):

Female ov. (8.5 mm): Body medium, relatively slender. Low mid-dorsal and dorso-lateral carinae or teeth present on peraeon segments 6 & 7, and more strongly on pleon segments 1-3.

Rostrum large, very deep, strongly deflexed to a broadly rounded or subtruncate apex. Antenna 1, flagellum 15-segmented. Antenna 2, flagellum 13-segmented.

Upper lip, epistomal process well marked, triangular, knife-like in front. Mandibular palp, length of segment 2 twice segment 1; segments 2 & 3 subequal in length. Maxilliped, inner plate half as long as outer. Other mouthpart structures probably much as in *grandirostris* and related members of the "duck-bill" subgroup of *Thorlaksonius*.

Coxae 1-4 deep, lower margins rounded. Coxa 4 not strongly produced behind. Coxa 5 posteriorly acute?

Gnathopod 1, propod twice as long as deep (wide) (angle) defined by a series of spines, distalmost palmar spine distinctly larger than adjacent spine. Gnathopod 2, propod deeper than in gnathopod 1, except that the posterior carpal lobe is larger and flattened cup-fashion over base of propod; angle of "step-down" margin very shallow, margin merging with posterior margin; D-TD barely discernible; at least 3 medium spines extend along outer palmar margin. PDSP formulae undeterminable.

Peraeopods 3-7 relatively short, segments stout. Peraeopod 4, dactyl stout, about 50% length of segment 6. Peraeopod 6, hind margin of basis nearly straight, posterior lobe rounded; segment 4 short, broad, hind lobe extending 50% length of segment 5; dactyl strong, length nearly 50% of segment 6.

Uropod 1, rami and peduncle subequal in length. Uropod 2, outer ramus 2/3 length of inner ramus. Uropod 3, outer ramus half as long as inner, and 50% longer than peduncle.

Telson flat, not constricted at base, rounded apically, length 40% greater than width.

Colour: light tan.

Length of specimens: 6.0 mm, 8.0 mm.

Distributional Ecology: In shallows along rocky shores, from Coos Bay, Oregon, to Carmel and La Jolla, California, in small numbers, variously associated with *Phyllospadix*, *Macrocystis*, and coralline algae. Two females, taken from kelp holdfasts, in 2 fathoms (about 4 m.) of water, at Moss Beach, San Mateo Co., California, July-August, 1933. Material similar to *T. depressus* was also listed by Barnard (1969b) from "Velero" Stns. 2280, and 1407.

Taxonomic Commentary: The weakly carinated body, large down-curved rostrum, short legs, and small size distinguish this species from all others known to date. Its combination of plesiomorphic and apomorphic character states relate it most closely to *Thorlaksonius platypus* and *T. grandirostris* (p. 54).

Thorlaksonius platypus (Barnard & Given)
(Fig. 27)

Pleustes platypa Barnard & Given, 1960: 41, fig. 1.—J. L. Barnard, 1969b: 206, fig. 58a, Table (sample 1871 mainly).—Crane, 1969: 200, pl. 1?—Field, 1974: 439, Figs. 1-3? *Pleustes platypus*—Gurjanova, 1972: 142-143.—Barnard,

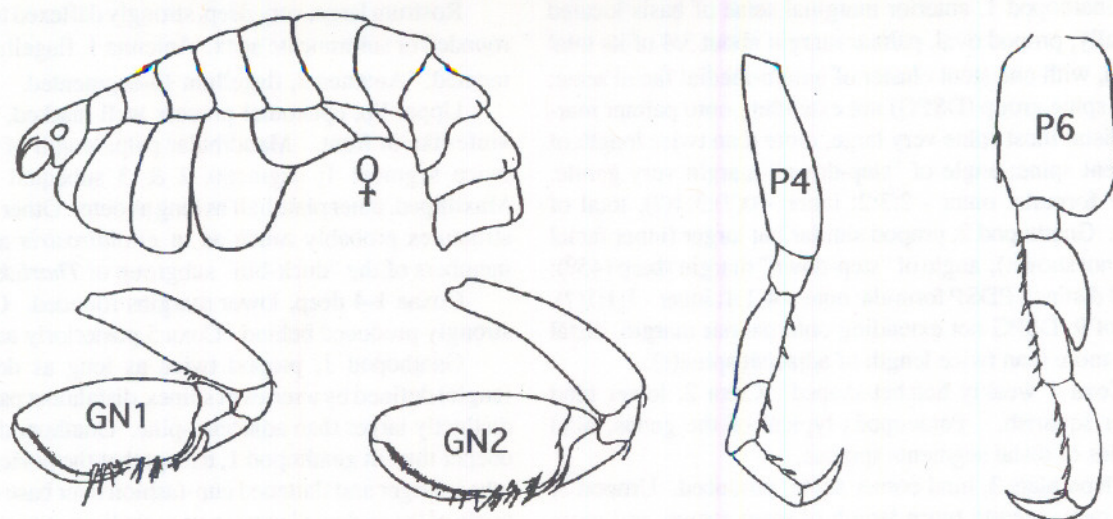


FIG. 26. *Thorlaksonius depressus* (Alderman). ♀ (8.5 mm).
Central California. (after Alderman, 1936, figs. 14-18).

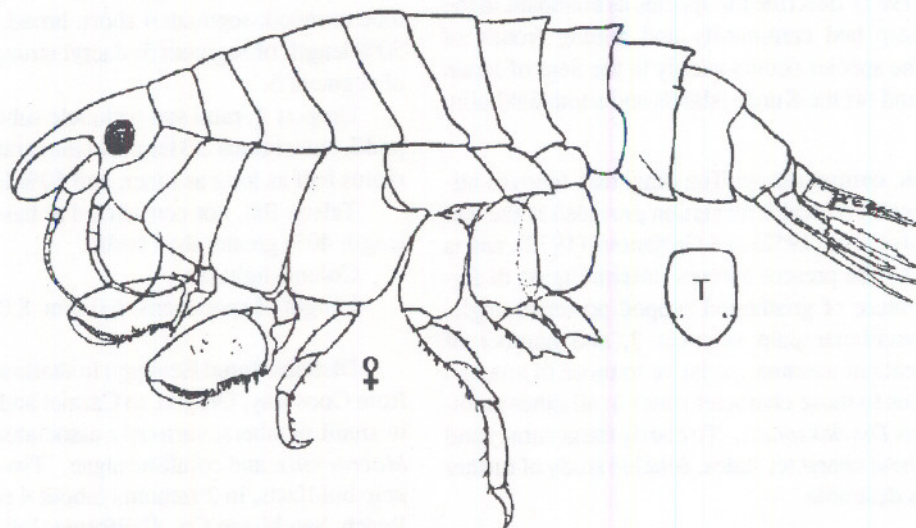


FIG. 27. *Thorlaksonius platypus* (Barnard & Given). ♀ (8.5 mm)
Southern California. (after Barnard & Given, 1960, fig. 1).

Bowers, & Haderlie, 1980: 559?—Carter & Behrens, 1980: 376, fig. 1.—Barnard & Karaman, 1991: 651.

Material Examined: None identified in present lots.

Diagnosis: The following diagnosis is collated from the original figure and brief descriptive remarks of Barnard & Given (loc. cit.).

Female ov. (8.5 mm): Mid-dorsal carinae lacking, or trace only, on pereaeon segments 5 & 6, distinct on pereaeon 7, medium to weak on pleon segments 1 & 2 respectively; dorso-lateral and lateral teeth lacking on all pereaeonal seg-

ments, weakly developed on pleon segments 1 & 2. Dorso-lateral ridges apparently lacking on pleon 3 and urosome 1.

Head, rostrum large, deep, "duck-bill" shaped, about 1.5X head length, slightly deflexed distally to bluntly rounded apex. Antenna 1, flagellum of 25-30 segments (estimated). Antenna 2, peduncular segment 4 extending well past peduncle of antenna 1; flagellum of 15-20 segments (estimated).

Barnard & Given (loc. cit.) referred to the mouthparts "as in *P. panopla* (Kroyer) (Sars, 1895, pl. 121)". However, in view of mouthpart distinctions between the genera *Thorlaksonius* and *Pleustes* (*Pleustes*), such does not seem likely, and the mouthparts remain, in effect, undescribed.

Coxae 1-4 broad deep, lower corners sharply rounded. Coxa 5 hind margin steeply sloped, not strongly produced posteriorly. Coxae 5-6 hind corners subacute (facially not ridged?); coxa 7 apparently without lateral ridge or toothed behind.

Gnathopods unequal; gnathopod 1, propod smaller more slender than in gnathopod 2, hind margins of both very short; angle of "step down" margin very gentle, imperceptibly merging with hind margin; distal spines extend onto outer palmar margin, distal-most spine distinctly stronger than adjacent spine; PDSP formulae not accurately determinable; that of gnathopod 2 close to: outer - 8:3:2.

Peraeopods 5-7, bases broad, hind margins nearly straight; segment 4 ordinary, postero-distal lobe overhanging segment 5 by about 40% of its length; dactyls stronger than in peraeopods 3 & 4, about half the length of segment 6. Uropods 1 & 2, inner ramus longer than peduncle, serially about 10-spinose. Uropod 3, length of outer ramus about 60% that of the inner ramus. Telson slightly longer than wide, slightly broadening distally, apex rounded. Coxal gills, brood plates, pleopods also not described.

Distributional Ecology: Pt. Conception, Catalina I., and La Jolla, S. California, on various bottom types (*Phyllospadix*, *Chaetopterus*, etc), in small numbers from the low water line to depths of more than 100 m.

Taxonomic commentary: Barnard (1969b, Table, p. 207) has listed a number of morphotypes (from "Velero" samples taken off the coast of southern California) that vary widely in type of rostrum, and dorsal carination of peraeon and pleonal segments. Variants of this species exhibit Batesian mimicry with mitrellid snails (Crane, 1969; Field, 1974; Carter & Behrens, 1980). Similar kinds of "variation" in the present material from British Columbia and adjacent coastal waters is here shown to have species-level taxonomic importance. Its possible applicability to Barnardian material awaits re-examination of the original "Velero" material in the Allan Hancock Foundation collections, and "mimicry" collections elsewhere (above).

Thorlaksonius brevirostris, new species
(Figs. 28, 29)

Material Examined: A total of 235 specimens in 74 station lots were examined (number of specimens taken at each station given in parentheses).

S.E. ALASKA: ELB & DEM Stns., 1961: 14 lots (31 specimens): A6(1), A7(1), A27(1), A80(2), A91(2), A96(1), A131(1), A136(1), A147(6), A151(3), A168 (2).

ELB, KEC Stns., 1980: 6 lots (14 specimens): S5B7(10), S8F3(2); S18F3(1), S19B1(1), S20B5(1), S23F1(1).

BRITISH COLUMBIA:

Queen Charlotte Islands: ELB Stns., 1957: 3 lots (6 specimens): E14a(3), W2(1), W4a(2).

North-central coast: ELB Stns., 1964: 11 lots, (82 speci-

mens): H1(1), H3(5), H7(11), H8(6), H10(4), H23(1), H29(3) H30(3), H33(14), H65 (31), H57(4).

Vancouver Island, north end, ELB Stns., 1959: 12 lots (83 specimens): O1(2), O5(3), O11(6), O13(2), O15(3), V5(5), V7(39), V10(1), V17(12), V46(6), N6(9), N16(1). ELB Stns., 1955: 1 lot (1 specimen).

TYPE LOT: Lady Ellen Point, north end of Vancouver I., B. C., ELB Stn. V7, LW, 7 Aug., 1959 - 1 female ov. (7.8 mm) + slide mount, HOLOTYPE, CMN Cat. No. NMCC 1994-352; male (7.0 mm), ALLOTYPE, CMN Cat. No. NMCC 1994-353; several males, females and immatures, PARATYPES, CMN Cat. No. NMCC 1994-354.

Vancouver Islands, south end, ELB Stns.: 10 lots (43 specimens): 1955 - 3 lots (31 specimens): G2(1), F1 (20), F2(10), F3(1); 1970 - 2 lots (3 specimens): P702(2), P719 (1); 1975 - 2 lots, (2 specimens): P3a(1), P17a(1); 1976 - 3 lots, (7 specimens): B4(1), B7(4), B27(2). Additional material from localities in southern Vancouver I.: E. Black, C. Low collns., (1980-81): -12 lots (21 specimens).

WASH.-OREGON, ELB Stns., 1966 - 5 lots (27 specimens): W30(2), W36(1), W40(1), W42(1), W60(22).

CALIFORNIA: Horseshoe Cove, Bodega Bay, CA. K. E. Conlan Stn. 06-2, July 6, 1986 - 3 males, 5 females, 12 im.

Diagnosis: Female ov. (7.8 mm): Body small to medium. Peraeon segments 1-5 lacking dorsal and dorso-lateral teeth or carinae. Peraeon segments 6, 7, and pleon segments 1-3 with very low mid-dorsal ridge, not toothed behind. Pleon segments 1 & 2 with small dorso-lateral teeth. Pleon 3 and urosome 1 with low dorso-lateral ridges, not toothed behind. Pleon plates 1-3, hind corners acute, slightly produced, lacking hind marginal cusps.

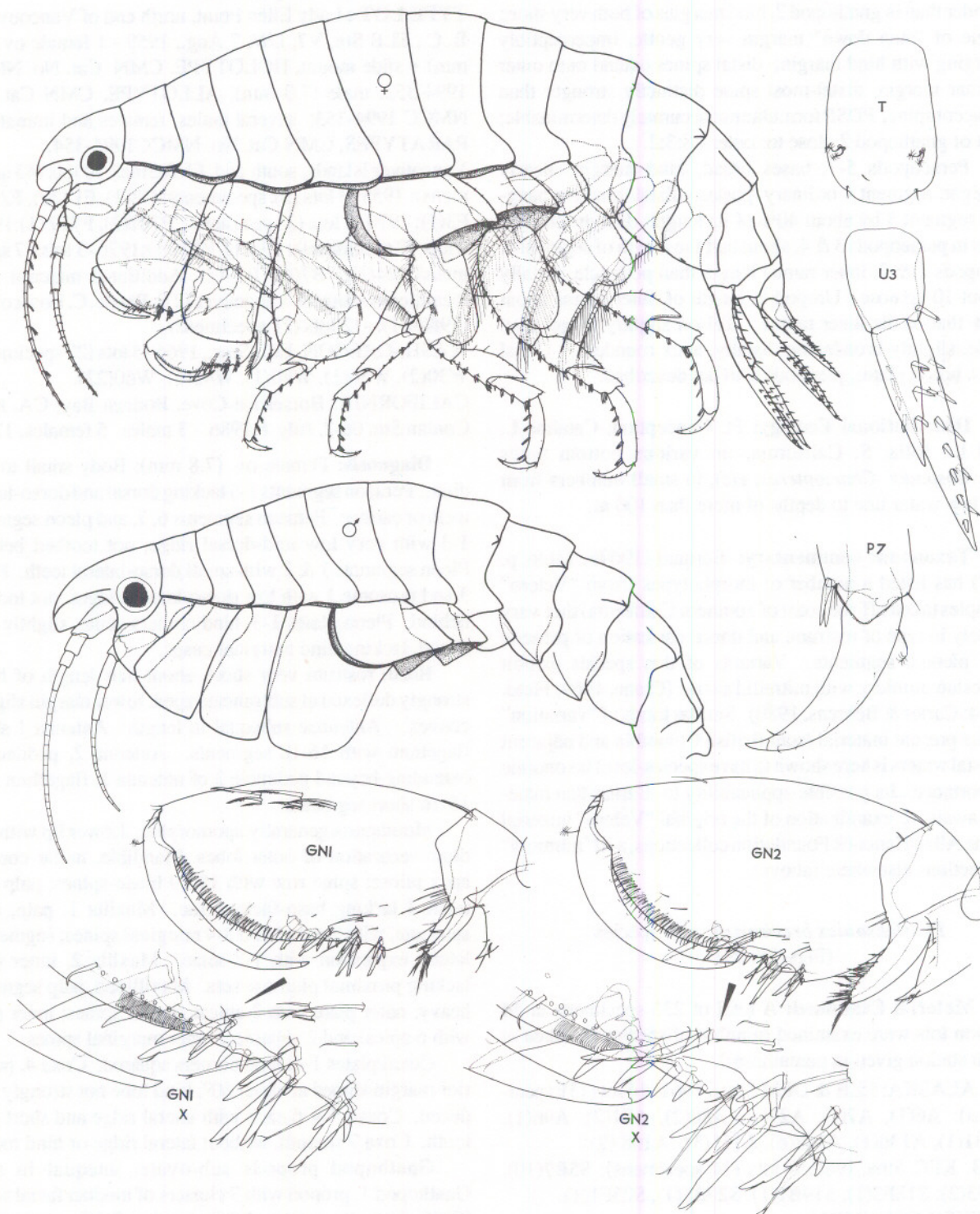
Head, rostrum very short, about half length of head, strongly deflexed at subtruncate apex, lower margin slightly convex. Antennae subequal in length. Antenna 1 short, flagellum with 16-18 segments. Antenna 2, peduncle 4 extending beyond peduncle 3 of antenna 1, flagellum with 15-16 short segments.

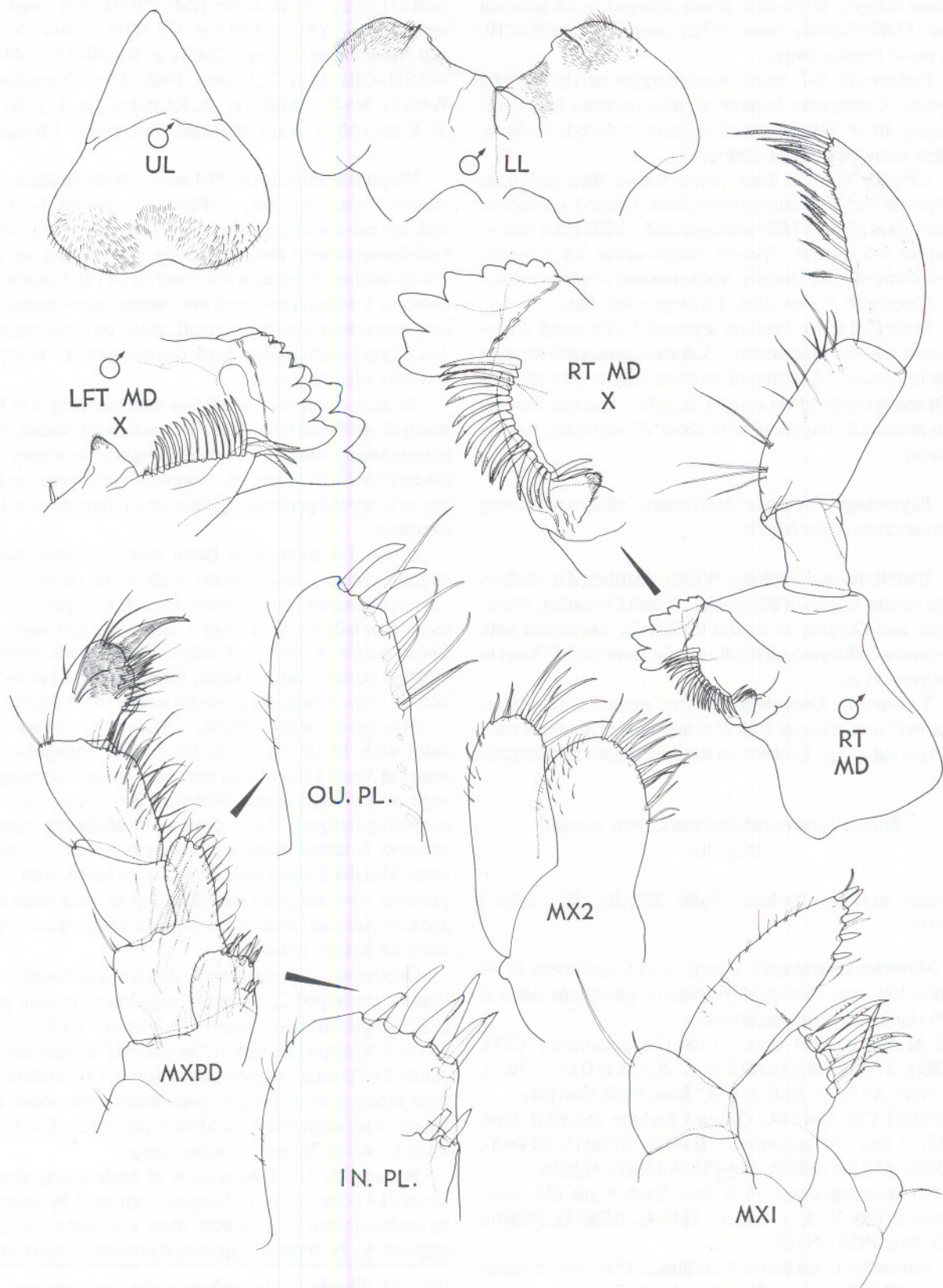
Mouthparts generally apomorphic. Lower lip with medium separation of outer lobes. Mandible, molar conical, apex pilose; spine row with 18-19 blade-spines; palp segment 3 lacking baso-facial setae. Maxilla 1, palp, apex subacute, with 2 apical and 3-4 marginal spines; segment 1, lateral expansion with 1-2 setae. Maxilla 2, inner plate lacking proximal plumose seta. Maxilliped, palp segments heavy; outer plate with 2 apical curved spines; inner plate with 6 apical and 2 subapical inner marginal spines.

Coxal plates 1-4, hind corners squared. Coxa 4, posterior margin sloped at about 60°, hind lobe not strongly produced. Coxae 5 & 6 each with lateral ridge and short hind tooth. Coxa 7 smooth, without lateral ridge or hind tooth.

Gnathopod propods sub-ovate, unequal in size. Gnathopod 1, propod with 3 clusters of median facial setae; PDSP formula: outer - 6:2:2; inner - 2:4:3, total of 19. FIGS. 28, 29. *Thorlaksonius brevirostris*, new species FEMALE ov. (7.8 mm) HOLOTYPE; MALE (7.0 mm)

ALLOTYPE. (SEE PAGES 50 AND 51)





Gnathopod 2, angle of "step-down" margin gentle, imperceptible, D-TD shallow; distal spines extend little onto outer palmar margin, distal-most much enlarged, > 2X adjacent spine; PDSP formula: outer - 6:3:2; inner - 3:3:2, total of 19-20; meral process large.

Peraeopods 5-7, bases, hind margins nearly straight; segment 4 somewhat broadened, postero-distal lobe overhanging about 50% length of segment 5; dactyls medium, length about half that of segment 6.

Uropods 1 & 2, inner ramus longer than peduncle, margins with 6-7 serially paired spines. Uropod 3, length of inner ramus about 2 1/2X peduncle and 1 1/2X inner ramus, margins 5-6 spinose. Telson, length about 1.4 X width, broadening slightly distally, apex rounded or subtruncate.

Coxal gills 2-3 sac-like, 4-6 large, plate-like.

Male (7.0 mm): Peraeon segment 7 with small dorso-lateral tooth. Pleon segments 1-3, dorso-lateral teeth stronger than in female. Rostrum of medium length, less strongly deflexed apically, lower margin straight. Antenna 1 longer than antenna 2, flagellum with about 22 segments, basally conjoint.

Etymology: The name "*brevirostris*" alludes to the very short rostrum of the female.

Distributional Ecology: Widely distributed in shallow outer coastal waters of SE Alaska, British Columbia, Washington and Oregon, to central California, associated with laminarian holdfasts and *Phyllospadix*, from the LW level to depths of 35 m.

Taxonomic Commentary: This species is closely related to *T. subcarinatus*, and other members of the *depressus-platypus* subgroup. Its character states are mainly apomorphic.

Thorlaksonius subcarinatus, new species

(Fig. 30)

Pleustes depressa Barnard, 1968b: 206, fig. 58c, Table I (part)?

Material Examined: A total of 118 specimens in 39 station lots were examined (number of specimens taken at each station given in parentheses).

S.E. ALASKA: ELB Stns., 11 lots (24 specimens): A3(1), A48(1), A71(1), A87(1), A92(3), A12(2), A131(1), A139(1), A174(4), A151(5); ELB & KEC Stns., 1980: S6B1(4).

BRITISH COLUMBIA: Queen Charlotte Ids., ELB Stns., 1957: 9 lots (30 specimens): E14(2), E14a(1), E14b(5), E25(2), H11 (1), W8(2), W4a(5), W15b(1), N2a(9).

North-central coast: ELB Stns., 1964: 6 lots (31 specimens): H5(8), H33(1), H43(1), H47(4), H53(11), H65(6); ELB Stn., 1959 - N1(3).

Vancouver I., north end, ELB Stns., 1959: 2 lots (5 specimens): N11(4), V22(1); ELB Stn., 1955: G4 (7).

Vancouver I., south end, ELB Stns., 1955 - 2 lots (13 specimens); ELB Stns., 1976 - 2 lots (5 specimens).

TYPE LOT: Telegraph Bay, Cadborough Bay, Vancouver I., B.C. ELB Sta. F6, Aug. 9, 1955. - 1 female ov. (9.3 mm), **HOLOTYPE**, CMN Cat. No. NMCC1994-355; 1 male (5.0 mm), **ALLOTYPE**, CMN Cat. No. NMCC1994-356; several males, females, & im., CMN Cat. No. NMCC1994-357. WASH.-OREGON: ELB Stns., 1966: 2 lots (3 specimens). W40(1), W64(2). Mill Bay, K.E. Conlan Stn. 1, 1980- (1). E. Black coll., Pultney Pt., Malcolm I, 1980 - 1 female.

Diagnosis: Female ov. (9.3 mm). Body medium sized, relatively short and deep. Peraeon segments 1-5 totally lacking mid-dorsal dorso-lateral and lateral teeth or carinae; mid-dorsal carinae low, posteriorly elevated but not posteriorly toothed on peraeon 6 & 7 and pleon 1 & 2; pleon 3 and urosome 1 with dorso-lateral low ridges. Dorso-lateral teeth on peraeon segments 6 & 7 small, acute, on pleon segments 1 & 2 larger and basally ridged; pleon segment 1 with small posterior marginal tooth.

Head, rostrum very short, less than half length of head, much deeper than long, apex deflexed and truncate, lower margin nearly straight. Antenna 1 slightly the longer, flagellum with 20-25 segments. Antenna 2, peduncle 4 extending well beyond peduncle 3 of antenna 1, flagellum of 18-20 segments.

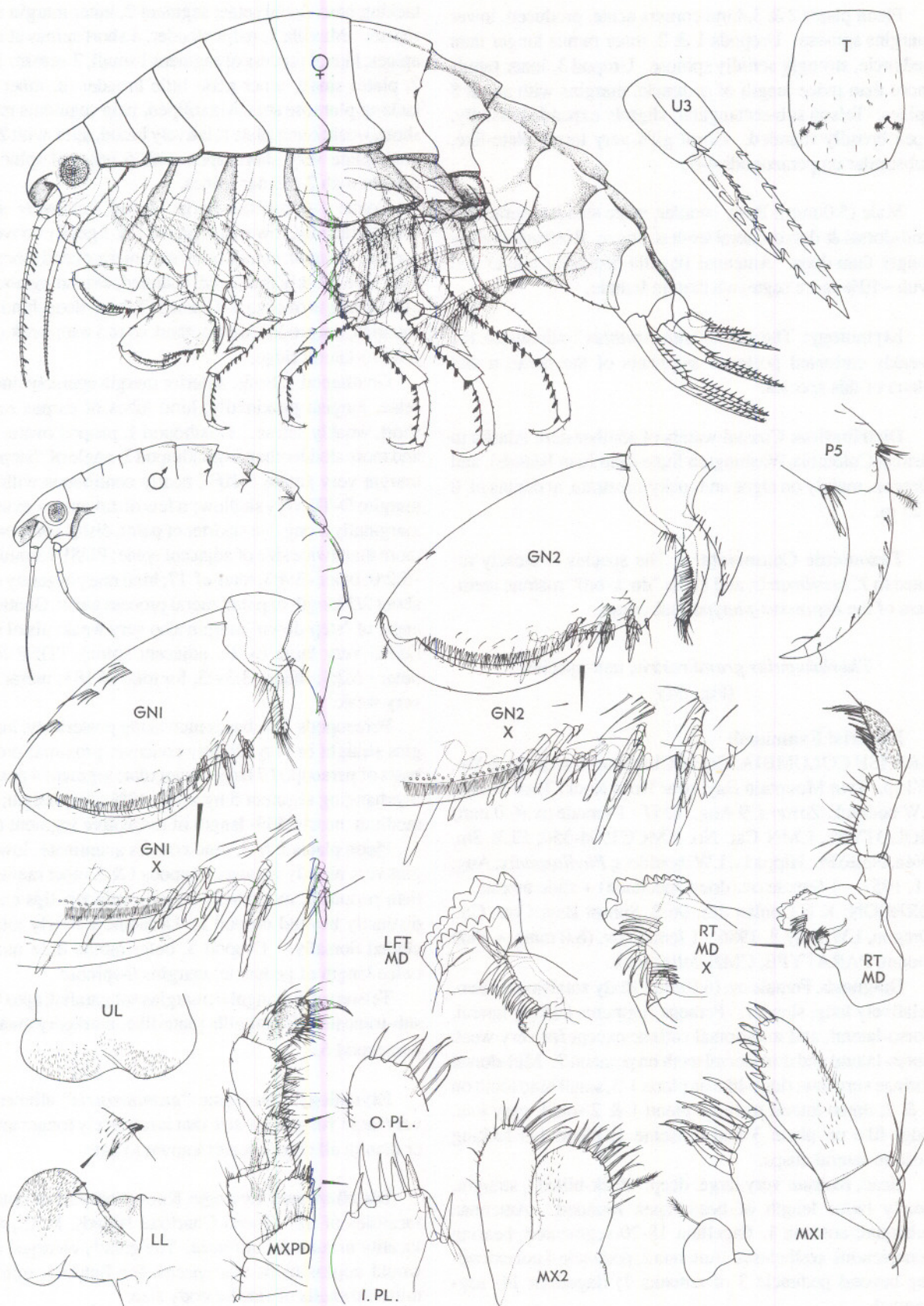
Coxae 1-4 deep, with facial mid-rib, lower margins slightly convex, hind corners with weak cusps; coxa 1 covering anterior head process; coxa 4, hind process long, more than half width of coxa 4, extending half-way along lower margin of coxa 5. Coxae 5-7 with weak, obliquely sloping, postero-lateral ridges, little produced but toothed behind; coxa 5 long, deep, length nearly twice depth.

Mouthparts unremarkable. Mandible, left and right sides with 16-18 blades; molar broadly triangular; palp segment 3 with 1 baso-facial seta, inner (posterior) margin of segment 2 strongly setose. Maxilla 1, apical spines and setae extending obliquely nearly to mid-point of slightly expanded segment 2; lateral process of segment 1 with 3-4 longish setae. Maxilla 2, inner plate slightly broadened, with 1 short plumose inner marginal seta. Maxilliped, outer plate short, apex 2-3 spinose; inner plate with six apical spines, innermost not basally broadened.

Gnathopod 1, propod more slender, less basally deep, than in gnathopod 2; angle of "step-down" margin gentle (~30°); PDSP formula: outer - 7:3:2; inner - 4:4:3-4, total of 23-24. Gnathopod 2, angle of "step-down" margin similarly gentle, D-TD small, shallow; distal spines extend about one-third along palmar margin, distal-most spine about twice length of adjacent spine; PDSP formula: outer - 8:4:3; inner - 4:4:3, total of 26; meral process large.

Peraeopods 5-7, hind margin of basis nearly straight; segment 4 posteriorly overhanging segment 5 by about half its length; dactyls long, slender, more than half the length of segment 6. Peraeopod 7, proximal process of basis blunt.

FIG. 30. *Thorlaksonius subcarinatus*, new species
FEMALE (9.3 mm) HOLOTYPE; MALE (5.0 mm)
ALLOTYPE. (SEE PAGE 53 - OPPOSITE)



Pleon plates 2 & 3, hind corners acute, produced, lower margins spinose. Uropods 1 & 2, inner ramus longer than peduncle, strongly serially spinose. Uropod 3, inner ramus more than twice length of peduncle, margins with about 8 spines. Telson sub-rectangular, slightly expanded distally, apex broadly rounded. Coxal gills very large, plate-like, subsimilar on pereopods 4-6.

Male (5.0 mm): Body smaller, more slender; peraeonal mid-dorsal & dorso-lateral teeth stronger. Rostrum slightly longer than deep. Antennal flagella distinctly longer and with ~10% more segments than in female.

Etymology: The name "*subcarinatus*" alludes to the weakly carinated posterior segments of the peraeon and pleon of this species.

Distribution: Coastal waters of southeastern Alaska to British Columbia, Washington State (San Juan Islands), and Oregon, mainly on algae and rocky substrata, at depths of 0 - 25 m.

Taxonomic Commentary: The species is closely related to *T. brevisrostris*, and to the "duck-bill" rostrate members of the *depressus-platypus* subgroup.

Thorlaksonius grandirostris, new species
(Fig. 31)

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands: ELB Stn. W15b, Two Mountain Bay, near Horn Rock, Tasu Sound, LW bedrock, *Zostera*, 9 Aug., 1957 - 1 female ov. (6.0 mm) HOLOTYPE, CMN Cat. No. NMCC1994-350; ELB Stn. W4a, Nesto Pt., Hippa I., LW, boulders, *Phyllospadix*, Aug. 11, 1957 - 1 female ov. (dried specimen) + slide mount. OREGON: K E Conlan Stn. 06-2, Sunset Bay, Coos Co., Oregon, LW, July 8, 1986 - 1 female ov. (6.0 mm) + slide mount, PARATYPE, CMN collections.

Diagnosis. Female ov. (6.0 mm): Body small to medium, relatively long, slender. Peraeon segments lacking lateral, dorso-lateral, and mid-dorsal carinae except for very weak dorso-lateral and mid-dorsal teeth on peraeon 7. Mid-dorsal carinae very low, ridge-like on pleon 1-3, small hind tooth on 1 & 2; dorso-lateral teeth on pleon 1 & 2 small, very low, ridge-like on pleon 3 and urosome 1; pleon 1-3 lacking postero-lateral cusps.

Head, rostrum very large, deep, "duck-billed", straight, nearly twice length of head, apex rounded. Antennae subequal; antenna 1, flagellum 18-20 segmented, bearing conspicuous aesthetascs. Antenna 2, peduncle 4 not extending beyond peduncle 3 of antenna 1; flagellum 14-segmented.

Mouthparts reduced. Mandible, left and right blade rows short, 15-16 blades on each side; molar short, thumb-like, apex subacute; left lacinia 8-9 dentate; palp segment 3

lacking baso-facial setae; segment 2, inner margin sparsely setose. Maxilla 1, palps slender, 4 short spines at rounded apices; lateral process of segment 1 small, 2-setose. Maxilla 2, plates small, inner plate little broadened, inner margin lacking plumose seta. Maxilliped, palp segments relatively short, weak; outer plate relatively broad, apex with 2 spines; inner plate very short, apex with 6 unequal spines, inner margin with 2 slender spines.

Coxae 1-4 medium large, broad, relatively shallow, smooth facially, lower margins of 2 & 3 gently convex, hind corners squarish; coxa 1 covering anterior head lobe; coxa 4, hind lobe weakly produced, rounded, extending about one-quarter length of coxa 5. Coxae 5-7 short, deep, hind corners squarish, not produced or toothed, coxa 5 with weak, oblique, postero-lateral ridge.

Gnathopod 1, basis, anterior margin sparsely lined with setae, longish proximally; hind lobes of carpus relatively short, weakly setose. Gnathopod 1, propod ovate, smaller and more slender than in gnathopod 2; angle of "step-down" margin very gentle (~10°), nearly continuous with palmar margin; D-TD very shallow; a few distal spines extend submarginally along one-quarter of palm, distal spine enlarged, more than twice size of adjacent spine; PDSP formula: outer - 5:2:0; inner - 3:4:3, total of 17; hind margin gently convex, about 2/3 length of palm; meral process weak. Gnathopod 2, angle of "step-down" margin also very weak; distal spine of DSPG very large (> 2X adjacent spine); PDSP formula: outer - 6:2:1; inner - 3:3+:3, for total of 18+; meral process very weak.

Pereopods 5-7, bases increasing posteriorly, hind margins straight or very slightly concave; proximal process of basis of pereopod 7 large, triangular; segment 4 posteriorly overhanging segment 5 by about 40% of its length; dactyls medium, nearly 50% length of respective segment 6.

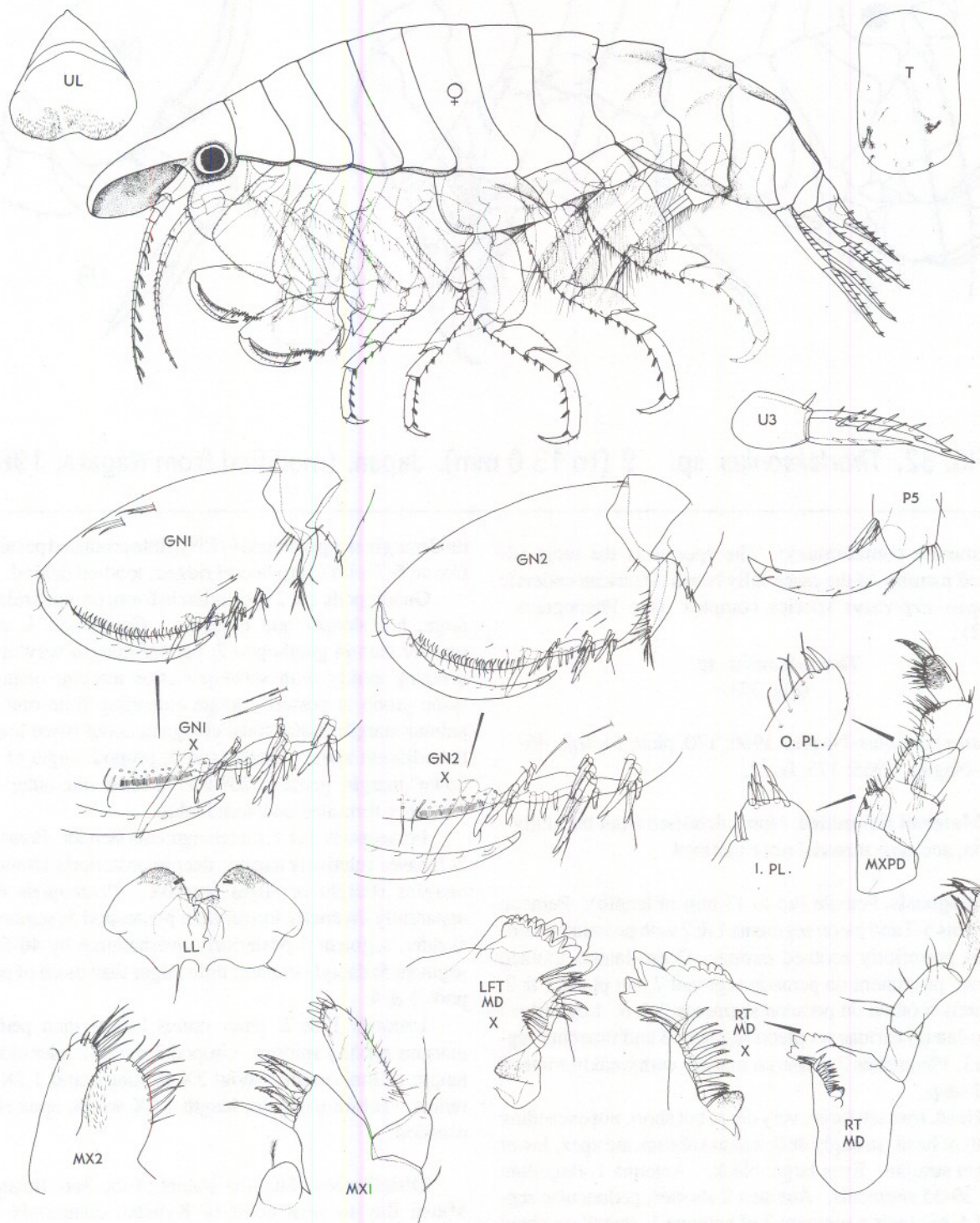
Pleon plates 2 & 3, hind corners acuminate, lower margins very weakly spinose. Uropods 1 & 2, inner ramus longer than peduncle, moderately serially spinose, tips extending distinctly beyond uropod 3. Urosome 2 nearly totally occluded dorsally. Uropod 3, outer ramus little more than twice length of peduncle, margins 6-spinose.

Telson subrectangular, margins subparallel, apex broadly sub-truncate. Coxal gills plate-like, markedly smallest on pereopod 6.

Etymology: The name "*grandirostris*" alludes to the very large rostrum, a size that is relatively longer and deeper than in all other species known to date.

Distributional Ecology: Known only from outer coast localities of the Queen Charlotte Islands, B. C., and one locality in central California. The greatly enlarged rostrum would appear to fit this species for Batesian mimicry of mitrellid snails of similar body size.

FIG. 31. *Thorlaksonius grandirostris*, new species
FEMALE ov. (6.0 mm) HOLOTYPE
(SEE PAGE 55 - OPPOSITE)



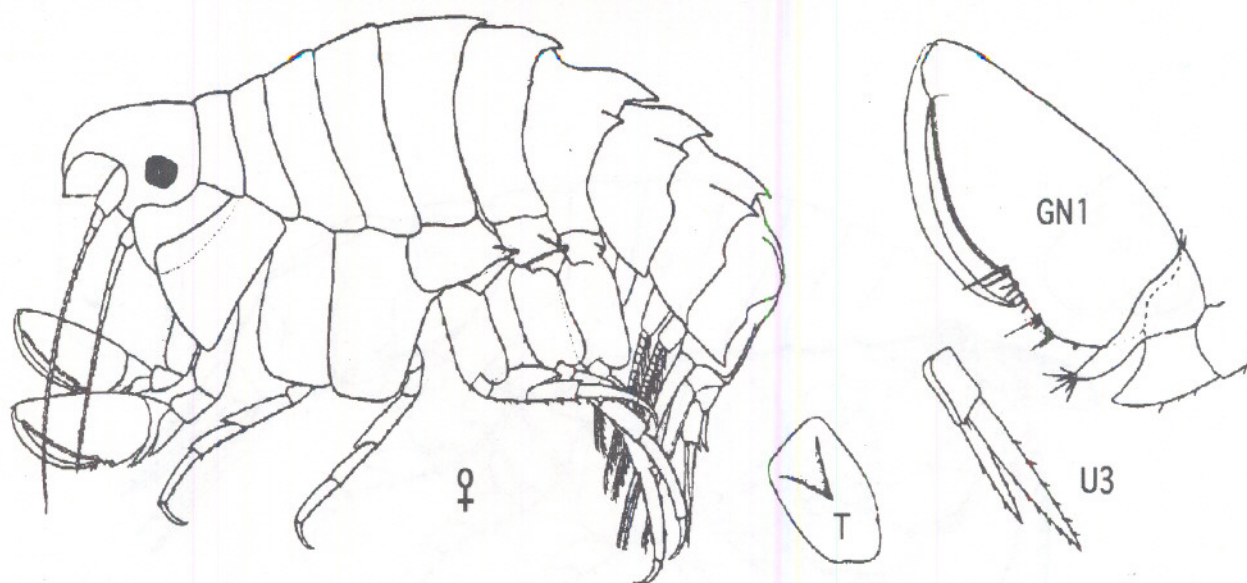


FIG. 32. *Thorlaksonius* sp. ♀ (to 13.0 mm). Japan. (modified from Nagata, 1965).

Taxonomic commentary: The species is the most advanced member of the essentially North American endemic *platypus-depressus* species complex (see Phenogram, p. 62).

Thorlaksonius sp.
(Fig. 32).

Pleustes panoplus Nagata, 1960: 170, plate 14, figs. 46-49.—Nagata, 1965: 175, fig. 2.

Material Examined: None identified from the study region, and type material not examined.

Diagnosis. Female (up to 13 mm in length): Peraeon segments 5-7 and pleon segments 1 & 2 with prominent mid-dorsal posteriorly toothed carinae. Dorso-lateral toothed carinae prominent on peraeon segment 7 and pleon 1 & 2, minutely toothed on peraeon segments 5 & 6. Low ridged dorso-lateral carinae on pleon segment 3 and urosome segment 1. Pleon plate 2, posterior margin with weakly toothed basal cusp.

Head, rostrum large, very deep, but short, not exceeding length of head, strongly deflexed at subtruncate apex, lower margin straight. Eyes large, black. Antenna 1, flagellum with 30-35 segments. Antenna 2 shorter, peduncular segment 4 exceeding segment 3 of antenna 1; flagellum about 20-segmented.

Mouthparts not described or figured by Nagata (*loc. cit.*); possibly similar to those of *T. truncatus* (p. 59).

Coxae 1-4 medium deep. Coxa 2 broadening distally, lower corners sharply rounded. Coxa 4 relatively narrow,

hind margin steeply sloped ($\sim 75^\circ$), little produced posteriorly. Coxae 5-7 with sharp lateral ridged, toothed behind.

Gnathopods 1 & 2 subsimilar in form; propods relatively large, but slender and elongate. Gnathopod 1, propod smaller than in gnathopod 2; palmar margin very oblique, merging gently with short posterior margin; distal-most spine group at posterior angle extending little onto outer palmar margin, distal spine elongate, about twice length of the adjacent spine. Gnathopod 2, propod, angle of "step-down" margin gentle ($\sim 20^\circ$); PDSP formula: outer - 7:3:2 (?), other formulae undeterminable.

Peraeopods 3 & 4, distal segments slender. Peraeopods 5-7, bases relatively narrow, deeply posteriorly lobate, hind margins straight or slight concave. Peraeopods 6 & 7 apparently distinctly longer than peraeopod 5, segment 5-6 slender, segment 5 posteriorly overhanging by 40-50% of segment 5; dactyls slender, little larger than those of peraeopods 3 & 4.

Uropods 1 & 2, inner ramus longer than peduncle, margins serially spinose. Uropod 3, rami slender elongate; length of inner ramus about 3X peduncle and 1.5X outer ramus. Telson elongate, length 1.5X width, apex sharply rounded.

Distribution: Shallow waters of the Seto Inland Sea, Mutsu Bay to west coast of Kyushu, commonly in the *Zostera* belt near low water mark (Nagata, 1965).

Taxonomic Commentary: This distinctive species conforms essentially with the diagnosis of genus *Thorlaksonius*. Cluster analysis relates it, not very closely, to the *truncatus*

subgroup (p. 62). However, the enlarged distal palmar spines of the gnathopods and deflexed form of the rostrum are more similar to the *subcarinatus-obesirostris* complex within the *depressus-platypus* subgroup. A more precise phyletic positioning within the genus awaits full re-examination of the original material.

Thorlaksonius carinatus, new species
(fig. 33)

Material Examined:

S.E. ALASKA: ELB Stn. S6L2, NW end Hogan I., Imperial Passage, shallow dive, 0-16 m. sand, stone, hydroid clumps, July 28, 1980 - 1 female (+slide mount).

BRITISH COLUMBIA: Queen Charlotte Ids., ELB Stn. E14c, Onward Pt., Skidegate Inlet, LW, fucoids, kelp, July 14, 1957 - 3 females ov., 1 female br. I.

Vancouver I., north end: ELB Stn. N22, Manson's Landing, Cortez I., boulders, kelp, LW, June 20, 1959 - 1 female (small) + slide mount.

Vancouver I., south end: ELB Stn. P710b, Cape Beale, bedrock, boulders, LW, July 19, 1970 - 2 males (+ 1 slide mount); Stn. B17, Off Cape Beale, 40-45 m., sand and tubeworms, 30 May, 1977 - 1 female (11.0 mm) + slide mount, HOLOTYPE, CMNCat. No. NMCC1994-360; ELB Stn. B8, Off Brady's Beach, 5-10 m. d, stones, algae, May 21, 1977 - 1 male (+ slide mount; specimen photographed).

Diagnosis. Female ov. (11.0 mm): Body medium large, elongate. Peraeon segments 1-4 lacking mid-dorsal, dorso-lateral, and lateral carinae except for small mid-dorsal trace on peraeon 5. Mid-dorsal carinae low, posteriorly elevated on peraeon 5, moderately strongly elevated and slightly toothed behind on peraeon 6 and 7 and pleon 1, centrally rounded on pleon 2, and a low ridge on pleon 3; dorso-lateral teeth increasingly strong on peraeon 5-7, proximally ridged and distally produced (above median line) on pleon 1 & 2, dorso-lateral carinae of pleon 3 and urosome 1 moderately elevated, but unevenly ridged; lateral ridges of peraeon 5-7 with sharp posterior teeth. Pleon plates 1 & 2 with posterior marginal tooth; pleon plate 3 smooth behind. Head, rostrum stout, deep, slightly shorter than head; apex bluntly rounded or subtruncate. Antenna 1 slightly the longer, flagellum with 26-30 short segments; antenna 2, peduncle 4 not extending beyond peduncle 3 of antenna 1; flagellum 22-segmented.

Coxa 1-4 deep, lacking facial mid-rib; lower margins of 2 & 3 nearly straight, hind corners squarish; coxa 1 covering anterior head lobe; coxa 4, posterior process acute, extending along 1/3 of lower margin. Coxae 5-7 medium deep, with weakly expressed postero-lateral ridge, each with weak posterior tooth.

Mouthparts modified. Lower lip, inner lobes relatively broad. Mandible, blade row relatively short, 15-18 blades; molar small, apex blunt; palp segment 3 lacking baso-facial setae, segment 2 moderately setose medially. Maxilla 1, palps medium broad, 8-9 apical spines extending along

oblique medial margin; segment 1, lateral process moderate, with 3 long outer marginal setae. Maxilla 2, inner plate broad, inner margin lacking plumose seta. Maxilliped, outer plate medium, apex with 3-4 slender spines; inner plate medium, apex with 8-9 closely crowded spines of various sizes and basal thicknesses.

Gnathopod 1 distinctly smaller and more slender than gnathopod 2; anterior margin of basis densely lined with longish setae; angle of "step-down" margin gentle; PDSP formula: outer - 10:4:2; inner - 4:4:6?, total of 30; meral process short. Gnathopod 2, propod, angle of "step-down" margin slightly stronger (~30°), tip of dactyl closing short of D-TD depression; distal spine group extends submarginally along 40% of palm, distal spine about twice as heavy and 50% longer than adjacent spine; hind margin short, about half length of palm; meral process short.

Peraeopods 5-7, bases increasing posteriorly, hind margins straight; proximal cusp of basis of peraeopod 7 weakly developed; segment 4 posteriorly overhanging segment 5 by about half its length; dactyls distinctly stronger than those of peraeopods 3 & 4, = 1/2 length of segment 6.

Pleon plates 2 & 3, hind corners acute, slightly produced, lower margins moderately spinose. Uropods 1 & 2 strongly spinose, inner ramus longer than peduncle, tips extending slightly beyond that of uropod 3. Uropod 3, inner ramus nearly 3X length of peduncle, and 1.6 X length of outer ramus; margins 7-8 spinose.

Telson linguiform, slightly broadening distally, apex broadly rounded.

Coxal gills medium, pallet-like on peraeopods 2 & 3, rounded, plate-like on 4-6.

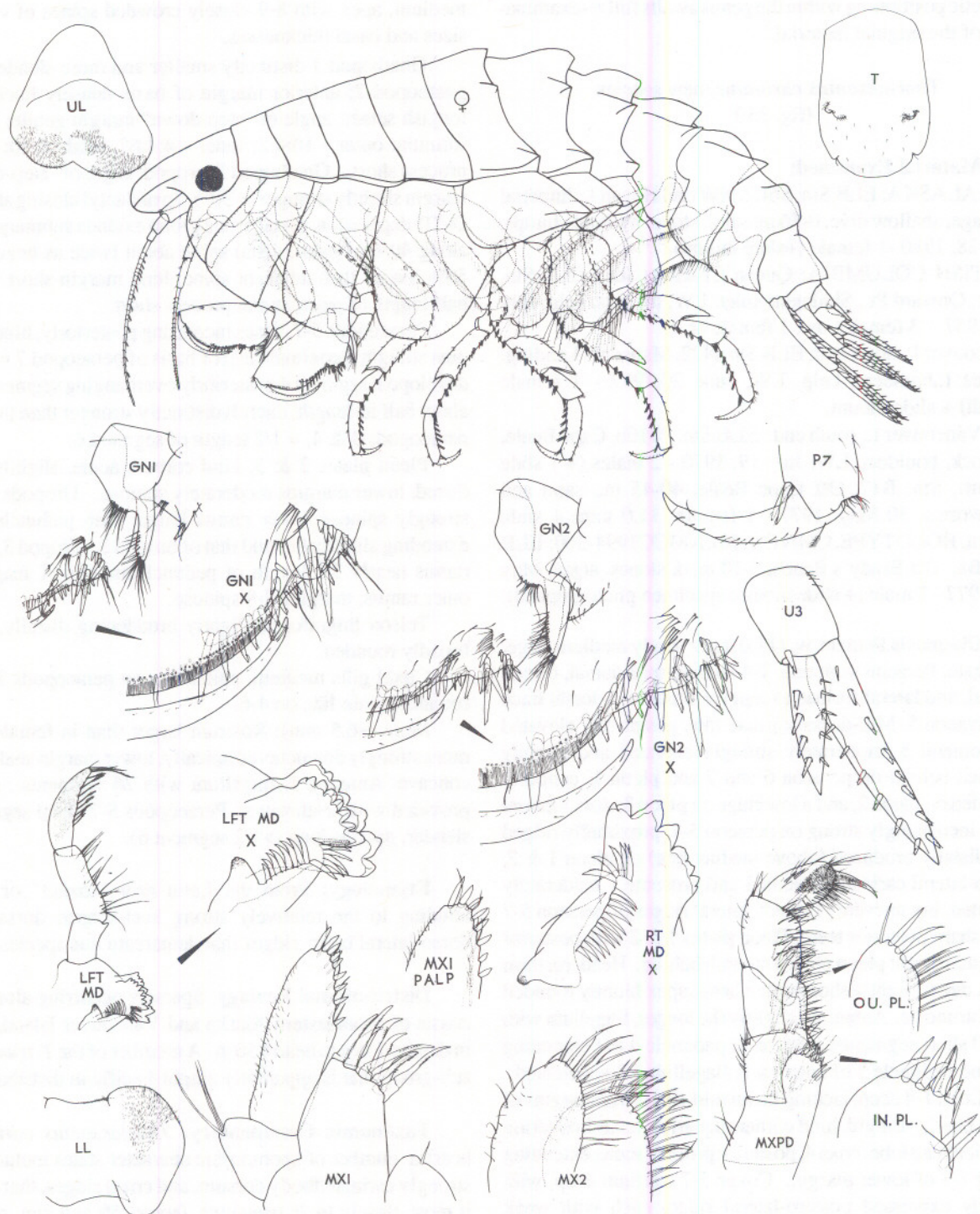
Male (~6.5 mm): Rostrum larger than in female, and more strongly downcurved apically, lower margin shallowly concave. Antenna 1, flagellum with 26 segments, richly provided with aesthetascs. Peraeopods 5-7 distal segments slender, dactyls long (>1/2 segment 6).

Etymology: From the Latin root "*karina*" or keel, alluding to the relatively strong keel-shaped dorsal and dorso-lateral body ridges that demarcate this species.

Distributional Ecology: Sparsely occurring along the coasts of southeastern Alaska and Vancouver Island, B.C., in depths down to nearly 50 m. A member of the *T. truncatus* sub-group that is apparently amphi-Pacific in distribution.

Taxonomic Commentary: *Thorlaksonius carinatus* bears a number of apomorphic character states including a strongly carinated body dorsum, and coxal ridges, that relate it most closely to *T. truncatus* (see p. 59 and key, p. 39). Mouthpart structure, especially the apical spination of the maxilliped plates, is relatively plesiomorphic, however.

FIG. 33. *Thorlaksonius carinatus*, new species
FEMALE ov. (11.0 mm) HOLOTYPE
(SEE PAGE 58)



Thorlaksonius truncatus, new species
(Figs. 34, 35)

Pleustes species, Bousfield, 1985: 32, fig. 2.

Material Examined:

BRITISH COLUMBIA: ELB Stn. B13, off Brady's Beach, 6-14 m., sand, stone, algae, 25 May, 1977 - 1 female ov. (10.5 mm) + slide mount, HOLOTYPE, CMN Cat. No. NMCC 1994-358; *Ibid.* - 1 male (8.7 mm) + slide mount, ALLOTYPE, CMN Cat. No. NMCC1994-359; *Ibid.* - 3 females, CMN Cat. No. NMCC1994-378.

North-central coast: ELB Stns., July-August, 1964: H30 (2 females, 1 male); H45 (1 female).

Vancouver Island, south end, Berkeley Sound & outer coast: ELB Stn. P9, 1955 (Amphitrite Pt.) - 1 male; ELB Stn. B9a, 16 m., rock, sand, June 28, 1976 - 1 male (+ slide mount), 3 females; ELB Stn. B27, SW end Diana I., 8-10 m., sand, July 8, 1976 - 1 male. ELB Stn. B18, mouth Trevor Channel, 36-40 m., sand, shell, May 30, 1977 - 6 males, 1 female, 2 im.; Stn. B21b, off Brady's Beach, 10-20 m., sand, kelp, June 1, 1977 - 1 male, 4 females + 2 slide mounts. CMN collections.

Diagnosis. Female ov. (10.5 mm): Body medium large, elongate. Ridge-like carinae, raised and toothed posteriorly, on pereon segments 5-7 and pleon 1, centrally raised on pleon 2, low on pleon 3; posteriorly acute dorso-lateral teeth on pereon segments 6 & 7 and pleon 1, strongly elevated (above dorsal ridge) and produced on pleon 2; medially incised and ridge-like on pleon 3 and urosome 1; postero-lateral ridge and teeth on pereon 5-7, cusped on pleon segments 1 & 2.

Head, rostrum massive, very deep, as long as head, lower margin straight, apex gently deflexed, truncate. Antenna 1 slightly the longer, flagellum about 35-segmented. Antenna 2, flagellum about 30-segmented.

Coxae 1-4 very large and deep, lower margins nearly straight, hind corners squarish; coxa 1 covering anterior head lobe; coxa 4 very large, hind process enlarged, extending posteriorly about half length of coxa 5; coxae 5-7, postero-lateral ridge strong, oblique, acutely produced behind; coxa 5 very large, length about 1.5 times depth.

Mouthparts modified. Mandible, left and right spine rows with 19-20 blades; molar process narrow, tip bluntly rounded. Maxilla 1, left palp broadened, apical spines and setae extending obliquely to about mid-point of segment 2; segment 1, lateral process with 3-4 longish setae. Maxilla 2, outer plate little broadened, inner margin lacking plumose seta. Maxilliped, inner plate medium, apex 4-spinose; inner plate very short, broad, inner apical spine broadened at base, apex with 7 apical and 4-5 inner marginal spines.

Gnathopod 1, basis, anterior margin lined with short setae; propod, angle of "step-down" margin medium (~30°); PDSP formula: outer - 9:3:2; inner - 4:3:4, total of 25; meral process short. Gnathopod 2, palmar margin strongly convex; angle of "step-down" margin medium large (~45°), distal spines extending fully half way along outer palmar

margin; D-TD medium; PDSP formula: outer - 9:4:2; inner - 3:4:1(?), total of 23; meral process short.

Pereopods 5-7, bases increasing posteriorly, hind margins straight or slightly concave, proximal hind cusp of basis of pereopod 7 relatively short, blunt; segment 4 strongly overhanging segment 5 posteriorly by about 60-70% of its length; dactyls slender, slightly longer than those of pereopods 3 & 4, each about 50% length of its segment 6.

Pleon plates 2 & 3, hind corners acute, lower margins weakly spinose. Uropods 1 & 2, inner ramus longer than peduncle, tips extending well beyond uropod 3. Uropod 3, inner ramus elongate, nearly 3 X length of peduncle, margins 7-spinose. Telson subrectangular, slightly expanded distally, apex broadly rounded.

Coxal gills sublinear on pereopods 2 & 3, plate-like on pereopods 4-6.

Male (8.7 mm): Body relatively small, slender. Rostrum elongate, more than twice as long as deep, and about 1.5 X length of head, straight, lower margin gently convex, apex narrowly truncate. The eye appears relatively large and placed closer to the anterior head margin. The flagella of the antennae are relatively longer, and segments more numerous, than in the female.

Colour: Mottled rosy red; body segments of some individuals may have grayish white vertical stripes.

Etymology: The name "*truncatus*" alludes to the deep, apically squared or truncated rostrum of the female.

Distributional ecology: The species occurs along the outer coast of Vancouver I., in subtidal depths to about 30 m., on hard sand bottoms on which were deposited mats of laminarians and other kelp.

Taxonomic commentary: Material from the present series of stations exhibits some degree of morphological and colour variation, as well as sexual dimorphism. Thus, a 13.5 mm female from B9 Second Beach differed slightly from the TYPE female in the maxilliped (outer plate with only 2 apical spines), uropod 3 (rami slightly longer and more spinose), and telson (distally slightly narrowing, apex more sharply rounded). These and other minor other differences are here considered to be within the range of size and individual variation for the species.

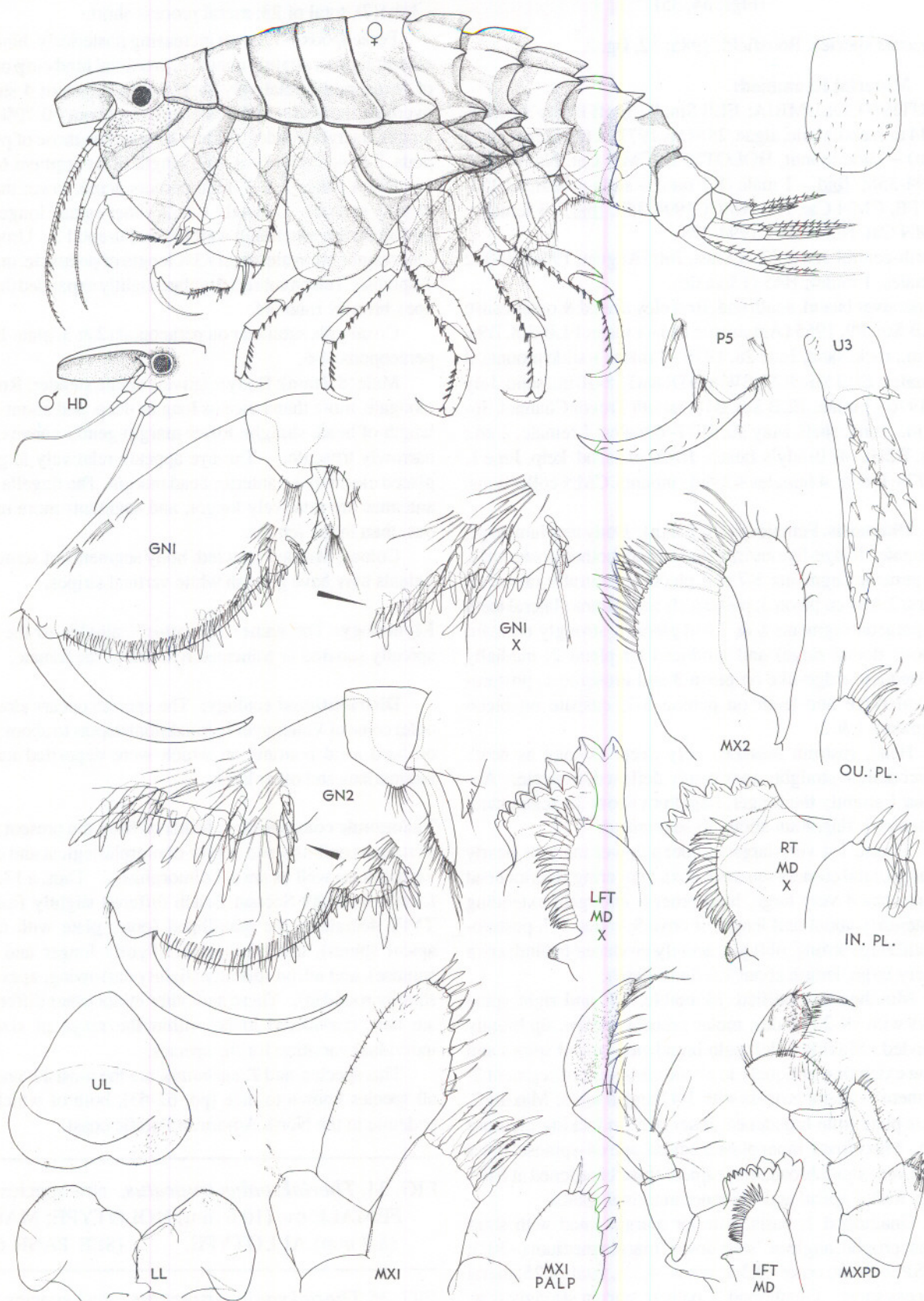
This species, and *T. carinatus*, are the most advanced of all species known to date (pp. 62-63), both of which are endemic to the North American Pacific coast.

FIG. 34. *Thorlaksonius truncatus*, new species.

FEMALE ov. (10.5 mm) HOLOTYPE; MALE (8.7 mm) ALLOTYPE. (SEE PAGE 60)

FIG. 35. *Thorlaksonius truncatus*, new species, var.

FEMALE (13.5 mm) VARIANT (SEE PAGE 61)



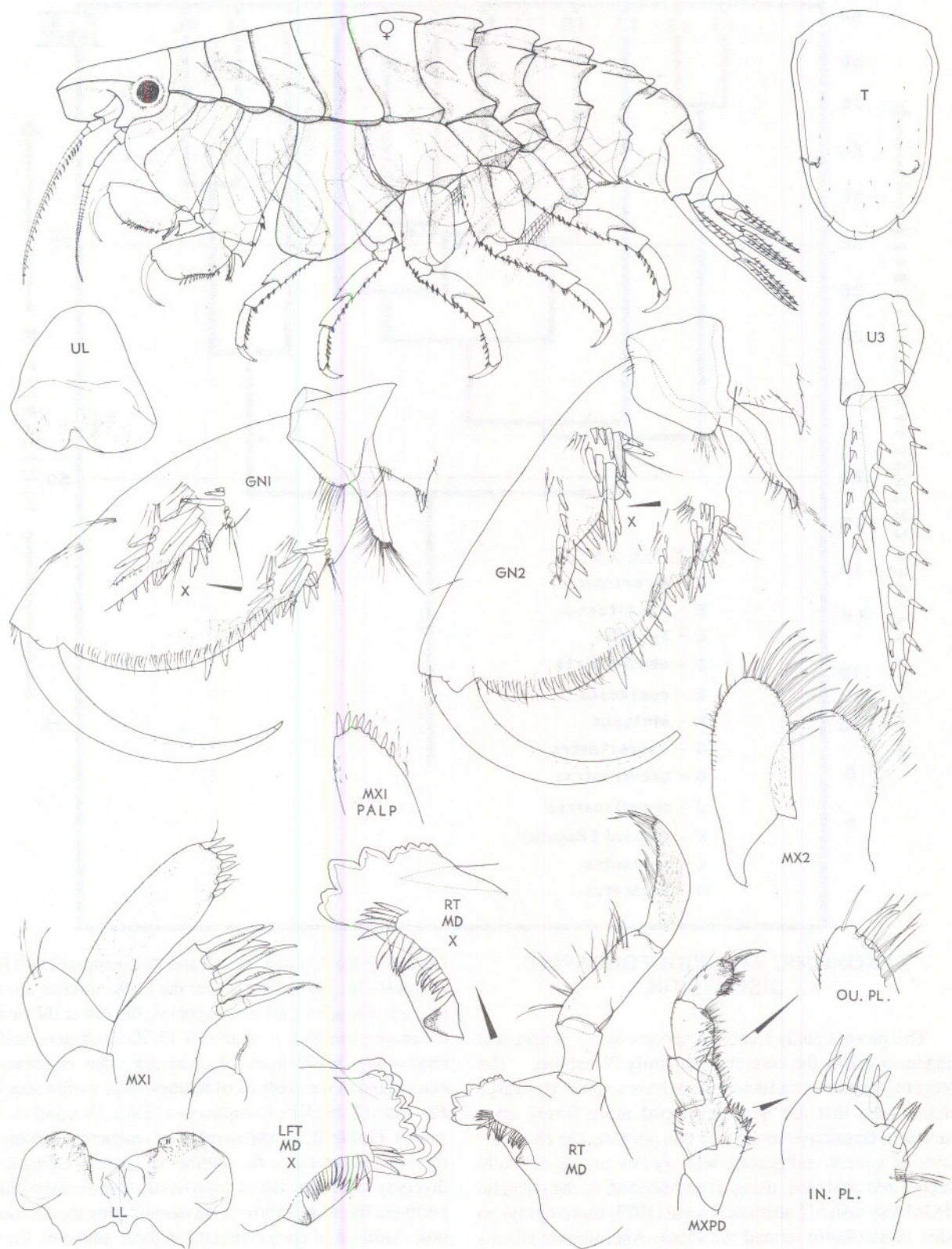
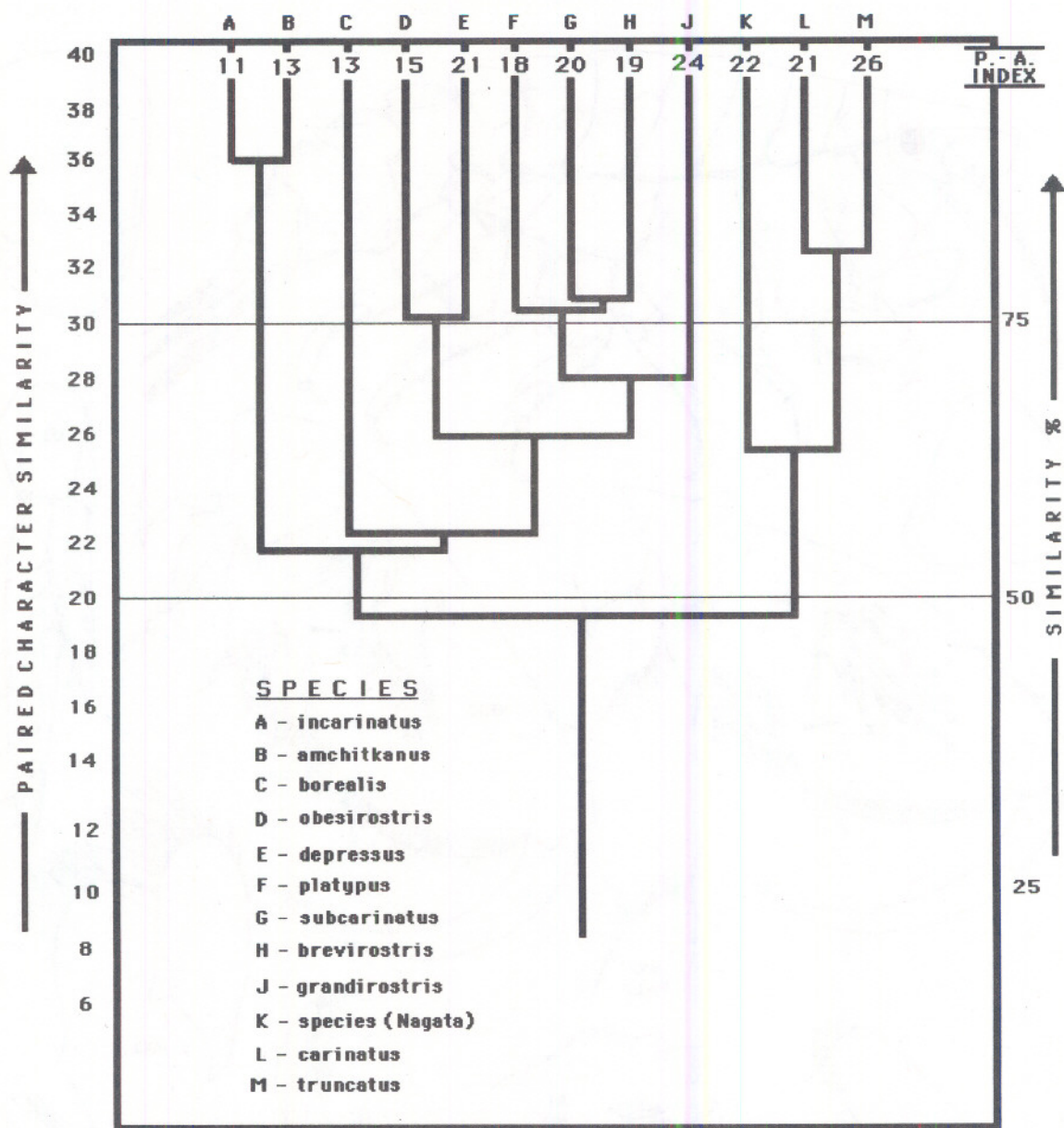


FIG. 36. PHENOGRAM OF SPECIES OF *THORLAKSONIUS*



TAXONOMIC AND BIOGEOGRAPHIC DISCUSSION

The present study treats 24 species and 3 genera and subgenera within the holarctic subfamily Pleustinae. The foregoing diagnoses and descriptions have suggested phyletic relationships that are here developed more firmly on a numerical taxonomic basis. For this purpose, the character states of genera, subgenera, and species are phyletically ordered and analyzed, using a modification of the phenetic UPGMA system of Sneath and Sokal (1973) that employs an index of similarity termed the Plesio-Apomorphic (P.-A.) Index. This modification has been utilized previously in developing natural relationships within similar taxonomic units of the Ampeliscidae (Dickinson, 1982), various

Corophioidea (Conlan, 1983), and Phoxocephalidae (Jarrett & Bousfield, 1994). The higher the P.-A. number, the more phyletically advanced is the species, the lower the number, the more primitive. A matrix of 15-20 characters, and corresponding 30-40 pairs of character state extremes, are considered in the analysis of relationships within species of *Pleustes* (Table III), *Catapleustes* (Table IV), and *Thorlaksonius* (Table II.). The number of characters employed is therefore about twice the number of corresponding taxa, a diversity level considered analytically significant within the pertinent literature (above). In demarcating the discontinuous condition of each character in these analyses, the plesiomorphic condition is coded as 0, the apomorphic condition as 2, and the intermediate condition as a value of 1.

The quality and number of characters and character

TABLE II. THORLAKSONIUS: CHARACTERS AND CHARACTER STATES

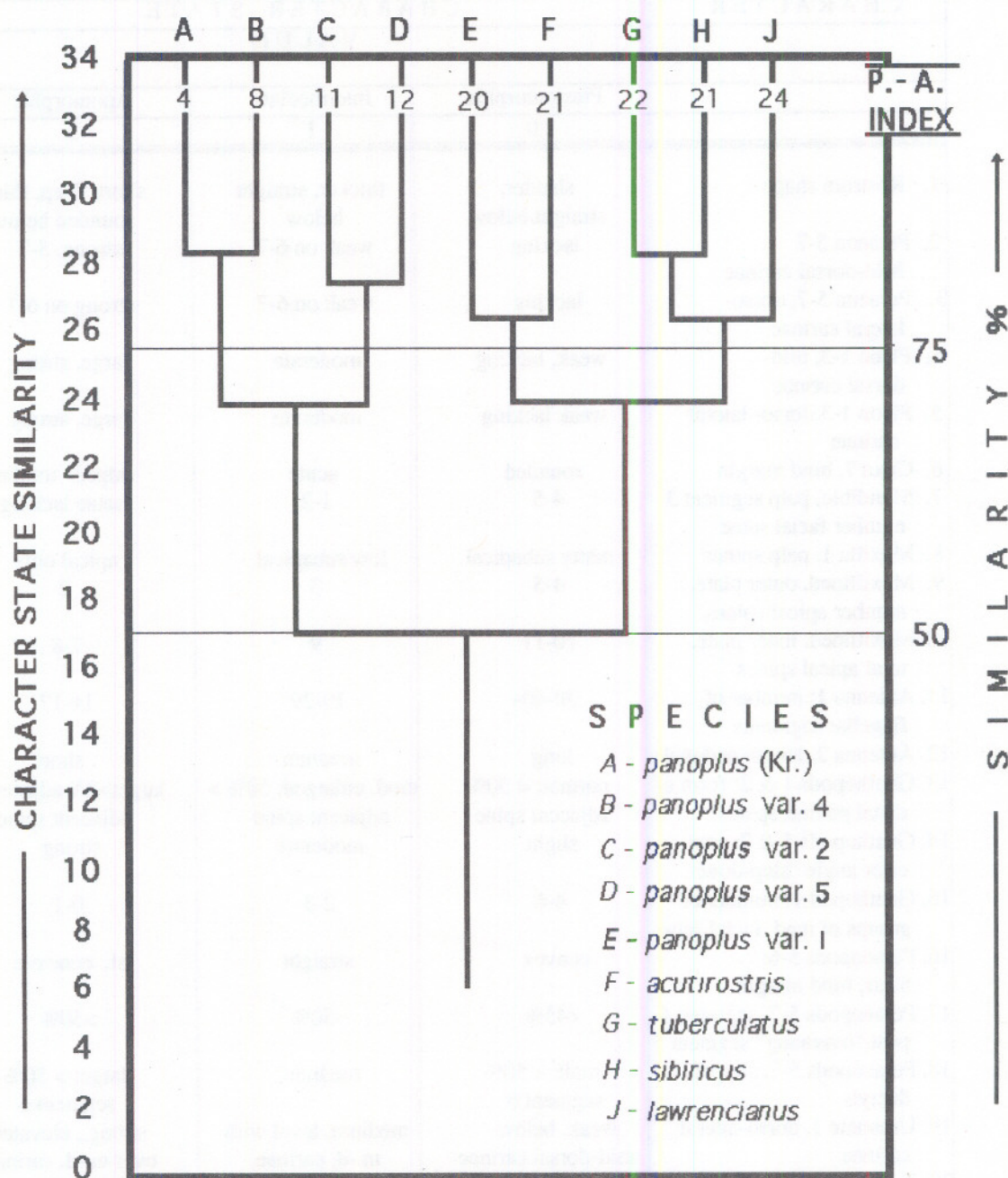
CHARACTER	CHARACTER STATE		
	VALUE		
	Plesiomorphic	Intermediate	Apomorphic
	0	1	2
1. Rostrum shape	slender, straight below	thicker, straight below	short, deep, thick rounded below
2. Peraeon 5-7 Mid-dorsal carinae	lacking	weak on 6-7	strong, 5-7
3. Peraeon 5-7, dorso- lateral carinae	lacking	weak on 6-7	strong on 6-7
4. Pleon 1-3, mid- dorsal carinae	weak, lacking	moderate	large, strong
5. Pleon 1-3, dorso- lateral carinae	weak lacking	moderate	large, strong
6. Coxa 7, hind margin	rounded	acute	ridged, toothed
7. Mandible, palp segment 3 number facial setae	4-5	1-2	setae lacking
8. Maxilla 1, palp spines	many subapical	few subapical	apical only
9. Maxilliped, outer plate, number apical spines	4-5	3	2
10. Maxilliped, inner plate, total apical spines	10-11	9	7-8
11. Antenna 1: number of flagellar segments	30-40+	19-29	14-17
12. Antenna 2, length peduncle	long	medium	short
13. Gnathopods 1 & 2; form of distal palmar spines	normal; < 50% adjacent spine	mod. enlarged; 50% > adjacent spine	large: >2X adjacent adjacent spine
14. Gnathopods 1 & 2: post- erior angle "step-down"	slight	moderate	strong
15. Gnathopod 1: number of groups of med. facial setae	4-6	2-3	0-1
16. Peraeopods 5-6: basis, hind margin	convex	straight	sl. concave
17. Peraeopods 5-7, segment 4 post. "overhang" segment 5	<45%	~50%	>50%
18. Peraeopods 5-7, size of dactyls	small, < 50% segment 6	medium	large; > 50% segment 6
19. Urosome 1, dorso-lateral carinae	weak, below mid-dorsal carinae	medium, level with m.-d. carinae	strong,, elevated over m.-d. carinae
20. Telson, shape	narrowing distally	rectangular	slightly broadened

states used here depends very significantly on the quality of descriptions and illustrations in the pertinent literature. Some proved to be of uneven quality and completeness, and did not always treat, in satisfactory or uniformly applicable detail, phylogenetically significant character states of gnathopods and peraeopods, and frequently not at all character states of mouthparts, antennal armature, gills, brood plates, pleopods, and/or uropods 1 & 2. In the case of *Pleustes* (*Pleustes*), and especially *Pleustes* (*Catapleustes*), groups in which rela-

tively little material and few species were obtained from the field study region, and material from other sources was not readily available, such dependence was high. Thus, in analytical treatment of those groups, similarity correlations and coefficients may have less phyletic significance than had a full range of morphological characters been utilized.

With respect to overall relationships between genera and subgenera within subfamily Pleustinae, both plesiomorphic and advanced character states occur widely.

FIG. 37. PHENOGRAM OF SPECIES OF *PLEUSTES* (*PLEUSTES*)



In balance, however, members of the genus *Thorlaksonius* entrain the largest number of plesiomorphies of character states treated herein, especially of rostral form and body armature. The most primitive members of this genus are therefore considered closest to the hypothetical subfamily ancestral type (see Bousfield & Hendrycks, 1994). Similarly, members of the subgenus *Catapleustes* are considered to contain the most advanced forms of pleustinids, with members of the nominate subgenus *Pleustes* intermediate in phylogeny.

With respect to numerical taxonomic analysis of component species, the characters and characters states are provided in Tables II-IV and the corresponding phenograms in Figures 36-38. Within the genus *Thorlaksonius*, the phenogram of species similarities (Fig. 36), based on a 20-character analysis (Table II), suggests that the 12 recognized species form three basic subgroupings at 50-60% similarity level. These encompass a primitive and phylogenetically distant slender-rostrate *incarinatus* group (P.-A. indices of 11-13), an intermediate "duck-bill"-rostrate *platypus-depressus*

TABLE III. *PLEUSTES* (*PLEUSTES*) CHARACTERS AND CHARACTER STATES

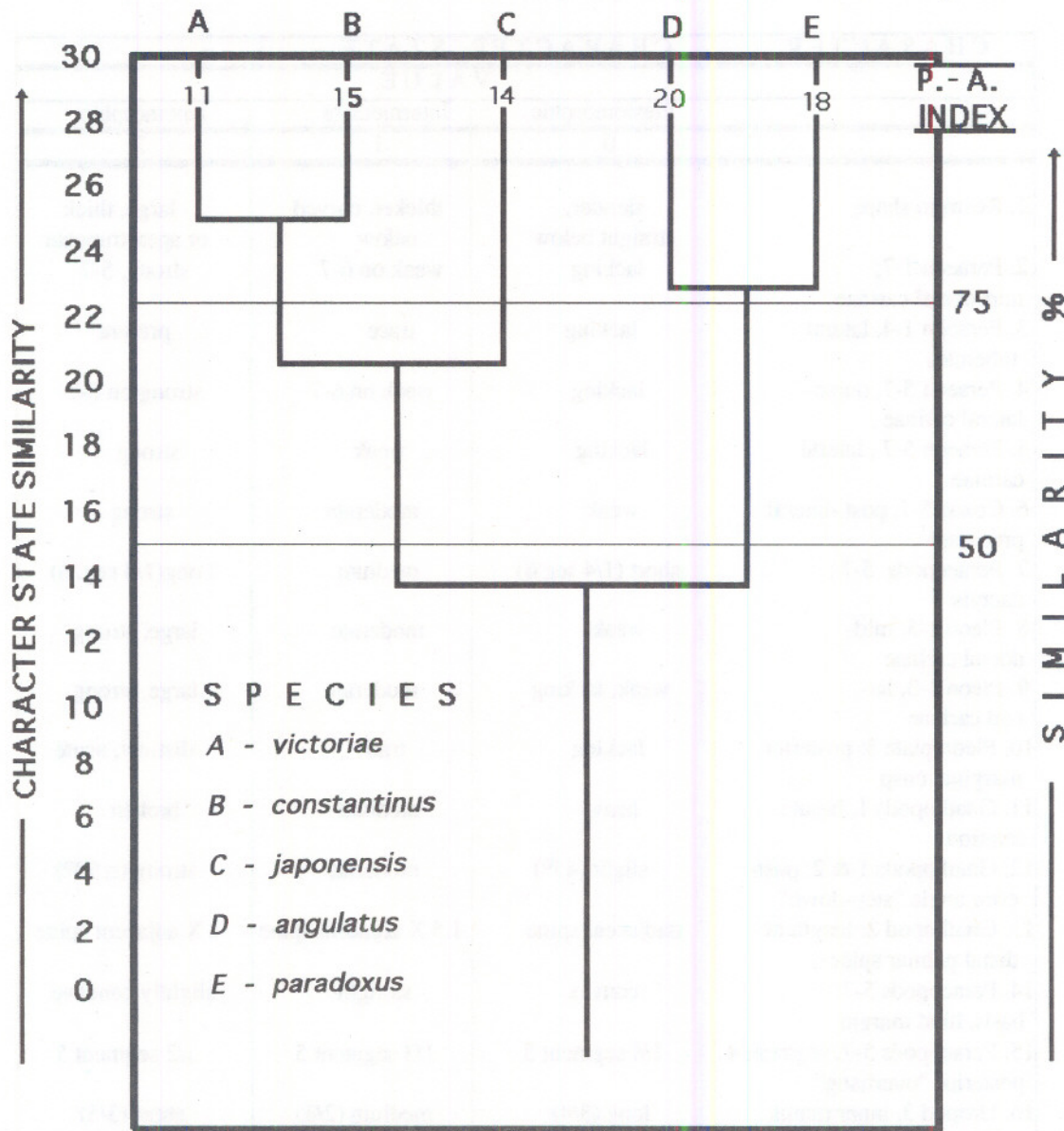
CHARACTER	CHARACTER STATE		
	VALUE		
	Plesiomorphic	Intermediate	Apomorphic
	0	1	2
1. Rostrum shape	slender, straight below	thicker, curved below	large, thick or apex truncate
2. Peraeon 1-7; mid-dorsal carinae	lacking	weak on 6-7	strong, 5-7
3. Peraeon 1-4, lateral tubercles	lacking	trace	present
4. Peraeon 5-7, dorso- lateral carinae	lacking	weak on 6-7	strong on 6-7
5. Peraeon 5-7, lateral carinae	lacking	weak	strong
6. Coxae 5-7, post.-lateral processes	weak	moderate	strong
7. Peraeopods 5-7; dactyls	short (1/4 seg 6)	medium	long (1/3 seg. 6)
8. Pleon 1-3, mid- dorsal carinae	weak,	moderate	large, strong
9. Pleon 1-3, lat- eral carinae	weak, lacking	moderate	large, strong
10. Pleon plate 3: posterior marginal cusp	lacking	trace	distinct, acute
11. Gnathopods 1, basal : setation	heavy	medium	broken
12. Gnathopods 1 & 2: post- erior angle "step-down"	slight (45°)	moderate	strong ($\cong 90^\circ$)
13. Gnathopod 2: length of distal palmar spine	\cong adjacent spine	1.5 X adjacent spine	2 X adjacent spine
14. Peraeopods 5-7: basis, hind margin	convex	straight	slightly concave
15. Peraeopods 5-7, segment 4 posterior "overhang"	1/4 segment 5	1/3 segment 5	1/2 segment 5
16. Uropod 3, inner ramus relative to outer ramus	long (3/4)	medium (2/3)	short (3/5)
17. Telson shape	tapering to apex	medium	short, broad

group (P.-A. indices of 13-24), and an advanced truncate-rostrate *truncatus* sub-group (P.-A. indices of 21-26). Biogeographically, the genus *Thorlaksonius* is endemic to the North Pacific region. Members of the primitive group are the most northern, and are confined to the summer-cold waters of the Bering, Okhotsk, and Japan seas. The intermediate group consists of relatively closely related forms (63-76% similarity, except for the relatively primitive *T. borealis*), that are mainly endemic to the North American coastal region. The advanced group contains a *truncatus-carinatus* species pair in the eastern boreal Pacific that is

relatively distantly related (63% similarity) to a carinated but yet unnamed species in the boreal western Pacific.

Within subgenus *Pleustes*, the phenogram of species similarities (Fig. 37), based on a 17-character matrix (Table III), clusters the 10 recognized species and varietal complexes into two main subgroups at the 50-60% similarity level. These encompass a primitive, weakly carinate *panoplus* group (P.-A. indices of 4-17) and an advanced, strongly carinated *tuberculatus* group (P.A. indices of 20-24). Members within each species complex are relatively closely related (73-85% similarity). Biogeographically, the subgenus

FIG. 38 PHENOGRAM OF SPECIES OF
PLEUSTES (*CATAPLEUSTES*)



Pleustes is essentially holarctic and high arctic in distribution, extending southward in the western (N. American) N. Atlantic region, via the cold Labrador Current, to the Gulf of Maine and in the western (Asiatic) Pacific, via cold Oyashio surface waters. The most advanced species occur in the western Bering Sea, the Sea of Okhotsk and the northern Sea of Japan. Only one species (*P. panoplus*) is known from the eastern North Atlantic and no species has yet been recorded from the eastern North Pacific south of the Bering Sea.

Within subgenus *Catapleustes*, based on a matrix of 15 characters and corresponding character states (Table IV), the relatively small complex of 5 recognized species can be clustered into three main subgroups at 50-70% similarity

levels (Fig. 38). These consist of a primitive, less strongly carinated and spinose *constantinus* subgroup of two North America Pacific and Beringian species (P. A. indices of 11-15), the slightly more advanced and more strongly carinated *P. (C.) japonensis* in the western N. Pacific (P. A. index of 14), and a highly advanced, strongly carinated and spinose *paradoxus*-*angulatus* pair of species in colder waters of the Chukchi-Bering-Okhotsk marine region. As in the genus *Thorlaksonius*, no members have yet been recorded from outside the North Pacific and immediately adjacent waters. *Catapleustes* co-occurs regionally with *Thorlaksonius*, but in deeper waters.

Ecologically, pleustinid species form a relatively small

TABLE IV. *PLEUSTES* (*CATAPLEUSTES*) CHARACTERS AND CHARACTER STATES

CHARACTER	CHARACTER STATE		
	VALUE		
	Plesiomorphic	Intermediate	Apomorphic
	0	1	2
1. Rostrum shape	slender, straight below	thicker, slightly curved below	large, thick, distinctly arcuate below
2. Antenna 1, number flagellar segments	35-45	26-34	15-25
3. Peraeon 1-7; dorso-lateral carinae	very weak or lacking	weak (ht < width)	strong (height > width)
4. Peraeon 1-4, supra-lateral tubercles	lacking	trace	present
5. Peraeon 1-7, mid-lateral processes	rounded ridge	intermediate	acute, tooth-like
6. Peraeopod 5, coxal process	sub-triangular	acute, blade-like	
7. Coxa 4 lower marginal excavation	shallow	intermediate	wide, deep
8. Coxae 1-5, proximal tubercles	absent	trace	present
9. Pleon 1-3, mid-lateral teeth or processes	weak, lacking	moderate	large, strong
10. Peraeopods 5-7; dactyls	short (1/4 seg 6)	medium	long (1/2 seg. 6)
11. Peraeopods 5-7: basis, hind margin	convex	straight	slightly concave
12. Gnathopod 2: number of palmar outer marginal spines	many (8-10)	intermediate	few (4 - 5)
13. Gnathopod 2: length of distal palmar spine	≅ adjacent spine	intermediate size	1.5 X adjacent spine
14. Uropod 3, inner ramus relative to outer ramus	long (3/4)	medium (2/3)	short (3/5)
15. Telson shape	tapering to apex (L > W)	medium (L ≅ W)	short, apex broad

and inconspicuous part of regional pleustid faunas and total hard-bottom amphipod communities as a whole. As a specialized group of micro-predators, and micro-carnivores, they occupy niches on open stony bottoms and on the fronds of marine grasses and kelp, that would seem highly vulnerable to fish predation. However, low-level populations are apparently maintained there, despite such presumed predation pressure, by factors not yet fully understood. These factors may include, variously within the genera and subgenera, heavily spinose and sharply toothed body armature that resists manipulation by small-mouthed predators, and Batesian mimicry of other hard-shelled invertebrates of similar size that are presumably less attractive to larger predators (as noted by Crane, 1969; Field, 1974; and Carter & Behrens, 1980). Other factors may encompass protective

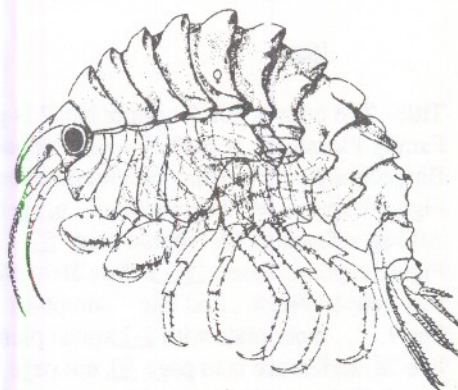
body coloration that, on the one hand, may be classically cryptic, phaneric, or camouflaging or, on the other hand, may be proaposematic or warning of the presence of body compounds (e.g. terpenes) that are noxious, unpalatable, or otherwise harmful to potential fish predators (Williams & Anderson, 1987).

In summary, the subfamily Pleustinae (including the morphologically most primitive and most advanced species) may be considered essentially endemic to coastal shelf waters of the North Pacific Ocean. A morphologically intermediate element, containing the type genus and species, has penetrated arctic shelf waters, in both directions from the Pacific, into arctic-subarctic regions of the North Atlantic Ocean where it may be actively in the process of speciation.

LITERATURE CITED

- Alderman, A. L., 1936. Some new and little known amphipods of California. Univ. Calif. Publ. Zool. 41(7): 53-74, 51 figs.
- Austin, W. C., 1985. An Annotated Checklist of Marine Invertebrates in the Cold Temperate Northeast Pacific. Publ. Khyotan Mar. Lab., Cowichan Bay, B. C. Vols. I-III: 1- 682.
- Barnard, J. L., 1954. Marine Amphipoda of Oregon. Oregon State Monogr., Stud. in Zool. 8: 1-103, 33 pls.
- , 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. Natl. Mus. Bull. 258:1-230, figs. 1-173.
- , 1975. Amphipoda: 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 edition. Univ., California Press, Berkeley, CA. 716 pp.
- , D. Bowers, & E. C. Haderlie, 1980. Chapter 22: Amphipoda. The amphipods and allies. pp. 559-556. in R. H. Morris, D. P. Abbott, & E. C. Haderlie (eds). Intertidal Invertebrates of California. Stanford Univ. Press. Stanford, California.
- , & R. R. Given, 1960. Common pleustid amphipods of southern California, with a projected revision of the family. Pac. Nat. 1(17): 37-48.
- , & G. S. Karaman, 1991. The Families and Genera of Marine Gammaridean Amphipoda (Except Marine Gammaroids) Parts 1 & 2: 1-866. 133 figs., 7 maps.
- Bate, C. S., 1858. On some new genera and species of Crustacea Amphipoda. Ann. Mag. Nat. Hist. (Ser. 3) 1: 361-362.
- Bousfield, E. L., 1958. Ecological investigations on shore invertebrates of the Pacific coast of Canada, 1955. Bull. Natl. Mus. Canada, 147: 104-115.
- , 1963. Investigations on sea-shore invertebrates of the Pacific coast of Canada, 1957 and 1959. I. Station list. Bull. Natl. Mus. Can. 185: 72- 89.
- , 1968. Studies on littoral marine invertebrates of the Pacific coast of Canada, 1964. I. Station list. Natl. Mus. Can. Bull. 223: 49-57.
- , 1985. Mysterious insects of the sea. Rotunda, 18 (3): 30-36.
- , 1987. Amphipod Parasites of Fishes of Canada. Can. Bull. Fish. Aqu. Sci. 217: 1-37.
- , & 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 south-eastern Alaska and Prince William Sound. Natl. Mus. Can. Bull.183: 76-103.
- , & E. A. Hendrycks, 1994. A Revision of the Family Pleustidae (Crustacea: Amphipoda:Leucothoidea) Part I. Systematics and Biogeography of Component Subfamilies. Amphipacifica I(1): 17-57.
- Bulycheva, A. I., 1952. New species of amphipods (Amphipoda: Gammaridea) from the Sea of Japan (in Russian). Trud. Zool. Inst. Akad. Nauk, SSSR. 12:195-251.
- Carter, J. W. & D. W. Behrens, 1980. Gastropod mimicry by another pleustid amphipod in central California. The Veliger 22: 376-377, 1 fig.
- Conlan, K. E., 1983. The amphipod superfamily Corophioidea in the northeastern Pacific region. 3. Family Isaeidae: systematics and distributional ecology. Natl. Mus. Natur. Sci., Publ. Natur. Sci. 4: 1-75.
- Crane, J. M., 1969. Mimicry of the gastropod *Mitrella carinata* by the amphipod *Pleustes platypa*. The Veliger 12: 200, pl. 36.
- Dickinson, J. J., 1982. The systematics and distributional ecology of the family Ampeliscidae (Amphipoda: Gammaridea) in the northeastern Pacific region. I. The genus *Ampelisca*. Publ. Biol. Oceanogr., Natl. Mus. Can. 10: 1-39, 21 figs. 3 tables.
- Dunbar, M. J., 1954. The amphipod Crustacea of Ungava Bay, Canadian eastern Arctic. Jour. Fish. Res. Bd. Canada, 11: 709-798.
- Field, L. H., 1974. A description and experimental analysis of Batesian mimicry between a marine gastropod and an amphipod. Pac. Sci. 28(4): 439-447.
- Gurjanova, E. F., 1938. Amphipoda Gammaroidea of Siau-kua Bay and Sudzukhe Bay (Japan Sea). Rept. Hydrobiol Expd. Zool. Inst. Acad. Sci. USSR in 1934. 1: 241-404, 59 figs., (In Russian)
- , 1951. Bokoplavyy Morei SSSR, i sopredelnyk vod. Opred. Faune SSSR, Izd. Zool. Inst. Akad. Nauk. No. 41, 1029 pp.
- , 1955. Order Amphipoda, pp. 180-390. In E. N. Pavlovskii (ed). Atlas of the Invertebrates of the Far Eastern Seas of the USSR. Akad. Nauk SSSR. Zool. Inst. Moscow-Leningrad. 760 pp., illustr.
- , 1972. New species of amphipods (Amphipoda, Gammaridea) from the northern part of the Pacific Ocean. Trud. Zool. Inst. Akad. Nauk SSSR 52: 129-200, figs. 1-43 (in Russian).
- Hirayama, A. 1988. Taxonomic Studies on the Shallow-Water Gammaridean Amphipoda of West Kyushu, Japan. VIII. Pleustidae, Podoceridae, Priscomilitaridae, Stenothoidae, Synopiidae, and Urothoidae. Publ. Seto Mar. Biol. Lab. 33(1/3): 39-7.
- Holmes, S. J., 1905. The Amphipoda of southern New England. U.S. Bur. Fish. Bull. 24: 459-529, pls. 1-13.
- 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.

- Karaman, G. S., & J. L. Barnard, 1979. Classificatory revisions in gammaridean Amphipoda (Crustacea), Part 1. Proc. Biol. Soc. Wash. 92(1): 106-165.
- Kroyer, H., 1838. Gronlands amfipoder beskrevne af Henrik Kroyer Kongel. Danske Vidensk. Selsk. Naturvid. Math. Afhandl. 7: 229-326, pls. 1-4.
- , 1842. Une Nordiske slaegter og Arter af Amfipodernes Orden, henorende til Familien Gammarina (Forelobigt Uddrag af et Storre Arbejde). Naturh. Tidskr. 4: 141-166.
- Kudrjaschov, V. A., 1972. K faune i ekologii bokoplavov (Amphipoda-Gammaridea) prilivo-otlivnoi zony Kuril'skikh ostrovov (Litoral'o-vov Iturup, Urup, Simuschir, Paramuschir. Uchenye Zapiski Dvgu 60: 79-116.
- Nagata, K., 1960. Preliminary notes on benthic gammaridean Amphipoda from the *Zostera* region of Mihara Bay, Seto Inland Sea, Japan. Publ. Seto Mar. Biol. Lab. 8: 163-182, 2 figs., pls. 13-17.
- , 1965. Studies on marine gammaridean Amphipoda of the Seto Inland Sea. II. Publ. Seto Mar. Biol. Lab. 13(3): 171-186.
- 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.
- Sars, G. O., 1895. Amphipoda. An account of the Crustacea of Norway with short descriptions and figures of all the species. Christiana and Copenhagen. vol. I. Amphipoda. pp. i-viii, 1-711, pls. 1-240, 8 suppl. pls.
- Shoemaker, C. R., 1930. The Amphipoda of the Chetiacamp Expedition of 1917. Contr. Can. Biol. & Fish. n. s. 5(10): 1-141, figs. 1-54.
- , 1955. Amphipoda collected at the Arctic Laboratory, Office of Naval Research, Point Barrow, Alaska, by G. E. MacGinitie. Smithson. Misc. Coll. 128(1): 1-78, 20 figs.
- Slaterry, P. N., and J. S. Oliver, 1987. Barnacle settlement on *Pleustes panopla tuberculata* (Amphipoda) in the Chukchi Sea. J. Crustacean Biol. 7(2): 358-363.
- Sneath, P. H. A., and R. R. Sokal, 1973. Numerical Taxonomy. W.H. Freeman and Company, San Francisco. 573 pp.
- Staude, C. P. 1987. Gammaridean Amphipoda. in Kozloff, E. N. Marine Invertebrates of the Pacific Northwest. Univ. Wash. Press. Seattle. 18: 346-391.
- Stebbing, T. R. R., 1906. Amphipoda I: Gammaridea. Das Tierreich, 21: 1-806 figs. 1-127.
- Stephensen, A. 1938. The Amphipoda of Northern Norway and Spitzbergen with adjacent waters. Tromso Mus. Skr. 3: 141-278, figs. 20-31.
- Stimpson, W., 1853. Synopsis of the Marine Invertebrata of Grand Manan: or the Region about the mouth of the Bay of Fundy, New Brunswick. Smiths. Contr. Knowl. 6: 5-66, pl. 1-3.
- , 1864. Descriptions of new species of marine Invertebrata from Puget Sound, collected by the naturalists of the Northwest Boundary Commission, A. H. Campbell, Esq., Commissioner. Proc. Acad. Nat. Sci., Philad. v. 16: 153-165.
- Tzvetkova, N. L., & V. A. Kudrjaschov, 1985. Ecological Studies on the fauna of South Sakhalin. Acad. Naul. Trud., 1985: 1-45.(?)
- Williams, D. E., & R. J. Andersen, 1987. Terpenoid metabolites from skin extracts of the dendronotid nudibranch *Tochuina tetraquetra*. Can. Jour. Chem. 65(9): 2244-2247.



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List of Subject Matter Errata for Vol. I(1)

Page No.	Column	Paragraph	Item
17.			Title. The correct title for paper No. 2 is given on the cover: "A Revision of the Family Pleustidae (Crustacea: Amphipoda: Leucothoidea). Part I. Systematics and Biogeography of Component Subfamilies. E. L. Bousfield and E. A. Hendrycks.
24.	2		Figure Caption. M " <i>Parapleustes</i> ", <u>n. sp.</u> (not <i>P. oculatus</i>)
24.	2	2,3	All Fig. references "S" should read " <u>5</u> ".
26	2		Figure caption. Insert " <u>H</u> " before <i>Stenopleustes pulchellus</i>
34			Key couplet No. 8., 2nd line "...uropod 1 with <u>small</u> disto-lateral spine . . ."
37	2	1	line 7. "... inner plate with <u>1-2</u> apical plumose setae . . ."
40	1	5	line 28. Reference is to page <u>30</u> , not page 31.
42	2	1	line 4. Reference is to page <u>35</u> , not page 45.
43	1	1	line 8. Reference is to fig. <u>3</u> (O), not fig. 4(O).
50	2	1	line 11. Correct reference is to pages <u>12-13</u> of article No. 1 (Tribute to J. L. Barnard) by E. L. Bousfield and C. P. Staude.
54	1	3	line 32. Reference is to page <u>35</u> , not page 45.
57			Correct reference is "Slattery, P. <u>N.</u> , and J. S. Oliver . . ."

THE AMPHIPOD SUPERFAMILY PHOXOCEPHALOIDEA ON THE PACIFIC COAST OF NORTH AMERICA. FAMILY PHOXOCEPHALIDAE. PART II. SUBFAMILIES PONTARPINIINAE, PARHARPINIINAE, BROLGINAE, PHOXOCEPHALINAE, AND HARPINIINAE. SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

by Norma E. Jarrett¹ and E. L. Bousfield²

ABSTRACT

The systematics and distributional ecology of component members of phoxocephalidean amphipod subfamilies Parharpiniinae, Pontarpiniinae, Broilginae, Phoxocephalinae, and Harpiniinae in coastal waters of the Pacific coast of North America, from the Bering Sea to northern California, are analyzed. Of the 22 regional species here recorded, the following 11 species (50%) are new to science: Pontarpiniinae: *Mandibulophoxus mayi*, new species; *M. alaskensis*, new species; Broilginae: *Paraphoxus rugosus* new species, *P. pacificus*, new species, *P. communis*, new species, *P. gracilis*, new species, and *P. similis*, new species; Phoxocephalinae: *Parametaphoxus quaylei*, new species; Harpiniinae: *Pseudharpinia inexpectata*, new species; *Heterophoxus conlanae*, new species, and *H. ellisi*, new species.

The following taxon from outside the study region is also newly described: *Griffithsuis*, new genus (South Africa). The following species are identified but not named: *Eyakia* species 1 (California), *Eyakia* species 2 (Alaska); *Parametaphoxus* species 1 (Japan), and *Heterophoxus* species 1 (California). The following taxa are newly recorded from the study region: *Mandibulophoxus gilesi* Barnard, 1957; *Eyakia robusta* (Holmes, 1908); *Harpiniopsis gurjanovae* (Bulycheva, 1936); *H. fulgens* (Barnard, 1960); *Paraphoxus simplex* Gurjanova, 1938; and *Cephalophoxoides homilis* (Barnard, 1960). The following species are re-recorded, redescribed and refigured on the basis of regional material: *Eobrolgus chumashi* Barnard & Barnard, 1981; *Metaphoxus frequens* Barnard, 1960; *Heterophoxus affinis* (Holmes, 1908); and *Harpiniopsis fulgens* (Barnard, 1960). The copulatory apparatus of the male peraeopod 7 was found to be remarkably diverse in the present material, and proved helpful in clarifying taxonomic relationships.

Biogeographically, the subfamilies Parharpiniinae and Pontarpiniinae, dominant along temperate-tropical Indo-Pacific and antipodean shores, appear to be relict along northeastern Pacific shores. The Broilginae, common in protected coastal shallows of the northern and southern hemispheres, the Phoxocephalinae, world-wide mainly in deeper shelf waters, and the Harpiniinae, dominant on finer sediments and in deeper waters of the northern hemisphere, are well represented in the present study region. The Coxophoxinae and Joubinellinae, known from deep waters of adjacent regions, probably occur here also but were not identified.

Within the present study region, the total number of species of these five subfamilies combined is slightly less than that of the single regional subfamily Metharpiniinae (Jarrett and Bousfield, 1994). The present species were also taken less abundantly at stations with sandy sedimentary bottoms. Such bias may reflect their overall preference for finer, softer sediments, at greater depths, habitats that were not extensively sampled in present surveys. Only a few species of these subfamilies, notably within the primitive sand-burrowing Pontarpiniinae, occur commonly intertidally.

INTRODUCTION

Members of the gammaridean amphipod family Phoxocephalidae are sediment-burrowing crustaceans of distinctive morphology, life style, and reproductive behaviour. They are world-wide in distribution, and are abundantly represented on the Pacific coast of North America, from Alaska to California. In a previous systematic account of the large, mainly shallow-water subfamily Metharpiniinae in this region, Jarrett and Bousfield (1994) treated 29 species in 5 genera. With respect to seven other subfamilies (of Barnard and Drummond, 1978) recorded from (or probably occurring on) the North American Pacific coast, previous

records of 20 component species have been summarized variously by Austin (1985), (Cadien, 1991), and Barnard & Karaman (1991). These include the following (subfamily of this study in parentheses): *Mandibulophoxus gilesi* Barnard, 1957 (Pontarpiniinae); *Eyakia robusta* (Holmes, 1908) and *E. calcarata* (Gurjanova, 1938) (Parharpiniinae); *Eobrolgus chumashi* Barnard & Barnard, 1981, *E. pontarpinioides* (Gurjanova, 1953), and *Paraphoxus oculatus* Sars, 1895 (Broilginae); *Cephalophoxoides homilis* (J.L. Barnard, 1960), *Metaphoxus frequens* (J. L. Barnard, 1960), and *Parametaphoxus fultoni* (Scott, 1890) (Phoxocephalinae); *Heterophoxus oculatus* (Holmes, 1908), *Heterophoxus affinis* (Holmes, 1908), *Harpinia crenulata* Boeck, 1871, *Harpin-*

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iopsis emeryi Barnard, 1960, *H. fulgens* Barnard, 1960, *H. galera* Barnard, 1960, *H. naiada*, Barnard, 1960, *H. percellaris* Barnard, 1971, *H. triplex* Barnard, 1971, and *Pseudoharpinia excavata* (Chevreux, 1887) (Harpiniinae); and *Coxophoxus hidalgo* J. L. Barnard, 1966 (Coxophoxinae). Members of the bathypelagic subfamily Joubinellinae (e.g. *Joubinella strelkovi* Gurjanova, 1952) are expected to occur in deep offshore waters but have not been recorded from the region and are not treated here.

The history of the development of systematic knowledge of these free-burrowing phoxocephalid amphipods in North Pacific regional waters has been summarized by Jarrett & Bousfield (1994) and by Bousfield & Staude (1994). Briefly, very few records from the Asiatic coast existed prior to the work of Gurjanova (1938, 1951, 1953, 1977, 1980), or from the North American coast prior to the studies of J. L. Barnard (1957, 1958, 1960, 1971, 1979) and in co-authorship with Charlene Barnard (1980, 1981, 1982). Since then, work on the Asiatic coast has been expanded mainly by Hirayama (1987, 1992) and on the North American coast by Coyle (1982), and the present authors (Jarrett *et al.* 1990; Jarrett and Bousfield, 1994). The most significant single study affecting the higher level classification of North Pacific phoxocephalids was the monumental compendium on Australian Phoxocephalidae by J. L. Barnard and Margaret Drummond (1978), a work that has been basic to the present undertaking.

Despite the extensive contributions of previous workers on North Pacific phoxocephalid amphipods, a large gap has existed between the inshore material coverage of Barnard and co-workers in California and Oregon, on the one hand, and that of Gurjanova and colleagues in the far-eastern seas of the former Soviet Union, on the other. It is fortunate, therefore, that this geographical hiatus has to a large degree been filled by much new material from the region of coastal British Columbia and Southeastern Alaska, obtained mainly since 1955, through expeditions of the Canadian Museum of Nature in Ottawa (formerly the National Museum of Natural Sciences). The material, supplemented by other collections, particularly from the Bering Sea region, forms the basis of this report. About 300 lots of specimens from more than 150 sampling stations were examined, as ecologically detailed and mapped in the station lists of Bousfield (1958, 1963, 1968), Bousfield & McAllister (1962), and Bousfield and Jarrett (1981).

The present study formally treats all the species occurring in this extensive material, classifies them in relation to previous work and to new taxonomic and phyletic concepts, and contributes to the solution of a number of problems in phoxocephalid systematics and distributional ecology that have been revealed during the course of the work.

ACKNOWLEDGEMENTS

This study could not have been completed without the help of many biological research agencies and interested colleagues. The field surveys were carried out with the full

support of the National Museum of Natural Sciences (now Canadian Museum of Nature) in Ottawa, and received vital technical assistance and ship-time from Canadian Pacific research centres and their staffs. These included the Pacific Biological Station, the Bamfield Marine Station, the Pacific Environmental Institute, the Royal British Columbia Museum, the University of Victoria, University of British Columbia, and the Institute of Ocean Sciences, Sidney, and, in the United States of America, the Friday Harbor Marine Laboratories and the College of Fisheries, University of Washington. Full acknowledgement to individuals of those agencies, and to many others, are provided in the previously published station lists (above), to whom we again express our deepest appreciation. For advisory assistance in preparation of this report, we are especially grateful to museum colleagues Kathleen E. Conlan and Ed Hendrycks, and for curatorial assistance especially to Ed, and to Judith C. Price. Preparation of the line illustrations was most capably assisted by Susan Laurie-Bourque, Hull, Quebec. Marjorie Bousfield provided translations of pertinent Russian literature. Work by the senior author, and by the artist, was also supported by operating grants from the Royal Ontario Museum, Toronto, and the Natural Sciences and Engineering Research Council, Ottawa.

SYSTEMATIC SECTION

The subfamily classification utilized here follows the system proposed initially for Australian phoxocephalids by Barnard and Drummond (1978) but modified by later studies on the world-wide fauna (e.g., Barnard and Barnard, 1982a; Barnard & Karaman, 1991). The arrangement of subfamilies is basically phyletic, as in Barnard & Drummond (1978), modified by phyletic principles developed on a broader basis across the Amphipoda in general (e.g. Bousfield, 1979, 1982, 1983; Schram, 1986; Bousfield & Staude, 1994; Jarrett & Bousfield, 1994). The technical format follows that of Barnard and Karaman (1991).

Although previous work on the systematics and classification of phoxocephalid amphipods has been extensive, relatively little significance has hitherto been placed on structures bearing on the reproductive process. The usefulness of character states of presumed mate-sensing structures of pelagic males, especially the antennal callynophore (Lowry, 1986) and calceoli (Lincoln and Hurley, 1981) has only recently been recognized, but not yet universally applied. Within the Phoxocephalidae some taxonomic attention has been paid to modifications in the form and armature of distal segments of pereopod 7 in the pelagic male (e.g. Barnard & Drummond, 1978) but their character states have seldom been incorporated into the classification of the species, or even utilized in keys to the species (e.g. Barnard & Barnard, 1981; Karaman, 1993). This copulatory apparatus, de-

FIG. 1. Phoxocephalid Subfamilies: Copulatory Spines of Male Pereopod 7.
(SEE PAGE 73 - OPPOSITE)

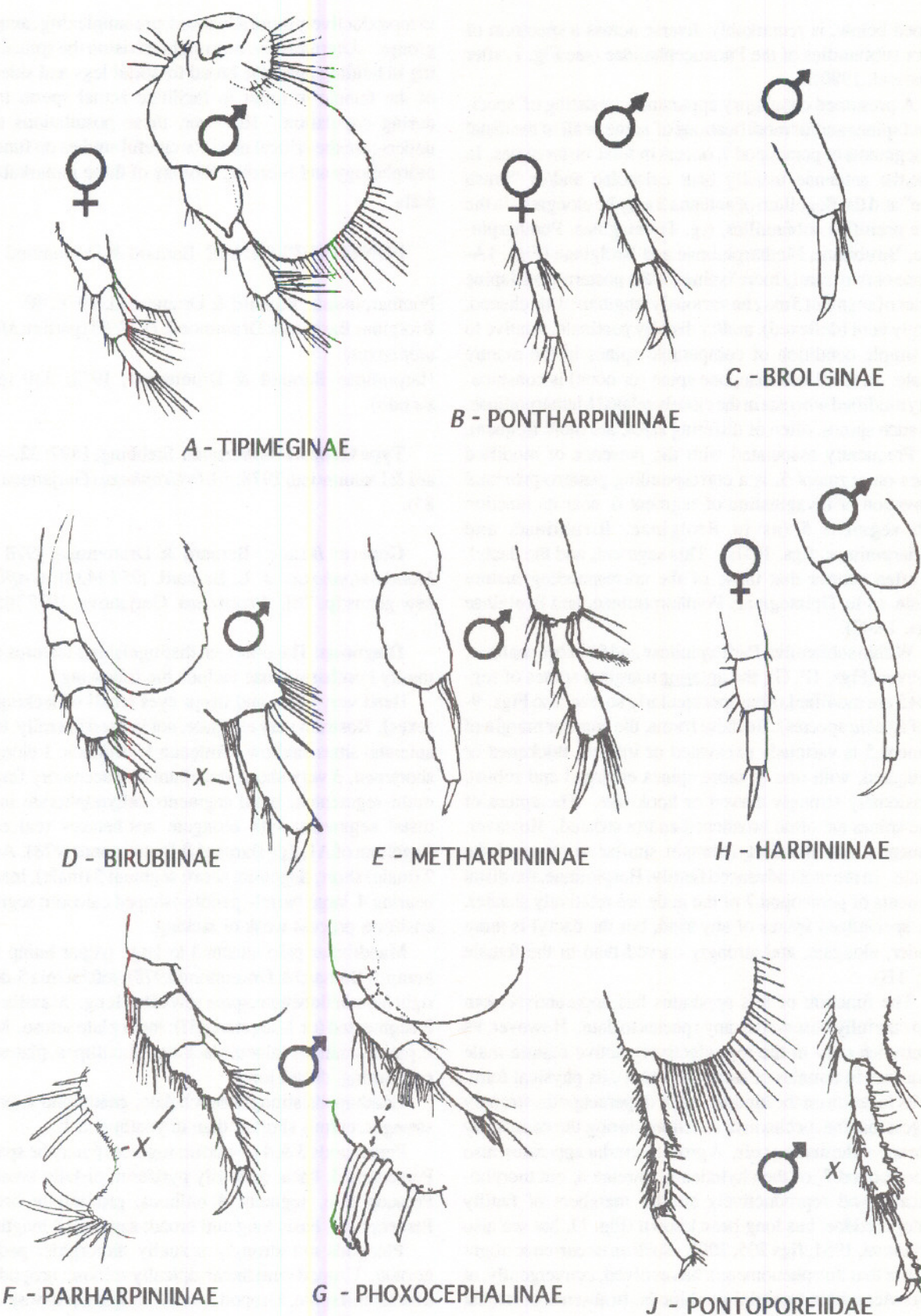


FIG. 1. PHOXOCEPHALID SUBFAMILIES: COPULATORY SPINES OF MALE PERAEPOD 7

scribed below, is remarkably diverse across a spectrum of major subfamilies of the Phoxocephalidae (see Fig. 1, after Bousfield, 1990).

A presumed copulatory apparatus, consisting of specialized spines and/or modifications of some or all of the distal 4-5 segments of pereopod 7, occurs in final instar males. In these, the antennae usually bear calceolae and/or "brush setae" and the flagellum of antenna 2 may be elongate. In the more primitive subfamilies, e.g. Tipimeginae, Pontharpiinae, Birubiinae, Metharpiinae and Brolginae (Figs. 1A-E), one or two (rarely more) spines of the postero-distal spine cluster of segment 5 may be variously lengthened, thickened, sharply bent (deflexed), and/or distally pectinate, relative to the simple condition of comparable spines in the mature female. In the Birubiinae, one spine (or none) is conspicuously modified whereas in the closely related Metharpiinae, two such spines, often of differing sizes, are more frequent.

Frequently associated with the presence of modified spines on segment 5, is a corresponding postero-proximal excavation or invagination of segment 6, near its junction with segment 5 (as in Brolginae, Birubiinae, and Metharpiinae, figs. 1C-E). This segment, and the dactyl, are often shorter than those of the corresponding mature female, as in Tipimeginae, Pontharpiinae, and Brolginae (Figs. 1A-C).

Within subfamilies Parharpiinae and Phoxocephalinae, however (Figs. 1F, G), the anterior marginal spines of segment 5 are modified, often spectacularly so (see also Figs. 9-11 of *Eyakia* species). In these forms, the anterior margin of segment 5 is variously excavated or incised, thickened or corrugated, with one or more spines enlarged and robust, occasionally strongly curved or hook-like. The apices of these spines are often broadened and/or striated. However, segment 6 and the dactyl remain similar to those of the female. In the most advanced family, Harpiinae, the distal segments of pereopod 7 of the male are relatively slender, lack specialized spines of any kind, but the dactyl is more slender, elongate, and strongly curved than in the female (Fig. 1H).

The function of this apparatus has apparently seldom been carefully observed in any species to date. However, its occurrence only in the reproductively active mature male instar (not in females or subadult males), its physical form, and its location on the hindmost pair of pereopods, strongly suggest that the mechanism functions during the copulatory embrace of the mating pair. A grossly similar apparatus, also on pereopod 7, of the phylogenetically unrelated, but morphologically and reproductively similar members of family Pontoporeiidae, has long been known (Fig. 1J, but see also Gurjanova, 1951, figs 205, 209). Such an occurrence might indicate that this phenomenon has evolved, convergently, at least twice within fossorial amphipods. In absence of critical observation, one is tempted to speculate on the mechanical functioning of this apparatus. Conceivably, it may help secure the female during actual copulation, and thereby perform, analogously, the principal role of the male gnathopods

in reproductively more advanced, pre-amplexing, amphipod groups. Alternatively, one might envision the spines assisting in holding apart the broad fossorial legs and side plates of the female in order to facilitate actual sperm transfer during copulation. However, these postulations merely underscore the critical need for careful studies on functional morphology and breeding biology of these remarkable animals.

PONTHARPINIINAE Barnard & Drummond

Pontharpiinae Barnard & Drummond, 1978: 40.

Brolginae Barnard & Drummond, 1978: 87 (partim: *Mandibulophoxus*).

Harpiinae Barnard & Drummond, 1978: 530 (partim: *Basuto*).

Type Genus. *Pontharpinia* Stebbing, 1897: 32.—Barnard & Drummond, 1978: 40. (= *Urophoxus* Gurjanova, 1977: 85).

Genera: *Basuto* Barnard & Drummond, 1978 [530]; *Mandibulophoxus* J. L. Barnard, 1957 [432]; *Griffithsius*, new genus [p. 76]; *Urophoxus* Gurjanova, 1977 [85].

Diagnosis: The principal distinguishing features of subfamily Pontharpiinae include the following:

Head very short and deep; eyes small or lacking (both sexes). Rostrum very elongate, not incised laterally, inferior antennal sinus shallow. Antenna 1, peduncle 1 elongate, 2 shortened, 3 very short; flagellum and accessory flagellum multi-segmented; basal segments callynophorate in male; distal segments with elongate aesthetascs (calceoli on flagellum of A1, vide Barnard & Drummond (1978). Antenna 2 (male) short, flagellum short; segment 5 (male), inner face bearing 4 large barrel-(paddle-)shaped calceoli; segment 1, ensiform process weak or lacking.

Mandibular palp attached to large palpal hump (molar hump of Barnard & Drummond 1978); left lacinia 5-dentate, right lacinia flabellate, spine row often long. Maxilla 1, palp 2-segmented (or 1-segmented?); inner plate setose. Maxilla 2, plates small, facial setae lacking. Maxilliped, plates small, palp strong, dactyl long.

Gnathopods strongly subchelate; gnathopod 2, propod stronger, carpus shorter, than in gnathopod 1.

Pereopods 3 & 4 powerful; segment 6 may be spatulate. Pereopod 5, basis variously pyriform, distally broadened. Pereopod 6, segment 4 bulbous, proximally broadest. Pereopod 7, basis long and broad; segment 3 lengthened.

Pleopods not strongly sexually dimorphic; peduncles normal. Uropod rami linear, apically spinose; uropod 1 with distolateral spine. Uropod 3, rami elongate, plumose-setose, sexually subsimilar.

Telson lobes subapically spinose; penicillate setae proximal to medially inserted. Coxal gills sac-like, small on pereopod 7. Brood plate 5 slender, often broadened distally.

Taxonomic Commentary: The Pontharpiniinae comprises a very distinctive and specialized subfamily group that entrains both plesiomorphic and apomorphic character states. The austral subgroup of 3 genera appears more plesiomorphic than North American members in the presence of pigmented eyes, less strongly developed molar (palpar) hump, and aequiramous, plumose-setose uropod 3. A more comprehensive revision of this subfamily complex awaits the collection and analysis of further material, especially from the southern hemisphere, and especially the careful characterization of mature males of the austral genera.

The north Pacific genus *Mandibulophoxus* is apomorphic in these and most other character states. The pyriform shape of the basis of peraeopod 5 (in *Basuto*) may be narrowed superficially almost to the linear condition, a single character state which may have led Barnard & Drummond (1978) to mis-classify it within the Harpiniinae (see fig. 2). The genus *Mandibulophoxus* had been classified with the genus *Paraphoxus* Sars in subfamily Brolginae by Barnard and Drummond (1978) and maintained there by Barnard and Karaman (1991). Perceptively, they had noted its overall generic similarity to *Pontharpinia* (loc. cit., p. 90) but "overruled" such an alliance by the taxonomic weight they gave to an apparently dissimilar condition of the mandibular molar. Paradoxically, this range of molar character states was not deemed inimical to their phyletically correct decision to include (within subfamily Phoxocephalinae) such molar-disparate types as *Phoxocephalus* and *Limnoporeia*. Mindful of this precedent, the inclusion of *Mandibulophoxus* within the Parharpiniinae seems fully justified here.

Sexual dimorphism is relatively weakly expressed within the Pontharpiniinae. Thus, in antenna 2 of the male of *Mandibulophoxus*, the flagellum is short and non-calceolate, as in the female. However, peduncular segment 5 is broadened and bears 4 large, barrel-shaped calceoli on its inner surface. The condition of the male antennae in the other genera has not been critically described (e.g., in Barnard and Drummond, 1978; Griffiths, 1973; 1976a,b). However, the close similarity of antenna 2 of the female of *Pontharpinia*, *Basuto*, and *M. "latipes"* to that of *Mandibulophoxus* suggests that the condition of antennae 2 of the males of these genera is also similar. "*Mandibulophoxus*" *latipes* Griffiths (1976b) is so distinctive in the form of its peraeopods 3 & 4, and uropods 1 & 2, that a new genus is warranted for its reception, aligned naturally also within the Pontharpiniinae (see below).

Urophoxus Gurjanova (= *Pontharpinia* Stebbing)

Pontharpinia Stebbing 1897: 32 (*Urothoe pinguis* Haswell, 1879, monotypy).—Stebbing, 1906: 146 (part).—Barnard & Drummond, 1978: 40.

Type species: *Urothoe pinguis* Haswell, 1879, by monotypy.

Diagnosis: (Condensed from Barnard & Karaman, 1991). Eyes weakly pigmented. Rostrum distally downcurved. Mandible with 5-dentate left lacinia; palpar hump weak; molar triturative, small, margin spinose.

Gnathopod 1, carpus slender, elongate. Gnathopod 2, carpus short, hind lobe cryptic. Peraeopods 3 & 4 similar distally, segment 6 long, dactyl short. Peraeopod 5, basis medium, broad distally, segment 4 broader than deep.

Pleon plate 3, hind corner strongly hooked, falciform. Uropod 3, rami aequiramous, margins spinose-setose in female. Telson lobes with proximo-lateral setal clusters.

Taxonomic Commentary: The type species has been quite fully described and illustrated by Barnard and Drummond (1978, pp. 41-46, figs. 8-10). In mature males in their possession, they did find large calceoli on proximal flagellar segments of antenna 1. However, they did not describe calceoli on antenna 2, either on the peduncle or on the relatively short flagellar segments. Is it possible that the relative shortness of the flagellum in these males may have led to their belief that they were not "advanced" (ie. reproductively fully mature)? As in males of *Mandibulophoxus*, calceoli might very well have been present on antenna 2 but, not being marginal in position, may have been "concealed" against the face of segment 5 in unstained material. In this regard, therefore, it is suggested that this material be made available for re-examination.

Basuto Barnard & Drummond

Basuto Barnard & Drummond, 1978: 530.—Barnard & Karaman, 1991: 598.

Species. *Basuto stimpsoni* (Stebbing, 1908) (Barnard 1957 [436] fig. 4.)(Reid, 1951 [222])(Griffiths, 1974a,b). *Basuto* species (Griffiths, 1976b, figs. 39 D,G).

Diagnosis: (see Barnard and Drummond, 1978, loc. cit.). Eyes present, weakly pigmented. Mandible with medium strong palpar hump; molar reduced, with a few spines.

Gnathopods dissimilar in size, and otherwise typical of the subfamily. Peraeopods 3 & 4 subsimilar in size and form. Peraeopod 5, basis sublinear, weakly or narrowly pyriform, segments 4 & 5 not strongly broadened.

Pleon plate 3 rounded behind, ordinary. Uropod 2, rami slender, unequal, posterior margins spinose or smooth. Uropod 3 inaequiramous, inner ramus non-setose.

Telson lobes lacking lateral setal clusters, apices each with simple spine.

KEY TO GENERA OF PONTARPINIINAE

1. Pigmented eyes present; mandibular palpal hump moderate; telson often with lateral setae; uropod 3, margins plumose-setose; Austral-S. African 2.
 —Pigmented eyes lacking; palpal hump strongly developed (half the length of palp segment 2); telson laterally smooth; uropod 3, ramal margins spinose, or weakly setose; Asian-North American. *Mandibulophoxus* (p. 77)
2. Pleon plate 3, hind corner produced, hook-like; telson with baso-lateral setal clusters; mandibular molar triturative *Urophoxus* (= *Pontharpinia*) (p. 75)
 —Pleon plate 3 squarish or rounded behind; telson with single lateral seta; mandibular molar process reduced, 2-3 spine-tipped; African-Madagascar 3.
3. Peraeopods 3 & 4., segment 5 not shortened, segment 6 unlike in both; peraeopod 5, basis broadly pyriform; uropods 1 & 2, rami short and stout, with heavy distal spines. *Griffithsius* n. g. (p. 76)
 —Peraeopods 3 & 4, segment 5 shortened (much shorter than segment 4), segment 6 alike in each; uropods 1 & 2, rami as long as peduncles, spined heavily throughout *Basuto* (p. 75)

Taxonomic Commentary: The species *Basuto latipes* (Griffiths, 1976) (Barnard & Karaman, 1991) is transferred to a new genus, *Griffithsius* (see below). The species illustrated by Griffiths (1976b) as *Mandibulophoxus stimpsoni* differs from *M. stimpsoni* as illustrated by Barnard (1957) and represents an unnamed species of *Basuto*.

Griffithsius, new genus (Fig. 2)

Mandibulophoxus Griffiths, 1976: 27 (partim).

Type species. *Mandibulophoxus latipes* Griffiths, 1976b: 27, figs. 9-10 (here designated).—Barnard & Karaman, 1991 [598].

Species. *Griffithsius* sp. (= *Metaphoxus* sp. Griffiths, 1973 [296].

Diagnosis: Generally similar to *Basuto* but with the following combination of character states:

Rostrum narrowly hood-like, very elongate, down-turned apically. Eyes small, weakly pigmented. Antenna 1, flagellum elongate, with weak basal calynophore (male). Antenna 2, peduncular segment 4 expanded and setose posteriorly; flagellum not elongate in male(?).

Mandibular palpal hump short; molar lacking, spine row long; palp expanding distally, with strong apical spine cluster. Maxilla 1, palp 2-segmented (or indistinctly so?), distal segment oblique, slender-spinose or setose; inner plate with 3-4 apical setae. Maxilliped plates short; palp, segment 4 (dactyl) elongate.

Gnathopods stoutly subchelate. Gnathopod 1 propod the smaller; palm of propod short, nearly vertical; carpus elongate. Gnathopod 2, carpus short, hind margin cryptic, palm of propod oblique, smooth.

Peraeopods 3 & 4 differing markedly; in peraeopod 3, segments 4, 6 and 7 (dactyl) relatively short, segment 6

spatulate, strongly spinose behind or reduced; in peraeopod 4, segments 4, 6, and 7 normal or elongate, segment 5 relatively short. Peraeopod 5, basis pyriform, broadening distally, segments 4 & 5 broad. Peraeopod 6, segment 4 little expanded posteriorly.

Pleon plate 3 quadrate behind, not hooked or falciform; outer face variously setose. Uropods 1 & 2, rami short, stout; rami strongly spinose posteriorly and apically; uropod 1 with displaced spine. Uropod 2, rami markedly unequal (outer shorter). Uropod 3 aequiramus, variously plumose-setose (both sexes).

Telson lobes each with apical spines only.

Etymology: Named in honour of Charles Griffiths who has significantly advanced knowledge of marine and freshwater amphipods of the greater South African region.

Taxonomic and Distributional Commentary. The type species (*latipes*, above) figured by Griffiths (1976) is unquestionably pontharpiniid in every feature, including the pyriform shape of peraeopod 5 basis, and the typically deeply lobate basis of peraeopod 7. However, Griffiths (1973) placed a single undetermined, larger male specimen (Stn. PED 18 V) questionably in the genus *Metaphoxus*, based on what he believed to be a 1-segmented palp of maxilla 1. However, his observations on maxilla 1 require confirmation, as the palp may be indistinctly 2-segmented in pontharpiniid species. In all other features, the animal is clearly pontharpiniid, including the very long downcurved rostrum, elongate primary and accessory flagellum, with short, obtusely angled, peduncular segment 3, short peduncular segments 3 & 4 of antenna 2, subequal rami of uropod 3 (outer segment short), and form of the mandible. The gnathopods are typically pontharpiniid. In Fig. 10 (*Ibid.*, 1973), peraeopod 7 is apparently not shown. Instead, what appear to be the distal segments (4, 5, 6, and 7) of peraeopod 5 are illustrated. Segment 4 (mistakenly described as segment 2 of peraeopod 7) is much expanded; segments 5, 6, & dactyl are short and slender.

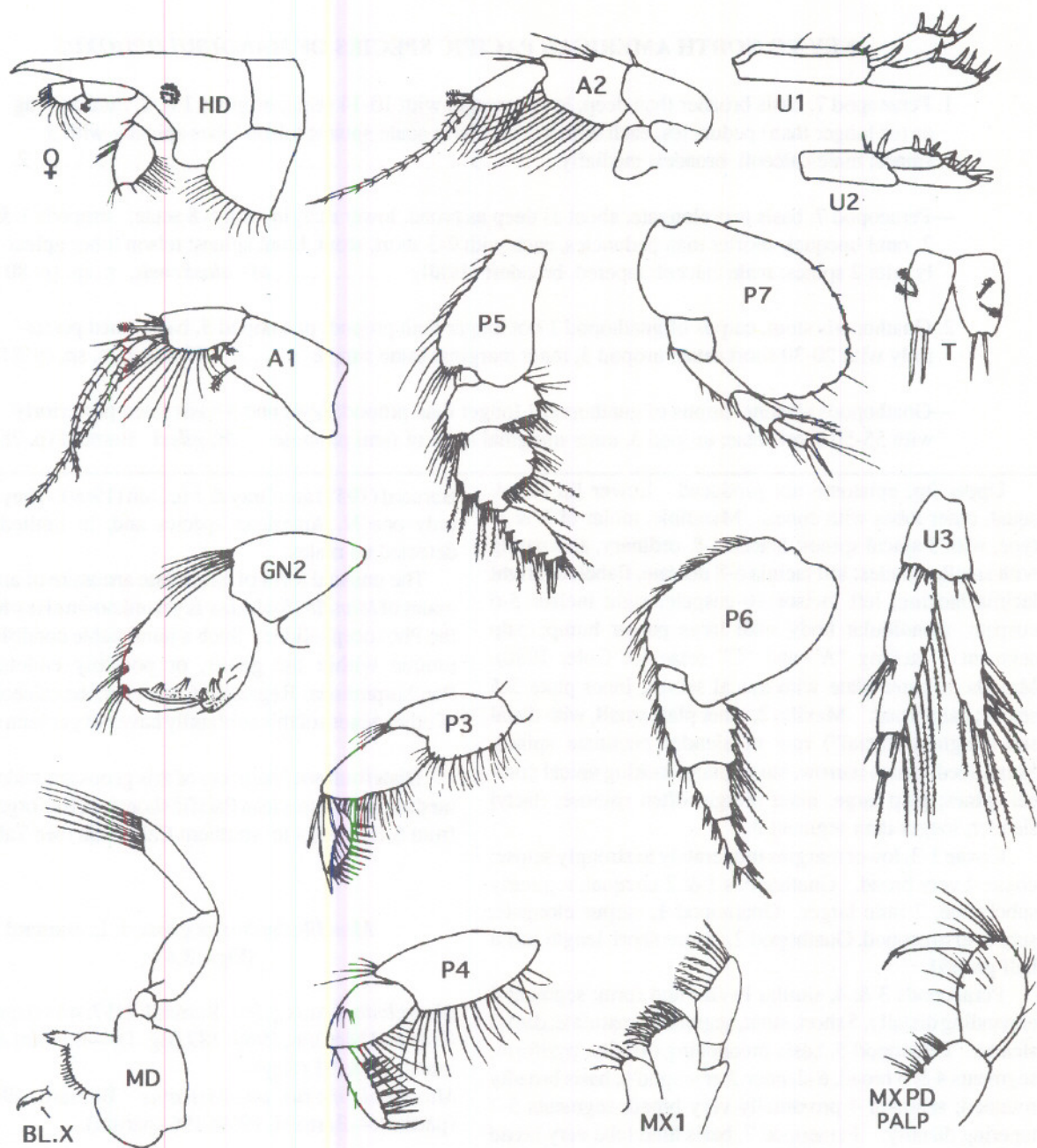


FIG. 2. *Griffithsius latipes* (Griffiths) ♀ (7.0 mm) S. W. Africa.
(modified from Griffiths, 1976).

Mandibulophoxus J. L. Barnard

McCain, 1969 [189].

Mandibulophoxus Barnard, 1957: 432.—Gray & McCain, 1969: 189.—Barnard & Drummond, 1978: 90.—Barnard & Karaman, 1991: 619.

Type species: *Mandibulophoxus gilesi* Barnard, 1957, original designation.

Species: *Mandibulophoxus alaskensis*, new species [p. 80]; *M. mayi*, new species [p. 81]; *M. uncistrostratus* (Giles, 1890 [65]); (J.L. Barnard, 1957 [435]); (Gray &

Diagnosis: With the characters of the subfamily. Rostrum elongate, unstricted. Pigmented eyes lacking or vestigial. Antenna 1, flagellum and accessory flagellum multisegmented; peduncular segment 2 short, posterior marginal setae confined distally; segment 3 very short, unarmed. Antenna 2, segment 1 normal (not ensiform); segment 3 with 2 setules; segment 4 deeper than 5, both spinose behind. Antennae of male shorter, with fewer flagellar segments; antennae 2, peduncular segment 5 deep, with 4 very large medial facial calceoli inserted near posterior margin.

KEY TO NORTH AMERICAN PACIFIC SPECIES OF *MANDIBULOPHOXUS*

1. **Peraeopod 7, basis broader than deep, lower margin with 10-14 setae; uropods 1 & 2, rami as long as (or longer than) peduncles, each with 4-5 regularly acute spines; telson lobes apically with 3 spines; male calceoli broadest medially** 2.
- Peraeopod 7, basis less elongate, about as deep as broad, lower margin with 6-8 setae; uropods 1 & 2, rami unequal, shorter than peduncles, each with 2-3 short, stout, blunt spines; telson lobes apically with 2 spines; male calceoli tapered, broadest distally *M. alaskensis*, n. sp. (p. 80)
2. **Gnathopods stout, carpus of gnathopod 1 not longer than propod; peraeopod 5, basis lined posteriorly with 20-30 short setae; uropod 3, inner marginal setae simple** *M. mayi*, n. sp. (p. 81)
- Gnathopods slender, carpus of gnathopod 1 longer than propod; peraeopod 5 basis lined posteriorly with 35-50 short setae; uropod 3, inner marginal setae of rami plumose *M. gilesi* Barnard (p. 78)

Upper lip, epistome not produced. Lower lip broad, squat, outer lobes with cones. Mandible, molar of B & D type, with 3 apical spines; blades 6-8, ordinary, alternating with smaller blades; left lacinia 6-8 dentate, flabellate; right lacinia lacking; left incisor 10-cusped; right incisor 5-6 cusped; mandibular body with large palpal hump; palp segment 3 lacking "A" and "C" setae (of Cole, 1980). Maxilla 1, outer plate with apical spines, inner plate 3-5 setose; palp broad. Maxilla 2, inner plate small, with distal sub-marginal (facial?) row of slender pectinate spines. Maxilliped, plates narrow, small, inner lacking apical conical spines; palp large, inner margin often spinose; dactyl slender, longer than segment 3.

Coxae 1-3, lower margins moderately to strongly setose; coxae 4 very broad. Gnathopods 1 & 2 unequal, regularly subchelate, 2 little larger. Gnathopod 1, carpus elongate, subequal to propod. Gnathopod 2, carpus short, length about half propod.

Peraeopods 3 & 4, similar in size and form; segment 4 expanding distally, 5 short, stout, segment 6 spatulate; dactyl slender. Peraeopod 5, basis broadening distally, pyriform; segments 4 & 5 broad, 6 slender. Peraeopod 6, basis broadly rounded; segment 4 proximally very broad, segments 5-7 tapering distally. Peraeopod 7, basis hind lobe very broad and deep, exceeded below only by segment 6 and dactyl; dactyl may be short in male.

Pleon plate 2 smooth behind, setose anteriorly below; pleon 3 squarish and weakly cusped and setose behind. Uropods 1 & 2, inner ramus the shorter; rami with few stout distal marginal and apical spines; peduncle of uropod 1 with stout disto-lateral spine. Uropod 3 slender, inner ramus medium long; inner margin of rami usually setose (both sexes).

Telson lobes medium broad, apices rounded, each with 2-3 strong spines but no lateral setae. Brood plates slender, with long distal setae. Coxal gills slender, simple, smallest on peraeopod 7.

Taxonomic Commentary: Difference between the N. American *M. gilesi* and the Indian subcontinental *M. uncistrostratus* were noted and confirmed at species level by

Barnard (1957) and Gray & McCain (1969). They examined only one N. American species and, in limited material, detected no males.

The unusual form of calceolate armature of antenna 2 in males of *Mandibulophoxus* is yet unknown elsewhere within the Phoxocephalidae. Such a remarkable condition may be unique within the genus, or possibly endemic to the Pontarpiiniinae. Regrettably, however, the calceoli of males of other genera of this subfamily have not yet been described.

Distribution: Members of this genus are widely distributed along N. American Pacific shores, in fine organic sands, from S.E. Alaska to southern California (see Table I).

Mandibulophoxus gilesi, J. L. Barnard (Figs. 3,4)

Mandibulophoxus gilesi Barnard, 1957: 433 (figs. 1-2).—Gray and McCain, 1969: 189 (fig. 1).—Barnard & Drummond, 1978: 91 (Key).

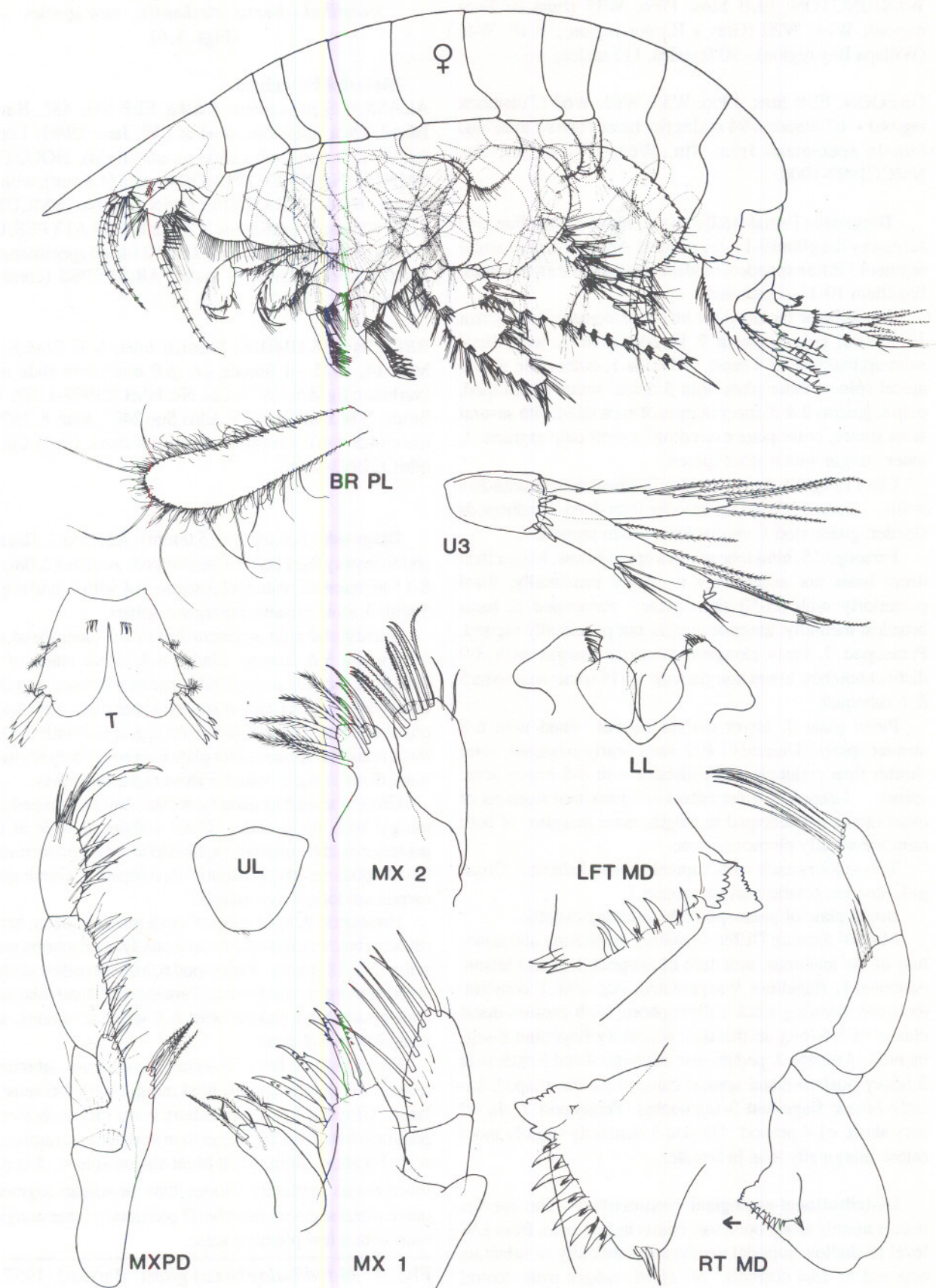
Mandibulophoxus uncistrostratus Barnard, 1960: 359 (partim).—Barnard, 1969: 196 (partim).

Material Examined: More than 400 specimens, about 5/8 females (mostly ovigerous) from 14 stations, at or slightly below LW level, along open sandy beaches, ranging north from central California and Oregon to the Strait of Juan de Fuca. CMN collections, as follows:

BRITISH COLUMBIA: Vancouver Island: Experiment Bight, Cape Scott, ELB Sta 01, July 18, 1959. - 1 female, 3 males; Grant Bay, Quatsino Sound, ELB Sta. 03, Cape Scott, July 21, 1959. - ~ 30 specimens; Clo-oose, outer coast, ELB Stn. P713, main beach, steep coarse sand, July 23, 1970. - 1 female, 4 males.

FIG. 3. *Mandibulophoxus gilesi* Barnard, 1957.

FEMALE ov. (6.0 mm)
(SEE PAGE 79 - OPPOSITE)



WASHINGTON: ELB Stns, 1966: W35 (Juan de Fuca region); W14, W20 (Gray's Harbor region); W18, W46 (Willapa Bay region) - 90 females, 115 males;

OREGON: ELB Stns, 1966: W53, W61, W63 (Tillamook region) - 67 females, 94 males (includes figured male and female specimens from Stn. W61, CMN. Cat. No. NMCC1992-1000.

Diagnosis: Female (6.0 mm): Antenna 1, flagellum and accessory flagellum 9-11-segmented. Antenna 2, peduncular segment 5 little expanded, hind margin with 6-8 stout spines; flagellum 10-11-segmented.

Mandibular molar, right incisor 7-dentate; left incisor 10-dentate; palp segment 2 broader than 3, with distal submarginal row of 4 setae. Maxilla 1, outer plate with 9 apical spines, inner plate with 5 apical setae. Maxilliped, palp segments 2 & 3, inner margin of each lined with several stout spines; outer plate extending beyond palp segment 1, inner margin with 4 stout spines.

Coxa 1 slightly deeper anteriorly, lower margin with 20+ setae. Coxa 4 distinctly broader than deep. Gnathopods slender; gnathopod 1, carpus longer than propod.

Peraeopod 5, hind lobe of coxa broad below, longer than deep; basis not excessively narrowed proximally, lined posteriorly with 35-50 short setae. Peraeopod 6, basis broadest medially, anterior margin not proximally incised. Peraeopod 7, basis elongate, posterior margin with 8-9 distinct notches, lower margin with 10-14 setae; segments 5 & 6 subequal.

Pleon plate 3, lower margin convex, lined with 6-8 slender spines. Uropods 1 & 2, rami nearly subequal, outer shorter than peduncle, each distally with 4-5 heavy acute spines. Uropod 3, inner ramus and proximal segment of outer ramus are subequal in length, inner margins of both rami are weakly plumose-setose.

Telson lobes each with 3 apical spines, 1 shorter. Coxal gills slender, smallest on peraeopod 7.

Brood plate of peraeopod 5 broadening distally.

Male (4.5 mm.): Differing mainly in the form and armature of the antennae, armature of uropods 1-3, and telson. Antenna 1, flagellum 9-segmented, segment 1 conjoint, elongate, forming weak callynophore, with postero-distal cluster of 5-6 long aesthetascs; accessory flagellum 8-segmented. Antenna 2, peduncular segments 4 and 5 each with 5 heavy postero-distal spines; calceoli paddle-shaped, basally broad; flagellum 9-segmented. Peraeopod 7, dactyl very short, <1/4 propod. Uropod 3 rami only slightly more setose marginally than in female.

Distributional-ecological commentary: The species occurs mainly along open surf coasts in fine sand, from LW level to shallow subtidal depths and subtidally in substrata exposed to tidal currents. *M. gilesi* ranges from central British Columbia to southern California. Males are present in July and August in the northern part of the species range.

Mandibulophoxus alaskensis, new species
(Figs. 5, 6)

Material Examined:

ALASKA: South-eastern Alaska, ELB Stn. A81, Hawkins Island, Orca Inlet, fine sand at LW, June 29/61: Lot #1 - female (5.0 mm), with slide mount (fig'd), HOLOTYPE, CMN Cat. No. NMCC1992-1104; male (4.5 mm), with slide mount (fig'd), ALLOTYPE, CMN Cat. No. NMCC1992-1105; 43 female (mostly ov.), 29 male PARATYPES, CMN Cat. No. NMCC1992-1106. Lot # 2 (dried specimens) - 20 females (mostly ov.), 19 male PARATYPES (combined, above).

BRITISH COLUMBIA: Saanich Inlet, K E Conlan coll., Mar. 14, 1975 - 1 female ov. (5.0 mm) with slide mount (variation fig'd?), CMN. Cat. No. NMCC1992-1107. Haro Strait, NW James I., D.V. Ellis Sta. 2403, Mar. 8, 1979. - 1 male (4.5 mm), 1 subadult male (4.5 mm), CMN Cat. No. NMCC1992-1108.

Diagnosis: Female ov. (5.0 mm): Antenna 1, flagellum and accessory flagellum 8-9 segmented. Antenna 2, flagellum 8-11 segmented; peduncular segment 4 with 7, and segment 5 with 5, stout posterior marginal spines.

Mandibular palp, segment 2 with 2-3 inner distal setae; left lacinia 5-6 dentate; blades 6-8, distal blade of right mandible forming a short bifid pseudo-lacinia. Maxilla 1, outer plate with 11 apical spines; inner plate with 4 apical plumose setae. Maxilliped, palp segment 2 with 2-3 distal inner marginal spines; outer plate exceeding palp segment 1, inner distal margin with 3-5 stout raptorial spines.

Coxa 1 expanding distally, weakly hatchet-shaped, distal margin with 10-12 setae. Coxa 4 about as wide as deep, posterior excavation shallow, hind lobe very broadly rounded. Gnathopods relatively stoutly developed. Gnathopod 1, carpus not longer than propod.

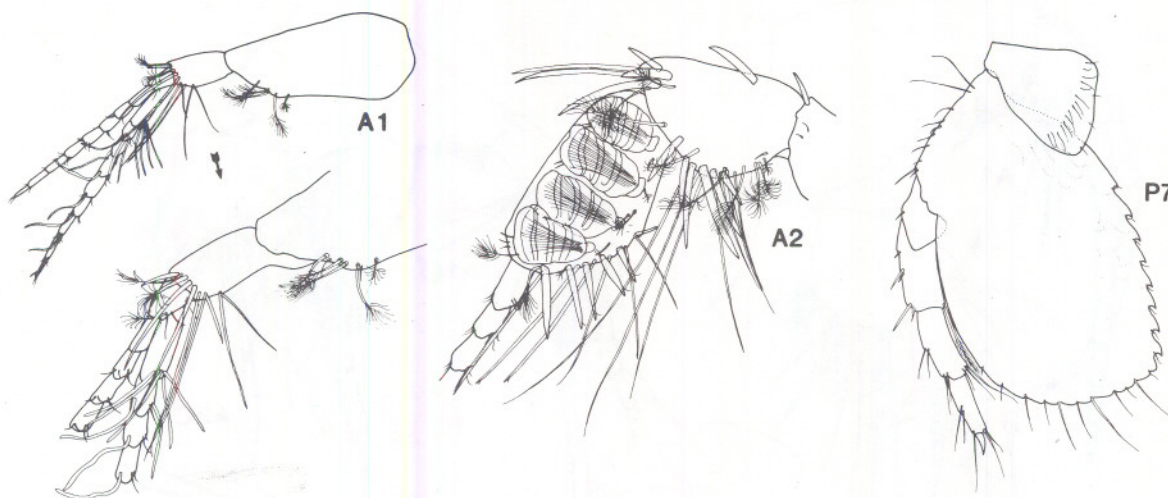
Peraeopod 5, hind lobe of coxa medium deep, broadly rounded below; basis narrow proximally, hind margin weakly setose (12-18 setae). Peraeopod 6, basis broadest medially, anterior margin unindented. Peraeopod 7, hind lobe deeper than broad, hind margin with 6-8 weak serrations, lower margin with 6-8 setae.

Pleon plate 3, lower margin convex, with submarginal row of 5-6 slender spines; hind margin with 4-6 setae, one large. Uropods 1 & 2, rami short, outer ramus shorter than peduncle but distinctly longer than inner ramus; rami distally with 2-3 short, stout, often blunt-tipped spines. Uropod 3, inner ramus distinctly shorter than proximal segment of outer, distal segment short (<1/3 proximal); inner margins of rami with a few plumose setae.

FIG. 4. *Mandibulophoxus gilesi* Barnard, 1957.

MALE (4.5 mm)

(SEE PAGE 81 - OPPOSITE)



Telson lobes each with two subequal apical spines.

Male (4.5 mm): Antenna 1, flagellum 7-segmented, basal segment weakly conjoint, length equal to two successive segments, postero-distally with cluster of 7-8 elongate aesthetascs. Accessory flagellum 7-segmented. Antenna 2, peduncular segment 4 with 5, and segment 5 with 4 strong posterior marginal spines; calceoli balloon-shaped (proximally narrow, distally broadest); flagellum 7-9-segmented. Pereopod 7, dactyl normal, about half length of propod.

Taxonomic and biogeographic commentary: *Mandibulophoxus alaskensis* is distinct from *M. gilesi* in characters noted in the key and text (above). The differences hold in both males and females. Moreover, the distributions are essentially disjunct, overlapping only in the Vancouver Island region. The northern species may yet be found in suitable localities to the west and northwest of Prince William Sound, and to the south in northwestern British Columbia. Recent surveys (Slattery & Conlan, personal communication) suggest that bottom faunas were not seriously affected, let alone extirpated, by the great Exxon oil spill of 1989, and full re-establishment of subtidal populations may soon be completed.

Subtidal specimens from Saanich Inlet and Haro Strait show slight variations in setation of pereopod bases, and armature of uropods, etc., but numbers are too few to assess the range of variation and hence the level of taxonomic significance. However, in a female (5.0 mm) from Saanich Inlet (fig. 6), the following differences (from Alaska females of similar size) were noted:

Gnathopod 1, superior lateral setae of propod in 4-5 groups; pereopod 5, basis, posterior marginal setae short, close-set, 10-12 in number; brood plate of pereopod 5, margins with short supernumerary setae; pereopod 7, basis slightly broader, with 5-6 posterior serrations and 5-6 postero-distal setae; uropods 1 & 2, marginal and apical spines less slender, more blunt; uropod 3, inner margin of inner ramus with fewer plumose setae; telson lobes each with one short and one long stout spine.

***Mandibulophoxus mayi*, new species**
(Fig. 7)

Material Examined:

BRITISH COLUMBIA: North-central coast: ELB Stn.H1, 1964 (Calvert I.) - 2 females, 1 male. Vancouver Island, outer coast: ELB Stn. P703, 1970 - 1 female ov., with slide mount, (HOLOTYPE), CMN Cat. No. NMCC1922-1101; 1 mature male, with slide mount, (ALLOTYPE), CMN Cat. No. NMCC1992-1102; *Ibid.* - 100 females (many ov.), 71 males, PARATYPES, CMN CAT. NO. NMCC1992-1103; ELB Stn. P10, 1975, and P. Slattery, 1983, 25-30 m. (off Long Beach) - 4 females ov. Other material from: ELB Stn. H44, 1964; P711, 1970; B19b (Brady's Beach), 1977 - 141 females (mostly ov.), 89 males. Also ELB Stns., 1975: P21 (Bordelais Ids.), 30 m. - 3 females (ov.); P14a (Keeha Bay), 4-12 m. - 3 females, 9 males. ELB Stn. H41 (Jordan R.), LW, 1964 - 1 female, 1 male.

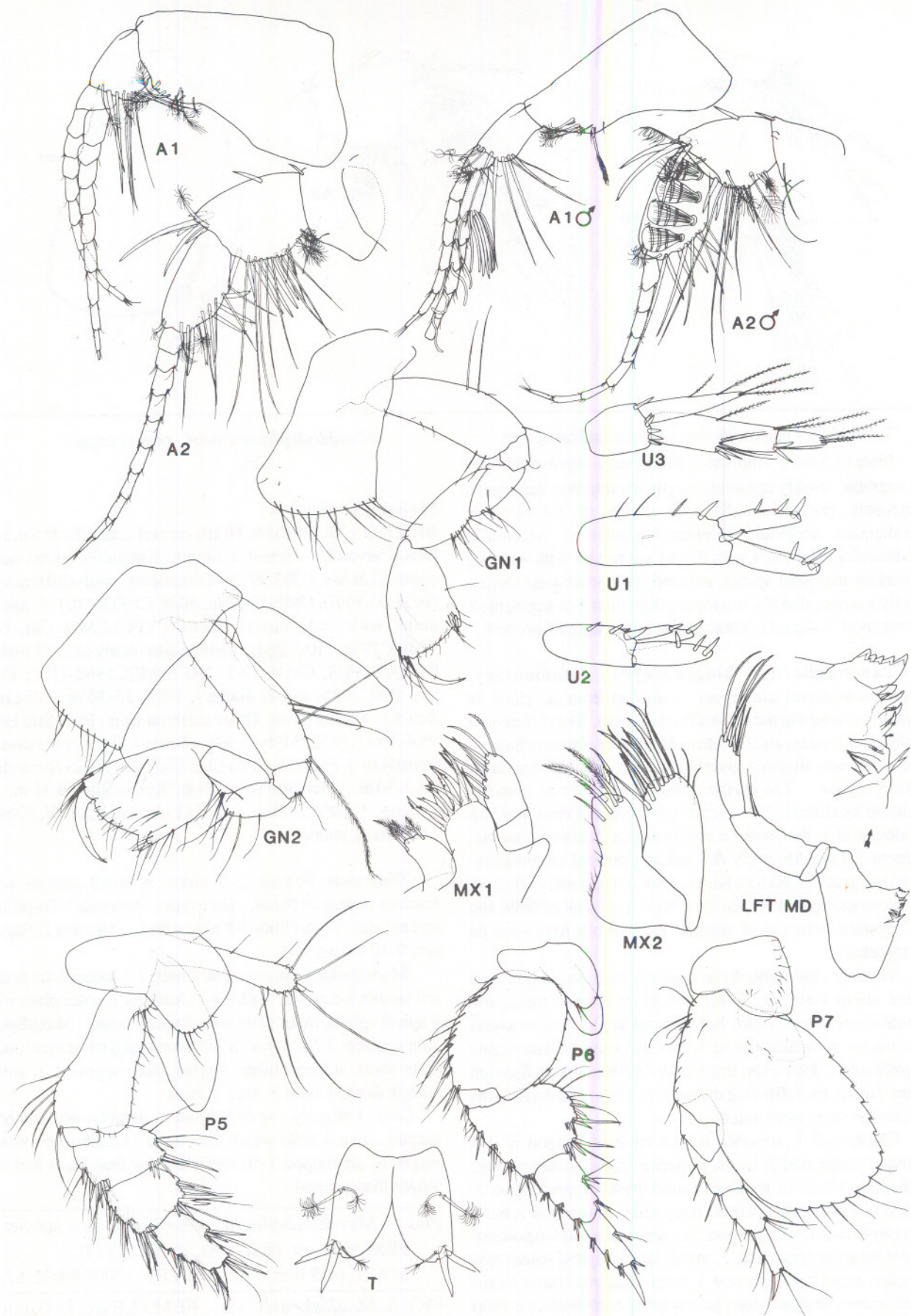
Diagnosis. Female (3.5 mm.): A small species with features mainly of the *M. gilesi* type. Antenna 1, flagellum and accessory flagellum 7-8 segmented. Antenna 2, flagellum 9-10 segmented.

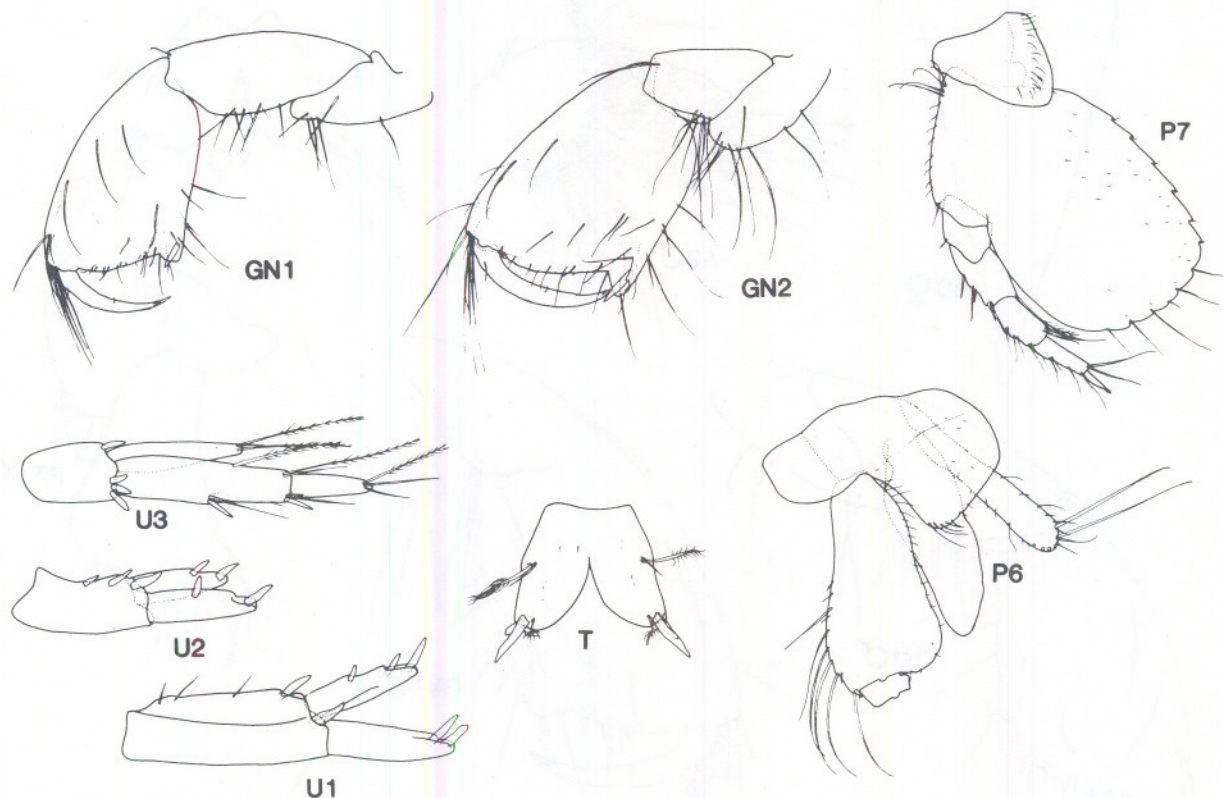
Mandibular palp, segment 2 with 2-3 inner distal setae; left lacinia 6-dentate; blades 5-7. Maxilla 1, outer plate with 9 apical spines, inner plate with 4 apical setae. Maxilliped, palp segment 2 distally with 2-3 inner marginal spines; outer plate short, not extending beyond palp segment 1, inner margin distally with 3 stout spines.

Coxa 1 slightly expanded antero-distally, not hatchet-shaped; coxa 4 little wider than deep. Gnathopods stout; carpus of gnathopod 1 distinctly shorter than basis and not longer than propod.

FIG. 5. *Mandibulophoxus alaskensis*, new species
FEMALE ov. (5.0 mm), HOLOTYPE;
MALE (4.5 mm), ALLOTYPE. (SEE PAGE 82)

FIG. 6. *M. alaskensis* var. FEMALE ov. (5.0 mm)
Saanich Inlet. B. C. (SEE PAGE 83)





Pereopod 5, hind lobe of coxa deep, narrow; basis narrow proximally, length about $2\frac{1}{2}$ X distal width, hind margin with 25-30 close-set setae. Pereopod 6, basis widest distally, anterior margin weakly incised proximally. Pereopod 7, basis elongate posteriorly, hind margin with 5-6 weak serrations, junction with convex lower margin sharply angled, lower margin with 10-13 medium setae; segments 4-6 with slender anterior marginal spines.

Pleon plate 3, lower margin nearly straight, with 3-4 submarginal spines. Uropods 1 and 2, ramal pairs long, outer equal in length to peduncle, each distally with 4-5 regular, acutely tipped marginal spines and single stouter apical spine; peduncle with very stout distolateral spine. Uropod 3, inner ramus nearly equal to first segment of outer ramus, with single inner marginal and apical simple setae.

Telson lobes each with 3 subequal apical spines.

Brood plate on pereopod 5 not expanded distally.

Male (3.5 mm). Antenna 1, flagellum 8-segmented, first conjoint, about equal in length to next three segments combined, bearing postero-distal cluster of 8 long aesthetascs; accessory flagellum 8-segmented. Antenna 2, flagellum 9-segmented; peduncular segment 4 with 7 stout postero-distal spines; segment 5 with 5 postero-distal spines and 4 median facial balloon-shaped calceoli.

Pereopod 7, basis with 5-6 weak posterior marginal notches; dactyl about $\frac{1}{4}$ length of propod. Uropod 3, inner

ramus longer than peduncle, with single simple inner marginal seta.

Etymology: Named in honour of Dr. Arthur S. May, former President and Chancellor, Memorial University, St. John's, Newfoundland, and former President, Natural Sciences and Engineering Research Council, for his outstanding support of aquatic biological research in Canada.

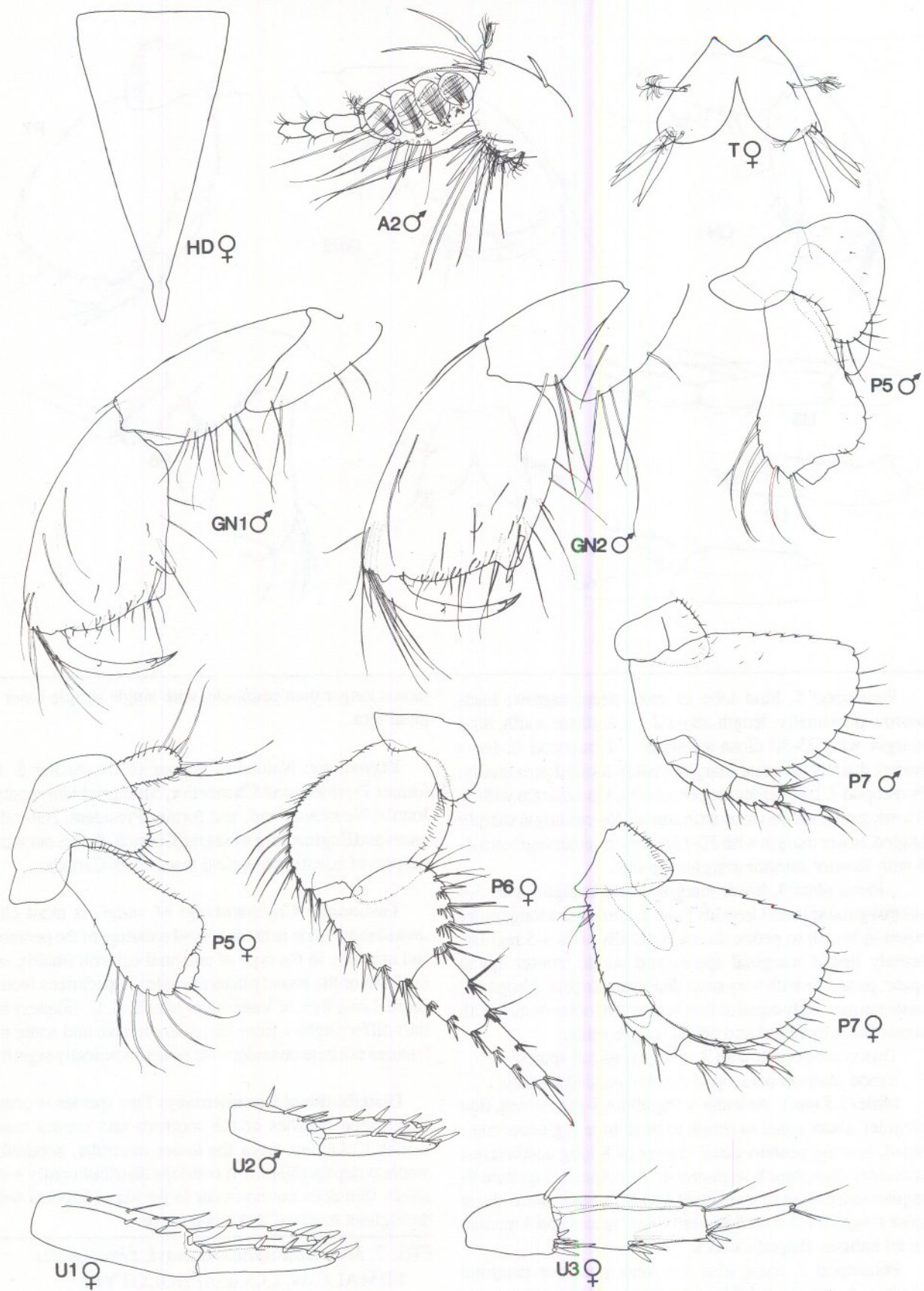
Taxonomic Commentary: *M. mayi* is most closely related to *M. gilesi* in the form and armature of the pereopods and uropods, in the type of antennal calceoli (male), and in the form of the brood plates (female). Specimens from offshore, Long Beach, Vancouver Island, B. C. (Slattery material) differ slightly from the others in size and some minor features not here considered to be taxonomically significant.

Distributional Commentary: This species is common along open beaches of the southern and central coast of British Columbia, from the lower intertidal, subtidally to medium depths (30 m.). It overlaps distributionally with *M. gilesi* (but does not co-occur in the same habitats with it) throughout much of its known range.

FIG. 7. *Mandibulophoxus mayi*, new species

FEMALE ov. (3.5 mm) HOLOTYPE;

MALE (3.5 mm) ALLTYPE. (SEE PAGE 84)



Parharpiniinae: Barnard & Drummond, 1978: 174 (part).— Barnard & Karaman, 1991: 595 (key to genera).

Type genus: *Parharpinia* Stebbing, 1899: 207.

Other Genera: *Protophoxus*, K. H. Barnard, 1930: 335; *Eyakia*, J. L. Barnard, 1979b: 375; *Phoxorgia* J. L. & C. M. Barnard, 1980: 867.

Diagnosis: Rostrum fully hooded, elongate. Eyes small or lacking in female, very large, pigmented, in male.

Antenna 1, peduncular segment 2 long; proximal segments of flagellum calceolate in male. Antenna 2, peduncular segments 4 & 5 with facial and marginal clusters of stout spines; segment 5 and elongate flagellum strongly calceolate in male.

Mandible, molar process not triturative, apex with articulated serrate spine(s); spine row strong; right lacinia bifid or trifid, left lacinia irregularly 4-5 dentate; palp segments 2 & 3 slender, 3 usually with baso-facial setae. Maxilla 1, inner plate with 1-4 apical setae; outer plate with 11 apical spines, palp 2-segmented. Maxilla 2, plates subequal. Maxilliped, palp powerfully raptorial, dactyl long; outer plate tall, inner plate short, with 1-2 apical spines and setae.

Coxal plates 1-4 deep, not very broad, lower margins usually strongly setose. Gnathopods regularly subchelate, propods subequal, carpus with free lower margin.

Peraeopods 3 & 4 strong; segment 5 with strong postero-distal spine; dactyls medium. Peraeopod 5, basis broad, narrowing distally; segments 4-6 spinose not greatly expanded, margins generally strongly setose and spinose. Peraeopod 6 elongate; basis irregularly broad; segments 4-6 not broadened. Peraeopod 7, basis very broad, plate-like; segments 4 & 5 somewhat broadened, margins setose; in male, segment 5 of specialized copulatory form; anterior margin variably incised, and lined with spines of specialized form; one or two spines may be enlarged, curved, and striated or otherwise modified at the apex.

Pleopods strong, rami long. Pleon plates 1-3 broad, lower margins setose. Pleon 3, outer margin usually with facial row of seta; hind corner often produced, tooth-like.

Uropods 1 & 2 powerful, rami tapering, marginal and apical spines distinct, not shortened or fused with rami. Uropod 1, peduncle with special apical spine. Uropod 3 (female), rami unequal but outer ramus with setose margins; in male, rami subequal and fully plumose-setose, terminal segment short or lacking.

Telson lobes broad, apical spines few, short. Coxal gills plate-like on peraeopods 2-6, smaller, sac-like on peraeon 7.

Taxonomic and Distributional Commentary: One genus of this subfamily, *Eyakia*, is endemic to Asiatic and North American shores of the North Pacific. A key to world genera is provided by Barnard & Karaman, 1991, p. 595.

Eyakia J. L. Barnard, 1979b: 375.— Barnard & Barnard, 1981: 305.—Barnard & Karaman, 1991: 608.

Mesophoxus Gurjanova, 1977: 77.

Type species: *Parharpinia calcarata* Gurjanova, 1938b (original designation).

Species (North Pacific region): *Eyakia robusta* (Holmes, 1908); *E. ochotica* (Gurjanova, 1953); *E. uncigera* (Gurjanova, 1938b); *E. subuncigera* (Gurjanova, 1938b); *E. lap-erusi* (Gurjanova, 1977); *Eyakia* species 1 (= *E. calcarata*, Barnard, 1960); *Eyakia* species 2 (= *E. robusta*, large Aleutian form, Barnard & Barnard, 1981).

Diagnosis: Rostrum entire, not or little incised in front of eyes. Antenna 2 (male), segment 5 with 7 anterior marginal calceoli; flagellar segments regularly calceolate; in female, segment 4 with facial spines in 2 rows.

Mandibular palpal hump distinct; molar with 1-3 spines; palp segment 3 usually with single baso-facial setal cluster. Maxilla 1, inner plate with 4 apical setae. Maxilliped, inner plate with 1 apical stout spine and 1 outer narrow spine.

Coxal plates, distal margins often heavily setose. Gnathopods regular, carpus of gnathopod 1 the longer.

Peraeopods 3-4 strongly setose and spinose posteriorly. Peraeopod 5 small, segments 4 & 5 not much broadened, segments 5 & 6 subequal in length. Peraeopod 6, basis shallowly concave behind; distal segments little broadened. Peraeopod 7, hind margin of basis with numerous small teeth. Segment 5 (male) usually with strong anterior marginal copulatory notch and clasping spine.

Pleon plate 3, hind corner usually produced acute, outer face with single row of long setae. Uropod 1, peduncle with strong baso-facial setal row, but lacking displaced spine. Uropod 2, peduncle with strong outer marginal spine row. Uropod 3, rami short, nearly bare in female; in male, outer ramus slightly the shorter, all margins plumose-setose.

Telson lobes medium long, apices with 1-3 spines, unequal in the female, subequal in the male.

Coxal gills large, plate-like, smallest on peraeopod 7.

Distributional Commentary: Members of the genus are confined to the coastal waters of the North Pacific shelf region, from immediately subtidal to depths of nearly 700 m. At least three species occur along the N. American Pacific shelf, from the Aleutians to Baja California.

Taxonomic commentary. The genus appears to be well represented along both Asiatic and North American Pacific shores. Numerical taxonomic analysis of component species was not attempted because study material was available for only one species. However, the group appears divisible into two major subgroups. The *robustus* subgroup, occurring on both sides of the Pacific, is marked by a strongly

KEY TO KNOWN SPECIES OF *EYAKIA*

1. Pleon plate 3 with stout posterior tooth or hook; pereopod 7, hind margin of basis with 5-10 distinct serrations; telson lobes each about twice as long as wide 2.
—Pleon plate 3 squarish or rounded behind; pereopod 7, hind margin of basis with small or indistinct teeth of with one large process telson lobes about three times as long as wide 4.
2. Pleon plate 3, tooth heavy rounded; antenna 2, peduncular segments 4 & 5 with single groups of stout facial spines *E. robusta* group 3.
—Pleon plate 3 short, acute; antenna 2, peduncular segments 4 & 5 lacking facial spines
..... *E. ochotica* (Gurj.) (p. 92)
3. Pereopod 7 (male), segment 5 with distinct notch and anterior clasping spine; antenna 2, peduncle 5 with 6-7 anterior marginal calceoli; animals large (12-15 mm) *Eyakia* species 2 (p. 90)
—Pereopod 7 (male), segment 5 with weak anterior notch and no clasping spine; antenna 2, peduncle 5 with 2-5 anterior marginal calceoli; animals medium (9-11 mm) *E. robusta* (Holmes)(p. 86)

Animals small (6.5 mm) *E. laperusi* (Gurjanova)
4. Pereopod 7 segment 2 lacks large spike; uropod 2 at least one ramus with marginal spines 5.
—Pereopod 7, segment 2 with large posterior spike; uropod 2, rami lacking marginal spines 6.
5. Antenna 2 (male), peduncular segment 5 with 4 anterior marginal calceoli; pleon plate 3 rounded behind; pereopod 7 (male) with strong notch and copulatory spine ... *E. calcaratus* (Gurj.)(p. 90)
—Antenna 2 (male), peduncular segment 5 with 5-7 anterior marginal calceoli; pleon plate 3 subsquarish, pereopod 7 (male), segment 5 with weak anterior marginal notch and no copulatory spine ...
..... *Eyakia* species 1 (p. 89)
6. Coxa 2 with postero-ventral tooth; uropod 1, outer ramus with marginal spine(s)
..... *E. subuncigera* (Kudrjasch.) (p. 92)
—Coxa 2 lacking postero-ventral tooth; outer ramus of uropod 1 lacking marginal spines
..... *E. uncigera* (Gurj.) (p. 92)

toothed pleon plate 3, strongly setose coxal plates 1-4, and relatively short, broad, telson lobes. At least two species occur on both coasts. The *calcaratus* group is mainly Asiatic Pacific. Member species lack a pleonal tooth, the coxal plates are less strongly setose below, and the telson lobes are relatively long and slender. *Eyakia laperousi* is removed from the genus *Mesophoxus*, on the logical recommendation of Barnard & Karaman (1991: 621).

Eyakia robusta (Holmes) (Figs. 8, 9)

Paraphoxus robustus Holmes, 1908: 518, fig. 27.—Barnard, 1960: 235, pl. 25.

Eyakia robusta: Barnard & Barnard, 1981: 309 (partim).—Barnard & Karaman, 1991: 609.

Material Examined:

BRITISH COLUMBIA: North Central coast: Swanson Bay, C. Levings coll., Nov., 1978 - 2 specimens.
Southern Vancouver I., Saturna I., J.F.L. Hart coll., Aug. 24, 1955: 1 female ov. (9.0 mm), with slide mount. CMN Cat. No. NMCC1992-0999 (fig'd); 1 male (7.0 mm), with

slide mount, CMN Cat No. NMCC1992-0999 (fig'd). French Creek, P. O'Rourke coll., August, 1977 - 1 female; Saanich Inlet, 3 stations, K. E. Conlan, August, 1977- 4 females ov., with 1 slide mount.

Victoria region: Off Clover Point, G. O'Connell, 1982 - 1 female.

WASHINGTON: Strait of Juan de Fuca, 3 localities, C. P. Staude coll., May, 1976 - 3 females, 2 im.

Diagnosis. Female (9.0 mm): Rostrum medium. Eye small, oval. Antenna 1, peduncular segment 2 with postero-distal cluster of 7-8 setae; flagellum 10-12 segmented, accessory flagellum 7-segmented. Antenna 2, peduncular segment 4 with anterior marginal cluster of 6-8 strong setae and 2 facial clusters of 2-5 spines; segment 5 with central facial cluster of 3 spines and distal group of 2-3 spines; flagellum 10-segmented.

Mandibular molar, apex flat, not tritulative, with single movable serrated blade and seta; right lacinia irregularly bifid; spine row with 8-12 serrated blades, left lacinia 4-

FIG. 8. *Eyakia robusta* (Holmes 1908).

FEMALE (9.0 mm) HOLOTYPE; MALE (7.0 mm)

ALLOTYPE (SEE PAGE 87 - OPPOSITE)



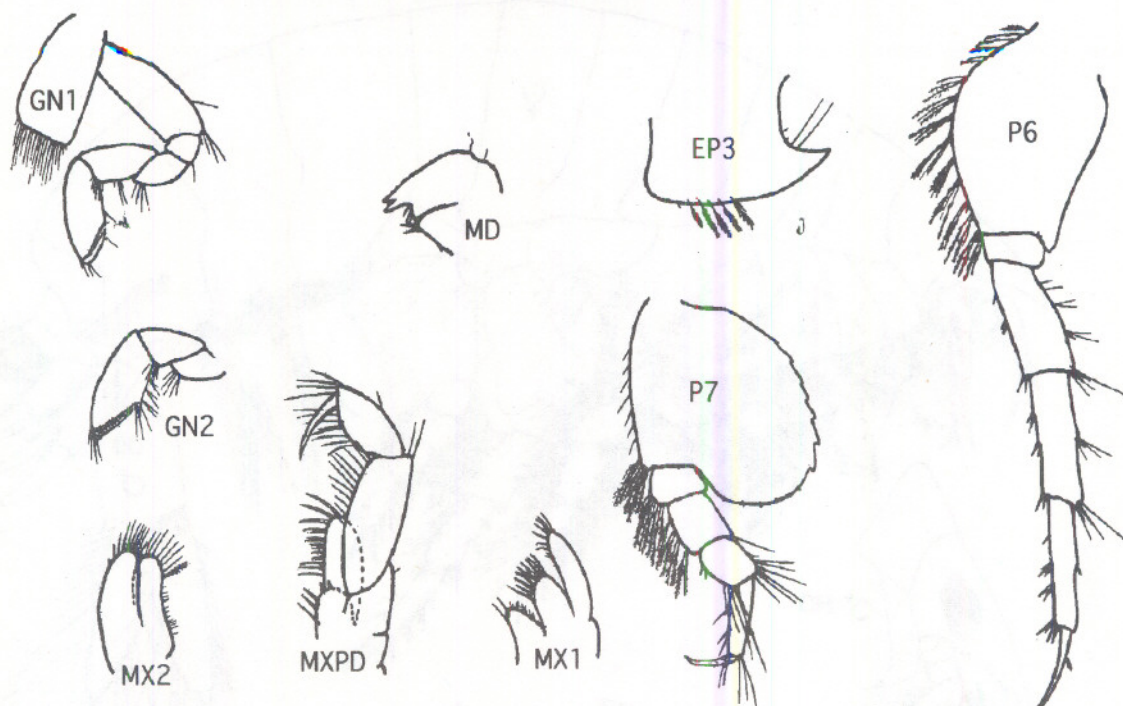


FIG. 9. *Eyakia robusta* (Holmes) ♀ (8.0 mm). off Point Loma, CA.
(modified from Holmes, 1908).

dentate; palp segment 3 with baso-facial cluster of 4-5 medium setae. Maxilla 1, inner plate with 2 apical setae, bluntly conical apex of palp with 4-5 spines. Maxilliped outer plate tall, with 4-5 strong apical spines, and 2-3 outer marginal setae.

Coxal plate 1, lower margin with ~ 20 long setae, corners rounded. Coxa 4 broad, hind margin vertical. Gnathopod propods subequal, ordinary. Gnathopod 1, carpus nearly as long as propod, lower margin with 2 clusters of setae. Gnathopod 2, carpus short, free lower margin with single setal cluster. Pereopods 3 & 4, postero-distal spine of segment 5 stout, length nearly equal to segment 6; posterior margin of segment 6, distal half spinose; dactyl strong, > half length of segment 6. Pereopod 5, segments 4 & 5 little expanded, margins heavily setose, segments 5 & 6 subequal in length, dactyl short. Pereopod 6, segment 4 slightly wider than 5, hind margins long-setose. Pereopod 7, hind margin of basis with 8 medium teeth; segments 4 & 5 slightly expanded, as wide as long, margins strongly setose; dactyl medium.

Pleon plate 3, hind corner produced as strong tooth; facial row of 18-20 long setae; lower margin with 5 plumose setae. Uropod 1, peduncle with baso-facial fan of 10 setae; rami each with 2 closely set marginal spines. Uropod 2, peduncular outer margin with 12-15 tall spines, rami with 2-3 close-set marginal spines. Uropod 3, peduncular distal fan of spines strong; outer ramus twice length of inner ramus, inner distal margin setose, terminal segment short.

Telson lobes, length about twice width, apex with 2 unequal spines.

Male (7.0 mm): Eye large, irregular. Antenna 1, single calceolus on peduncular segment 3 and on proximal 3 of 10 flagellar segments. Antenna 2, peduncular segment 4 with 3 facial clusters of spines; segment 5 with one cluster of facial spines and 5 anterior marginal calceoli; flagellum 30+ segmented; proximal 9 segments with calceoli.

Pereopod 7, copulatory apparatus of segment 5 consists of a slightly emarginated anterior border lined with short spines but none specialized as a copulatory spine.

Uropod 3, rami broadly lanceolate, subequal; all margins setose; terminal segment of outer ramus very small.

Distributional Commentary: *Eyakia robusta* (Holmes, sens. str.) has now been recorded from central and southern British Columbia to southern California, in shelf waters to depths of 20 - 250 m.

Taxonomic Commentary: Except for its slightly larger size, the present material compares closely with that originally described from southern California by Holmes (1908) and redescribed and figured by Barnard (1960) (fig. 9, above). It differs significantly from the large species from the Aleutian Islands described by Barnard and Barnard (1981, fig. 1) by the characters given in the key (p. 86).

This male of this large unnamed species has a very distinctive copulatory spine on pereopod 7 (see fig. 10A), and more closely resembling that of *E. calacurata* (fig. 11).

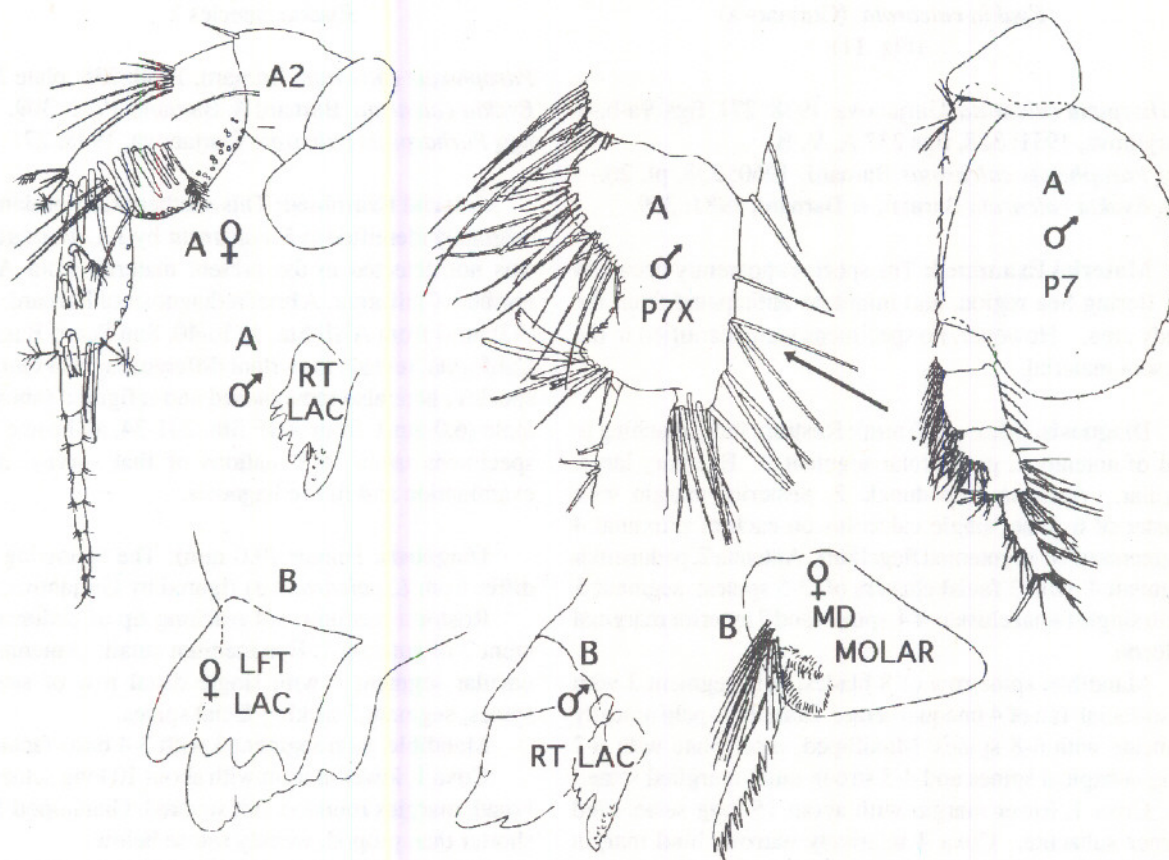


FIG. 10. SPECIES OF *EYAKIA* (AFTER BARNARD & BARNARD, 1981)

A. - *Eyakia* species 1. Male (12.0 mm); Female (15.0 mm) Adakh I.

B. - *Eyakia robusta* (Holmes)?

Eyakia species 1
(Fig. 10A)

Eyakia robusta J. L. and C. M. Barnard, 1981: 305, fig. 1.

Material Examined: No specimens of this species were identified in the present extensive phoxocephalid material from the Aleutians to Washington and Oregon states.

The description and figures of Barnard and Barnard apply to a large male "m" (12.0 mm) and a larger female "y" (15.0 mm), from an "Albatross" Stn. off. Adakh Island, Alaska, July, 1893, surface. Other material from Alaska is listed by Barnard & Barnard (loc. cit.).

Diagnosis: Female (15.0 mm): Antenna 2, peduncular segment 2 with 2 weakly separated facial clusters of heavy spines; segment 5 with a single median facial cluster of 3 spines and a terminal cluster of 2 spines.

Male (12.0 mm): The copulatory apparatus of peraeopod 7 differs markedly from that rediagnosed for *E. robusta* (p. 87). Anterior margin of segment 5 deeply and broadly, lower corner subacute, with a fan of stout spines, the largest of which is much thicker than the others, is slightly curved upwards, and has a striated apex. The excavated margin is

lined with very short blunt spines and some longish setae. The basis of peraeopod 7 is much deeper and less broad, and the 8-10 teeth of the posterior margin are low and barely discernible.

Distribution: Barnard & Barnard (loc. cit.) list material from the inner Aleutian Islands, through Prince William Sound and SE Alaska to Friday Harbor, Washington. Their material from Bahia de San Quintin, Baja California, Mexico, is referable to *E. robusta* (Holmes).

Taxonomic commentary: This large species from southern Bering Sea and SE Alaska differs from *E. robusta* (Holmes) by the characters given in the key and by the following. Especially significant in the male is the deeply concave anterior marginal notch, and short copulatory spine of segment 5 of peraeopod 7, and in the female, the short peduncular segment 2 of antenna 1.

The Barnardian description (1981, p. 305, fig. 1) of female "w" (9.12 mm) from VELERO IV Stations, southern California, applies reasonably closely to Holme's TYPE 8.0 mm female of *E. robusta* from off Pt. Loma, CA. (Fig. 10B, above).

Eyakia calcarata (Gurjanova)
(Fig. 11)

Parharpinia calcarata Gurjanova, 1938: 271, figs. 9a-b.—
Gurjanova, 1951: 388, figs 237 A, V, B.
non *Paraphoxus calcaratus* Barnard, 1960: 238, pl. 26.—
non *Eyakia calcarata* Barnard & Barnard, 1981: 309.

Material Examined: The species apparently occurs in the Bering Sea region, and might be anticipated from the study area. However, no specimens were identified in the present material.

Diagnosis. (Male, 12.0 mm): Rostrum long, reaching to end of antenna 1, peduncular segment 2. Eye very large, regular. Antenna 1, peduncle 2, posterior margin with cluster of 6 setae; single calceolus on each of proximal 4 segments of 10-segmented flagellum. Antenna 2, peduncular segment 4 with 3 facial clusters of 3-5 spines; segment 5 with single facial cluster of 4 spines, and 7 anterior marginal calceoli.

Mandible, spine row of 8 blades; palp segment 3 with baso-facial fan of 4 unequal setae. Maxilla 1, palp apically truncate with 6-8 spines. Maxilliped, outer plate with 6-7 long subapical spines and 4-5 strong outer marginal setae.

Coxa 1, lower margin with about 15 long setae, hind corner subacute. Coxa 4 relatively narrow, hind margin steeply oblique. Gnathopod propods subsimilar. Gnathopod 1, carpus as long as propod, lower margin with 3-4 clusters of setae.

Peraeopods 3 & 4, hind margin of segment 6 apparently lacking distal spines; dactyl stout, half length of segment 6. Peraeopod 6, basis little broadened, hind margin straight; segments 4-6 slender, margins not strongly setose or spinose; dactyl large. Peraeopod 7, basis broadly rounded, hind margin nearly smooth; copulatory apparatus of segment 5 very distinctive: anterior margin deeply and narrowly notched, with one large, apically striated, upward-curving spine inserted at lower corner.

Pleon plate 3, hind corner subtruncate; facial row of about 18 medium setae, and lower margin with 6 setae. Uropod 2, outer margin with 9 tall slender spines; outer ramus with 5 close-set spines, inner ramus bare. Uropod 3, peduncular fan of 10 stout spines; outer ramus slightly the shorter, all margins densely plumose-setose.

Telson lobes slender, length 3X width, apex with 2 very unequal slender spines.

Distributional Ecology: Taken near Vladivostok, Russian coast of the Sea of Japan, in depths to 75 m.

Taxonomic Commentary: The female of this species from the type locality has yet to be described. The species is quite distinct from that from southern California identified under this name by Barnard (loc. cit.).

Eyakia species 2

Paraphoxus calcarata Barnard, 1960: 238, plate 26.
Eyakia calcarata Barnard & Barnard, 1981: 309.
non *Parharpinia calcarata* Gurjanova, 1938: 271.

Material Examined: This southern Californian species, originally identified as *E. calcarata* by J. L. Barnard (1960), was not detected in the present material from Alaska to northern California. A brief rediagnosis of Barnard's female (9.0 mm) from AHF Stn. 1156-40, San Pedro Basin, off S. California, reveals important differences from Gurjanova's species, here also rediagnosed and refigured (above). A male (6.0 mm) from AHF Stn. 201-34, and some 16 other specimens taken at 8 stations of that survey, await re-examination and full rediagnosis.

Diagnosis. Female (9.0 mm): The following features differ from *E. calcarata*, as figured by Gurjanova, 1951:

Rostrum medium, not reaching tip of peduncular segment 2 of antenna 1. Eye medium small. Antenna 2, peduncular segment 4 with single distal row of stout facial spines; segment 5 lacking facial spines.

Mandible, palp segment 3 with 3-4 baso-facial setae.

Coxa 1, lower margin with about 10 long setae. Coxa 4 broad, margins rounded, not squared. Gnathopod 1, carpus shorter than propod, weakly setose below.

Peraeopods 3 & 4, distal segment slender, segment 6 lacking posterior marginal spines. Peraeopod 5, segments 4 & 5 little expanded. Peraeopod 7, basis, hind margin with about 4 small but distinct teeth.

Pleon plate 3, hind corner rounded, not squared. Uropod 3, inner ramus very short, < 1/3 outer ramus; terminal segment relatively large, 1/4 length of proximal segment.

Telson lobes very long relative to width ($L > 3X$ width).

Male (7.5 mm): Eyes large, subrotund, nearly meeting mid-dorsally. Antenna 2, peduncular segment 4 with distal facial row of 4-5 spines; segment 5 with 2 slender facial spines. Copulatory apparatus of peraeopod 7 not described. Uropod 3, rami less setose than in *E. calcarata*.

Taxonomic and Distributional Commentary: Barnard's material was taken on the east side of San Pedro Basin and the western slope of Santa Monica Basin at depths to 380 m.

Material from the Galapagos Islands (Barnadian female "n" (6.41 mm), and other material from off Gorgona island, Columbia, is probably referable to different, yet undescribed, species.

FIG. 11. *Eyakia calcarata* (Gurjanova, 1938).
MALE (12.0 mm) HOLOTYPE
(SEE PAGE 91 - OPPOSITE)

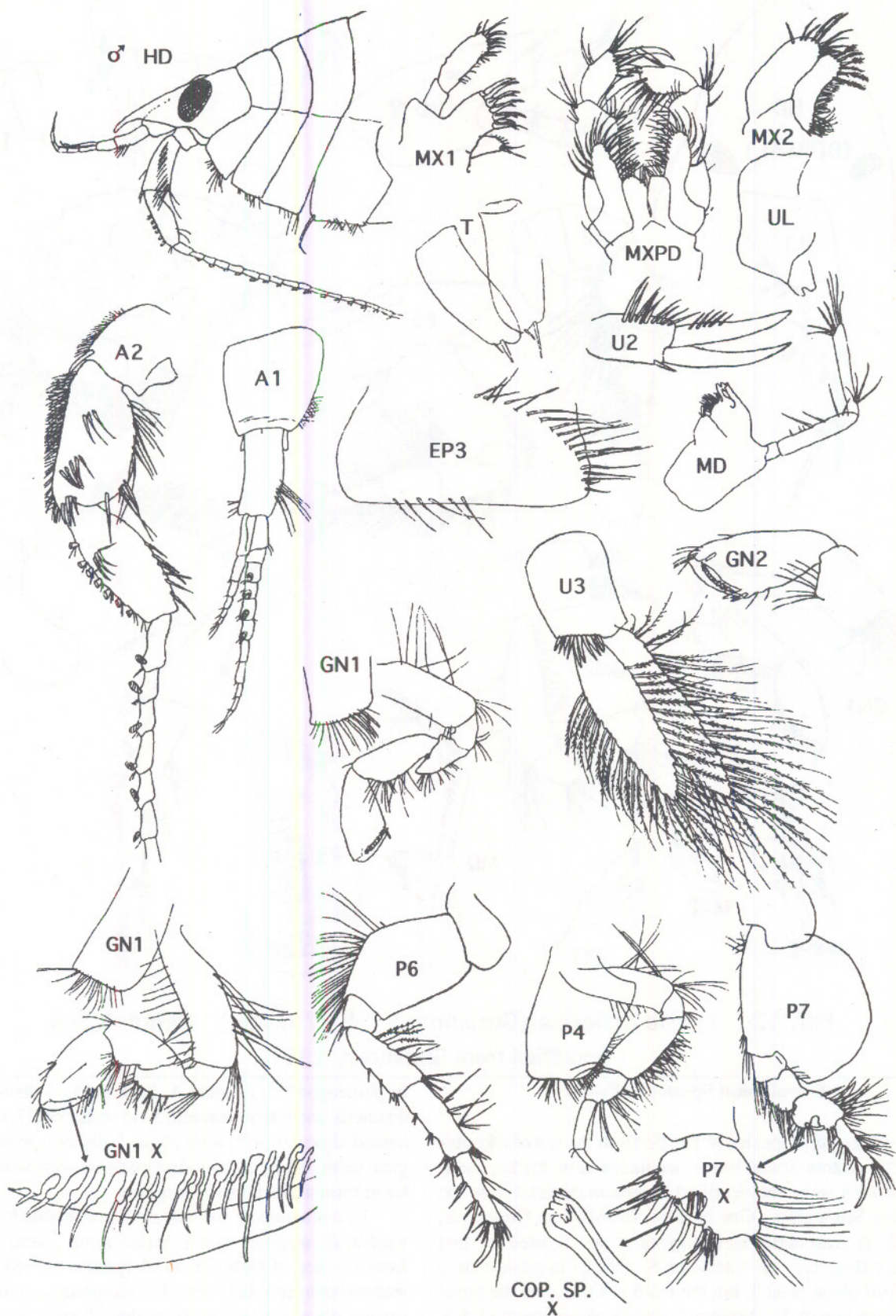


FIG. 11. *Eyakia calcarata* (Gurjanova). ♂ (12.0 mm) Japan Sea.
(modified from Gurjanova, 1951).

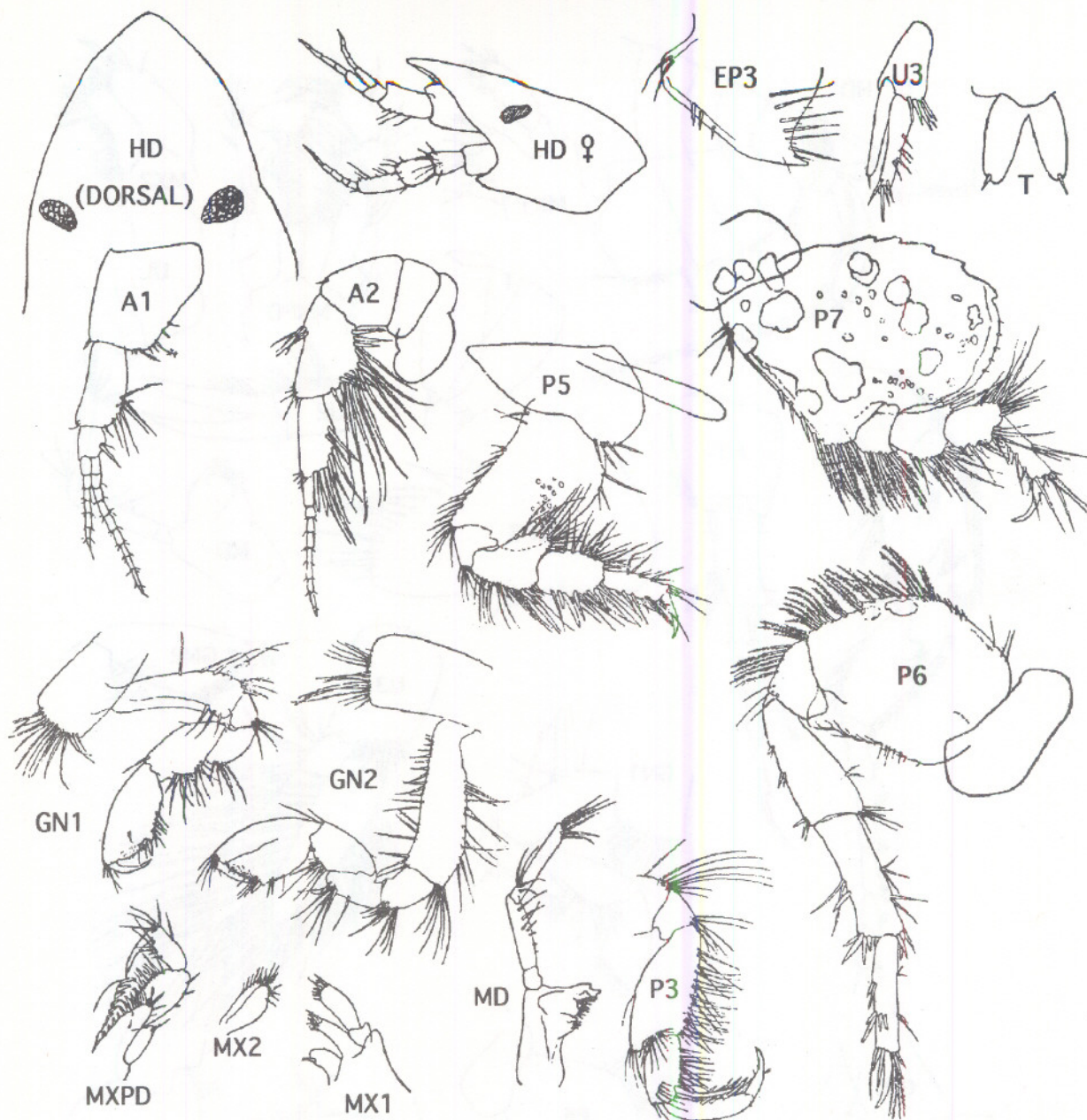


FIG. 12. *Eyakia ochotica* (Gurjanova). ♀ (7.0 mm). Okhotsk Sea
(modified from Gurjanova, 1951).

Extralimital Species of *Eyakia*

Three other species of *Eyakia* from the sea of Okhotsk and far eastern Soviet waters are included in the key here (p. 86) but were not identified in present material from the Bering Sea region. One of these, *E. ochotica* Gurjanova, 1953, is reasonably well diagnosed and figured by that author (Fig. 12). It resembles *E. robusta* in possessing a toothed pleon plate 3, but the tooth is small, and the facial setae are few (6-7). Antenna 1, peduncular segments 4 & 5, apparently lack clusters of facial spines, but the hind margins are richly spinose and setose. Pereopods 3 & 4 are robust, with strong distal spine, and posteriorly spinose segment 6.

In pereopod 5, segment 4 is broadened distally and is distinctly wider than segment 5. In pereopod 7, the basis is extended posteriorly, with about 5 distinct posterior marginal teeth. The gnathopod propods are somewhat dissimilar in form although similar in size.

Two other small species, clearly referable to the genus *Eyakia*, *E. uncigera* and *E. subuncigera*, were described from the Sea of Okhotsk by Gurjanova (1938), but have seldom been recorded since. The morphology of these small species departs markedly from that of previous species in having weakly or sparsely armed coxae, pereopods, and uropods, and the basis of pereopod 7 is produced posteriorly as a large tooth or process.

Brolginae Barnard & Drummond

Brolginae Barnard & Drummond, 1978: 87-89; Barnard & Karaman, 1991: 595 (Key).

Type Genus: *Brolgus* Barnard & Drummond, 1978: 96.

Genera: (N. American Pacific):

Paraphoxus G. O. Sars, 1895: 148 (part).

Eobrolgus J. L. Barnard, 1979: 376.—J. L. Barnard and C. M. Barnard, 1981: 295.

Paramesophoxus Gurjanova, 1977: 76.

Diagnosis: Body regular. Rostrum well developed, hood-like, lacking lateral incisions. Antenna 1, segment 2 short, little longer than 3, segments of accessory flagellum and flagellum transversely separated; in male, basal segments calceolate or calynophorate (conjoint, with strong posterior cluster of long aesthetascs). Antenna 2, peduncular segments 4 & 5 short to medium but not strongly expanded or heavily spinose behind; in male, segments 3 & 4 with anterior marginal brush setae, segment 5 with 2 anterior submarginal calceoli, flagellum elongate, often calceolate on alternate segments.

Mandibular molar non-tritulative, bearing 3 or fewer tightly clumped apical spines; left lacinia 5-6 dentate; right lacinia small or vestigial; blades strong; palp slender, segment 3 usually with "A"-setae. Maxilla 1, outer plate with 9-11 apical spines, inner plate with 1 apical seta. Maxilla 2, inner plate small. Maxilliped, inner and outer plates short, outer with stout inner marginal raptorial spines, palp ordinary, inner margins lacking stout spines.

Coxae 1-4 broad, deep, lower margin setose posteriorly. Gnathopods strongly subchelate, unequal; Gnathopod 1, propod more slender, but carpus longer than in gnathopod 2.

Peraeopods 3 & 4, segments 4 & 5 stout, 6 slender, not spatulate, weakly armed; dactyls normal. Peraeopod 5, basis and segments 4 & 5 expanded behind. Peraeopod 5, segments 4, 5, & 6, slender or little expanded, usually elongate. Peraeopod 7, basis normally expanded posteriorly, lower margin exceeded fully by segment 5, in which (male) the postero-distal copulating spines are weak or lacking.

Pleon plate 3 subquadrate, hind corner not produced, lower margin lacking long marginal and submarginal setae. Pleopod peduncles slightly broadened. Uropods 1 & 2 short, peduncle with disto-lateral and usually medio-lateral spine(s); rami subequal, each with single apical spine. Uropod 3, inner ramus variable, strong, larger and more strongly plumose-setose in male than in female.

Telson lobes narrow, each with single subapical spine.

Coxal gills large, plate-like on peraeopods 2-6, medium small, sac-like on peraeopod 7. Brood plates, small, narrow.

Taxonomic Remarks: The genus *Mandibulophoxus* is here transferred from Brolginae (in which it was initially placed by Barnard and Drummond (*loc. cit.*), to the Pont-

harpiiniinae with which it agrees in nearly all principal character states (see p. 75). Members of family Brolginae are closely related to the Phoxocephalinae in general form of rostrum, antennae, and uropods, but retain a 2-segmented palp in maxilla 1. This feature may be considered convergent, but other differences in the peraeopods and uropod 3 justify retention of the two groups as separate subfamily entities. The genus *Paramesophoxus* Gurjanova is hereby transferred from Phoxocephalinae to Eobrolginae because of eobrolgin characteristics of the male copulatory apparatus

Eobrolgus J. L. Barnard

Eobrolgus Barnard, 1979: 376.—Barnard & Barnard, 1981: 295.—Barnard & Karaman, 1991: 607.

Type species. *Paraphoxus spinosus* Holmes, 1905.

Species: (North Pacific region): *Eobrolgus chumashi* J. L. & C. M. Barnard, 1981: 301, Fig. 1e; *E. pontarpioides* (Gurjanova, 1953): 286, Fig. 15.

Diagnosis (per Barnard & Karaman, 1991: 607). Eyes pigmented (both sexes). Antenna 1, segments of flagellum and accessory flagellum not strongly oblique. Antenna 2, peduncular segment 1 not ensiform; segment 4 with 2+ strong facial rows of thick spines; in male, peduncular segment 5 with 1 antero-distal calceolus (Barnard 1960, pl. 29-2), flagellar segments alternately calceolate.

Mouthparts regular. Mandibular molar medium, with 4+ marginal spines; blade spines prominent; left incisor 5-dentate? Maxilla 1, inner plate with 3-4 apical setae. Maxilliped, palp segment 2 lacking outer marginal setae.

Gnathopods medium, somewhat dissimilar, segment 5 of gnathopod 2 much shorter and more cryptic than in gnathopod 1.

Peraeopods 3 & 4 not stoutly developed, segment 6 with short postero-distal armature; dactyls medium. Peraeopod 6 much longer than peraeopod 5, segments 4 & 5 not (or little) broadened. Peraeopod 7 (male) segment 5 posteriorly with paired slender simple copulating spines; segment 6 with distal comb fringe.

Pleon plate 3, hind margin with 1 to several long setae. Uropod 3 (female) inaequiramous, outer ramus weakly setose, terminal segment with paired apical setae.

Telson regular, lobes smooth above.

Taxonomic Remarks: *Eobrolgus* is distinguished from *Paraphoxus* by the multi-spinose mandibular molar, segment 4 of antenna 2 with 2+ rows of thick facial spines; maxilla 1, inner plate with 3+ apical setae; and pleon plate 3 with posterior marginal seta(e). In *Foxiphalus*, segment 1 of antenna 1 is typically weakly ensiform, and segment 6 of peraeopod 7 (male), is armed with a distal fringe.

This taxon appears to link the Eobrolginae to the Metharpiiniinae through its close resemblance to *Foxiphalus*.

KEY TO SPECIES OF *EOBROLGUS* (after Barnard & Barnard 1981)

1. Telson lobes, each with 2 apical spines *E. pontarpinioides* (Gurjanova) (p. 96)
 ---Telson lobes each with one apical spine 2.
2. Pleon plate 3, lower margin lacking setae or spines; outer plate of maxilla 1 with 9 spines
 *E. spinosus* (Holmes)
 --- Pleon plate 3, lower margin with 1- 3 setae ; maxilla 1, outer plate with 11 apical spines
 *E. chumashi* Barnard & Barnard (p. 94)

Eobrolgus chumashi Barnard & Barnard (Fig. 13)

Paraphoxus spinosus J.L. Barnard, 1960: 243 pl. 29 (partim).
Eobrolgus chumashi J. L. and C. M. Barnard, 1981: 301 (part).—J.L. and C.M. Barnard, 1982a: 370 (partim).

Material Examined: ALASKA: Amchitka I., Banjo Point, C.E.O'Clair: 8 specimens; S.E. Alaska, June-July, 1961, ELB Stns. A19(1); A30 (25); A33(30), July, 1980, ELB Stn. S13B1 (2).
 BRITISH COLUMBIA: Queen Charlotte Islands, ELB Stns. E25 (1); H4a(1); H8(a & b) (15 specimens including 1 female ov (3.5 mm); H9 (15 specimens including 1 male (3.5 mm); H14 (10).
 North Central coast: ELB Stns, 1964: H13 (3); H39 (1). ELB Stns., 1964: H10 (several, including female (3.5 mm) variant.
 Vancouver Island: ELB Stns, 1955: F9 (1); ELB Stns. 1970: P710 (14); P711 (1); P715 (c 100); P716 (c 200); P717 (c. 200); P721 (15). ELB Stns., 1976: B5 (1); B11b (6); ELB Stns., 1977: B5a (50 specimens, including 1 male (3.5 mm)); B6a (2); B6b (30); B7a (1); B7b (20); B11b (2). Shoal Bay, J. F. L. Hart, 1935: 1 specimen. Discovery Passage, R. Rafi coll., Aug. 21-23, 1984: about 90 males and females, including 1 female ov (3.5 mm), slide mount, and 1 male (3.0 mm), + slide mount CMN Cat. No. NMCC1992-1115.
 WASHINGTON and OREGON: ELB Stns. 1966: W31 (6); W50 (several, including 1 female ov. (4.5 mm); W63 (1). Strait of Juan de Fuca, C. P. Staude colls., 1976: 80 specimens in 9 lots, including 1 female ov. (3.0 mm).

Diagnosis: Female ov. (4.5 mm): Rostrum medium, nearly reaching end of antennal peduncle segment 2, apex obtuse. Eye relative large, oval. Antenna 1, peduncle 2 with strong postero-distal setal cluster; flagellum 6-segmented; accessory flagellum 5-segmented. Antenna 2, peduncular segment 4 with 2 major facial clusters of strong spines, anterior margin with cluster of single spine and seta; segment 5 with single distal spine, and medial facial cluster of stout spines; flagellum 8-segmented.

Mandible, apex flat but not tritulative, bearing 1 stout spine and 3-4 movable spines, spine row with 8 heavy pectinate blades; left lacinia irregularly 5-dentate, right lacinia bifid; palp segment 5 with 2 medium baso-facial setae. Maxilla 1, inner plate with 2 strong apical setae; outer plate with 11 apical spines; palp 2-segmented, apex subconical, 5-

6 spinose. Maxilliped, outer plate short, apically with 3-4 curved pectinate spines; inner plate with 1 peg spine; palp, dactyl heavy, basally exceeded slightly by segment 3.

Coxa 1 not expanded distally, lower hind corner with 6-8 long setae. Coxa 4 very deep, excavation shallow, hind margin steeply straight. Gnathopods 1 & 2, propods subsimilar; gnathopod 2, carpus with free hind margin and cluster of setae.

Peraeopods 3 & 4 stout, segment 5, distal spine shorter than segment 6, dactyls short. Peraeopod 5, basis broad, hind margin nearly straight; segments 5 & 6 expanded, width greater than depth, margins spinose and setose; dactyl short. Peraeopod 6, basis broadening distally, hind margin straight; segments 4 & 5 little broadened, weakly setose. Peraeopod 7, basis produced postero-ventrally, hind margin rounded, with 4-5 small but distinct teeth, segments 4 & 5 little broadened

Pleon 3, hind corner squarish, hind margin with 3 longish setae, lower margin with 2 slender spines. Uropod 1 peduncle nearly bare, with single baso-facial seta and inner distal displaced spine, rami subequal, each with single marginal spines. Uropod 2, peduncle with 4- 5 stout outer marginal spines. Uropod 3 stout, inner ramus very short, terminal segment of outer ramus short.

Telson lobes, length about 2X width, each with single short apical spine.

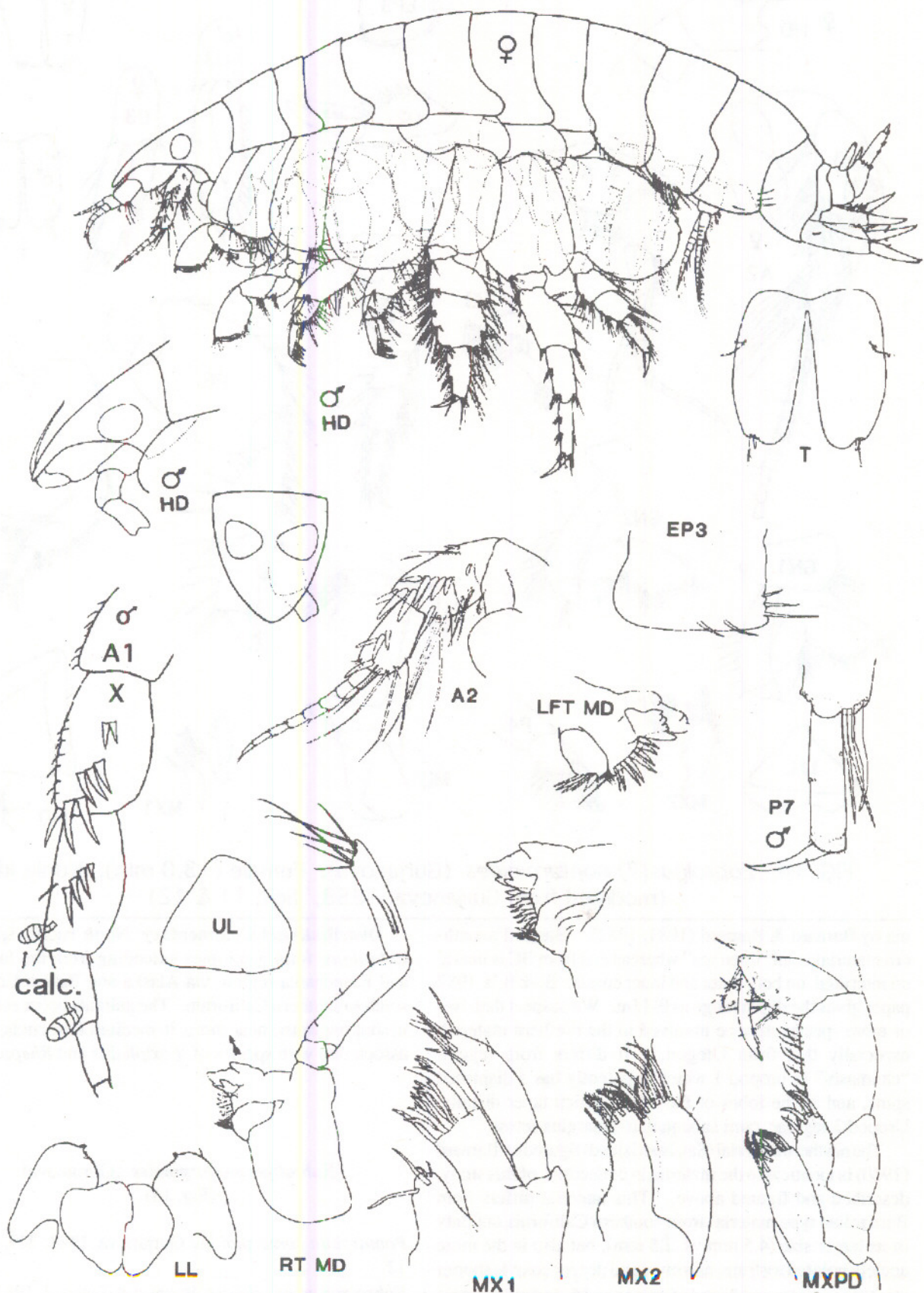
Coxal gills large, plate-like on peraeopods 2-5, smaller on peraeopod 6, small and sac-like on peraeopod 7.

Male (3.0 mm): Eyes large, about twice size of female's. Antenna 1, proximal 3-4 segments of flagellum calceolate. Antenna 2, peduncular segment 3 & 4 with typical anterior marginal brush setae; segment 5 with single antero-distal calceolus; flagellum elongate, alternate segments calceolate.

Peraeopod 7, segment 5 postero-distally with 2 slender pectinate, and one heavy bent, copulatory spines; segment 6 straight, with distal marginal pectinations.

Taxonomic Commentary: This material is identical with that figured from the San Juan Islands, Wash., by Barnard 1960, plate 29. It is distinct from that described and figured as "*P. spinosus*" by Barnard, 1960, pls 30, 31, but reasonably close to "*E. chumashi*" described from Califor-

FIG.13. *Eobrolgus chumasi* Barnard & Barnard.
 FEMALE ov. (3.5 mm); MALE (3.0 mm). Discovery Passage, B.C. (SEE PAGE 95 - OPPOSITE)



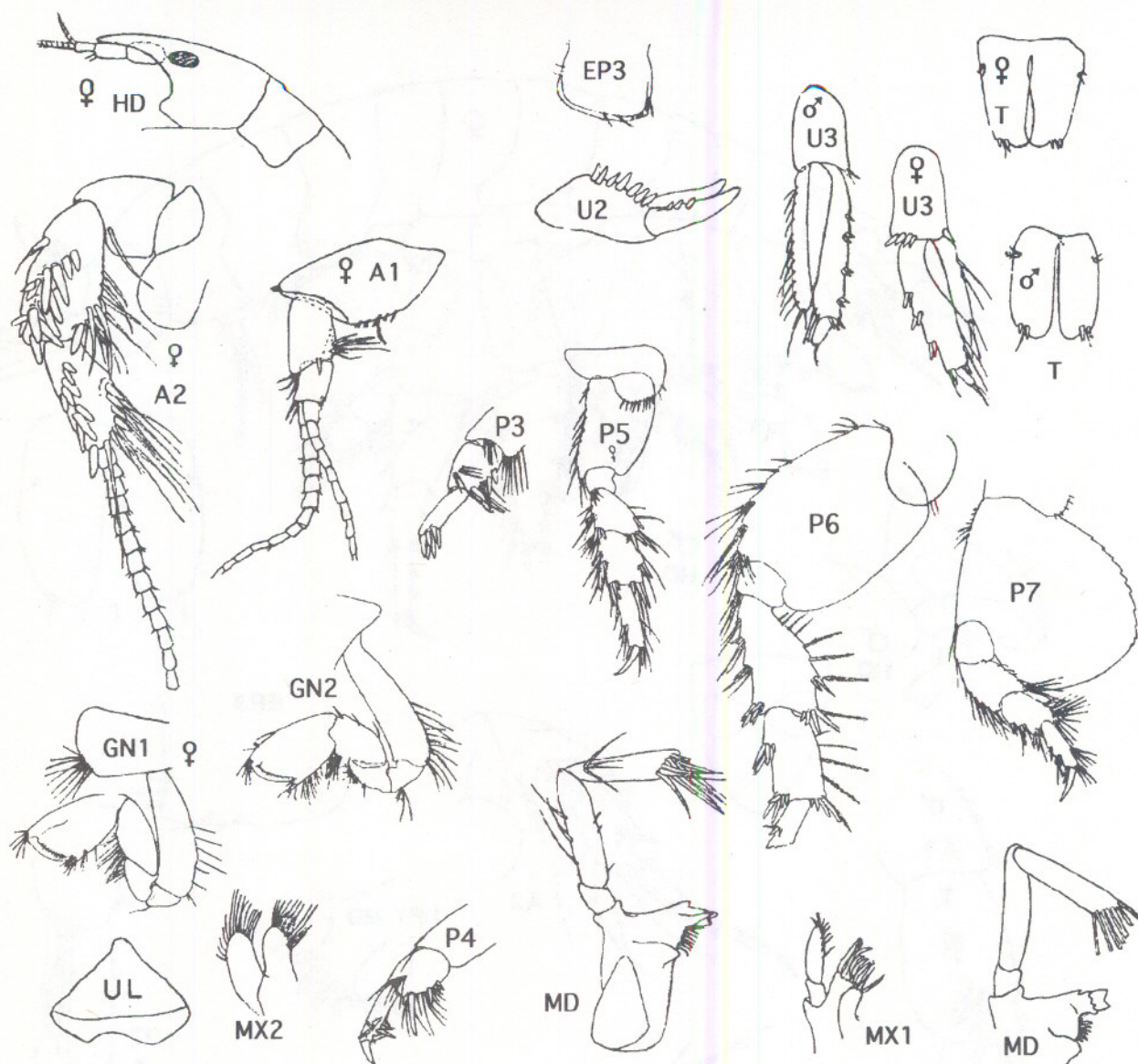


FIG. 14. *Eobrolgus(?) pontarpioides* (Gurjanova). Female (13.0 mm). Kurile Ids. (modified from Gurjanova, 1953, figs. 11 & 12)

nia by Barnard & Barnard (1981, 1982). Barnard's southern material is all "open sea" whereas that from BC is nearly all intertidal, on both outer and inner coasts. B. & B.'s 1982 paper gives the depth range as 0-11 m. We suspect that two or more species may be involved in the northern material, especially that from Oregon. It differs from regular "chumashi" in uropod 1 which apparently has a displaced spine, and in the lobes of the telson which taper distally. Uropod 3 regular, rami subequal and margins setose.

The northern material (San Juan Island) figured by Barnard (1960) is identical to the material in collections of this study, described and figured above. This material differs from Barnardian type material from southern California not only in its larger size (4.5 mm vs. 2.5 mm), but also in the more acutely pointed rostrum, narrower and deeper coxa 4; shorter stouter segments and dactyl of peraeopod 6, and more setose anterior margins of peraeopod 7, segments 4 & 5.

Distributional Commentary: North Pacific species of *Eobrolgus* form a complex extending from the Japan Sea and Kamchatka region, via Alaska and British Columbia, south to southern California. The animals occur essentially in shallow water, near shore, in medium fine sands, often in association with species of *Foxiphalus* and *Rhepoxynius*.

Eobrolgus pontarpioides (Gurjanova)
(Fig. 14)

Pontarpinia pontarpioides Gurjanova, 1953: 229, figs. 11, 12.

Eobrolgus pontarpioides Barnard & Barnard, 1981: 304, + Key—Barnard & Karaman, 1991: 607.

Taxonomic Commentary: This large northwestern Pacific form (female to 13 mm) differs from typical southern Californian material of *E. chumasi* in several character states. The flagellum and accessory flagellum of antenna 1 are long (both 10+ segmented); antenna 2, peduncular segment 5 with 2 clusters of very stout facial spines and 4 strong posterior marginal spines. The mandibular palp has a cluster of 4 baso-facial setae. In gnathopod 2, carpus short, hind margin nearly cryptic. In peraeopod 5, segments 4 & 5 stoutly spinose; in peraeopod 6, segments 4 & 5 somewhat broadened and setose behind; and in peraeopod 7, hind margin with about 10 weak teeth. Pleon plate 3, hind margin with 1 posterior marginal seta. Uropod 2, outer ramus with 3 marginal spines. Uropod 3, inner ramus > 1/2 outer ramus. Telson lobes apically with 3 short spines. Resolution of the taxonomic significance of such differences requires a geographically more extensive series of specimens than available to the authors.

Distribution. Sea of Okhotsk: Kurile Islands, Ekatera I.

Paraphoxus G. O. Sars

Paraphoxus G. O. Sars, 1895: 148.—Gurjanova, 1951: 364.—Barnard, 1969: 420 (partim).—Barnard & Drummond, 1976: 524.—Barnard & Drummond, 1978: 144.—Barnard & Karaman, 1991: 625.

non *Paraphoxus* Bousfield, 1973: 124. (= *Eobrolgus*).

Type Species. *Phoxus oculatus* Sars 1879, monotypy. (E. North Atlantic).

Species (North Pacific regional): *Paraphoxus beringiensis*, new species; *P. similis* new species (Bering Sea); *P. simplex* Gurjanova 1938 [272] (Japan Sea); *P. tomiokaensis* Hirayama, 1987 [48], (Japan Inland Sea); *P. gracilis*, new species (B.C. fiords); *P. rugosus* new species (Bering sea); *P. communis*, new species (and variations) (B.C.); *P. pacificus*, new species; *Paraphoxus* sp. 1 (= *P. oculatus* Barnard, 1960 [240] (S. California); and *Paraphoxus* sp. 2 (= *P. oculatus* Hirayama, 1992 [118] (Hong Kong).

Diagnosis. (see Barnard & Karaman, 1991: 625): Ros-trum fully hooded, not laterally constricted, apex bluntly rounded. Eyes pigmented (both sexes), much larger in male. Antenna 1, flagellum short, 6-9 segmented, proximal 4-5 segments calceolate in male; accessory flagellum 4-5 segmented. Antenna 2, segment 1 not ensiform; peduncle 4 with distal marginal fan of 6-12 stout fossorial spines; segment 5 (male) with 2 antero-distal marginal calceoi; flagellum of female short, 5-8 segmented, of male, elongate (15-30+ segmented), alternate segments calceolate.

Mandibular molar, apex with 2-4 spines; blade row with 5-10 spines, left lacinia 4-dentate; incisor tricusate; palp segment 3 with 0-4 basofacial "A" setae, and 6-8 distal "C"

setae. Maxilla 1, inner plate with 2 apical setae; outer plate basically with 9 or 11 (occ. 10) apical spines; palp 2-segmented (occ. segments fused), spines and/or setae apical. Maxilla 2, plates weakly apically setose, outer plate distinctly the larger. Maxilliped, outer plate narrow, inner margin with 5-9 distally longer curved masticatory spines; inner plate short, apex with plumose setae; palp, dactyl slender, curved.

Coxae 1-4, postero-distal margins variously lined with simple setae; coxa 1 with 5-12 setae. Gnathopods 1 & 2, propods smoothly subchelate, subsimilar in size and form or, gnathopod 1, propod smaller and more slender, carpus longer than in gnathopod 2; basis of gnathopod 1 variously with longish posterior marginal setae.

Peraeopods 3 & 4, postero-distal fossorial spine and/or adjacent spine of segment 5 stout, often equal to (or longer than) segment 6; dactyl variable, often nearly equal in length to segment 6. Peraeopod 5, coxa with deep rounded hind lobe; basis variably broad, hind margin straight or convex; segment 4 slightly expanded and spinose; segment 6 with 1-3 anterior marginal spines and 0-3 posterior marginal setae. Peraeopod 6 elongate, segments 5-6 slender, with variable numbers of marginal spines and setae. Peraeopod 7, basis variously extended posteriorly, hind margin weakly toothed. segment 5 lacking posterior copulatory spine(s).

Pleon plate 3, hind corner variously produced, broadly rounded, lower margin bare, often straight. Pleopods normal, not sexually dimorphic. Uropods 1-2, rami and peduncles subequal in length. Uropod 1, peduncle with baso-facial cluster of 2-5 setae, but lacking distal displaced spine; rami with 0-3 marginal spines. Uropod 2, peduncle, outer margin usually strongly spinose, rami with 0-2 marginal spines. Uropod 3 (female), outer ramus variably much shorter than inner, terminal segment large (1/4-1/2 proximal segment), apex with 2 unequal simple setae; in male, rami large, subequal, margins plumose-setose. Telson longer than wide, lobes longer in male, slightly diverging, apices slightly oblique, each with 1-3 spines, paired penicillate setae about mid-point. Coxal gills large, plate-like on peraeopods 2-6, small, sac-like on peraeopod 7. Brood plates regular.

Distribution: Mainly amphi-North Pacific, in subarctic and boreal coastal shelf waters; two species (including the type species) are known from eastern North Atlantic and Mediterranean coastal regions.

Taxonomic Commentary: North Pacific species apparently form two principal sub-groups, viz: a relatively primitive *oculatus* subgroup and a more advanced *pacificus* subgroup (see key to species (p.98), and also phenogram). The *oculatus* subgroup is characterized by: gnathopods subsimilar in size and form; peraeopod 3 & 4, dactyls long; maxilla 1, outer plate with 11 apical spines; mandible with 8-10 relatively slender blades; uropods 1 & 2, some rami with 2-3 marginal spines; and telson lobes with 2-3 apical spines.

KEY TO NORTH PACIFIC SPECIES OF *PARAPHOXUS* (FEMALES & IMM.ATURES)

1. Telson lobes each with 1 apical spine 2.
—Telson lobes each with 2(3) apical spines 3.
2. Peraeopod 5, basis rounded behind; peraeopods 3 & 4, segment 5 with postero-distal subequal pair of stout spines *P. simplex* Gurj. (p. 113)
—Peraeopod 5, basis hind margin straight; peraeopods 3 & 4, segment 5 with single stout postero-distal spine *P. beringiensis* n. sp. (p. 114)
3. Coxa 1, lower margin with 12-14 close-set long setae; maxilla 1, outer plate with 9 apical spines . . 4.
—Coxa 1, lower margin with 6-9 widely spaced long setae; maxilla 1, outer plate with 11 apical spines 7.
4. Pleon plate 3 produced behind; peraeopods 3 & 4, segment 5 with single stout postero-distal spine 5.
—Pleon plate 3 not produced behind; peraeopods 3 & 4, segment 5 with subequal pair of stout distal spines 6.
5. Uropod 1, basal peduncular fan with 3 spines; mandibular palp segment 3 lacking "A" seta; antenna 2, peduncular segment 4 with distal fan of 6-8 stout spines *P. similis* (p. 110)
—Uropod 1, basal peduncular fan with 4-5 short spines; mandibular palp with 1 "A" seta; antenna 2, peduncular segment 4 with distal fan of 10+ stout spines *P. oculatus* Sars (p. 99)
6. Peraeopod 5, segment 5, anterior spines long; mandibular palp segment 3 lacking "A" seta; peraeopods 3 & 4, segment 5 postero-distal paired spines extend beyond segment 6 . . *P. rugosus* (p. 111)
—Peraeopod 5, segment 5, anterior spines short; mandibular palp 3 with single "A" seta; peraeopods 3 & 4, segment 5 postero-distal paired spines not extending beyond segment 6 . *P. pacificus* (p. 107)
7. Peraeopods 3 & 4, segment 5, distal spines long (beyond segment 6); accessory flagellum 4-5 segmented; mandibular palp segment 3 lacking "A" seta 8.
—Peraeopods 3 & 4, segment 5, distal spines short, (not beyond segment 6); accessory flagellum 4-segmented; mandibular palp, segment 3 with single "A" seta 9.
8. Pleon plate 3, hind corner narrowly rounded; gnathopod 1, propod slender, length 2X depth; peraeopod 6, segment 6, anterior margin with setae only *P. gracilis*, n. sp. (p. 107)
—Pleon plate 3, hind corner broadly rounded; gnathopod 1, propod robust, length 1.5 X depth; peraeopod 6, segment 6, anterior margin with paired spines and setae *P. communis*, n. sp. (p. 102)
9. Pleon plate 3 produced behind; peraeopods 3 & 4, segment 5 with 2 subequal postero-distal stout spines; uropod 1, peduncular basal fan with 2 spines, outer ramus with 2 marginal spines; mandibular palp segment 3 with 1 baso-facial seta *Paraphoxus* sp. 1. (p. 99)
—Pleon plate 3 not produced; peraeopods 3 & 4, segment 5 with single postero-distal stout spine; uropod 1, peduncular basal fan of 4 spines, outer ramus with single marginal spine; mandibular palp with 3 baso-facial setae 10.
10. Antenna 1, flagellum 7-8 segmented; propod (GN1), palm vertical . *P. tomiokaensis* Hiray. (p. 104)
—Antenna 1, flagellum 6-segmented; propod, (GN1), palm oblique *Paraphoxus* sp. 2 (p. 102)

The *pacificus* subgroup generally has, in combination: gnathopods somewhat dissimilar in size and/or form; peraeopods 3 & 4, dactyls short; maxilla 1, outer plates with 9 apical spines; mandible with 4-7 short thick blades; uropods

1 & 2, rami usually with 0-1 marginal spines; and telson lobes each with 1-2 apical spines. The distinctions may yet merit formal subgeneric or generic recognition.

Paraphoxus oculatus (G. O. Sars)

(Fig. 15)

Phoxus oculatus Sars, 1879: 441.149, pl. 51.

Paraphoxus oculatus (Sars, 1895: 149, pl. 51.—Gurjanova, 1951: 364.—Karaman, 1972: 91, figs. 25-28.—Barnard & Karaman, 1991: 625.

non Paraphoxus oculatus Barnard, 1960: 240, pls. 27, 28.—Bousfield, 1973: 125, pl. 34.1.—Lincoln, 1979: 368, fig. 174.—Hirayama, 1987: 42.—1992: 118, figs. 1-4.

Diagnosis (after Sars, 1895): Female ov. (5.0 mm): Eyes small, rounded. Antenna 1, flagellum 7-segmented, accessory flagellum 4-segmented. Antenna 2, peduncular segment 4 with distal fan of 10-12 stout spines; flagellum 8-segmented.

Mandibular molar with 2 apical spines, blade row of 7-8 spines; palp segments 2 & 3 subequal, segment 3 with 1 (2?) facial "A" seta, segment 2 with strong distal, and weak middle, marginal seta. Maxilla 1, outer plate with 11 apical spines; palp 2-segmented (1-segmented in Sars' description, but his illustration shows marginal separation lines). Maxilliped, outer plate with 9-10 stout inner marginal masticatory spines.

Coxal plate 1 with about 14 tightly grouped lower marginal simple setae; coxa 4 broader than deep. Gnathopods 1 & 2, propods stout, closely subequal in size, segment 5 of pereopod 2 distinctly shorter than in pereopod 1, with 3-4 posterior setae.

Pereopods 3 & 4, segment 5 postero-distally with unequal pair of medium spines not exceeding apex of segment 6 that has 4 inner marginal spines; dactyls subequal in length to segment 6. Pereopod 5, basis relatively broad, hind margin slightly convex; segment 6 with 2 anterior marginal spines and one posterior marginal seta. Pereopod 6 elongate, segments 5 & 6 moderately spinose with total of about 10 clusters of spines and long setae. Pereopod 7, hind margin of basis with 12-14 weak teeth, lower margin evenly convex.

Pleon 3 posteriorly produced, hind corner rounded. Uropod 1, baso-facial fan of 4-5 short slender spines; outer ramus equal to peduncle, with 2-3 slender marginal spines, inner ramus with 2 marginal spines. Uropod 2, rami longer than peduncle, with 1-2 marginal spines; peduncle with 4-5 long stout outer marginal spines. Uropod 3, peduncle with weak distal fan of spines; inner ramus slender, > 1/2 proximal segment of outer ramus, terminal segment slender, elongate. Telson lobes each with pair of apical spines and setae.

Male (4.0 mm): Conforming with the generic diagnosis.

Distributional Remarks: North Atlantic region: coastal Norway to northwestern Russia, and south to the Mediterranean (as *P. maculatus*?) in depths of 12-200 m. Not known authentically from the North Pacific region.

Taxonomic Remarks: The material of "*Paraphoxus oculatus*" from S. California (Barnard, 1960 loc cit) is distinct from Sars species, and may be a distinct new species (see p. 99). The small (4.0 mm) species figured as *P. oculatus* Sars by Lincoln, 1979 (loc. cit.), is very distinct from Sars' species in the heavily setose pereopod 6, weakly setose coxae 1-4, and single spine of the telson lobes, among other features. It may prove to be a species of *Brolgus* or *Eobrolgus*. Hirayama's well illustrated material of "*Paraphoxus oculatus*" from Hong Kong (loc. cit) appears to be a distinct new species, very closely related to *P. tomioakaensis* from Japan (see p. 102). Except for the small body size of his material, the description and figures of Karaman (loc. cit) agree well with those of Sars (1895) and confirm the form and number of the mandibular blades, and segmentation and armature of maxilla 1, as diagnosed above. Karaman has also formally submerged *P. maculatus* Chvereux, 1989, in this species, but further analysis of all previous N. Atlantic material would seem desirable to confirm this decision.

Paraphoxus sp. 1 (Barnard, 1960)

(Fig. 16)

Paraphoxus oculatus Barnard, 1960: 240, pls. 28, 29 (part).—Austin, 1985: 598?—Staudé, 1987: 365?

Material Examined: The diagnosis is based on the description and figures of J. L. Barnard (loc. cit). No material was re-examined.

Diagnosis: This small species differs from Sars' nominate species *oculatus* in the following features:

Female 4.75 mm (stns. 2293-53, above): Rostrum relatively short, not reaching antenna 1 peduncular segment 3. Eyes small, almond-shaped. Antenna 1, flagellum 6-segmented, accessory flagellum 4-segmented; Antenna 2, peduncle 4 with distal facial fan of 9 spines; flagellum 7-segmented.

Mandible, molar with 2-3 apical spines, and 6-7 stout blades; palp segment 3 with 1 baso-facial seta. Maxilla 1, outer plate with 11 apical spines; palp distinctly 2-segmented.

Coxal plates weakly setose below; coxa 1 with 7-8 distal marginal setae; coxa 4 wide, strongly rounded behind. Gnathopods, propods subsimilar.

Pereopods 3 & 4, postero-distal spine heavy, exceeding apex of segment 6; dactyls slender, length about equal to segment 6. Pereopod 5, basis not very broad, hind margin gently convex; segment 6 with 2 anterior marginal spines and

FIG. 15. *Paraphoxus oculatus* (Sars, 1879)

FEMALE (5.0 mm); MALE (4.0 mm). Norway.

(SEE PAGE 100)

FIG. 16. *Paraphoxus* species 1. (Barnard, 1960).

FEMALE (4.75 mm); MALE (4.5 mm). S. California
(SEE PAGE 101)

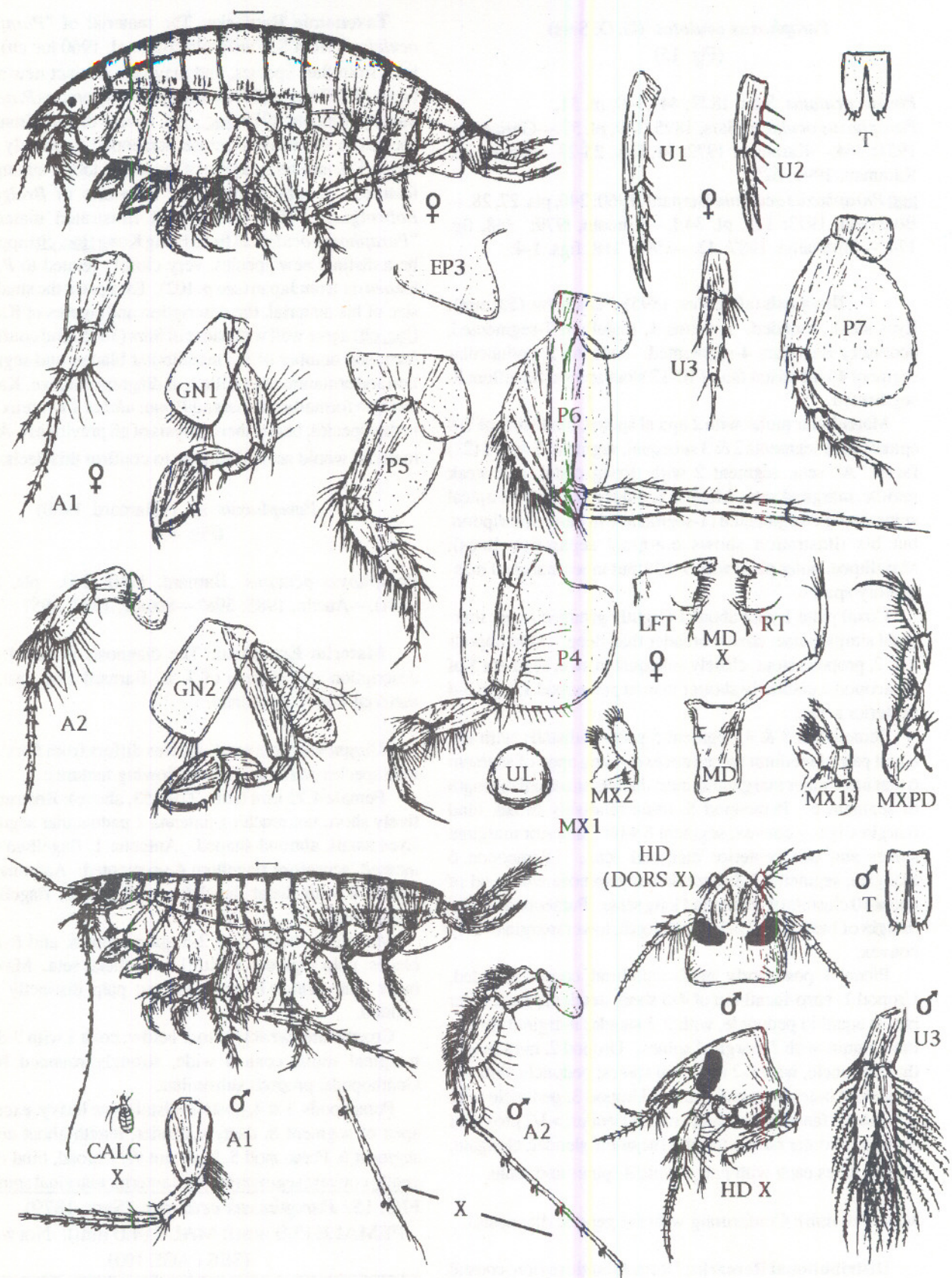


FIG. 15. *Paraphoxus oculatus* Sars ♀ ov. (5.0 mm) ♂ 4.0 mm) Norway (20-100m)
(modified from Sars, 1895)

1 posterior marginal seta. Peraeopod 6 not short, segments 5 & 6 not heavily spinose or setose. Peraeopod 7, basis broad, hind margin with 5-7 small teeth.

Pleon plate 3 produced at hind corner, sharply rounded, lower margin straight. Uropod 1, peduncle with 2 basofacial setae. Uropods 1 & 2, outer rami with 2-3 marginal spines. Uropod 3, peduncle with distal fan of 5-6 spines; outer ramus 2X inner, terminal segment about 1/2 length of proximal segment.

Male penult (4.5 mm): Eyes medium large, subreniform. Uropod 3, inner ramus equal to basal segment of outer ramus, margins bare.

Adult male not described.

Distribution: Known authentically only from southern California: J. L. Barnard stations in San Pedro and Santa Catalina Basins, and in Santa Monica Bay, 30 - 100 m. Not identified in the present study material.

Taxonomic-Distributional Commentary: The species is similar in most respects to the northeastern Atlantic type species, *P. oculatus* Sars, but differs in characters of the key, especially in antennal setation and in setation of the coxal plates. It clusters more closely with the North American Pacific coastal *P. gracilis*, and *P. communis* than with counterpart species from the Asiatic Pacific coast. (p.144). Material from Galapagos Islands, listed under this name by Barnard (loc. cit.), is probably also distinct. The material of Staude (loc. cit.) was not re-examined but it, and the records of Austin (loc. cit.), may be referable, at least in part, to *P. communis* (p. 104).

Paraphoxus species 2.
(Fig. 17)

Paraphoxus oculatus Hirayama, 1992: 118, figs. 1-5.—Hirayama, 1987: 48, fig. 253?

Diagnosis: The detailed figures of Hirayama (1992) are utilized here to develop additional diagnostic character states for the key (p. 98) and phenetic analysis (p. 143).

Female ov. (3.2, 3.3 mm). Rostrum short, not attaining segment 3 of antenna 1. Eye small to medium, about 20-faceted. Antenna 1, flagellum 6-segmented; accessory flagellum 5-segmented. Antenna 2, peduncular segment 4 with distal facial fan of 8-9 fossorial spines; flagellum of 6-7 segments.

Mandibular molar with 3 thick apical spines; spine row with 5-6 medium blades; palp segment 3 with 3 basofacial setae. Maxilla 1, outer plate with 11 apical spines, palp 2-segmented. Maxilliped, inner plate distally with 4 large plumose spines.

Coxal plate 1, with 7 lower marginal setae. Coxae 2 & 3, setae posterior only. Coxa 4 deeper than broad, hind margin strongly convex. Gnathopods subsimilar. Gnathopod 1, basis with 3 long posterior marginal setae.

Peraeopods 3 & 4, distal spine of segment 5 heavy, subequal in length to segment 6; dactyl medium long, about 3/4 length of segment 6. Peraeopod 5, basis medium broad, hind margin nearly straight; segment 6 with 2 anterior marginal clusters of spines and 2 posterior marginal stiff setae. Peraeopod 6, segments slender, well armed, marginal spine clusters totalling 13, anterior margin of segment 6 with 2 spine clusters. Peraeopod 7, basis relatively little broadened, hind margin with 8 weak teeth.

Pleon plate 3 not produced, broadly rounded behind, with 1 setule. Uropods 1 & 2, rami with 1-2 marginal spines. Uropod 1, peduncle with 3-4 basofacial setae. Uropod 3, peduncle with distal fan of 4-5 longish spines; inner ramus very short (< 1/2 outer ramus); terminal segment of outer ramus short, with 2 long apical setae.

Telson, lobes medium, each with 1-2 apical spines.

Distribution: Known from the Hong Kong region of the South China Sea and possibly from the coastal waters of Japan.

Taxonomic Commentary: This species is very close to *P. tomiokaensis* Hirayama from coastal waters of Japan. It differs, however, by characters of the key (above) and by the much more strongly spinose and setose segments 4-6 of peraeopod 6. Material previously recorded from Japan (Tomioka Bay) as *P. oculatus* (Hirayama, 1987) may also be this species.

Paraphoxus communis, new species
(Fig. 18)

Paraphoxus oculatus Austin, 1985: 598?—Staude, 1987: 380?

Material Examined:

BRITISH COLUMBIA: Southern Vancouver island: Berkeley Sound, North of Diana Island, ELB Stn. B26, 25-35 m. July 8, 1976. - 1 female Br. III (3.4 mm), with slide mount (fig'd) HOLOTYPE CMN Cat. No. NMCC1992-1123; 1 male penult (3.5 mm) with slide mount (fig'd) ALLOTYPE. CMN Cat. No. NMCC1992-1124; 3 males, penult., with slide mounts, 2 females, with slide mounts, PARATYPES. CMN Cat. No. NMCC1992-1125. plus 51 other females and 36 other male subadults. Off Edward King Island, ELB Stn B28, bed-rock and boulders, *Phyllospadix* community, LW - HW levels, July 10, 1976 - 4 females, 1 male. Off McCauley Point, Victoria, G. W. O'Connell coll., 39 m., Aug. 26, 1976 - 1 female (ov).

Diagnosis: Female (3.4 mm): Rostrum short, reaching little beyond peduncle 1 of antenna 1. Eye small, almond-shaped. Antenna 1, flagellum 6-segmented; accessory flagellum 5-segmented. Antenna 2, peduncular segment 4 with distal facial fan of 8-10 slender spines; flagellum 6-segmented.

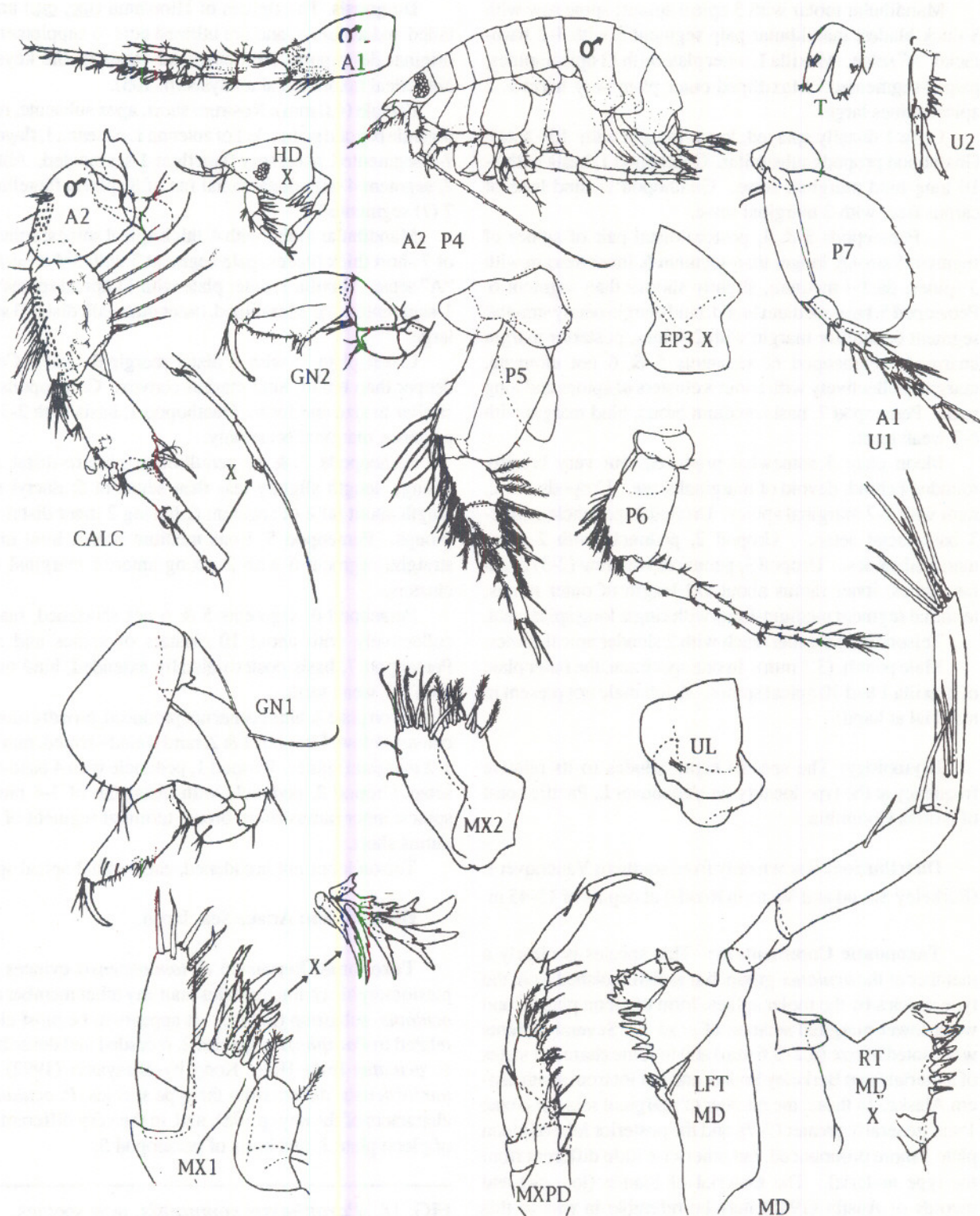


FIG. 17. *Paraphoxus* species 2. Male (3.3 mm); Female (3.3 mm). Hong Kong. (modified from Hirayama, 1992)

Mandibular molar with 3 apical spines; spine row with 8 thick blades; mandibular palp segment 3 with 1-2 baso-facial "A" setae. Maxilla 1, outer plate with 11 apical spines; palp 2-segmented. Maxilliped outer plate very narrow, 2 apical spines large.

Coxa 1 distally splayed, lower margin with 10+ setae. Gnathopod propods subsimilar. Gnathopod 1, basis with 8-10 long hind marginal setae. Gnathopod 2, hind lobe of carpus free, with 2 marginal setae.

Peraeopods 3 & 4, postero-distal pair of spines of segment 5 strong, longer than segment 6, inner margin with 3 spines; dactyl medium, slightly shorter than segment 6. Peraeopod 5, basis medium broad, hind margin nearly straight; segment 6, anterior margin with 2 spines, posterior margin unarmed. Peraeopod 6, segments 5 & 6 not elongate, margins collectively with about 8 clusters of spines and long setae. Peraeopod 7, basis medium broad, hind margin with 6-7 weak teeth.

Pleon plate 3 somewhat produced, but very broadly rounded behind, devoid of marginal setae. Uropods 1 & 2, rami with 1-2 marginal spines. Uropod 1, peduncle with 2-3 baso-facial setae. Uropod 2, peduncle with 2 outer marginal spines. Uropod 3, peduncle with few (2-3) distal fan spines; inner ramus about 1/2 length of outer ramus; terminal segment medium-long, with single long apical seta.

Telson lobes slender, each with 2 slender apical spines.

Male penult. (3.5 mm). In one specimen, the outer plate of maxilla 1 had 10 apical spines. Adult male not present in material at hand.

Etymology: The species name alludes to its relative frequency at the type locality on Vancouver I., Pacific coast of British Columbia.

Distribution: Known only from southern Vancouver I. (Berkeley Sound and Victoria Roads) at depths of 15-45 m.

Taxonomic Commentary: This species is clearly a member of the *oculatus* group, but is distinguished from the type species by the molar spines, form of pleon plate 3, and weak lower marginal setation of coxa 1. Several variants were noted in size (3.2-3.6 mm) and in some character states of material from Berkeley Sound, and in 1 lot from southeastern Alaska. In these, the number of marginal setae of coxae 1 was generally greater (7-9), and the posterior lobe of pleon plate 3 more pronounced, but otherwise little different from the type material. The material of Staude (loc. cit.) and records of Austin (1985) may be referable in part to this species.

Paraphoxus tomiokaensis Hirayama

(Fig. 19)

Paraphoxus tomiokaensis Hirayama, 1987: 42, figs. 254-256.

Diagnosis. The figures of Hirayama (loc. cit.) are detailed and accurate, and are utilized here to supplement the original description with character states of the keys and numerical taxonomical analysis (p. 105).

Female (4.0 mm): Rostrum short, apex subacute, reaching little beyond peduncle 1 of antenna 1. Antenna 1, flagellum 7-8 segmented, accessory flagellum 4-segmented. Antenna 2, segment 4 with distal facial fan of 8 spines, flagellum 6-7 (?) segmented.

Mandibular molar with 4 thick apical spines; spine row of 7 short thick blades; palp segment 3 with 3-4 baso-facial "A" setae. Maxilla 1, outer plate with 11 apical spines; palp 1-segmented (?). Maxilliped, outer plate tall, distal 3 spines large.

Coxal plate 1, with 8 distal marginal setae. Coxa 4 deeper than broad, hind margin convex. Gnathopods subsimilar in size and form. Gnathopod 1, basis with 2-3 long posterior marginal setae only.

Peraeopods 3 & 4, penultimate postero-distal spine strong, length slightly less than segment 6; dactyl stout, length about 80% of segment 6, having 2 inner distal spine groups. Peraeopod 5, basis medium broad, hind margin straight; segment 6 with 2 strong anterior marginal spine clusters.

Peraeopod 6, segments 5 & 6 not shortened, margins collectively with about 10 clusters of spines and setae. Peraeopod 7, basis postero-distally extended, hind margin with 6-7 weak teeth.

Pleon plate 3, hind corner not produced, broadly rounded, convex below. Uropods 1 & 2, rami weakly armed, rami with 1-2 marginal spines. Uropod 1, peduncle with 4 baso-facial setae. Uropod 3, peduncle with distal fan of 3-4 medium spines; inner ramus short, broad, terminal segment of outer ramus short.

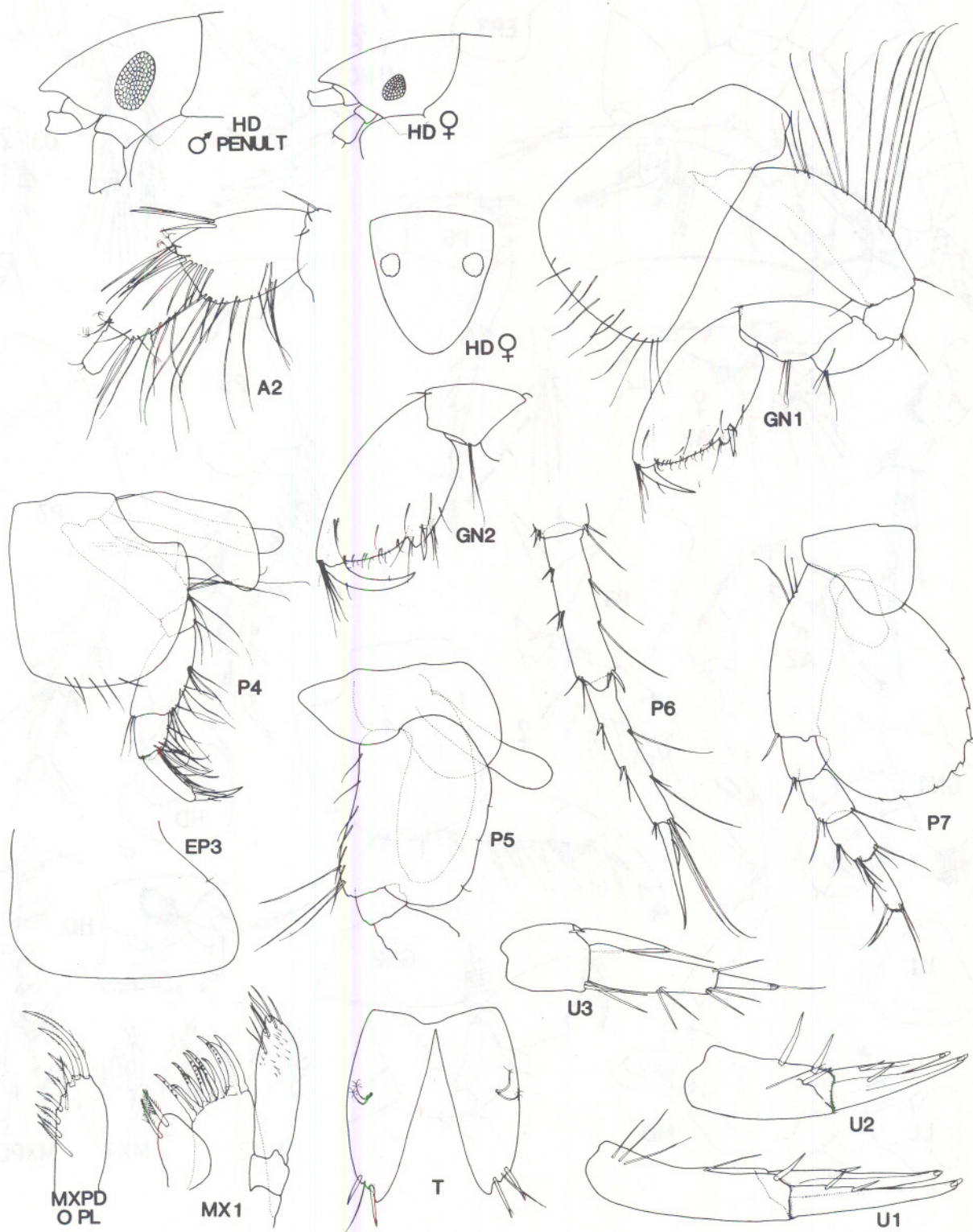
Telson lobes not broadened, each with 2 apical spines.

Distribution: Ariake Sea, Japan.

Taxonomic Remarks: *P. tomiokaensis* evinces more plesiomorphic character states than any other member of the *oculatus* subgroup (p. 99). It appears to be most closely related to *Paraphoxus* species 2, recorded and described as *P. oculatus* from Hong Kong by Hirayama (1992). *P. tomiokaensis* differs from the type species, *P. oculatus*, in characters of the key (p. 98), and in the very different form of pleon plate 3, and basis of peraeopod 5.

FIG. 18. *Paraphoxus communis*, new species.
FEMALE ov (3.4 mm) HOLOTYPE; MALE (3.5 mm)
Berkeley Sound, B. C. (SEE PAGE 105-OPPOSITE)

FIG. 19. *Paraphoxus tomakiensis* Hirayama, 1987.
FEMALE (4.0 mm); MALE (3.75 mm). JAPAN.
(SEE PAGE 106)



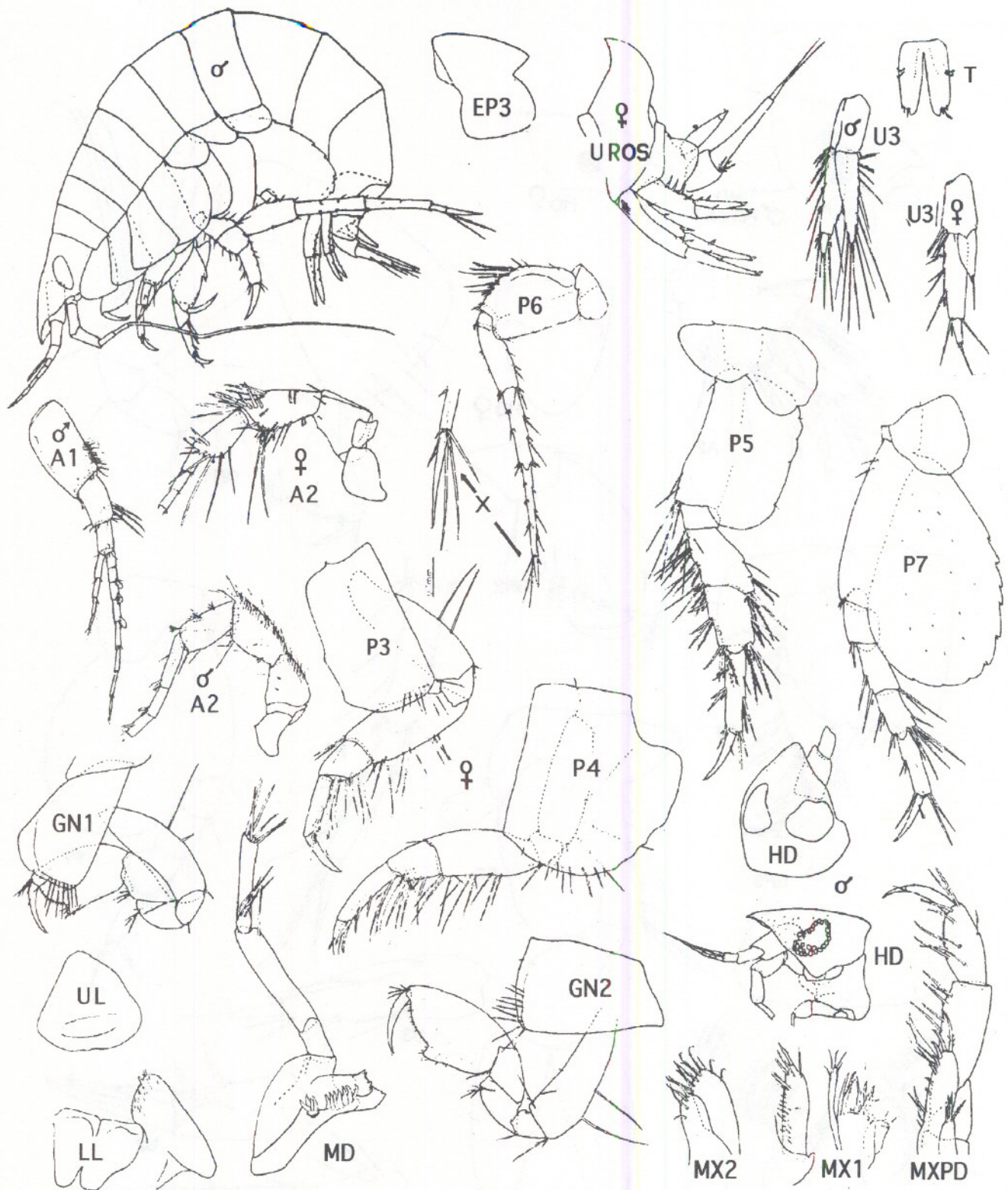


FIG.19. *Paraphoxus tomiokaensis* Hirayama. Male (3.5 mm). Female (4.0 mm). Japan. (after Hirayama, 1987)

Paraphoxus gracilis, new species
(Fig. 20)

Material Examined:

BRITISH COLUMBIA: Southeastern Mainland coast: Queen Charlotte Channel, off Passage Island, ELB Sta. P8, 130 m., Nov. 3, 1977. - 1 mature male; Sta. P7, 250 m. - 1 mature male; Strait of Georgia, off Passage I., 160 m - 1 female (ov.). Mouth of Burrard Inlet, ELB Stn. P4, 225 m, Nov. 2, 1977 - 1 female ov. (3.0 mm) with slide mount (fig'd), HOLOTYPE. CMN Cat. No. NMCC1992-1126; 1 mature male (3.75 mm), with slide mount (fig'd) ALLOTYPE. CMN Cat. No. NMCC1992-1127. Indian Arm, ELB Stn. E5, 60 m., Nov. 4, 1977 - 1 male, mature.

Diagnosis Female ov. (3.0 mm): Rostrum medium, apex subacute, reaching nearly to peduncular segment 3 of antenna 1. Eye very small, round. Antenna 1, flagellum with 6-7 segments, accessory flagellum with 4 segments. Antenna 2, peduncular segment 4 with distal facial fan of 9-10 fossorial spines; flagellum 6-segmented.

Mandibular molar with 3 apical spines; spine row with 6-8 blades; palp segment 3 with 1-2(?) baso-facial "A" setae. Maxilla 1, outer plate with 11 apical spines; palp distinctly 2-segmented, apex appearing subacute. Maxilliped, outer plate, apex with 2 long pectinate spines.

Coxa 1 with 8-9 distal marginal setae. Coxa 4 broad, hind margin steeply and strongly convex. Gnathopod 1, propod smaller and more slender than in gnathopod 2; basis with 8-10 long posterior marginal setae. Gnathopod 2, carpus short, hind margin not cryptic, with 3-4 posterior setae.

Peraeopods 3 & 4, segment 6, postero-distal pair of spines slender, subequal, length about equal to segment 6; dactyls medium, length about 80% segment 6. Peraeopod 5, basis broad, hind margin nearly straight; segment 6 with 1-2 anterior marginal spines and 2 posterior marginal setae. Peraeopod 6 slender, segments 5 & 6 well armed, margins collectively with about 12 clusters of short spines and longish setae. Peraeopod 7, basis medium broad, hind lobe not deep, hind margin with 7-8 small teeth.

Pleon plate 3, hind corner produced, rounded, lower margin straight, hind margin with a few short setae. Uropods 1 & 2, rami with 1-2 slender spines. Uropod 1, peduncle with 3 baso-facial setae. Uropod 2, peduncle outer margin with 3 long spines. Uropod 3, peduncle with distal fan of 5 long spines; outer ramus about twice length of inner ramus; terminal segment slender, about half length of proximal segment, apex with 1 long and 1 short seta.

Telson lobes relatively broad, acute, each apically with 2 long slender spines.

Male (3.75 mm). Eyes large, vertically subovate. Antenna 1, proximal 3-4 flagellar segments calceolate. Antenna 2, peduncular segment 4 with weak antero-distal fan of spines; peduncular segment 5 with 2 antero-distal calceoli; flagellum medium, 18-segmented, proximal 3, and alternate

distal segments calceolate. Peraeopod 7, segment 5 with 2 slender postero-distal copulatory spines; segment 6, distal margin gently convex, minutely pectinate.

Etymology: From the Latin *gracilis*, alluding to the relatively slender spines and appendages of this species.

Distribution: Known only from the environs of Burrard Inlet and Howe Sound, in deep muddy bottoms (60 - 160 m).

Taxonomic Commentary: Basically a member of the *oculatus* group but with character states (e.g. of gnathopods, and broadened telson lobes) transitional to the more advanced *pacificus* group. In mature males, the flagellum of antenna 2 (male) is relatively short (< 20 segments).

Paraphoxus pacificus, new species
(Fig. 21)

Material Examined. A total of 11 females and 6 subadult males, as follows:

S. E. ALASKA: ELB Sta. A103, Unakivik Inlet, near mouth of Siwash bay, 20-40 m, mud and stones, July 5, 1961 - female (3.75 mm), male (3.0 mm), slide mounts, 2 subadult males (3.0 mm), 2 females, 2 male subadults.

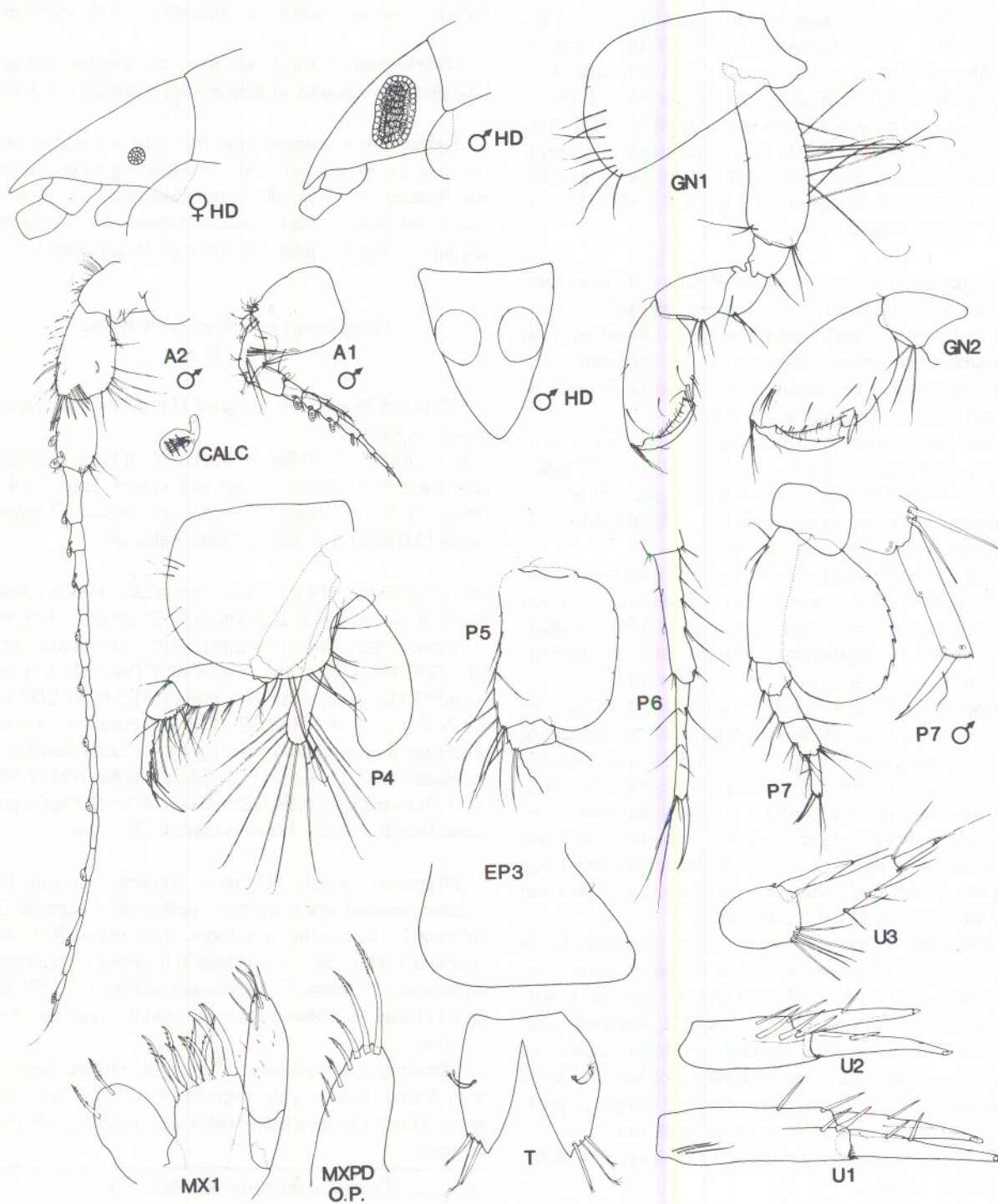
BRITISH COLUMBIA: Vancouver Island: Berkley Sound, North of Diana Island, ELB Stn. B26, 25-25 m., July 8, 1976 - 1 female, interbrood (3.6 mm), with slide mount (fig'd), HOLOTYPE, CMN Cat. No. NMCC1992-1119; 1 male subadult (3.0 mm) with slide mount (fig'd) ALLOTYPE, CMN Cat. No. NMCC1992-1120; 1 female ov. (4.0 mm) with slide mount (mouth parts fig'd), + 6 other females and 1 subadult male, PARATYPES, CMN Cat. No. NMCC1992-1121. Edward King I., ELB Stn. B28, LW level, *Phyllospadix* zone, July 10, 1976 - 1 male subadult (3.75 mm).

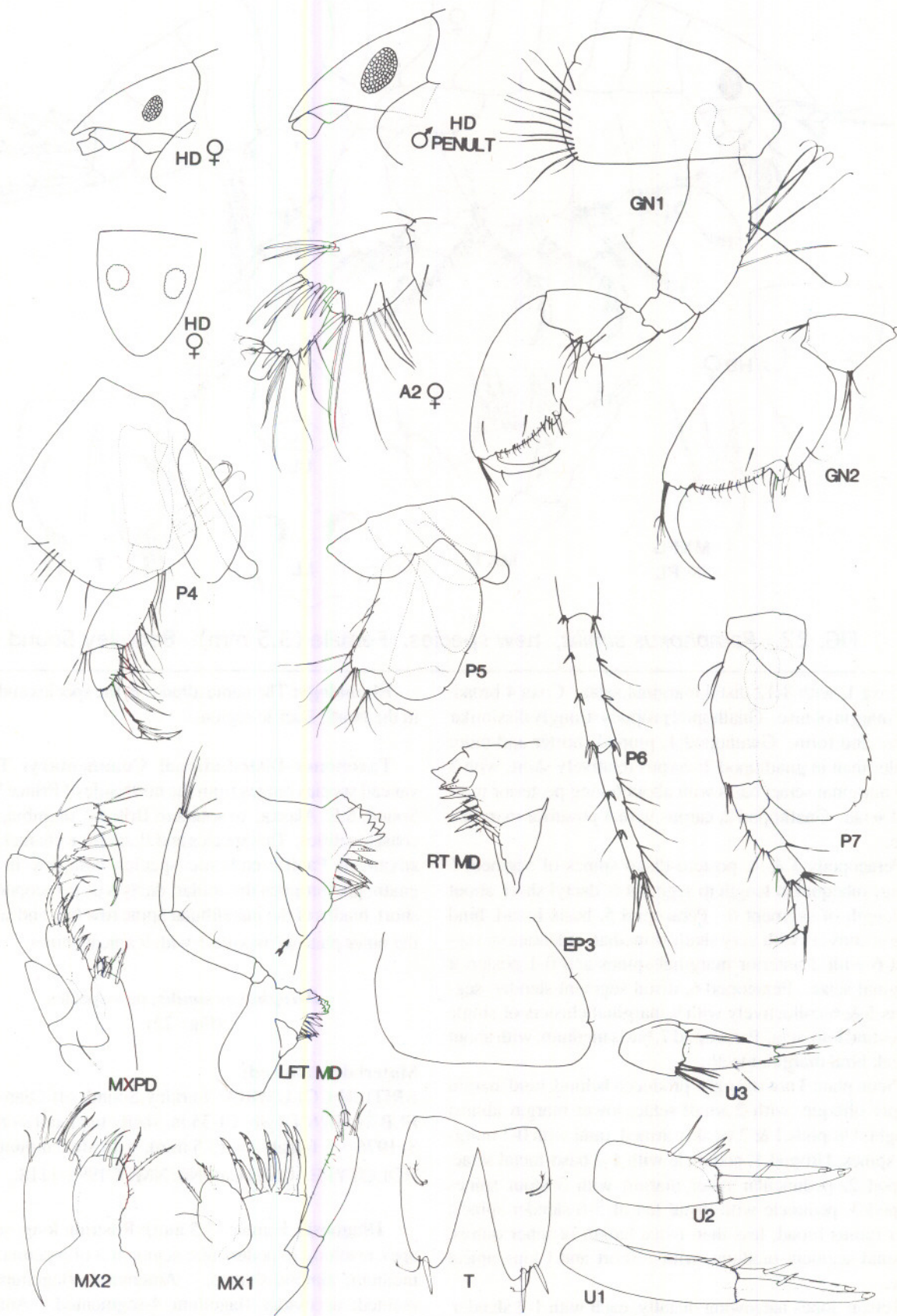
Diagnosis Female (3.6 mm): Rostrum medium long, bluntly rounded apex reaching peduncular segment 3 of antenna 1. Eyes relatively large, oval, about 40-faceted. Antenna 1, flagellum 6-segmented; accessory flagellum 4-segmented. Antenna 2, peduncular segment 4 with distal facial cluster of about 8 fossorial spines; flagellum 6-segmented.

Mandibular molar with 2-3 elongate spines; spine row with 5 stout blades; palp segment 3 with 1-2 baso-facial setae. Maxilla 1, outer plate with 9 apical spines; palp 2-segmented.

FIG. 20. *Paraphoxus gracilis*, new species.
FEMALE ov (3.0 mm) HOLOTYPE; MALE (3.7 mm) ALLOTYPE. (SEE PAGE 108).

FIG. 21. *Paraphoxus pacificus*, new species.
FEMALE ov (3.6 mm) HOLOTYPE; MALE (3.0 mm) (SEE PAGE 109).





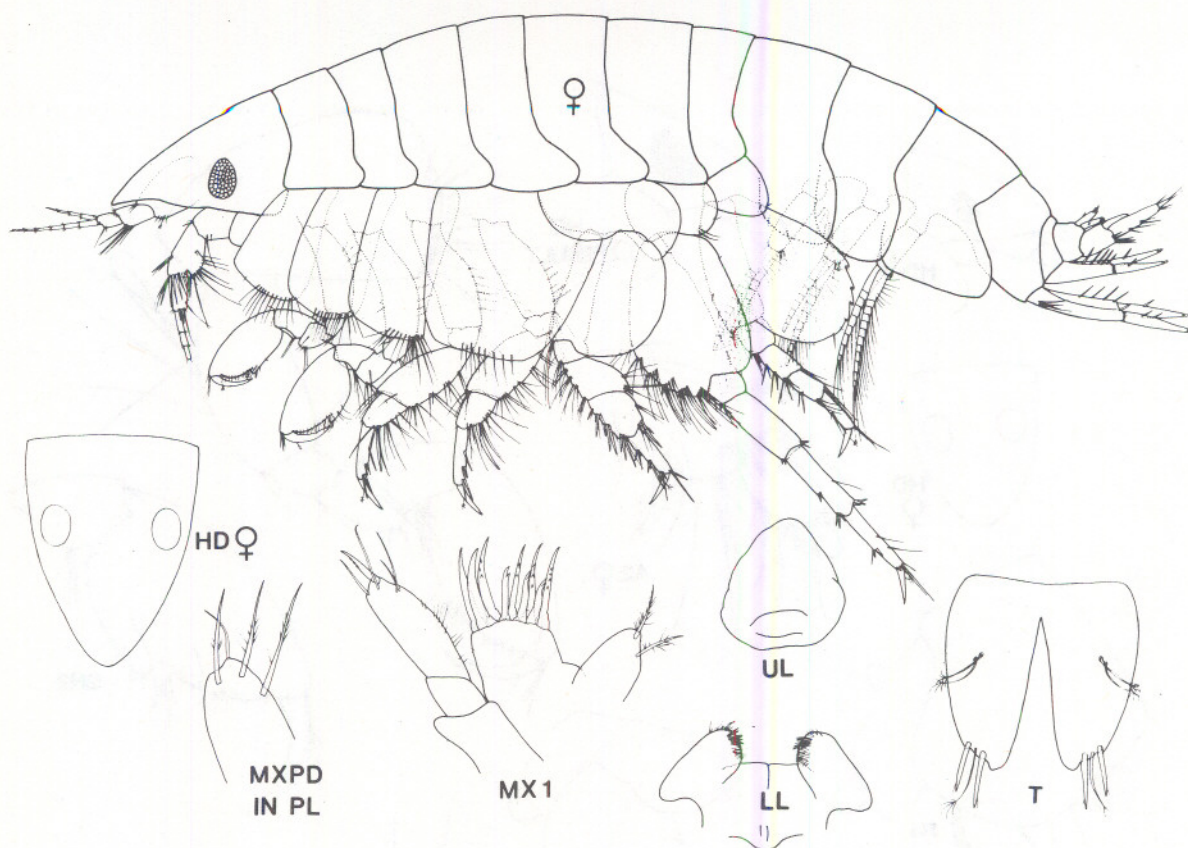


FIG. 22. *Paraphoxus similis*, new species. Female (3.5 mm). Berkeley Sound.

Coxa 1, with 8-12 distal marginal setae. Coxa 4 broad, hind margin obtuse. Gnathopod propods strongly dissimilar in size and form. Gnathopod 1, propod shorter and more slender than in gnathopod 2; carpus relatively short, with 3 hind marginal setae; basis with about 6 long posterior marginal setae. Gnathopod 2, carpus with 3 posterior marginal setae.

Peracopods 3 & 4, postero-distal spines of segment 5 strong, subequal in length to segment 6; dactyl short, about 2/3 length of segment 6. Peracopod 5, basis broad, hind margin convex, with very shallow median indentation; segment 6 with 2 anterior marginal spines and 0-1 posterior marginal setae. Peracopod 6, distal segment slender, segments 5 & 6 collectively with 9 marginal clusters of single spines and long seta. Peracopod 7, basis medium, with about 8 weak hind marginal teeth.

Pleon plate 3 not strongly produced behind, hind margin steeply oblique, with 2 small setae, lower margin almost straight. Uropods 1 & 2 weakly armed, rami with 0-1 marginal spines. Uropod 1, peduncle with 1-2 baso-facial setae. Uropod 2, peduncular outer margin with 3 stout spines. Uropod 3, peduncle with distal fan of 5-6 slender spines; outer ramus broad, less than twice length of inner ramus; terminal segment medium, with 1 short and 1 long apical setae.

Telson lobes narrowing distally, each with 1-2 slender apical spines.

Male, penult. (3.0 mm): No special features noted.

Etymology: The name alludes to the species endemicity in the North Pacific region.

Taxonomic-Distributional Commentary: This advanced species ranges from the north side of Prince William Sound, S.E. Alaska, to southern British Columbia, at outer coast localities. This species and *P. simplex* characterize the advanced Pacific-endemic species complex in having gnathopod propods dissimilar, dactyls of peracopods 3 & 4 short, blades of the mandibular spine row few and stout, and the outer plate of maxilla 1 with 9 apical spines.

Paraphoxus similis, new species
(Fig. 22)

Material Examined:

BRITISH COLUMBIA: Berkley Sound, off Diana island, ELB Stn B26, Depth 24-35 m, shelly mud and stones, July 8, 1976 - 1 female ov. (3.5 mm), with slide mount (fig'd), HOLOTYPE, CMN Cat. No. NMCC1992-1118.

Diagnosis. Female (3.5 mm): Rostrum long, subacute, apex reaching to peduncular segment 3 of antenna 1. Eye medium, almond-shaped. Antenna 1, flagellum 6-segmented; accessory flagellum 4-segmented. Antenna 2, peduncular segment 4 with distal fan of 7-8 fossorial spines; flagellum of 6(?) segments.

Mandibular molar with 3(?) apical spines; spine row with 8(?) blades; palp segment 3 lacking(?) basofacial setae. Maxilla 1, outer plate with 9 apical spines; palp 2-segmented. Maxilliped, inner plate with 3 apical plumose setae.

Coxa 1, distal margin with 10-12 setae. Coxa 4 broad, hind margin oblique, nearly straight. Gnathopod propods dissimilar in size and form, that of gnathopod 1 smaller and more slender; carpus with free posterior border.

Peraeopods 3 & 4, penultimate postero-distal spine of segment 5 strong, slightly shorter than segment 6; dactyl slender, about 3/4 length of segment 6. Peraeopod 5, basis very broad, hind margin strongly convex; segment 6, anterior margin with 2 spines, hind margin bare. Peraeopod 6, distal segments not elongate, segments 5 & 6 nearly bare, margins collectively with only 5-6 clusters of spines and setae. Peraeopod 7, basis broad behind, margin with 6-8 weak teeth.

Pleon plate 3, hind corner produced, broadly rounded, lower margin straight. Uropods 1 & 2, rami shorter than peduncles, with 1-2 marginal spines. Uropod 1, peduncle with 3 slender baso-facial setae. Uropod 2, peduncular outer margin with 4-5 stout spines. Uropod 3, peduncle with distal fan of 3-4 medium spines; inner ramus about half the length of the outer ramus, terminal segment small, (1/3 proximal segment).

Telson little longer than wide, lobes broad basally, apex with 2 medium stout spines (and seta).

Etymology: From the Latin "*similis*" - like, alluding to its overall similarity to the morphologically more advanced species of *Paraphoxus*.

Taxonomic-Distributional Commentary. This species, known only from a single specimen from Berkeley Sound, B. C., is basically a member of the *pacificus* subgroup of *Paraphoxus*. Its character states are mainly apomorphic and thus only remotely related to the type species *P. oculatus*.

Paraphoxus rugosus, new species
(Fig. 23)

Material Examined:

ALASKA: Beaufort Sea (off the mouth of the McKenzie River, Yukon Territories), Aug. 24-28, 1986, M. Gordon, ERA coll., 147-275 m. bottom dredge: A total of 17 females, 5 males, and 34 juveniles, at 10 stations, as follows: BDS86-D1-002, 226 m. - 1 penult male, 1 im; *Ibid*-003, 152 m. - 1 female ov. (4.75 mm), with slide mount (fig'd) HOLOTYPE, CMN Cat. No. NMCC1992-1128; 1 female, 20 juveniles; *Ibid*-017, 240 m. - 1 male penult.; *Ibid*-021, 275 m. - 1 male subadult; *Ibid*-028, 231 m. - 1 female with slide mount, 7 females, 8 juvs. *Ibid*-030, 222 m. - 1 female ov., 1 im. BDS86-D2-006, 157 m. - 1 female (br. II), 2 im.; *Ibid*-018, 147 m. - 1 female; *Ibid*-024, 155 m. - 2 females; *Ibid*-028, 231 m. - 1 male penult (4.4 mm) with slide mount

(fig'd), ALLOTYPE, CMN Cat. No. NMCC1992-1130; 1 male penult. (3.9 mm), PARATYPE, CMN Cat. No. NMCC1992-1131; 1 female Br. II., 1 male im.

Diagnosis (Female, 4.75 mm): Rostrum relatively long, subacute apex reaching to peduncular segment 3 of antenna 1. Eye relatively large, vertically subovate. Antenna 1, flagellum 7-segmented; accessory flagellum 4-segmented. Antenna 2, peduncle 4 with distal facial fan of 7-8 stout fossorial spines; flagellum 6-segmented.

Mandibular molar with 3 apical spines; spine row with 6 stout blades; palp segment 3 with 1-2 baso-facial setae. Maxilla 1, outer plate with 9 apical spines; palp 2-segmented, apex subconical. Maxilliped, outer plate strong, distally with 4 large pectinate spines.

Coxa 1, with 11-12 distal marginal setae. Coxa 4 deep, short, convex hind margin steeply sloped. Gnathopod propods strongly dissimilar in size, less so in form. Gnathopod 1, basis with 3 long posterior marginal setae. Gnathopod 2, carpus, hind margin cryptic, with 2 long setae.

Peraeopods 3 & 4, postero-distal spines of segment 5 long and heavy, exceeding length of segment 6; dactyls short, about 2/3 length of segment 6. Peraeopod 5, basis very broad, hind margin gently convex; segment 6 anterior margin with 2 spines, hind margin with 0-1 setae. Peraeopod 6, distal segments relatively short, well armed, segments 5 & 6 collectively with 12-13 clusters of spines and long setae. Peraeopod 7, basis produced postero-distally, hind margin with about 12 weak teeth.

Pleon plate 3 little produced behind, broadly rounded, hind margin with 3 small setae, lower margin gently convex. Uropods 1 & 2, rami with 1-2 marginal stout spines. Uropod 1, peduncle with 4 slender baso-facial setae. Uropod 2, outer margin with 4 spines. Uropod 3, peduncle with distal fan of 7-8 long spines; outer ramus large (2X inner), terminal segment short, with 1 long and 1 medium apical setae.

Telson lobes relatively broad, each with pair of medium slender spines.

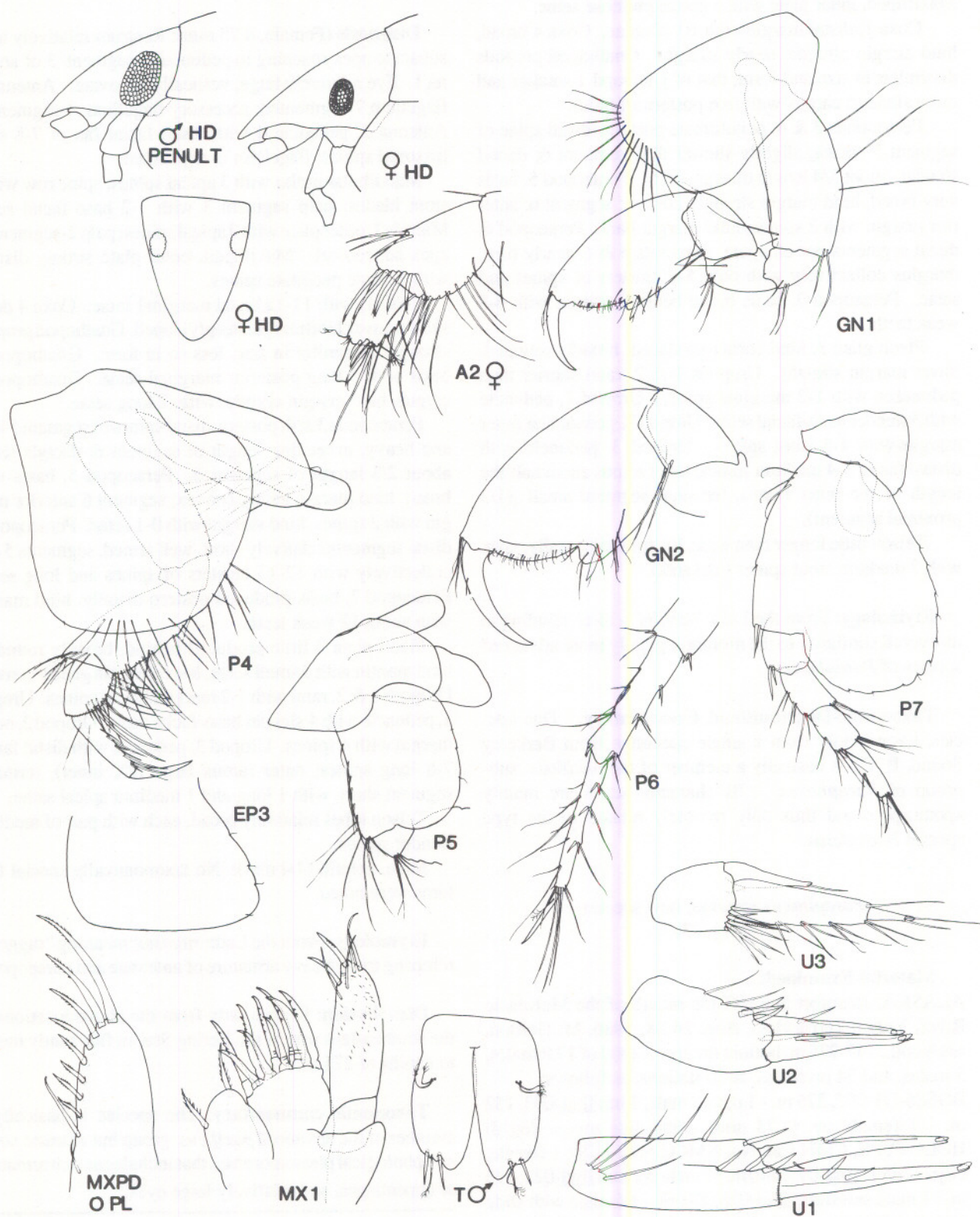
Male, penult. (4.4 mm): No taxonomically special features were noted.

Etymology: From the Latin *rugosus* meaning "rugged", referring to the heavy armature of antennae and peraeopods.

Distribution: Known only from the above locations in the southeastern part of the Bering Sea, in fine sandy muds, to depths of 275 m.

Taxonomic commentary: The species is basically a member of the advanced *pacificus* group but entrains some morphological plesiomorphies that include the rich armature of appendages, and relatively large eyes.

FIG. 23. *Paraphoxus rugosus*, new species.
FEMALE ov (3.6 mm) HOLOTYPE; MALE (3.0 mm)
(SEE PAGE 112)



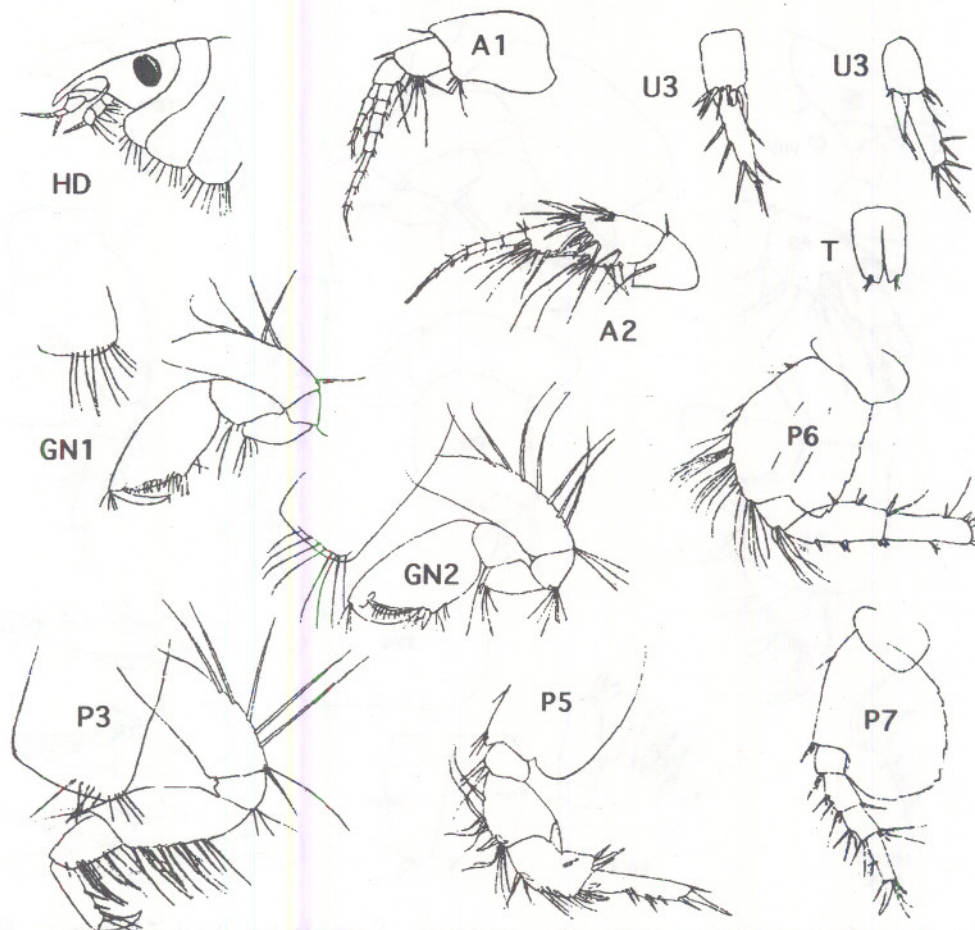


FIG. 24. *Paraphoxus simplex* Gurjanova. Female ov. (6.0 mm). Japan Sea.

Paraphoxus simplex (Gurjanova)
(Fig. 24)

Pararpinia simplex Gurjanova, 1938: 272, fig. 10.—
Gurjanova, 1951: 392, fig. 238.

Paraphoxus simplex Barnard & Karaman, 1991: 625.

Diagnosis: Since this species was not identified in present study material, the diagnosis is adapted from the description and figures of Gurjanova (*loc. cit.*).

Female (6.0 mm): Rostrum long, tip reaching end of peduncle of antenna 1. Eye medium, vertically oval. Antenna 1, flagellum 8-9 segmented; accessory flagellum 5-segmented. Antenna 2, peduncular segment 4 short, with distal facial cluster of 8-9 stout fossorial spines; flagellum 8-9 segmented.

Mouthparts not described or figured but are here presumed to be similar to those of *P. beringiensis* (p. 114) (i.e., mandible with 3 molar spines, about 5 blade spines; maxilla 1, outer plate with 9 apical spines, palp 2-segmented).

Coxa 1 with 9 distal marginal setae. Gnathopod propods somewhat dissimilar in size and form, that of gnathopod 1 long and more slender, that of gnathopod 2 shorter and deeper; carpus of gnathopod 1 with 2-4 hind marginal setae, carpus of gnathopod 2 with 1-2 long setae; basis of gnathopod 1 with 4 long posterior marginal setae.

Peraeopods 3 & 4, postero-distal spines of segment 5 subequal, slender, length about equal to segment 6 dactyl short, length about 60% of segment 6. Peraeopod 5, basis medium broad, hind margin convex; segment 6, anterior margin with 3 spine groups, hind margin bare. Peraeopod 6, distal segments short, relatively stout, margins sparsely setose-spinose collectively probably with only 5-6 marginal spine and setal clusters. Peraeopod 7, basis little broadened behind, with about 10 weak marginal teeth.

Pleon plate 3 and uropods 1 & 2 not shown. Uropod 3, peduncle with distal fan of 5 stout spines; inner ramus very short, length < 1/2 outer ramus; terminal segment medium, apex with 1 long and 1 medium slender seta.

Telson lobes medium broad, with single apical spine.

Male: unknown.

Distribution: Known only from the Russian coast of the, Sea of Japan, in the *Phyllospadix* zone.

Taxonomic Commentary: The advanced species is closely similar to *P. beringiensis* (below) but differs in several respects (see key). The eye is much larger, the armature of the peduncle of antenna 2 is slightly less strong, and the lower margins of the coxal plates are distinctly more heavily setose.

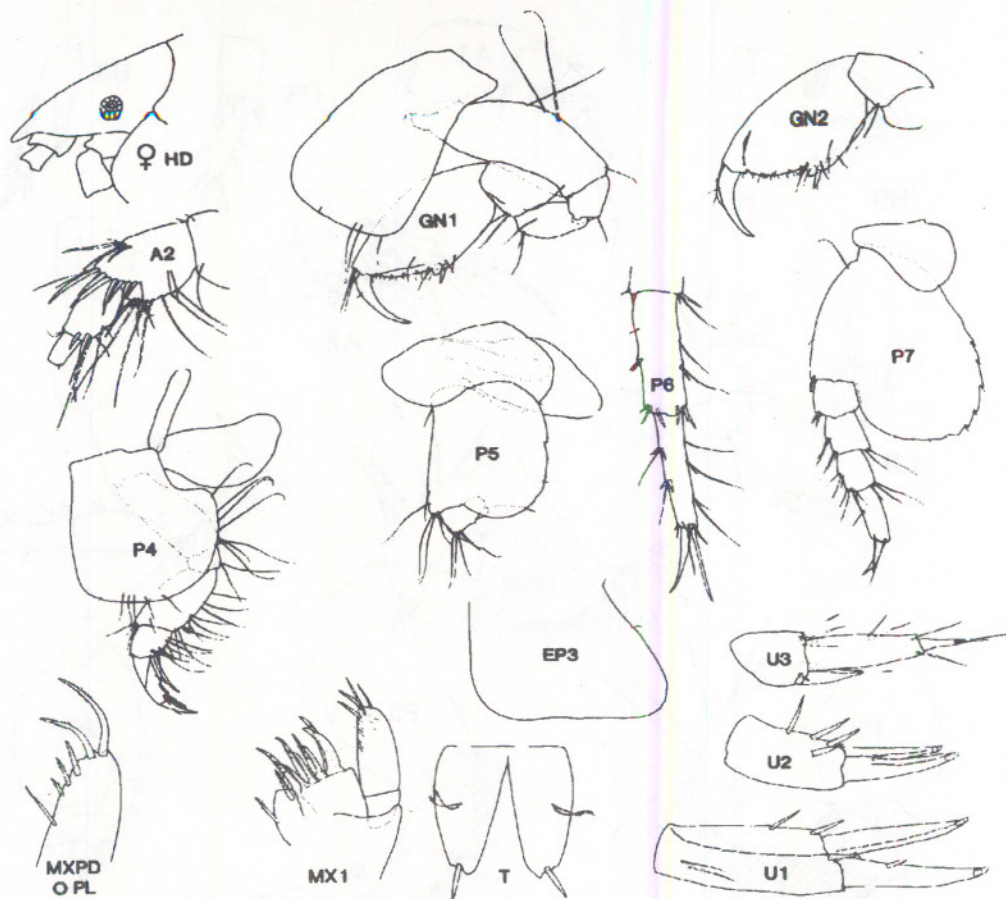


FIG. 25. *Paraphoxus beringiensis*, new species. Female br. II (2.75 mm). Bering Sea.

Paraphoxus beringiensis, new species
(Fig. 25)

Material Examined:

ALASKA: Bering Sea off St. Lawrence I., 45 m. sand, July 1, 1980 - 1 female br. II (2.75 mm), with slide mount HOLOTYPE (fig. 'd), 1 other female. CMN Cat No. NMCC1992-1122.

Diagnosis: Female br. II (2.75 mm): Rostrum short, apex reaching little beyond peduncular segment 1 of antenna 1. Eye small, round. Antenna 1, flagellum 5-segmented; accessory flagellum 4-segmented. Antenna 2, peduncle 4 with distal cluster of 8-9 strong facial fossorial spines; flagellum 5-segmented.

Mandibular molar with 3 apical spines; spine row with 4-6 stout blades; palp segment 3 with 2-3 baso-facial setae. Maxilla 1, outer plate with 9 apical spines, palp 2-segmented, short, weakly armed apically. Maxilliped, outer plate, distal 2 apical spines strong, sharply curved.

Coxa 1 with 4-5 distal marginal setae. Coxa 4 short, deep, hind margin steeply convex. Gnathopod propods subsimilar in size, that of 1 more slender, but not shorter than 2. Gnathopod 1, carpus short, with 2 posterior marginal setae; basis with 3 long hind marginal setae.

Pereopods 3 & 4, penultimate postero-distal spine of segment 5 stout, length nearly equal to segment 6; dactyls

short, about 2/3 length of segment 6. Pereopod 5, basis very broad, hind margin distinctly convex, weakly notched; segment 6, anterior margin with cluster of 3 strong spines, hind margin bare. Pereopod 6, distal segments short, relatively stout, segments 5 & 6 collectively with about 9 clusters of short spines and/or long seta. Pereopod 7, basis expanded posteriorly, with about 10 very weak hind marginal teeth.

Pleon plate 3, hind corner somewhat produced, rounded, lower margin straight. Uropods 1 & 2, rami nearly unarmed, each with 0-1 marginal spines. Uropod 1, peduncle with 2 slender baso-facial setae. Uropod 2, peduncular outer margin with 3 stout spines. Uropod 3, peduncle with weak distal fan of 3-4 slender spines; inner ramus very short, less than half outer ramus; terminal segment medium, apex with 1 long and 1 medium slender seta.

Telson lobes broad, each with 1 stout apical spine.

Etymology: The name alludes to the Bering Sea where the species may be endemic.

Taxonomic and Distributional Commentary: The species has been taken only at St. Lawrence I. in the Bering Sea. It is closely similar to *P. simplex* Gurjanova from the Sea of Japan (p. 113) but differs in characters of the key (p. 98), and in the plesiomorphically subsimilar gnathopod propods.

PHOXOCEPHALINAE Barnard & Drummond

Phoxocephalidae Sars, 1895: 142 (partim).—Gurjanova, 1951: 361 (partim).

Phoxocephalinae: Barnard & Drummond, 1978: 416.—Barnard & Karaman, 1991: 592 (key to genera).

Type genus. *Phoxocephalus* Stebbing, 1888: 810.

Genera. (North Pacific region): *Cephalophoxoides* Gurjanova, 1977 [81]; *Metaphoxus* Bonnier, 1896 [630]; *Parametaphoxus* Gurjanova, 1977 [81].

Diagnosis: Rostrum well developed, hood-like, lacking lateral incisions. Pigmented eyes usually present in male, often small or lacking in female. Antenna 1, segment 2 shortened, but longer than segment 3; segments of accessory flagellum and flagellum transversely separated; in male, peduncular segment 1 with strong posteromedial cluster of brush setae ("fuzz" of Barnard & Drummond); basal segments of flagellum calceolate and/or callynophorate. Antenna 2, peduncular segments 4 & 5 short to medium, 4 with distal facial fan of stout spines, posterior margin slender-spinose; in male, segments 3 & 4 with anterior marginal brush setae, segment 5 with anterior submarginal calceoli; flagellum usually elongate and calceolate, distally on alternate segments.

Mandibular molar mostly non-tritulative, bearing 4 or fewer tightly clumped apical spines; left lacinia 5-6 dentate; right lacinia various; blades strong, numerous; palp slender, segment 3 with few or no "A"-seta. Maxilla 1, outer plate with 7-11 apical spines, inner plate with 0-2 apical setae. Maxilla 2, inner plate small. Maxilliped, inner and outer plates reduced, outer with stout inner marginal raptorial spines; palp ordinary, inner margins lacking stout spines; dactyl slender, curved, nail elongate.

Coxae 1-4 broad, deep, lower margin setose. Gnathopods medium, strongly subchelate, subequal; carpus short-eusiroid, propod palm oblique, smoothly convex; in gnathopod 1, propod usually more slender and carpus slightly longer than in gnathopod 2.

Peraeopods 3 & 4, segments 4 & 5 stout, segment 5 short, postero-distal setae increasingly strong, usually spine-like; segment 6 slender (not spatulate) weakly armed, dactyls elongate. Peraeopod 5, basis variously expanded (narrow in harpiniid subgroup); segments 4 & 5 variously expanded and facially spinose. Peraeopod 6 elongate, basis broadest medially; segments 4, 5, & 6 slender or little expanded, usually elongate. Peraeopod 7 short, basis broadly expanded posteriorly but not deeply, lower margin exceeded fully by segments 5-7; segment 5 (male), anterior margin may be incised and/or bearing stout copulatory spines.

Pleon plate 3, hind corner variously subquadrate, rounded, or produced, outer facial and lower margin lacking rows of long setae. Pleopod peduncles slightly broadened, margins smooth. Uropods 1 & 2 and pleopods normal, peduncles

little broadened, margins bare. Uropods 1 & 2 medium, peduncle and rami subequal in length; peduncle with basofacial spine cluster, weak disto-lateral spine (not enlarged or spike-like), and distal comb-like lobes; rami subequal (inner shorter), unmodified, with 0-3 marginal spines and single short apical spine semi-fused with ramus. Uropod 3 parviramous (female) rami slender, outer much the longer, terminal segment large; in male, rami acquiramous subequal, margins plumose-setose.

Telson lobes narrow, separated to base, apices usually with 1-3 short spines and 1-3 supernumerary setae. Coxal gills medium to large on peraeopods 2-5, smaller on peraeopods 6 & 7. Brood plates, small, narrow, not broadened distally.

Taxonomic Remarks: Barnard & Karaman (1991) have provided an up-dated list of about 20 generic inclusions within subfamily Phoxocephalinae (world-wide). These genera encompass mostly Australian taxa, described initially by Barnard & Drummond (1978, loc. cit.) and taxa from other regions of the southern hemisphere including Madagascar. Records of the genera *Leptophoxus*, *Hopiphoxus*, and *Coxophoxus* from deep waters off southern California and Baja California are few and isolated. The latter genus was transferred to its own family, Coxophoxidae, by Gurjanova (1977). In this study, it is given intermediate taxonomic recognition, as subfamily Coxophoxinae.

Genera presently assigned to subfamily Phoxocephalinae exhibit a wide variety of mouthpart character states (see Barnard & Drummond, 1978). Thus, molars are fully tritulative in a number of genera, including *Phoxocephalus* (the type), but are small and non-tritulative in others (e.g. *Limnoporeia*). In most genera, however, the mandibular blades are short and thick. The present subfamily concept must eventually meet the rigorous test of conformity within other major character states, particularly of the male copulatory apparatus, as these phyletically significant taxonomic features become better known.

Phoxocephalus Stebbing

Phoxocephalus Stebbing, 1888: 810.—Gurjanova, 1977: 82.—Barnard & Drummond, 1978: 417.—Barnard & Karaman, 1991: 626.

Type species. *Phoxocephalus holbolli* Kroyer 1842, selected by Boeck, 1876.

Diagnosis: Rostrum unstricted. Pigmented eyes lacking or vestigial in both males and females. Antenna 1 & 2 slender, weakly armed; flagella (in male) lacking calceoli.

Mandibular molar small but tritulative, palp lacking basofacial setae, apically strongly setose. Maxilla 1, inner plate bare.

Key to North American Pacific Genera of Phoxocephalinae
(after Barnard & Karaman, 1991: 592)

1. Mandibular molar reduced but triturative; peraeopod 7 (male), segment 5 little modified 2.
—Mandibular molar weak, non-tritulative apex bearing spines; peraeopod 7 (male), segment 5, anterior margin with conspicuously modified, copulatory spines 3.
2. Eyes unpigmented or lacking (both sexes); gnathopods typically subsimilar in form and size.
..... *Phoxocephalus* (p. 115)
—Eyes pigmented, distinct; gnathopod 2 usually larger than gnathopod 1 ... *Cephalophoxoides* (p. 116)
3. Gnathopods either both subchelate or both parachelate; peraeopod 7 (male), segment 5, anterior copulatory spines are short, widely spaced, tips little modified *Metaphoxus* (p. 117)
—Gnathopod 1 slightly parachelate, gnathopod 2 subchelate; peraeopod 7 (male), segment 5 anterior copulatory spines are large, closely spaced, with strongly modified tips ... *Parametaphoxus* (p. 121)

Coxae 1-4 setose postero-distally. Gnathopods subequal, medium, obliquely subchelate, carpus cryptic or nearly so. Peraeopods 3 & 4 stout, segment 5 spine elongate; dactyls small. Peraeopod 5, basis broad, segments 4 & 5 not expanded. Peraeopod 7 (male), segment 5 little modified as a clasping organ.

Pleon plate 3 large, margins lacking setae. Uropods 1 & 2 not powerful, rami marginally spinose.

Telson lobes long, narrowing distally, apex with single spine.

Taxonomic Commentary: According to Barnard & Karaman (1991), the genus *Phoxocephalus* is not now represented in the North American Pacific region. *Phoxocephalus homilis* J. L. Barnard, 1960, and a number of species from the southern hemisphere, have been removed to *Cephalophoxoides*. *Metaphoxus fultoni* (J. L. Barnard) had previously been removed by Gurjanova to the genus *Parametaphoxus*, and its representative on the N. American Pacific coast is here renamed *Parametaphoxus quaylei*, new species (see p. 121). We may note that *Metaphoxus frequens* J. L. Barnard of this subfamily is here retained within the genus *Metaphoxus* (p. 117). The present authors here provide evidence that supports this major subdivision of the genus *Phoxocephalus* by Gurjanova (1977) and by Barnard and Karaman (1991). The genus *Phoxocephalus* thus reverts to monotypy, containing only its original type species *P. holbolli* Kroyer.

Cephalophoxoides Gurjanova

Cephalophoxoides Gurjanova 1977: 81.—Barnard & Karaman, 1991: 602.

Type Species. *Phoxocephalus bassi* Stebbing, 1888.

Species (North Pacific Region): *Cephalophoxoides homilis* (J. L. Barnard, 1960); *C. proluxus* (Hirayama, 1987)?

Diagnosis: Rostrum unconstricted. Pigmented eyes well developed. Antennae short (female). Antenna 2 (male), peduncular segment 5 weakly calceolate, flagellum elongate, calceolate.

Mandibular molar triturative; palp segment 3 much shorter than 2. Maxilla 1, outer plate 7-spinose; palp 1-segmented. Maxilliped, plates small, weakly armed; inner plate with apical spine(s).

Coxae 1-4 large, deep, setose below. Gnathopods large, subchelate, propods unequal in size, 2 enlarged; carpus short, hind lobes cryptic.

Peraeopods 3 & 4 stout, dactyls long. Peraeopod 5, basis very broad; segments 4 & 5 not expanded. Peraeopod 6 elongate, segments 4-6 slender; dactyl long. Peraeopod 7, basis very broad, hind margin not dentate; dactyl long; segment 5 (male) not modified, or equipped with copulatory spines.

Pleon plate 3 large, margins smooth. Uropods 1 & 2, inner rami marginally spinose. Uropod 1, outer ramus shorter than inner. Uropod 3, fully setose, aequiramous in male, non-setose but sub-aequiramous in female; terminal segment of outer ramus elongate. Telson lobes with single apical spine. Coxal gill on peraeopod 7 small.

Taxonomic-biogeographical Commentary: "*Phoxocephalus*" *prolixus* Hirayama, 1987, from the Ariake Sea, Japan, has fully pigmented eyes in both sexes, and is here tentatively assigned to the genus *Cephalophoxoides*. However, it differs markedly from the eastern Pacific species, *C. homilis*, in having a smaller triturating molar surface, gnathopod propods subequal in size, and possessing an elongated meral process in gnathopod 2, among other differences.

Both North Pacific species differ markedly from counterparts in the southern hemisphere, assigned by Barnard & Karaman (1991) to the genus *Cephalophoxoides*, of which the type species is *C. bassi* (Stebbing). The northern forms may eventually merit separate generic recognition.

Cephalophoxoides homilis (J. L. Barnard)

(Fig. 26).

Phoxocephalus homilis J. L. Barnard, 1960: 370.

Cephalophoxoides homilis Gurjanova, 1977:81.—Barnard & Karaman, 1991: 603.

Material Examined:

BRITISH COLUMBIA: Southern mainland region: Jervis Inlet, ELB Stn. P2, 360 m. fine mud, Nov. 2, 1977, - 1 female. Howe Sound, C. Levings coll., Nov. 2, 1976 - 1 male penult. (4.5 mm), with slide mount (fig'd). CMN Cat. No. NMCC1992-1116, female (2.25 mm). Off Passage I., Howe Sound, ELB Stn. V6, 160 m., July 5, 1978 - 1 female; West Bay, ELB Stn. P2, 25 m., Nov. 2, 1977 - 1 female ov. Southern Vancouver Island: Off McCauley Pt., G. W. O'Connell coll., 61 m., Aug. 26, 1976 - 4 females.

WASHINGTON: San Juan Channel, 80-90 m., K. E. Conlan coll., Jan. 1, 1987 - 1 female ov. Off Brown Island, 55-60 m., Nov. 3, 1983, ELB coll. - 1 female ov. (3.5 mm), with slide mount (fig.'d), 2 im. females. CMN Cat. No. NMCC1992-1117.

Diagnosis: Female ov. (3.5 mm): Eyes medium large, round. Antennae short. Antenna 1, flagellum 5-segmented; accessory flagellum 3-segmented. Antenna 2, peduncular segments 4 & 5, hind margin with fan of long setae; flagellum 4-segmented.

Mandible, left lacinia 4-dentate, right lacinia flabellate; spine row short (2-5 blades). Maxilla 1, inner plate 7-spinose; palp indistinctly 1-segmented. Maxilliped, outer plate short, with 4 short inner marginal spines.

Coxa 1 broadening distally, margin with 7-8 setae. Coxa 4 very broad, hind margin convex. Gnathopod propods large, unequal (2 larger), hind margin of carpus with single cluster of setae.

Peraeopods 3 & 4, postero-distal spine of segment 5 slender, length = segment 6; segment 6 with a few postero-distal spines; dactyls slender. Peraeopod 5, basis very broadly rounded behind. Peraeopod 6, segment 4 weakly spinose; dactyl long, ~ 2/3 segment 6.

Pleon 3, hind margin with slight notch but no setae. Uropod 1, outer ramus shorter than inner, marginally bare; inner ramus with long marginal spines. Uropod 2, outer ramus with 3-4 slender marginal spines. Uropod 3, peduncular distal fan of spines weak; outer ramus, margins nearly bare; terminal segment slender, half length of proximal segment; inner ramus ~ 1/2 length of outer ramus.

Telson, apices each with single long spine and plumose setule; dorsal penicillate setae large, long.

Male penult. (4.5 mm): Eyes large, vertically oval. Antenna 2, peduncle 4 with weak brush setae; flagellum with 30+ short segments. Peraeopod 7, segment 5. Uropod 3, inner ramus as long as proximal segment of outer ramus.

Taxonomic and Distributional Commentary: The species ranges from southern Vancouver Island to southern California, in depths of 40-600 m, shallower in the north. The northern material is virtually identical with that from California described and figured originally by Barnard (1960, pls. 49-50).

Cephalophoxoides homilis differs rather markedly from the type species and other species of the Australian antipodean region (see generic commentary, above).

Metaphoxus Bonnier

Metaphoxus Bonnier, 1896: 630.—Barnard, 1960: 379 (partim).—Barnard, 1969: 419 (partim).—Gurjanova, 1951: 363 (key).—Barnard & Karaman, 1991: 621.

Type species: *Metaphoxus typicus* Bonnier, 1896 (= *Metaphoxus simplex* (Bate, 1857)).

Species (North American Pacific): *Metaphoxus frequens* Barnard, 1960 [379].

Diagnosis: Eyes pigmented (both sexes). Antenna (female) very short. Antenna 1 (male), proximal 3 segments calceolate. Antenna 2 (male), segment 5 with 2 anterior marginal calceoli, flagellum elongate, proximal segments calceolate.

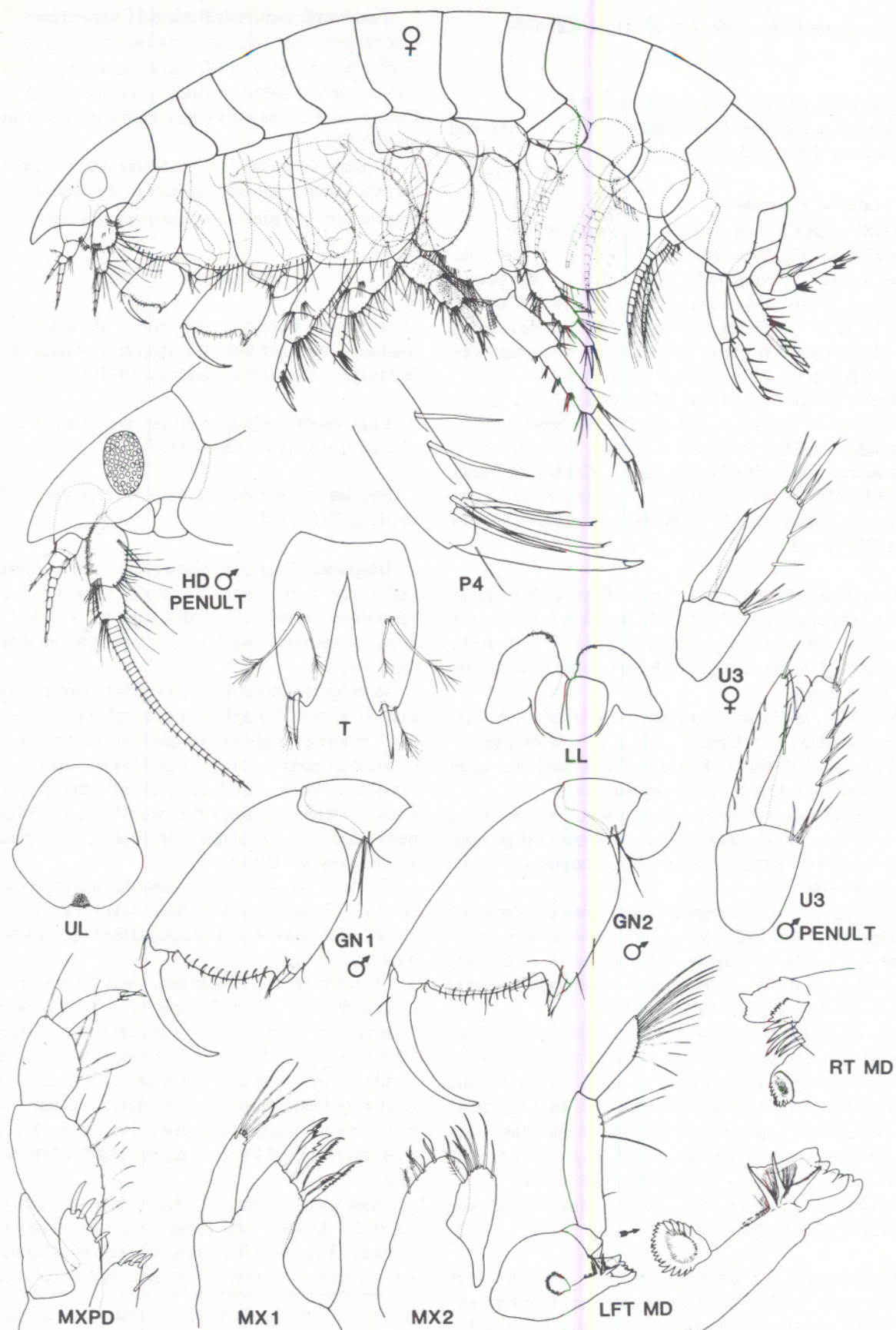
Mouthparts modified. Mandible, molar small, non tritulative, with 2-3 apical blades; spine row short, blades thick, powerful; right lacinia flabellate, left lacinia unevenly denticulate; palp segment 3 expanded and truncate distally. Maxilla 1, inner plate lacking distal setae; palp sparsely setose. Maxilla 2, plates small, weakly setose. Maxilliped, inner plate tall, with single apical spine; inner plate small, slender very weakly armed.

Coxae 1-4 broad, deep, postero-distal margins with setal cluster. Gnathopods powerfully subchelate, propods unequal in size and form, gnathopod 2 the larger; carpus short, hind lobe cryptic.

Peraeopods 3 & 4 medium, weakly spinose & setose behind; dactyls slender. Peraeopods 5-7, bases very broad. Peraeopod 5, segments 4 & 5 not expanded. Peraeopod 6, anterior margin of basis strongly long-setose; segments 4-6 slender, weakly armed; dactyl small. Peraeopod 7 (female), basis very broad, hind margin smooth; segment 6 short; in male, anterior margin of segment 5 not incised, but armed with singly spaced stout spines, tips slightly bent and pectinate.

Pleon plate 3 rounded, margins bare or weakly setose. Uropod 1 lacking inter-ramal or displaced spines; rami subequal. Uropod 3 (female) inaequiramous, margins lacking setae. Telson lobes slender, elongate, apical spines elongate.

FIG. 26. *Cephalophoxoides homilis* (J. L. Barnard)
FEMALE ov.(3.5 mm); MALE (4.5 mm)
(SEE PAGE 118)



Taxonomic Commentary: This genus is very little different from *Parametaphoxus* Gurjanova, 1977. Aside from differences in the gnathopods, another major character of significance is the form of the copulatory spines on segment 5 of pereopod 7 (male). In males of the Mediterranean *M. simplex* Bate, Karaman (1993, p. 658) noted: "pereopod 7, carpus, anterior margin with 3-4 stout spines", but did not use the information in analysis of species relationships.

Distributional Commentary: The five species of the genus occur in littoral marine shallows, from the tide lines to depths of 458 m. in the northeastern Pacific, from 0-80 m. in the northeastern Atlantic, and from 0-48 m. in southeastern Australia. Such a widely disjunct distribution of component species suggests that the generic concept may be artificial, and held together by homoplasies, rather than by true synapomorphies.

Metaphoxus frequens Barnard
(Fig. 27)

Metaphoxus frequens Barnard, 1960: 379, Pl. 51.—Barnard, 1975: 341, fig. 161.—Gurjanova, 1977: 80.—Austin, 1985: 598.

Material Examined:

ALASKA: Leo Anchorage, ELB Stn. A165, July, 1961 - 3 females.

BRITISH COLUMBIA: North-Central coast: Open Bight, ELB Stn. H37, July 22, 1964 - 1 female ov. (2.5 mm), with slide mount (fig'd), 2 other females, 1 subadult male. CMN Cat. No. NMCC1993-0053. Off Kennedy I., 20 ft. depth, May 15/64 - 1 female; Ocean Falls, C. Levings Stn. 51B-04 - 3 females; Stn. 51B-38 - 1 female; Swanson Bay, C. Levings Stn. 51B-008 - 1 male, subadult.; Stn. 51B-004 - 2 specimens.

Vancouver Island: Port Hardy, ELB Stn. V6, July 22, 1959 - 1 female; Trevor Channel, ELB Stn. B14, May 25, 1977 - 1 female ov. (3.25 mm), with slide mount, 1 male penult., with slide mount; Ibid, lot 2 - 1 female. Broken Id., ELB Stn. B7, June 27, 1976 - 1 female. ELB Stn. P13, Trevor Channel, July 29, 1975 - 1 male, 1 female; ELB Stn. P26, Koprino Hbr., Aug. 14, 1975 - 2 males, 2 females.

French Creek, near Nanaimo, P. O'Rourke Stations, August 13-28, 1977: FC2 - 2; FC5 - 1 mature male, with slide mount (fig'd), CMN Cat. No. NMCC1993-0054; FC6 - 1 male penult; FC7 - 1; FC13 - 1.

Sidney Channel, D.V. Ellis Stn. 1001, 1979 - 1 specimen. Shelf off Vancouver Island, Institute of Ocean Sciences, 1990: 14 stns (A4, A8, to 2C4) - 14 specimens, including juveniles, mature males, and females (ov.).

Diagnosis: Female ov. (2.5 mm): Rostrum long, reaching base of flagellum of antenna 1. Eye small, oval, weakly pigmented; Antenna 1, segments 2 & 3 very short; flagellum 4-segmented, accessory flagellum 2-3 segmented. Antenna 2, peduncular segment 4 with single facial cluster of slender

spines, hind margin sparsely long-setose; flagellum 4-5 segmented.

Mouthparts nearly typical of the genus. Mandibular palp segment 3 shorter than segment 2, tip expanded and subtruncate. Maxilla 1, inner plate large, margins bare. Maxilliped, inner plate columnar, with single apical slender spine; palp, dactyl heavy, nearly equal in length to segment 3,

Coxa 1 somewhat hatchet-shaped, hind corner with cluster of 6-7 setae. Coxa 4 very large, hind margin steeply convex. Gnathopod 1, propod smaller but more elongate, and palm less oblique, than in gnathopod 2.

Pereopods 3 & 4, postero-distal spine of segment 5 very slender, longer than segment 6; hind margin of segment 6 with single slender spine at mid-point; dactyls slender. Pereopod 5, basis extremely broad, hind margin convex. Pereopod 6, basis very broad, hind margin straight; segment 4, margins bare. Pereopod 7, basis very broad, orbicular, hind margin nearly smooth; segment 6 and dactyl short.

Pleon plate 3, hind margins with few very weak setae. Uropods 1 & 2, rami subequal, with 1 marginal spine. Uropod 3, rami bare; inner ramus short, < 1/2 outer ramus. Telson lobes narrowing distally, apical spines elongate, slender, tips curved. Coxal gills relatively small on pereopods 2, very small on pereopods 6 & 7.

Male (3.0 mm): Eye large, rounded, anterior ommatidia prominent. Antenna 1, peduncle 1 with strong posterior marginal brush setae; proximal 3 flagellar segments calceolate; antenna 2, peduncular segment 5 with 2 large anterior marginal calceoli; flagellum elongate, segments calceolate, distally alternately.

Pereopod 7, basis less broad than in female, hind margin with 3 small teeth; segment 5, anterior margin gently convex, armed with 3-4 well spaced, bent-tipped spines.

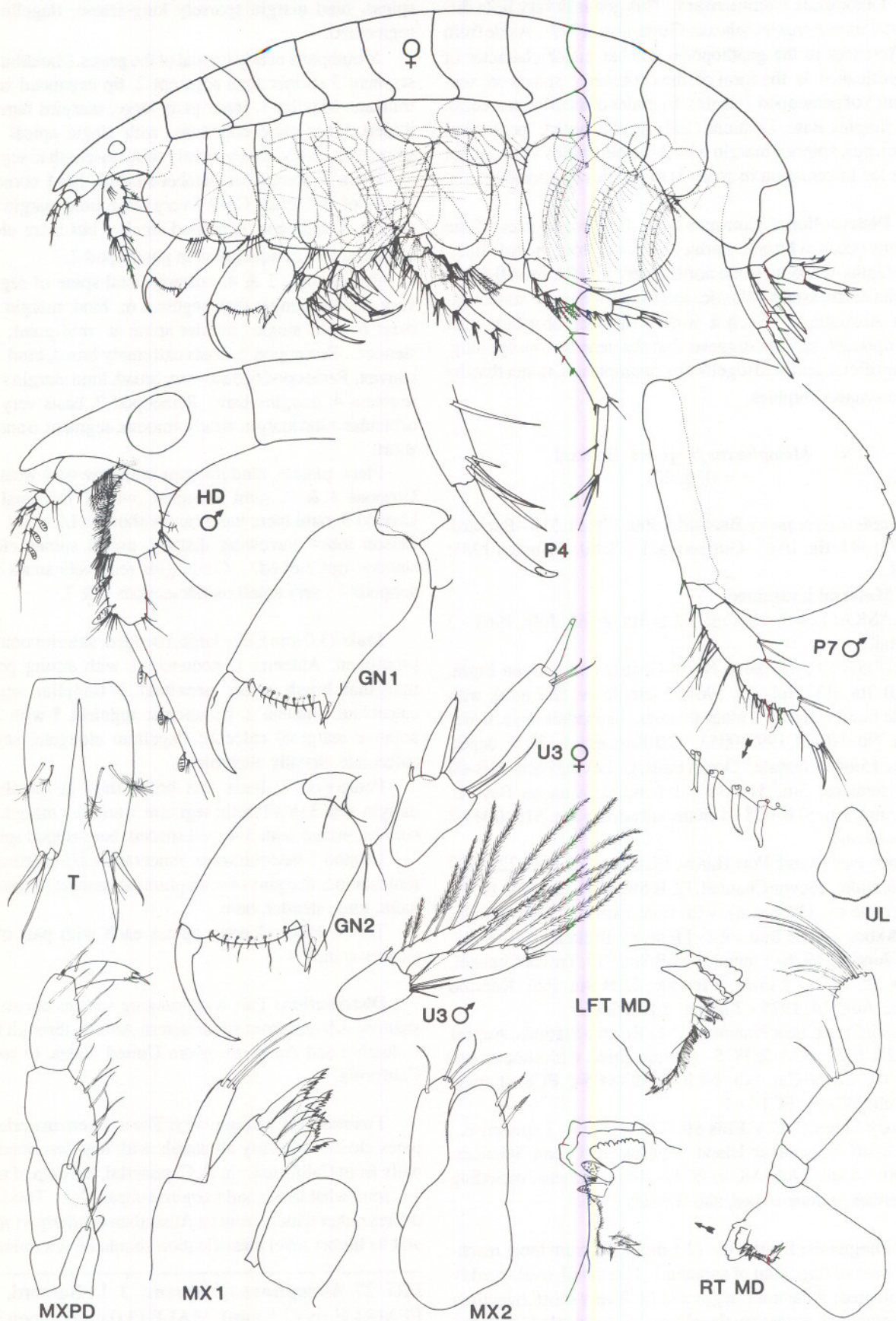
Uropod 3 inaequilateral; inner ramus 2/3 length of outer ramus; inner margins of rami plumose-setose; terminal segment, long, slender, bare.

Telson lobes slender, apices each with pair of long, slender spines

Distribution: This wide-ranging species occurs in the shallow subtidal from southeastern Alaska, through British Columbia and the northeastern United States, to southern California.

Taxonomic Commentary: The northern material compares closely in nearly all details with that described originally from California. In B. C. material, the palp of maxilla 1 is somewhat larger and margins subparallel. This species differs rather widely from its Australian counterpart species, and its higher level classification should be reexamined.

FIG. 27. *Metaphoxus frequens* J. L. Barnard, 1960. FEMALE ov (2.5 mm); MALE (3.0 mm). Open Bight, B. C. (SEE PAGE 120)



Metaphoxus Barnard, 1960: 304 (partim).—Barnard, 1969: 419 (partim).—Lincoln, 1979: 364 (partim?).

Parametaphoxus Gurjanova, 1977: 81 (partim).—Barnard and Karaman, 1991: 624 (partim).

Type Species. *Parametaphoxus quaylei*, new species

Additional Species: *Parametaphoxus asiaensis* (Hirayama, 1992)[127].

Diagnosis: Very close to *Metaphoxus* Bonnier, but differing mainly in the form of the gnathopods (Barnard & Karaman, *loc. cit.*). In *Metaphoxus fultoni* (Scott) (designated type of *Parametaphoxus*, as illustrated by Lincoln, 1979: 367), the palm of gnathopod 1 is parachelate and the posterior lobe of the carpus is free, whereas in gnathopod 2, the palm is nearly vertical, and the posterior lobe of the carpus is evanescent and cryptic.

Female: Rostrum short. Pigmented eyes present. Antennae short.

Mandible, molar non-tritulative, apex with 0-1 blade-spines; spine row short left lacinia unevenly 5-6 dentate, right lacinia blade-like; palp segment 3 with truncate apex. Maxilla 1, inner plate irregularly shaped, palp short. Maxilla 2, outer plate small. Maxilliped, outer plate small, weakly spinose. Coxae 1-4 deep, lower hind corners weakly setose. Gnathopods powerful, propods somewhat dissimilar in form and size, 1 smaller but longer, and palm somewhat parachelate, rather than vertical or truncate; carpus of 1 elongate, shallow, "semi-eusiroidean" in form.

Peraeopods 3 & 4 moderate, hind margin of segment 6 nearly bare. Peraeopod 5, hind lobe of coxa deep, basis very broad; segments 4 & 5 narrow. Peraeopod 6, basis very large, deeply lobate; distal segments slender, elongate. Peraeopod 7, basis extremely large, subtriangular.

Pleon plate 3 ordinary, unarmed. Uropods 1 & 2, rami subequal, weakly armed. Uropod 3 small, margins nearly bare, inner ramus short. Telson lobes slender elongate (length > 3X width), apices with 2 spines. Coxal gills relatively small, sac-like on peraeopods 2-6, minute or lacking on peraeopod 7.

Male: Antenna 1, flagellum calceolate. Antenna 2, peduncle 5 with 2 calceoli; flagellum elongate, segments calceolate. Peraeopod 7, segment 5, anterior margin incised, with close-set, copulatory spines. Uropod 3, rami unequal, margins weakly plumose-setose.

Taxonomic and Distributional Commentary: The genus, as here defined, is restricted to the North Pacific region, including the Sea of Japan in the west, and in the east from British Columbia to southern California. The type of Gurjanova's genus *Parametaphoxus* was based on *Metaphoxus fultoni* (Scott, 1890). The latter is an eastern Atlantic species having the same form of male peraeopod

KEY TO KNOWN SPECIES OF *PARAMETAPHOXUS*

1. Basis, hind margin with 3 small teeth; antenna 1, flagellum 4-5 segmented; gnathopod 2, propod distinctly longer than deep *P. quaylei* n. sp. (p. 121)

—Basis, hind margin with 5 distinct teeth; antenna 1, flagellum very short, 3-4 segmented; gnathopod 2, propod about as deep as long, squarish *P. asiaensis* (Hirayama)

copulatory apparatus as in *M. frequens* and other members of the genus *Metaphoxus* (e.g. *M. pectinatus*, Walker). However, the species from the N. American Pacific region, formerly identified as *M. fultoni*, has a different type of copulatory apparatus than that of the eastern Atlantic TYPE of *M. fultoni*. Thus, the eastern Pacific form is a distinctly different species (newly named *P. quaylei* below). Since Gurjanova (1977) was referring to the eastern Pacific form of "*M. fultoni*", that form becomes the type of her valid new genus, *Parametaphoxus*. *Metaphoxus* was originally described from the N. Atlantic, based on *M. typicus* Bonnier. It includes also *M. chelatus* (Calman, 1896) and several others from the Mediterranean and northeastern Atlantic region (Barnard & Karaman, 1991, p. 622).

Parametaphoxus quaylei new species
(Fig. 28)

Metaphoxus fultoni: Barnard, 1960: 304, plate. 18.—Barnard, 1975: 361, fig. 162.

Parametaphoxus fultoni Barnard & Karaman, 1991: 625 (partim)?

Material Examined:

BRITISH COLUMBIA: North-Central Coast: Rennison Island, ELB Stn. H30, 8-25 m., July 20, 1964 - 3 females, 1 juv.; Banks I., ELB Stn. H21, July 17, 1964 - 1 female. Ocean Falls, C. Levings Sta. 24B-009, 100 m., 1972 - 1 male; Swanson Bay, C. Levings Sta. 51B-031, 25 m., April 4, 1973 - 1 male; *Ibid.*, Sta. 51B-008, 66 m., Nov. 18, 1975 - 1 adult male, with slide mount.

Southern Vancouver Island: Berkeley Sound, Diana I, ELB Stn. B26, July 8, 1976 - 1 female; Off McCauley Pt., Victoria, G. O'Connell coll., 27 m., Aug. 26, 1976 - 1 female ov. (2.5 mm), with slide mount, + 1 other female. Off Clover Pt., Victoria, G. O'Connell, Aug. 28, 1976, 41 m. - 3 females. Saanich Inlet, K. E. Conlan coll., Jan. 16, 1976 - 1 female ov. (2.5 mm), HOLOTYPE, with slide mount, CMN Cat. No. NMCC1993-0050; 1 adult male (2.75 mm), ALLOTYPE, with slide mount, CMN Cat. No. NMCC1993-0051; 5 males, 7 females, PARATYPES, CMN Cat. No. NMCC1993-0052. D.V. Ellis Stns., 1979: Sidney Channel, Stn. 1001 - 2 specimens; Boatswain Bank, Stn. 1601-2-8 specimens; Haro Strait, Stn. 2202 - 1 specimen.

WASHINGTON: Brown Bay, San Juan Co., 50-60 m., ELB colln., Nov. 9, 1983 - 2 females.

Diagnosis: Female ov. (2.5 mm): With the characters of the genus. Differing from *P. asiaensis* by the character states of the key (above) and the following: Eyes medium round. Antenna 1, flagellum 4-5 segmented; accessory flagellum 3-segmented. Antenna 2, peduncular segment 4 with facial cluster of 2 spines; segment 5 short, with single anterior marginal and distal spine groups; flagellum 4-5-segmented.

Mandible, spine rows with 2-3 short thick heavy blades; palp segment 3 nearly equal in length to segment 2, with single long baso-facial seta. Maxilla 1, palp with 3 apical setae. Maxilla 2, plates apically with 3 setae. Maxilliped, outer plate with 1 apical spine; palp, dactyl weak.

Coxae 1 & 2 little broadening distally, lower posterior margin with 6-8 setae; coxa 4 very deep, hind margin nearly vertical. Gnathopod 1, propod longer than deep, slightly parachelate; carpus hind lobe with single setae. Gnathopod 2, propod rectangular, palm perpendicular, carpus with cryptic hind lobe.

Peraeopod 5, basis very broad, strongly rounded behind. peraeopod 6 very large, long; basis narrowing distally to large lobe, hind margin nearly straight; segments 4-6 slender, margins nearly bare; peraeopod 7, hind margin with 2-3 weak teeth; segment 5 short.

Pleon plate 3, hind corner produced, subquadrate, margins bare. Uropods 1 & 2, rami with 0-2 weak marginal spines. Uropod 3, terminal segment of outer ramus of medium length, < 1/2 proximal segment.

Telson, apex of each lobe with pair of unequal spines.

Male (2.75 mm): Pigmented eyes large, sub-orbicular. Antenna 1, proximal 3 flagellar segments calceolate. Antenna 2, peduncular segment 4 strongly brush-setose; peduncle 5 with 2 antero-distal calceoli; flagellum elongate, segments calceolate, distally alternately. Peraeopod 5, segment 5, anterior margin with 3 close-set, elongate, apically clavate copulatory spines and a single shorter spine. Uropod 3, rami with distal plumose setae.

Etymology: Named in honour of the late Dr. D. B. (Dan) Quayle, Nanaimo, British Columbia, whose life-long work in marine biology has contributed greatly to knowledge of invertebrate animals of the North American coastal marine region.

Taxonomic Commentary: In material of *Parametaphoxus* from the North American Pacific coast (represented by the present material from British Columbia, and by material from California formerly identified as *Metaphoxus fultoni* (Scott) by J. L. Barnard (*loc. cit.*), the condition of the gnathopods is closely similar to that of *M. fultoni* (Scott) from the European Atlantic region. However, in Pacific regional males, the anterior margin of segment 5, peraeopod 7, is slightly incised, and the protruding copulatory spines are relatively long, close-set, and bear complexly expanded tips. In European Atlantic males (as illustrated by Lincoln (*loc. cit.*)), the anterior margin of segment 5 is gently convex, and

the 3 copulatory spines are relatively short, simple, and widely spaced. Therefore, on the basis of this major character difference, and on lesser differences noted in the diagnosis above, the present species is considered distinct from *Parametaphoxus fultoni* (Scott) from the European Atlantic region and is herewith described as *P. quaylei*, new species.

The material described and figured by Barnard (1960, *loc. cit.*) is closely similar to the present northern species, esp. in the unique form of the gnathopods. However, the female of Barnard's material is slightly larger (3.0 mm), has larger pigmented eyes, coxa 1 is anteriorly subacute, coxa 5 has a very deep rounded posterior lobe, the basis of peraeopod 5 is irregularly rounded behind, and the basis of peraeopod 6 has an acute postero-distal lobe, etc. Regretably, the form of the copulatory spines of the male of the southern form have not yet been described. Such information is needed to elucidate the taxonomic value of the other character state differences noted above.

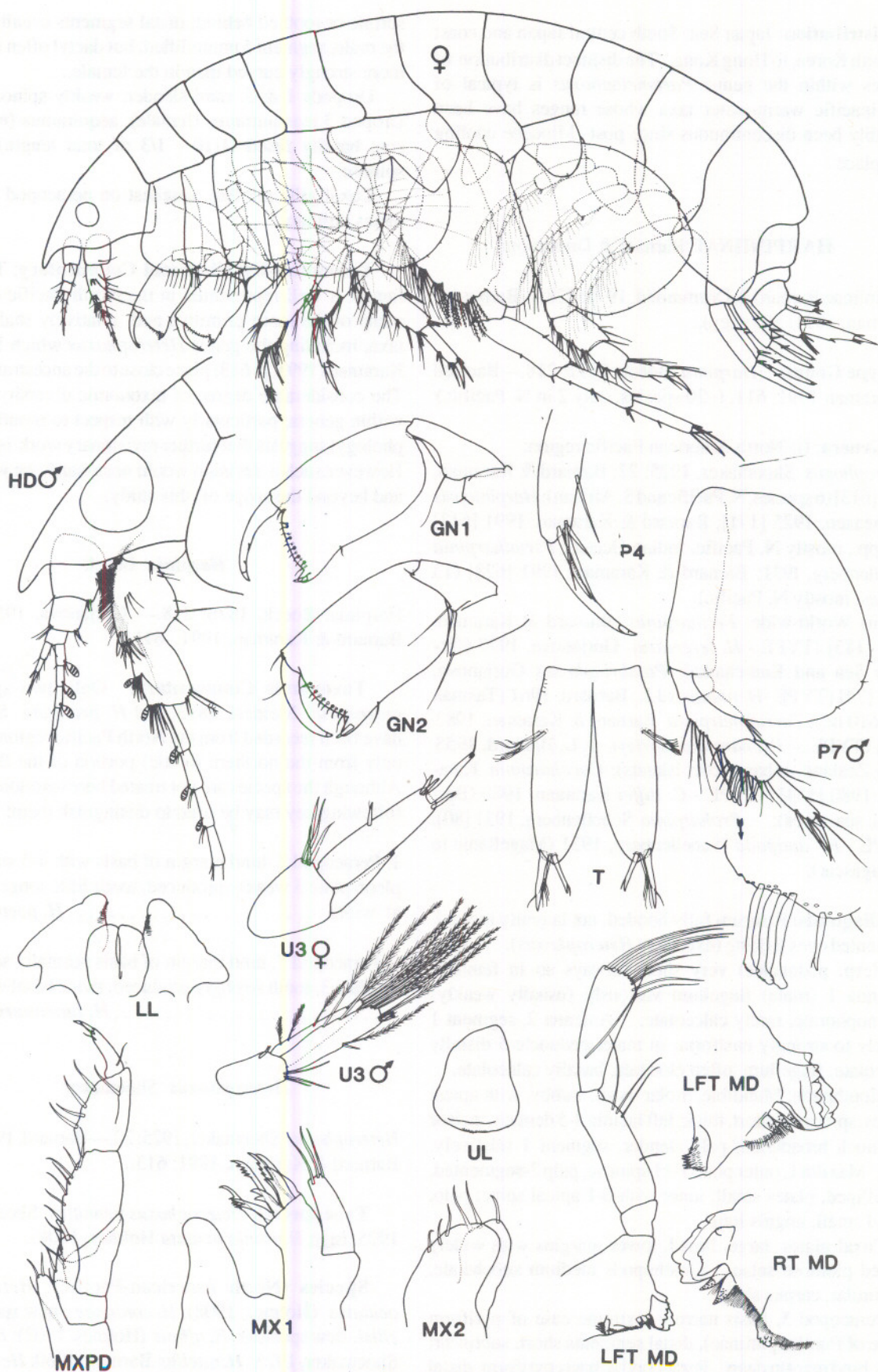
Distribution: Known only from British Columbia and Washington State, subtidally in coastal waters, in depths of 25-50 m, ranging to more than 100 m. in depth.

Parametaphoxus asiaensis (Hirayama, 1992)

Metaphoxus fultoni Hirayama, 1987: 58, figs. 260-263. *Metaphoxus fultoni asiaensis* Hirayama, 1992: 127, figs. 10-14.

Taxonomic Commentary: The material ascribed by Hirayama (1987) to *Metaphoxus fultoni* (Scott) of the N. Atlantic region is clearly much more similar to the N. American Pacific form, *Parametaphoxus quaylei*, new species (above). Hirayama's specimen (2.5 mm) was labelled as a male in figs. 260-262, but is certainly an adult female, since a brood plate is shown on peraeopod 1, the pigmented eye is small, antenna 2 is short, and peraeopod 7, segment 5, is unmodified. This specimen differs from females of the North American species, however, in the smaller, shorter antennae, less slender gnathopod 2, and in the different form and margination of the basis of peraeopod 7, among other features. Hirayama (1992, p. 127) has since merged the Japanese material with that from Hong Kong as a new species of *Metaphoxus*, *M. fultoni asiaensis* Hirayama. Hirayama did not figure the copulatory apparatus of peraeopod 7 of mature males in any of his material, but on general taxonomic grounds we presume it to be similar in generic form to that of *P. quaylei*. For reasons given above, we here transfer Hirayama's name to the genus *Parametaphoxus*, and elevate it to full species status, as *Parametaphoxus asiaensis*. (Hirayama, 1992).

FIG. 28. *Parametaphoxus quaylei*, new species.
FEMALE ov. (2.5 mm) HOLOTYPE; Male (2.75 mm)
ALLOTYPE (SEE PAGE 123 - OPPOSITE)



Distribution: Japan Sea; South central Japan and coast of North Korea, to Hong Kong. The disjunct distribution of species within the genus *Parametaphoxus* is typical of amphipacific warm-water taxa whose ranges have been probably been discontinuous since post-Miocene cooling took place.

HARPINIINAE Barnard & Drummond

Harpiniinae Barnard & Drummond, 1978: 528.—Barnard & Karaman, 1991: 591 (key).

Type Genus: *Harpinia* Boeck, 1872: 218.—Barnard & Karaman 1991: 611. (~20 species, only 2 in N. Pacific.)

Genera: (i) North American Pacific region:

Heterophoxus Shoemaker, 1925: 22; Barnard & Karaman, 1991 [613] (6 species, N. Pacific and S. African); *Harpiniopsis* Stephensen, 1925 [171]; Barnard & Karaman, 1991 [612] (20 spp., mostly N. Pacific, Indian Ocean); *Pseudharpinia* Schellenberg, 1931; Barnard & Karaman, 1991 [628] (13 species, mostly N. Pacific).

(ii) World-wide: *Feriharpinia* Barnard & Karaman, 1982 [183] (TYPE - *H. ferentaria* Gurjanova, 1977 (Okhotsk Sea and Kamchatka); *Palabriaphoxus* Gurjanova, 1977 [74] (TYPE - *H. palabris* J.L. Barnard, 1961 (Tasman Sea, 610 m.); *Torridoharpinia* Barnard & Karaman, 1982 [184] (TYPE - *Proharpinia hurleyi* J. L. Barnard, 1958 (New Zealand, subantarctic islands); *Cocoharpinia* Karaman, 1980 [154] (TYPE - *C. iliffei* Karaman, 1980 (Bermuda sea caves); *Proharpinia* Schellenberg, 1931 [80], (TYPE - *P. antipoda* Schellenberg, 1931 (Magellanic to Madagascar).

Diagnosis: Rostrum fully hooded, not laterally incised; pigmented eyes lacking (except in *Heterophoxus*). Antennae (esp. peduncles) very short (always so in female). Antenna 1 (male) flagellum variously (usually weakly) callynophorate, rarely calceolate. Antenna 2, segment 1 weakly to strongly ensiform; in male, peduncle 5 distally calceolate; flagellum often elongate, basally calceolate.

Mouthparts: Mandible, molar weak, stubby, with apical blades; spine row short, thick; left lacinia 4-5 dentate; incisor not much broadened; palp slender, segment 1 relatively long. Maxilla 1, outer plate 7-11 spinose, palp 2-segmented. Maxilliped, plates small, inner with 0-1 apical spine; palp, dactyl small, unguis long.

Coxal plates, large, broad, lower margins with widely spaced plumose setae. Gnathopods medium subchelate, subsimilar, carpus short.

Peraeopod 5, basis narrow (extreme case of pyriform shape of Pontoharpiniinae), distal segments short, sublinear; coxa, hind margin deep. Peraeopod 6, basis pyriform, distal segments elongate. Peraeopod 7, basis usually strongly

serrate or toothed behind; distal segments usually short; in the male, segment 5 unmodified, but dactyl often longer and more strongly curved than in the female..

Uropods 1 & 2, rami slender, weakly spinose behind. Uropod 3 inaequiramous (female), aequiramous (male). Telson, basally fused (1/10 - 1/3 of total length), slender-spinose.

Coxal gills sac-like, smallest on peraeopod 7. Brood plates ordinary.

Taxonomic-Distributional Commentary: This subfamily is well represented in the North Pacific region, by many of the more primitive and relatively shallow water taxa, including the genus *Heterophoxus* which Barnard & Karaman (1991, p. 613) place close to the ancestral harpiniin. The considerable degree of taxonomic diversity entrained within genera, particularly with respect to mouthpart morphology, suggests that further revisionary work is desirable. However, such a revision would necessarily be world-wide and beyond the scope of this study.

Harpinia Boeck

Harpinia: Boeck, 1876: 218.—Gurjanova, 1951: 365.—Barnard & Karaman, 1991: 611.

Taxonomic Commentary: Only two species, *H. antennaria* Meinert, 1893, and *H. pectinata* Sars, 1895, have been recorded from the North Pacific region, and these only from the northern (arctic) portion of the Bering Sea. Although the species are not treated here taxonomically, the following key may be used to distinguish them:

1. Peraeopod 7, hind margin of basis with 4-5 strong teeth; pleon plate 3 weakly produced, tooth little longer than basal width *H. pectinata* Sars

—Peraeopod 7, hind margin of basis normally serrate; pleon plate 3, tooth strongly produced, twice basal width *H. antennaria* Meinert

Heterophoxus Shoemaker

Heterophoxus Shoemaker, 1925: 22.—Barnard, 1960: 318.—Barnard & Karaman, 1991: 613.

Type species: *Heterophoxus pennatus* Shoemaker, 1925. (non *Harpinia oculata* Holmes, 1908).

Species (North American-Pacific): *Heterophoxus oculatus* (Holmes, 1908); *H. conlanae*, new species; *H. ellisi*, new species; *H. affinis* (Holmes, 1908); *H. pennatus* Shoemaker, 1925; *H. nitellus* Barnard, 1960; *Heterophoxus species* (part of Barnard, 1960, southern California).

KEY TO NORTHEASTERN PACIFIC GENERA OF *HARPINIINAE*

(partly after Barnard & Karaman, 1991: 591)

1. Pigmented eyes present (always in male); antenna 1 (male), flagellum calceolate, not callynophorate; antenna 2, peduncle 5 with 5-7 anterior marginal calceoli; telson broader than long. *Heterophoxus* (p.124)
—Eyes lacking or unpigmented (both sexes); antenna 1 (male) callynophorate, lacking calceoli; antenna 2 (male) peduncle 5 with 2 marginal calceoli; telson longer than broad 2.
2. Sexes strongly dimorphic; antenna 2 of male, flagellum elongate; antenna 1, male, basal flagellar callynophore weak 3.
—Sexes similar; antenna 2 of male short as in female; antenna 1, (male) flagellum with brushy basal callynophore *Harpinia* (p. 124)
3. Some rami of uropods 1-2 with posterior spines to apex; segment 2 of outer ramus of uropod 3 short; antenna 2, segment 1 usually ensiform *Pseudharpinia* (p.140)
—Uropod rami not spinose to apex; segment 2 of outer ramus of U3 elongate; antenna 1 weakly (or not) ensiform *Harpiniopsis* (p. 135)

Taxonomic Commentary: Holmes (1908) based his original descriptions of *H. oculatus* and *H. affinis* on very limited material from off the Channel Islands in southern California. Barnard's subsequent more extensive work (1960) confirmed and extended the species complexity (variation).

The present northern material contains additional morphological and ecological complexity which may indicate some or all of the following possible explanations: (1) Holmes' original species are wide ranging and variable; (2) Holmes' and Barnard's descriptions mask the presence of other North American species; (3) Holmes' species do not extend north to Alaska, and other northern species may be included in the BC material.

Without re-examination of the original material of both Holmes and Barnard (loc. cit.), and without consistent application of several diagnostic taxonomic characters not treated or illustrated by Holmes or Barnard (loc. cit.), but newly recognized herein, such explanations remain enigmatic. However, possibility (3) may be the likeliest correct scenario in view of what has been shown to be probably correct with other species complexes within other phoxocephaloidean subfamilies of the North American Pacific region.

Diagnosis: (see basic diagnosis in Barnard & Karaman, above). Rostrum entire, unstricted. Eyes pigmented, sexually dimorphic. Antenna 1 (male), peduncle 1 posterodistally pseudocallynophorate (with cluster of fine aesthetascs); flagellum basally calceolate, not callynophorate. Antenna 2, segment 1 strongly ensiform; in male, flagellum elongate, calceolate; peduncular segment 5 with 5-7 anterior marginal calceoli.

Mouthparts: Mandibular molar not tritirative, with marginal blades; palp slender; incisor not broadened, regularly

toothed. Maxilla 1, outer plate 9-spinose; palp broad, 2-segmented. Maxilla 2 weak. Maxilliped, inner plate setose, lacking apical spine(s); palp, dactyl short, with long apical spine.

Gnathopods, propods subsimilar, carpus of 1 with free hind margin. Peraeopod 5 short < peraeopod 7. Peraeopod 6 distal segments long. Peraeopod 7 (male), segment 5 unmodified but dactyl slender, curved forward.

Pleon plate 3, hind corner produced, lower margin setose. Uropods 1 & 2, outer ramus longer than inner. Uropod 2, outer ramus with special spines in some species. Uropod 3 variously inaequilateral, terminal segment of outer ramus minute; rami (male) marginally plumose-setose.

Telson lobes short, rounded, basally fused.

Taxonomic Remarks: Despite Barnard's re-examination of the type specimens of Holmes (1908) and Shoemaker (1925), the diversity of character states illustrated by Barnard (1960, plate 61) and his limited analysis of all characters states appears insufficient to justify synonymy of *oculatus*, *pennatus*, and *affinis* under Holmes' original name *oculatus*. Northern material differs significantly from Californian specimens in a number of character states involving the antennae, peraeopods, uropods, and pleon plate 3, for example. These differences are indicated in pertinent species descriptions, and in the key to North American Pacific species given below.

The South African species of *Heterophoxus* include the following: *Heterophoxus cephalodens* Griffiths, 1975; *H. opus* Griffiths, 1975; *H. ophthalmicus* (Schellenberg, 1925); and *H. trichosus* K. H. Barnard, 1932. These differ from North American counterparts mainly in having uropod 1 (and uropod 2?) with short bare outer ramus. The antarctic species, *H. videns* K. H. Barnard 1930, is similar to *H.*

KEY TO NORTH AMERICAN PACIFIC SPECIES OF *HETEROPHOXUS*

1. Peraeopod 6, segments 6, posterior marginal setae and/or spines lacking (or nearly so); telson lobes fused basally; pleon plate 3, hind process usually strong, upcurved 2.
—Peraeopod 6, segment 6 with posterior marginal setae; telson lobes separated nearly to base; pleon plate 3, hind process short or medium, but nearly straight, not strongly upcurve. 5.
2. Peraeopod 6, segment 5 lacking posterior marginal spines or setae 3.
—Peraeopod 6, segment 5 with posterior spines and setae 4.
3. Coxae 1 & 2, lower margins setose throughout; antenna 2 (male) peduncle 5 with 7 anterior marginal calceoli *H. affinis* (p. 126)
—Coxae 1 & 2, lower margins setose posteriorly only; antenna 2 (male), peduncle 5 with 5 marginal calceoli *H. pennatus* (p. 134)
4. Peraeopod 7, basis, hind margin normally toothed or serrate; pleon plate 3, hind process basally thick *H. nitellus* (p. 134)
—Peraeopod 7, basis, hind margin strongly (deeply) toothed; pleon plate 3, hind process slender *Heterophoxus* sp. 1 (p. 134)
5. Peraeopod 6, segment 6 with singly inserted posterior marginal setae; pleon 3 with medium hook; peraeopod 7 (female) lacking coxal gill 6.
—Peraeopod 6, segment 6 with doubly or triply inserted posterior marginal setae; pleon plate 3 with weak posterior process; peraeopod 7 (female) with small coxal gill 7.
6. Peraeopod 6, segment 5 with two short posterior marginal spines only; uropod 2 (male), spines not special; uropod 2, peduncular marginals very long *H. ellisi* n. sp. (p. 132)
—Peraeopod 6, segment 5, posterior margin with at least one spine and setal cluster; uropod 2 (male), outer ramus with row of elongate copulating spines; uropod 2, spines normal . *H. ellisi* variant (p. 134)
7. Peraeopod 6, segment 6 distinctly longer than segment 5; hind margin with distal doubly inserted setae; pleon plate 3 lower margin with 20 setae; California *H. oculatus* (p. 125)
—Peraeopod 6, segment 6 barely longer than segment 5; hind margin with doubly and triply (not (or rarely) singly) inserted setae, pleon plate 3, lower margin with 7-10 marginal setae. *H. conlanae* n. sp. (p. 130)

Heterophoxus affinis (Holmes) (Figs. 29A, 30)

Harpinia affinis Holmes, 1908: 523, fig. 29.

Heterophoxus oculatus Barnard, 1960, pl. 60: A - D. (WASH.);—pl. 60: L CAL., Velero Stn. 2414);—pl. 61: G, H, I (CAL., Stn. 2170).

non: *Heterophoxus pennatus* Shoemaker, 1925: 22, figs. 1-3. (Gulf CAL.).

Harpinia oculata Holmes, 1908: 521, fig. 28.—Barnard, 1960: 320, pl. 59 (= *Heterophoxus* sp. 1);—pl. 60, D-K;—pl. 61, J. (new).

Harpiniopsis oculatus nitellus Barnard, 1960, pl. 61: A-F.

Material Examined:

SE ALASKA: ELB Stns., 1961: Resurrection Bay, Stn. A135, 24 m., July 11 - 1 female ov. (9.0 mm), with slide mount; Leo Anchorage, Stn. A165, 40-50m, mud, July 23 - 6 females, 1 male; Ibid, Stn. A167 - 1 female (variant).

FIG. 29A. *Heterophoxus affinis* (Holmes)
29B. *Heterophoxus oculatus* (Holmes)
(SEE PAGE 127 - OPPOSITE)

FIG. 30. *Heterophoxus affinis* (Holmes)
FEMALE (ov.) (7.0 mm); MALE (7..25 mm).
(SEE PAGE 128)

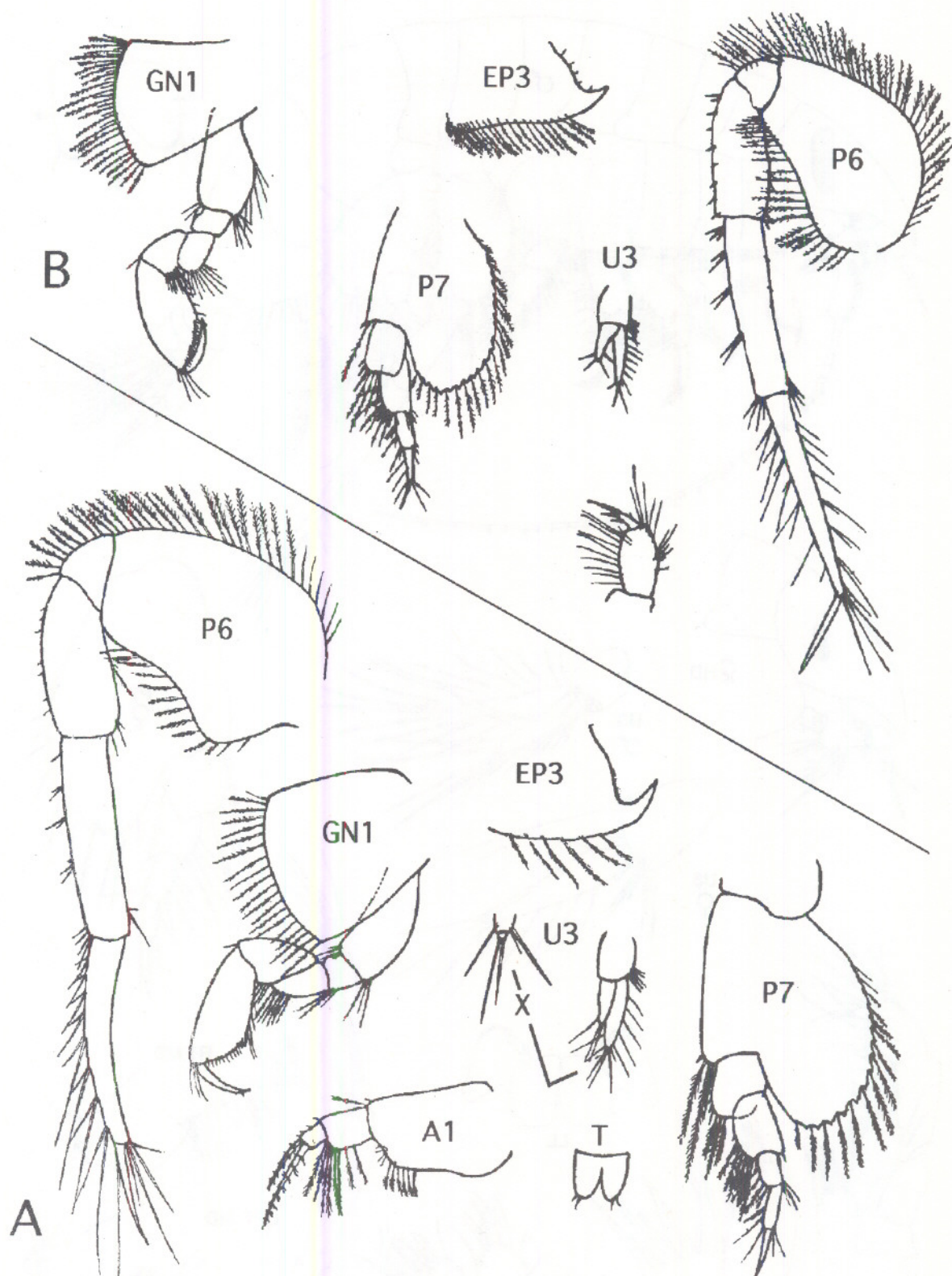
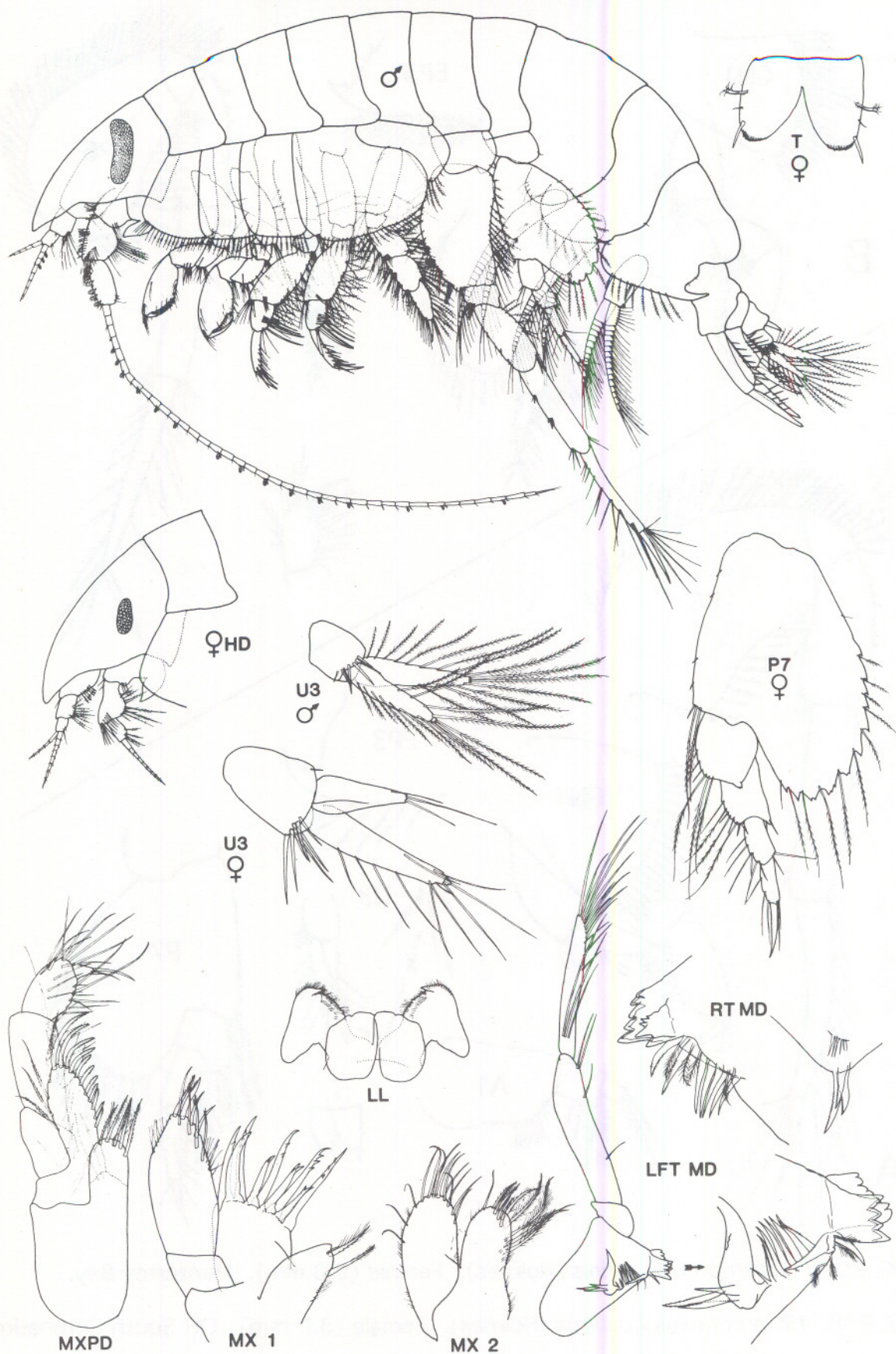


FIG. 29A. *Heterophoxus affinis* (Holmes). Female (9.0 mm). Monterrey Bay.

FIG. 29B. *Heterophoxus oculatus* (Holmes). Female (8.0 mm). Off South Coronado I.

(all figures modified from Holmes, 1908)



BRITISH COLUMBIA: Queen Charlotte Islands region: Dixon Entrance, J W Scoggan Stn. 105, 135 m., Aug. 12, 1965 - 2 females.

South-Central coast: ELB Stns. J1, Jervis Inlet, 360 m., mud, May 12, 1977 - 4 females, 8 juvs.; Ibid. J2, 576 m., - 15 specimens incl. males & females.

Burrard Inlet region: ELB Stns, Nov. 2, 1977: Stn. P4, 110 m., mud, (4 vials)- approx 100 specimens, incl. mature males, females, and immatures; Stn. P5, 80 m. (20); P6, 110 m. (40); Queen Charlotte Channel, St. P7, 240 m. - 1 male (7.5 mm), 1 female (7.0 mm); P8 (2 males, 2 females).

Pilot Cove, ELB Stn. P1, 44-50 m - 1 male (7.25 mm), 1 female ov. (7.0 mm), with slide mounts, + 15 other specimens. West Bay, Stn. P2, 20-24 m. (2 vials) - 87 specimens; Stn. P3, 60 m. (3 vials) - 1 female br. II (7.0 mm), with slide mount (fig'd), 1 male (7.5 mm), with slide mount (fig'd), + 40 specimens (males, females, juvs.) CMN Cat. No. NMCC1993-0040.

Burrard Inlet region, ELB Stns., July 4-5, 1978: V2, 3-8 m. - 3 females, 7 im.; V3, 25 m. - 10 specimens; V4, 50 m. - 40 mostly im.; V6, 160 m. - 60 specimens (males, females, im). C. Levings Stns., Sept. 1, 1977: B1, 51 m. - 6 females; Stn. B4, 112 m. - 2 females, 2 im.; B6, 24 m. - 2 males, 8 females, 5 im.

Vancouver Island: Haro Strait, D V Ellis Stns. 2701-2702, 20 m., March 8, 1979 - 3 females.

Outer Shelf, IOC Stn. DS 405-1, (3 lots) - 12 specimens including mature males and females.

Numukamis Bay, PF and HB Stns A2112, - 1 female; ROM, J P Tully cruise, Jan. 23, 1988, - 1 male.

WASHINGTON: Friday Harbor, KE Conlan colln, 20 m., Jan 1, 1987, - 6 females.

Diagnosis. Female ov. (6.5 mm): Rostrum large, down-curved apically. Eye small, remote from lower head margin. Antenna 1, flagellum 8-9 segmented; accessory flagellum 4-5 segmented. Antenna 2, peduncle 4 with distal fan of 8 medium spines, segment 5 short; flagellum with 9-10 segments.

Mandible, molar, apex with 3 blades; spine row with 8 blades; left lacinia unevenly 7-dentate, right lacinia flabellate; palp segment 3 with 3 strong baso-facial setae. Maxilla 1, palp very broad. 1 apical spine distinctly largest. Maxilla 2, inner plate with 3 facial setae. Maxilliped, inner plate broad, 5 apical setae; outer palte with 11 strong curved masticatory spines; palp segments 2 & 3 relatively broad, heavy.

Coxae 1-4 medium deep, lower margin setose throughout. Coxa 4 little broader than deep, front corner rounded. Gnathopod 1, posterior margin of carpus long, ~1/2 anterior margin; propods relatively small.

Peraeopods 3 & 4, segment 5 short; segment 6 hind margin with 5-6 spine clusters; dactyl medium, length about 1/2 segment 6.

Peraeopod 5, coxa, hind lobe relatively small and shallow, depth less than proximal margin; dactyl short ~1/2 segment 6. Peraeopod 6, basis shallowly emarginate behind, with proximal marginal bulge; segments 5 & 6 medium long, hind margins devoid of spines and setae, anterior margin of segment 5 with 2 spine groups; dactyl medium. Peraeopod 7, basis, hind lobe narrow, margin with 9-10 strong teeth.

Pleon plate 3 with strong posterior upcurving hook or process, lower margin sloping upwards posteriorly, with 9-10 medium long setae. Uropods 1 & 2, rami with 3-4 medium spines. Uropod 2, peduncle with relatively few (6-7) long outer marginal spines. Uropod 3, outer margin of outer ramus with several slender non-plumose setae, inner ramus longer than peduncle.

Telson little longer than wide, lobes fused basally 1/4 to 1/3 their length.

Male (7.5 mm): Eye large, slender-reniform, nearly vertical. Antenna 1, peduncle 2 with postero-distal fan of 3-5 plumose setae; basal 3 flagellar segments calceolate. Antenna 2, peduncle 5 short, little longer than segment 4, anterior margin with 6-7 calceoli; flagellum with 35-40 segments, alternately calceolate.

Peraeopod 7, dactyl shorter than segment 6, slender, curved forwards.

Uropod 3, peduncle with distal fan of 4-5 spines; ramal margins with 4-9 plumose setae.

Taxonomic Commentary: Barnard (1960, loc cit.) partially figured a mature male of this species from Friday Harbor, WA., that agrees in nearly every detail with the present northern regional collections. Holmes' original illustration (Fig. 29A) clearly shows the posterior margin of segment 6 of peraeopod devoid of spines or setae in *H. affinis*. This contrasts with the single and double pairs of setae shown on that margin in his drawings of *H. oculatus* (Fig. 29B). The posterior tooth of epimeral plate 3 also contrasts strongly in the two species.

The Californian material of Holmes (1908) from Monterey Bay, and Barnard (1960, pls. 60, 61, part) from the Santa Barbara region, differs slightly from more northerly specimens in that the basis of peraeopod 6 (female) bulges postero-proximally more strongly.

As Barnard (1960) has intimated, the male material of *H. pennatus* (Shoemaker, 1925) from the Gulf of California appears very close to the male of *H. affinis* described here. However, even though the female has not been described, the following features of the male of *H. pennatus* would appear to justify retention of Shoemaker's form as a distinct species: Antenna 2, peduncle 5, with 5 anterior marginal calceoli; coxae 1 & 2, lower margins are setose posteriorly only, (not throughout; mandible, palp lacks proximal group of "A" setae; maxilla 1, palp 1-segmented (rather than obscurely 2-segmented); and pleon plate 3, hind process is medium-small, straight, rather than large and upcurved.

The 7.0 mm. female of "*H. oculatus*" figured by Barnard (1960, pl. 60: G, I, J) from Californian Sta. 2142 also appears distinctive in the irregularly toothed hind margin of the basis of pereopod 7, and the weak hind process of pleon plate 3. In the male, peduncular segment 5 of antenna 2 is lined with 7 distinct calceoli, and the rami of uropod 3 are closely subequal and margins richly lined with plumose swimming setae. However, failing redescription of the type specimen, the information provided by Barnard (loc. cit.) is insufficient to justify its formal recognition at this time as a distinct species.

Distribution: From S. E. Alaska (near Sitka) through the Queen Charlotte Islands, north-central and south central coasts, especially in deep fiords, in bottom muds (to 600+ m. in depth), Southern Vancouver Island and San Juan Islands, south to southern California.

***Heterophoxus conlanae*, new species**

(Fig. 31)

Heterophoxus oculatus J. L. Barnard, 1960: 320-22, pls. 59-61 (part?).—Conlan 1978, lists (mainly?).—Bousfield, 1978 (in Conlan, 1978).

Material Examined:

SE ALASKA: ELB Stns. A165, Leo Anchorage, 40 m, July 23, 1961 - 2 females; ELB Stn. S13F1, Chichigof I., 0-3 m., July 31, 1980 - 2 females.

BRITISH COLUMBIA: Queen Charlotte Islands: Head of Big Inlet, C. McLean Fraser Stn. 3513, June 6, 1935 - 1 female; ELB Stn. E11, Transit I. 70 m., July 16, 1957 - 1 female ov. (7.0 mm) with slide mount, 15 other females. North-central coast: (14 station lots and 100+ specimens, as follows): ELB Stns., Calvert I. to Klakquot Channel, July-August, 1964: H17 (1); H21 (1); H25 (24 females, 12 males, 50 im. & juvs.); H27 (1); H34 (1); H36 (1 female, 2 antepenult. males); H62 (1); H64 (1). Swanson Bay, C. Levings Stns., 51-60 m., August 18, 1975: 51B-001 (1); 51B-002 (1); 51B-003 (2 females, 1 juv.); 51B-010 (1 female ov. (5.5 mm), with slide mount); 51B-013 (1); Ibid, 51B-028, 52 m., April 4, 1976 (1).

Vancouver Island, outer coast: ELB Stn. B28, Edward King I., LW, July 10, 1976 - 3 females.

Southeastern region and Strait of Georgia: :Saanich Inlet, KE Conlan Stns., January - May, 1975: Verdier Pt. (Stn 12101), <15 m., fine sand - 1 female ov. (7.0 mm) HOLOTYPE, CMN Cat. No. NMCC1993-0041; 1 male (6.5 mm) ALLOTYPE CMN Cat. No. NMCC-0042; 45 female and 2 juvenile PARATYPES, CMN Cat. No. NMCC1993-0043.; Stn. 11132, Jan. 16 - 1 female, 2 juvs.; Stn. 12155, 10 m., Jan 15 - 4 females, 2 juveniles; Stn. 75-1-3, 8 m., Feb. 7 - 1 female; Stn. 75-1-4, Feb. 2 - 1 male penult. (6.5 mm) with slide mount, 3 females, 2 im, PARATYPES, CMN Cat.

No. NMCC1993-0044; Stn. 75-4-9, 11 m., Mar. 19 - 1 female; Stn. 1979-109, 5.1 m., May 1 - 2 females.

Saanich Inlet, K. E. Conlan Stns. (unspecified), 5 lots 7.2 - 10.8 m., Jan.-May, 1975 - 11 females, 3 males antepenult., 2 juvs., 2 im. Saturna I., JFL Hart colln., Aug. 24, 1954 - 1 male (dissected).

Sidney Region, D.V. Ellis Stns., Feb-March, 1979: Sidney Channel, Stn. 1001, 40 m., - 7 females; Stns. 1601-1602, 20 m. - 7 females; Stn. 2201, 14 m., - 7 females; Stn. 2202, 14 m. - 2 males, 2 females; Stn. 2401-2402, 24 m. - 1 female; Stn. 2602, - 1 female br. I (7.8 mm) with slide mount, 5 other females, 1 male; Stn. 3401, 16 m. - 8 females; Stn. 3502, 17 m. - 1 female.

Strait of Juan de Fuca, Victoria region, McCauley Pt., G W O'Connell collns, 26 m., Aug. 26, 1976 - 1 female ov. (6.4 mm), with slide mount, 4 other females.

WASHINGTON: San Juan Islands: Friday Harbor, at marine labs, ELB Stn. F7, night light, July 21, 1955 - 5 males; Brown Island, ELB colln., 50-60 m., Nov. 9, 1983 - 1 male; Friday Harbor, K.E. Conlan Stn. 87-14-2, 20 m., Jan. 1, 1987 - 2 females.

Diagnosis. Female ov. (7.0 mm): Rostrum nearly straight. Eye medium, subreniform, 20-25 faceted. Antenna 1, peduncle 2 with fan of 8 postero-distal setae; flagellum 9-10-segmented; accessory flagellum 6-7-segmented. Antenna 2, peduncle 4 with fan of 8-10 antero-distal strong spines; peduncle 5 long, equal to segment 4; flagellum 8-9-segmented.

Mandible, molar short, with 3 stout apical blades; spine row with 7-9 blades; left lacinia 8-dentate; right lacinia flabellate flabellate; palp segment 3 with single short basofacial seta. Maxilla 1 palp slender, with 4 stout apical spines. Maxilla 2 inner plate with 2-3 facial setae and 3 stout inner marginal setae. maxilliped inner plate small, narrow with 3 apical setae; outer plate with few (8-9) curved masticatory spine; palp segments 2 & 3 relatively slender.

Coxae 1-4 broad, lower margin with 18 setae; coxa 4 very large, lower margin convex. Gnathopod 2, propod distinctly larger than in gnathopod 1; carpus of gnathopod 1 with short posterior margin.

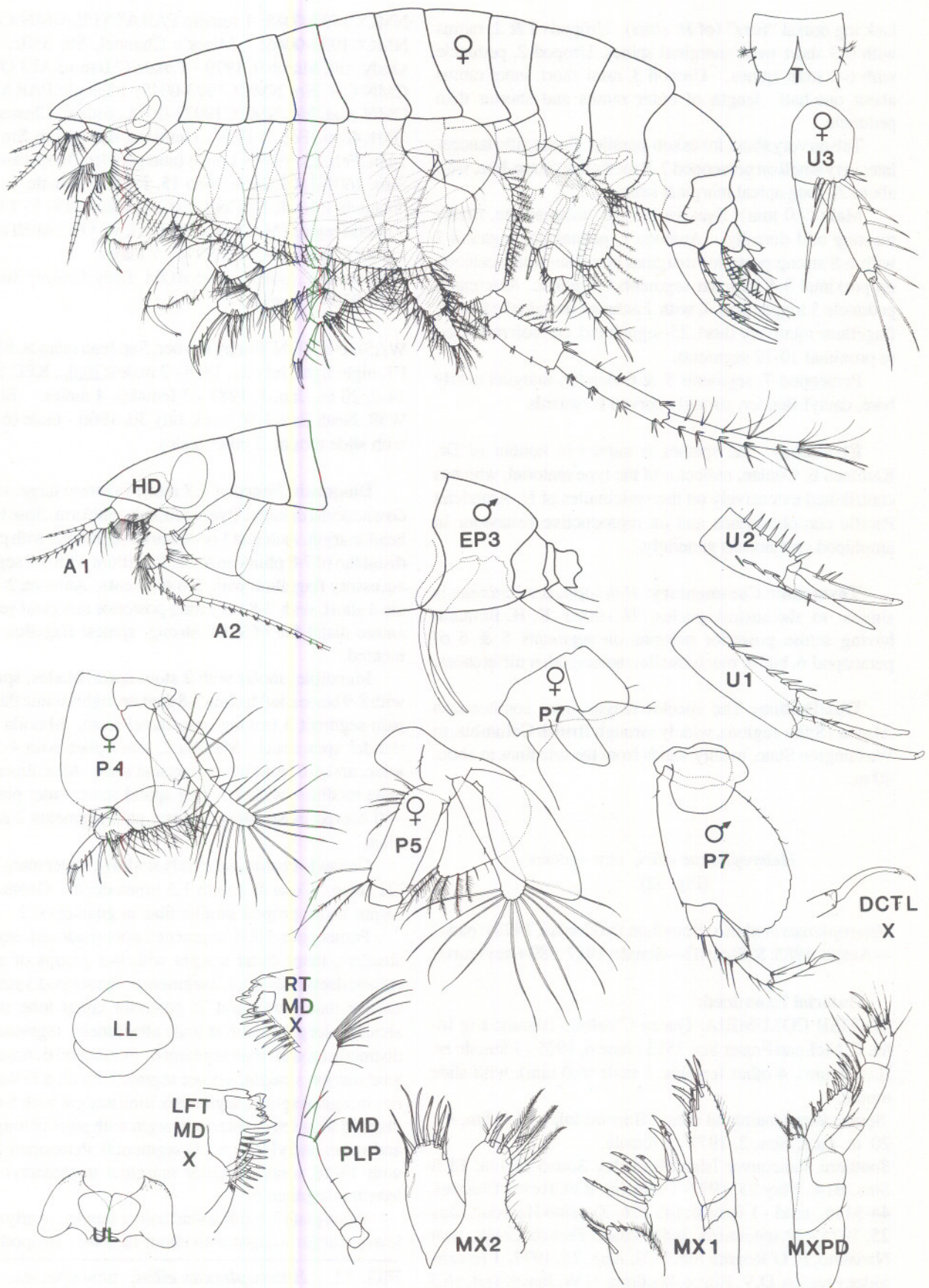
Pereopods 3 & 4, segment 5 not shortened; segment 6 with 2-3 single slender posterior marginal spines. Pereopod 5 strong, not shorter than pereopod 7; coxa, hind lobe very deep, greater than proximal margin at body. Pereopod 6, basis broad, hind margin not incised, hind setae short segment 5, hind margin with spine clusters, segment 6 with 3-5 clusters of doubly or triply grouped setae; dactyl short < 1/2 segment 6. Pereopod 7, basis not greatly expanded, hind margin with 14-16 median teeth; dactyl long > segment 6.

Pleon plate 3, hind corner very short, slightly upturned, lower margin with 7-10 setae. Pleosome 2 & 3 nearly clean,

FIG. 31 *Heterophoxus conlanae*, new species

FEMALE ov (7.0 mm) HOLOTYPE; MALE

(7.0 mm) ALLOTYPE. (SEE PAGE 131 - OPPOSITE)



lack ing dorsal "fuzz" (of *H. ellisi*). Uropods 1 & 2; ramus with 0-3 short weak marginal spines. Uropod 2, peduncle with 6-8 stout spines. Uropod 3, rami short, inner ramus about one-half length of outer ramus and shorter than peduncle.

Telson very short, lobes sub-parallel. Coxal gills lanceolate; very small on pereopod 7. Brood plates strap-like, with about 20 long apical marginal setae.

Male (7.0 mm): Eyes very large, subquadrate, nearly meeting mid-dorsally. Antenna 1, peduncular segment 2 with 6-8 strong posterior marginal plumose setae; calceoli on proximal 3-4 flagellar segments calceolate. Antenna 2, peduncle 5 longer than 4, with 7 anterior marginal calceoli; flagellum relatively short, 25-segmented, calceoli restricted to proximal 10-12 segments.

Pereopod 7, segments 5 & 6 slender, margins nearly bare, dactyl slender, strongly curved forwards.

Etymology: The species is named in honour of Dr. Kathleen E. Conlan, collector of the type material, who has contributed extensively on the systematics of N. American Pacific corophioideans and on reproductive behaviour in amphipod crustaceans generally.

Taxonomic Commentary: *Heterophoxus conlanae* is similar to the austral species, *H. videns* K. H. Barnard, having setose posterior margins on segments 5 & 6 of pereopod 6, but is much smaller, among other differences.

Distribution: The species ranges from southeastern Alaska (Sitka region), widely through British Columbia, to Washington State, in silty sands from the tide lines to about 40 m.

Heterophoxus ellisi, new species
(Fig. 32)

Heterophoxus oculatus: Bousfield (in Conlan, 1978) (part)?
—Austin, 1985: 598(part)?—Stauder, 1987: 380+key (part)?

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands: Big Inlet, C. McLean Fraser Sta. 3513, June 6, 1935 - 1 female br. II (8.0 mm), 4 other females, 1 male (6.0 mm), with slide mount.

Southeastern mainland coast. Burrard Inlet: ELB Stn. P2, 20 m. mud, Nov. 2, 1977 - 1 female.

Southern Vancouver Island: Berkeley Sound region: ELB Stns. B14, May 25, 1977 - 1 female; B14, Trevor Channel, 44-54 m., mud - 1 female; Stn P26, Koprino Harbour, May 25, 1975 - 12 specimens. Inner coast: French Creek, near Nanaimo, P. O'Rourke Stn. FC8, Aug. 23, 1977 - 1 female. Sidney region, D. V. Ellis collections: N.W. James Spit, 16.5 m. sandy silt, Mar. 8, 1979 - 1 female ov. (6.8 mm) with slide mount, 1 female (6.8 mm) HOLOTYPE, CMN Cat. No.

NMCC1993-0045; 1 female PARATYPE, CMN Cat. No. NMCC1993-0046; Miner's Channel, Stn 3502, 17 m., sandy silt, March 9, 1979 - 1 male (7.0 mm) ALLOTYPE, CMN Cat. No. NMCC1993-0047; 1 female PARATYPE, CMN Cat. No. NMCC19923-0048. Sidney Channel, Stn. 1001, 40 m., Feb. 9, 1979 - 3 females; Haro Strait, Stn. 2201, 14 m., Feb. 23, 1979 - 1 male (antepenult); Boatswain Bank, Stns. 1601-1602, 20 m., Feb. 15, 1979 - 1 female.

Saanich Inlet, K.E. Conlan colln, May 1, 1975 - 1 female. Victoria region: McCauley Point, G. W. O'Connell coll., 49 m., silty sand, Aug. 26, 1976 - 2 males.

Vancouver I., outer coast: ROM Tully Cruise, Stn. 11A, 1988-030 - 1 female.

WASHINGTON: Friday Harbor, San Juan Islands, ELB Sta. F7, night light, July 21, 1955 - 2 males; *Ibid.*, KEC Stn. 87-14-2, 20 m., Jan. 1, 1987 - 7 females, 4 males. ELB Sta. W39, Neah Bay, LW level, July 30, 1966 - male (6.2 mm) with slide mount, 2 other males.

Diagnosis. Female (6.8 mm): Rostrum large, slightly downcurved distally. Eye small, sub-reniform, close to lower head margin. Antenna 1 peduncular segment 2 with posterodistal fan of 7-8 plumose setae; flagellum with 8-9 segments, accessory flagellum with 5-6 segments. Antenna 2, peduncle 4 short, with 7-8 very long posterior marginal setae and antero-distal fan of 9-10 strong spines; flagellum 8-segmented.

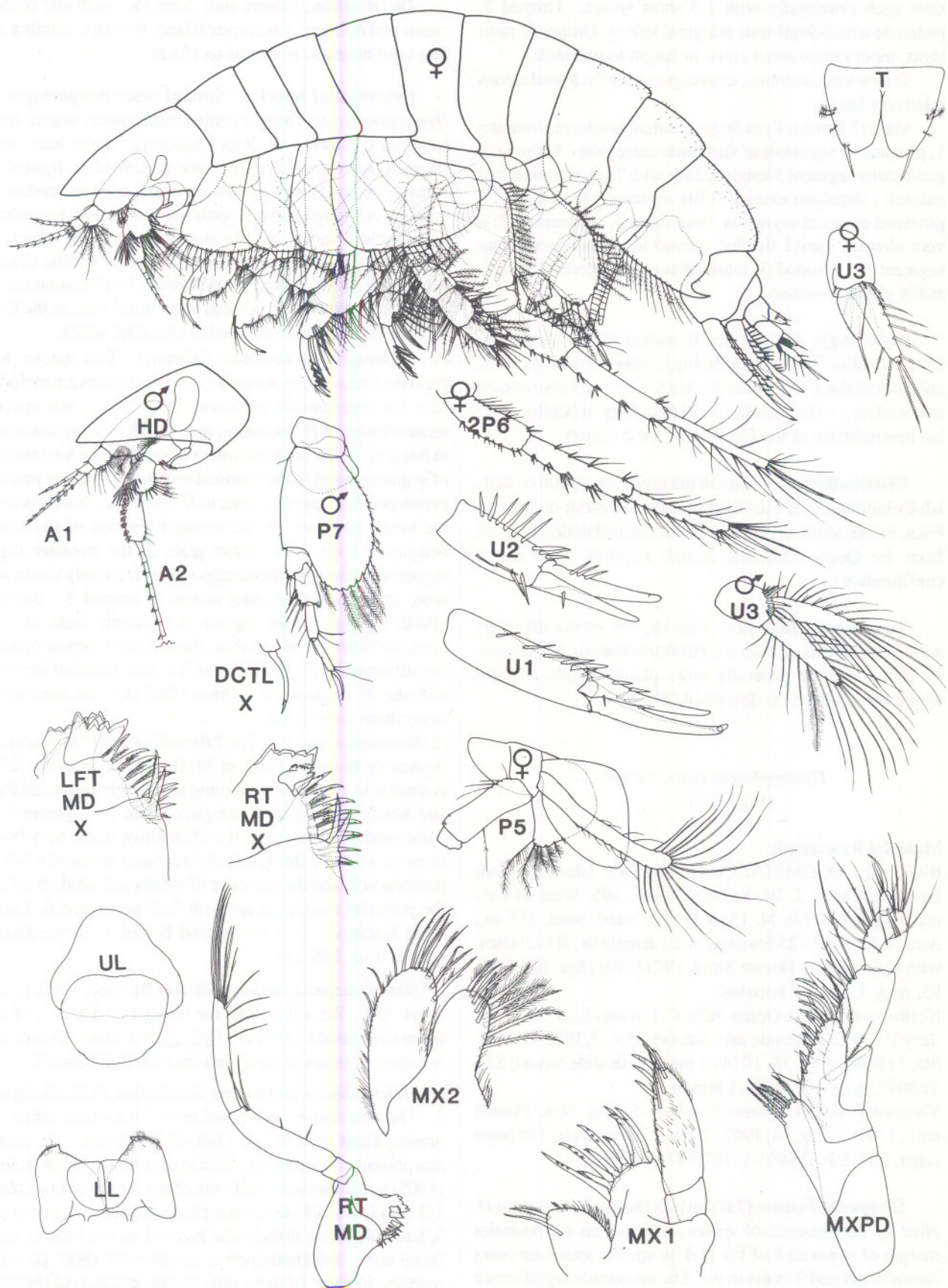
Mandible, molar with 2 stout apical blades; spine row with 8-9 blades, left lacinia 7-8 dentate, right lacinia flabellate; palp segment 3 lacking baso-facial setae. Maxilla 1, palp slender apex acute. Maxilla 2, inner plate with 4-5 facial setae, and 4-6 stout inner marginal setae. Maxilliped, inner plate medium, with 4-5 long apical setae; outer plate with ~10 curved masticatory spines; palp segments 2 & 3 medium.

Coxae 1-4 broad, relatively shallow, lower margins with ~21 setae. Coxa 4, length 1.5 times depth. Gnathopod 1, carpus short; propod smaller than in gnathopod 2.

Pereopods 3 & 4, segment 5 not broadened, segment 6 slender, inner distal margin with 4-5 groups of medium spines; dactyls short < 1.2 segment 6. Pereopod 5 strong, not shorter than pereopod 7; posterior coxal lobe medium, about as deep as width at body attachment; segments 4 & 5 distinctly broader than segment 6. Pereopod 6, basis broad, hind margin straight, setose; segment 5 with a fewer posterior marginal spines, segment 6, hind margin with 5-6 singly inserted long setae, anterior margin with pairs of long spines and setae; dactyl long > 1/2 segment 6. Pereopod 7, basis with 14-18 weak posterior marginal teeth; dactyl slender length > segment 6.

Pleon plate 3, tooth at hind corner slender, nearly straight, lower margin straight with about 12 setae. Uropods 1 & 2,

FIG. 32. *Heterophoxus ellisi*, new species
FEMALE ov (6.8 mm) HOLOTYPE; MALE ALLOTYPE (7.0 mm) (SEE PAGE 133 - OPPOSITE)



rami each proximally with 1-3 short spines. Uropod 2, peduncle with 8-9 tall outer marginal spines. Uropod 3, rami short, inner ramus about equal in length to peduncle.

Telson lobes medium, converging distally, apical spines relatively long.

Male (7.0 mm): Eyes large, medium reniform. Antenna 1, proximal 3 segments of flagellum calceolate. Antenna 2, peduncular segment 5 longer than 4, with 7 anterior marginal calceoli; flagellum elongate (30+ segments) with at least 6 proximal adjacent segments. Peraeopod 7, segments 5 & 6 very slender, dactyl slender, curved forward, shorter than segment 6. Uropod 3, rami subequal, margins relatively richly plumose-setose.

Etymology: The species is named in honour of Dr. Derek V. Ellis, Professor of Biology, University of Victoria, collector of the TYPE material, and a significant contributor to knowledge of the taxonomy and ecology of benthic marine invertebrates of the Canadian Pacific region.

Distribution: Occurring in the region of southern British Columbia to the San Juan Islands and Strait of Juan de Fuca, in fine sands at medium depth (an isolated record from the Queen Charlotte Islands requires more recent confirmation).

Taxonomic Remarks: This species shows affinities with *Heterophoxus conlanae*, but entrains a mixture character states that are generally more pleiomorphic. A more apomorphic variety is described below.

Heterophoxus ellisi, variant
(Fig. 32.2)

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands region: Dixon Entrance, J. W. Scoggan Stns. 105, West of Celestial Reef (54° 27' N, 131° 42' W), sand, mud, 155 m., August 12, 1965 - 25 females, incl. 1 female br. II (9.0 mm), with slide mount. Hecate Strait, JWS (FRB) Sta. 104 5-65-83, Aug. 11/65 - 2 females.

North-central coast: Ocean Falls, C. Levings Stns. 24B-013, July 19, 1972 - 1 female im.; Stn. O5, Dec. 3, 1972 - 1 male; Sta. 51B045, Aug. 18, 1974 - 1 male, with slide mount; Stn. 51B047, Aug. 18, 1974 - 1 female.

Vancouver Island: Queen Charlotte Sound, N.A. Powell coll., 190 m., Aug. 14, 1967 - 2 males, antepenult. Off outer coast, IOC Stn. DS405-1, 1979-81 - 1 female.

Diagnosis. Female (7.0 mm): Differing from typical *H. ellisi* by the presence of spines and setae on the posterior margin of segment 5 of P6, and by special spines on outer ramus of uropod 2 in the male. The taxonomic significance of these spines could not be fully ascertained because of the limited number of males in this material.

Distribution: Known only from the north and central coasts and northern Vancouver Island, British Columbia, on fine sand bottoms, in depths to 155 m.

Extralimital Species. Several other morphotypes of *Heterophoxus* have been recorded from coastal waters from southern California to Baja California. Some have been formally named, and others were described or figured as variants under the names *Heterophoxus oculatus* and/or *H. affinis*. Although these records are outside the immediate geographical scope of this study, because the genus is apparently endemic to the North American Pacific coastal marine region, we make the following brief comments on these forms, and have included them in the key, to the limit of their determinable distinctive character states.

(1) *Heterophoxus oculatus* (Holmes). This species was described reasonably accurately and his figures are included here for comparative purposes (Fig. 29B). His species seems closest to *H. conlanae*, and *H. ellisi* newly described in this text. In the double clusters of setae on the hind margin of segment 6 and in the rounded hind margin of the basis of peraeopod 6, it appears closer to *H. conlanae*. It differs from the latter, however, in the stronger setation of the lower margin of coxa 1, and pleon plate 3, the stronger distal segments of the maxilliped palp and the relatively longer and more strongly setose inner ramus of uropod 3. Barnard (1960, *loc. cit.*) partial figures of a mature male of "*H. oculatus*" from Friday Harbor, Puget Sound appear close to our illustrations of *H. conlanae*. To date, material identical with the *H. oculatus* of Holmes (1908) has not been found in northern collections.

(2) *Heterophoxus* sp. 1. The 7.0 mm female of "*H. oculatus*" figured by Barnard (1960, pl 59) from California Stn. 2448 is similar to *H. affinis* in having a strongly produced Ep3, and nearly lacking hind marginal setae on segment 6 of peraeopod 6. However, it is distinctive in the very broad form of coxa 4, the relatively elongate segments 4-6 of peraeopod 5, and the presence of spines and setal groups on the posterior margin of segment 5 of peraeopod 6, among other features. It is recognized herein as *Heterophoxus* species 1 (p. 126, key).

(3) *Heterophoxus oculatus nitellus* Barnard, 1960, p. 320, -1. 61 A-F. We agree with the distinctive features of this taxon illustrated by Barnard (*loc. cit.*) but would elevate it to full species status as *Heterophoxus nitellus* Barnard.

(4) *Heterophoxus pennantus* Shoemaker, 1925:25, figs. 1-3. The description was based on a 5 mm male taken at a marine night light in the Gulf of California. Its overall morphology is clearly referable to the *affinis* type of Holmes (1908) but differs in the following character states: coxa plates 1-3 with few (<10) lower marginal setae; coxa 5, peraeopod 5, hind lobe deep; mandibular palp segment 3 lacking basofacial setae; and gnathopod 1, carpus with short posterior margin. In view of these differences, and also of the small size of the mature animal and its isolated geographical location, we prefer to retain this taxon as a valid full species.

Harpiniopsis Stephensen

Harpiniopsis Stephensen, 1925: 171.—J. L. Barnard, 1958: —J. L. Barnard, 1960: 325.—Barnard & Karaman, 1991: 612.

Harpinia: Gurjanova, 1951: 365 (partim).

Type species. *Harpiniopsis similis* Stephensen, 1925, monotypy.

Species N. Pacific general region: *Harpiniopsis amundseni* Gurjanova, 1946 [227]. (Arctic-eastern Siberia); **H. fulgens* Barnard, 1960 [332] pls. 67, 68. (California to B. C.); **H. gurjanovae* (Bulycheva, 1936) [251]. (Bering Sea to B. C.); **H. kobjakovae* (Bulycheva, 1936) [254]. (Japan Sea to Bering Sea); *H. miharaensis* (Nagata, 1960) [395]; *H. moiseevi* (Gurjanova, 1953) [286]; *H. orientalis* Bulycheva, 1936 [391] (Japan Sea.); **H. pacifica* (Bulycheva, 1936) [252]. (Japan Sea); *H. percellaris* Barnard, 1971 [66] fig. 42; **H. salebrosa* (Gurjanova, 1936) [248]. (Chukchi & Bering Seas, med. d.); **H. schurini* (Bulycheva, 1936) [250]. (Japan Sea to Bering Sea); **H. tarasovi* (Bulycheva, 1936) [248] (Japan Sea, Bering Sea); **H. triplex* Barnard, 1971 [310A] fig. 43.

Diagnosis: Pigmented eyes lacking. Rostrum large, unconstricted laterally, often mid-dorsally ridged. Antenna 1, peduncular segment 2, posterior setae confined apically; basal flagellar segment(s) (in male) forming a weak calynophore (with group of enlarged aesthetascs). Antenna 2, segment 1 not (or weakly) ensiform; peduncular segment 3 with fan of 3 (or more) posterior marginal setae; segment 5 distinctly narrower than segment 4; in males, segments 3 & 4 with anterior marginal brush setae; segment 5 normally with 2 antero-distal calceoli; flagellum elongate, proximal segments (in some species?) with vestigial calceoli.

Lower lip, outer lobes with distal cones. Mandibular palpal hump of medium size; molar of type 6 (2-3 apical blade spines); left lacinia 4-dentate, right lacinia simple, bifid, or flabellate, with multiple teeth(?); right incisor with 3-6 teeth. Maxilla 1, outer plate with 7-11 slender apical spines; inner plate with 2-3 apical plumose setae. Maxilla 2, plates subequal, facial setae of inner plate subapical. Maxilliped, outer plate short, spines medium, pectinate; palp slender, segment 3 not distally produced; dactyl usually reduced, but with distinct elongate unguis.

Coxae 1-4 wide, deep. Gnathopods 1 & 2, propods small, similar, palms oblique; carpus short, shallow, weakly setose free hind margin.

Peraeopods 3 & 4, segment 6 slender, not spatulate. Peraeopod 5, segment 2 narrow; coxa, hind lobe deep, subacute. Peraeopod 6 basis broad, distal segments

slender, weakly armed. Peraeopod 7, segment 5 apparently unmodified, but dactyl longer, curved, in male.

Pleon plate 3, hind corner usually produced as an up-turned tooth. Uropod 1, peduncle lacking apical displaced spine. Uropod 3 aequiramous, rami bare, terminal segment of outer ramus large.

Telson lobes medium to long, fused basally 1/8 to 1/2.

Distributional Ecology: The genus is well represented in the North Pacific region especially in deeper softer sediments of the outer shelf. Three species are not uncommon in coastal sediments from the Bering Sea to Central California, but relatively rare south of Pt. Conception.

Taxonomic Commentary: The generic status of *Harpiniopsis* was reconfirmed by Barnard (1958) mainly on the basis of the very elongate flagellum of antenna 2 in the male; this character separates it from the genus *Harpinia* whose members are more specialized, and occur mainly in the North Atlantic region. Although males of most of the N. Pacific species of Harpiniinae are unknown, those studied here (and in lit.) conform with Barnard's distinctive male antennal character state (above). Thus, species for which females only are known are also assigned (tentatively) to *Harpiniopsis*. However, the diversity of mouthpart structure (in mandibular palp, maxilla 1 and maxilliped armature, etc.) exhibited by component species may provide bases for subgeneric, if not full generic subdivision, within the species complex.

A key to world species of the genus was provided by Barnard (1960, *loc. cit.*) with further detailed commentary on regional species (e.g. *H. triplex*) by Barnard (1971). Regretably, this deeper water genus was represented by very few species in present study material, and so the authors are able to add little to previous information or usefulness of previous keys. Species likely to be obtained in deep offshore waters of British Columbia would include the following taxa:

- (1) *H. gurjanovae* Bulycheva, 1936 (Bering Sea to B. C.)
- (2) *H. percellaris* Barnard 1971 (off Oregon)
- (3) *H. triplex* Barnard, 1971 (Oregon, v. deep)
- (4) *H. salebrosa* (Gurjanova, 1936) (Japan, Bering Sea)
- (6) *H. kobjakovae* (Bulycheva, 1936) (Bering Sea)
- (7) *H. schurini* Bulycheva, 1936 (Japan, Bering Seas)
- (8) *H. tarasovae* Bulycheva, 1936 (Japan, Bering Seas)
- (9) *H. galera* Barnard, 1960 (C. Calif, shallow)
- (10) *H. fulgens* Barnard, 1960. (British Columbia to C. California?)

Harpiniopsis fulgens J. L. Barnard
(Fig. 33)

Harpinia fulgens Barnard, 1960: 310, plate 67.

Material Examined: More than 260 specimens (in 180 lots) of which 140 were mature females, 55 juveniles or immatures, 7 penultimate males, 9 mature males, and 50 dried indeterminates (mostly subadult females), all in collections of the CMN, as follows:

BRITISH COLUMBIA: North-Central coast: Ocean Falls, 1974, C. Levings Stns. 51B-142, -047 - 10 females; 1977 C. Levings Stn. 28B-18 - 1 female.

Southeastern coast: Jervis Inlet, 1977, ELB Stn. J1 - 2 females; Queen Charlotte Channel, 1977, ELB Stns.: P7, off Bowen Island 1 female ov (3.5 mm), with slide mount (fig'd), CMN Cat. No. NMCC1992-1111; ELB Stn. P8, off Passage I. - 1 male (3.5 mm), with slide mount (fig'd), CMN Cat. No. NMCC1992-1110. Burrard Inlet, C. Levings Stn. B9, 1977 - 1 female; Jervis Inlet, ELB Stns. P1, P2, 300-400 m., Nov. 2, 1977 - 11 females; Indian Arm, ELB Stn. E5, 60 m. mud & coarse sand, Nov. 4, 1977. - 10 females.

South Vancouver Island: French Creek, P.O'Rourke Stn. FC3, August, 1977 - 1 female.

Vancouver Island, outer shelf, Institute of Ocean Sciences Patricia Bay, B. C.: 1979 (May, July, August,) Queen Charlotte Islands, 100-300 m. 10+ females. NMNS Access. No. 1983-57. Additional IOS lots taken off Vancouver Island during June-August, and the following year, from April - August, 1981, contained numerous lots of material tentatively identified as this species, but not examined in detail.

Diagnosis. Female ov. (3.5 mm): Rostrum with weak mid-dorsal keel, apex slightly downturned. Inferior lateral head lobe strongly produced, upturned. Antenna 1, flagellum 6-segmented; accessory flagellum 5-segmented.

Mandible, molar with 2 large apical blades; spine row with 5-6 blades, left lacinia 6-7 dentate; right lacinia flabellate; palp segment 3 with proximal facial cluster of 3 long "A" setae and a few posterior marginal "C" setae. Maxilla 1, outer plate with 11 apical spines; inner plate with 2 apical setae; palp weakly 2-segmented, apex with 5-6 slender spines. Maxilla 2, inner plate with 2 sub-apical facial setae. Maxilliped, inner plate apically with single spine and 4-5 plumose setae; outer plate slender, straight, with 8-9 marginal pectinate spines; unguis of dactyl elongate (2 X body).

Gnathopods, propods closely subsimilar; carpus of both short, hind lobe narrow.

Peraeopods 3 & 4, segment 5 short, nearly as deep as long; segment 6, hind margin distally long-spinose, dactyls medium. Peraeopod 5, coxal hind lobe distinctly shorter than basis; segments 5 & 6 elongate, subequal. Peraeopod 6, basis, anterior margin expanded medially, hind margin

straight; distal segments elongate (segment 6 longer than basis), very weakly spinose. Peraeopod 7, basis, postero-distal margin rounded, with numerous shallow serrations; segment 4-6 with anterior pairs of slender spines; dactyl very slender, longer than segment 6.

Pleon plate 3, hind process short, straight, not upturned; lower margin proximally with about 6 slender spines. Uropods 1 & 2, peduncles with several slender outer marginal spines; both rami with 2-3 slender posterior marginal spines. Uropod 3, rami smooth, outer slightly longer, terminal segment elongate ($> 1/2$ proximal segment).

Telson lobes medium, fused 1/5 basally, apices subacute, each with 2 disto-lateral slender spines; paired penicillate setae long,, disto-laterally inserted.

Coxal gills irregularly sac-like, medium broad, subacute distally, small on peraeopod 7. Brood plates regular.

Male (3.5 mm.): Antenna 1, flagellar segment 1 with 3-4 aesthetascs (weakly callynophorate), but no calceoli. Antennae 2, segment 4 strongly expanding antero-distally, with strong antero-distal fan of 8-10 slender spines; segment 5 slightly broadened behind, with 2 antero-distal calceoli; flagellum with 30-35 segments; segments 1, 3, 5 & 7 with minute vestigial calceoli. Peraeopod 7, distal segments and dactyl only slightly less robust than in female.

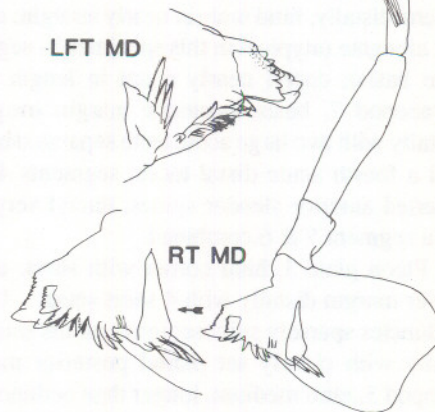
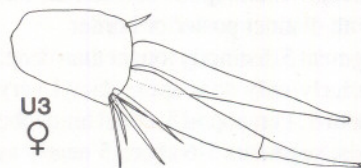
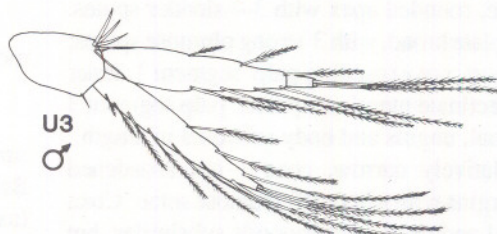
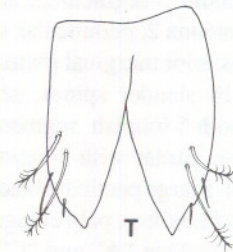
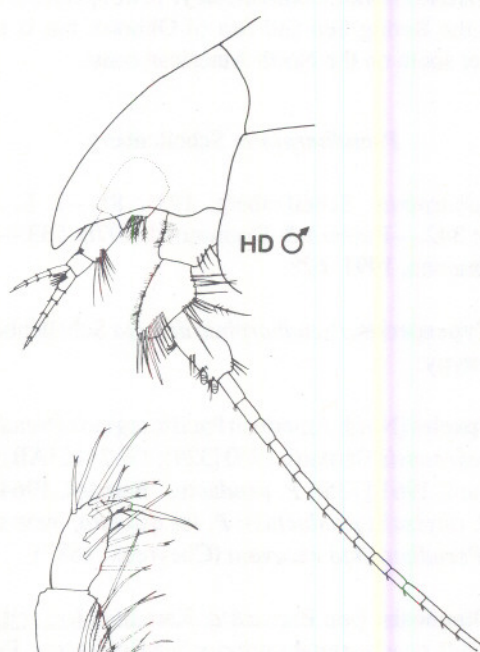
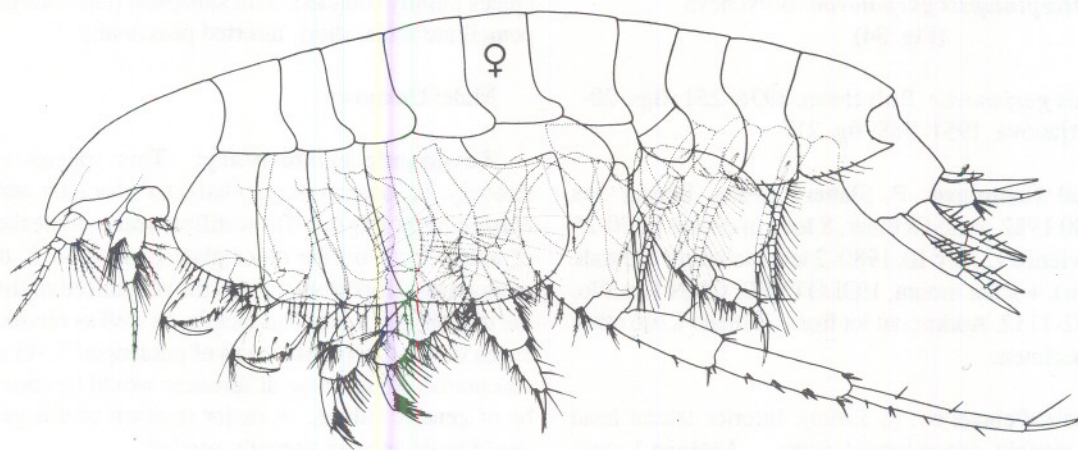
Uropod 3, rami slender, subequal, marginals with 3-6 plumose setae, outer ramus lacking distinct terminal segment.

Taxonomic commentary: Northern material is closely similar to that illustrated by Barnard (1960, pls. 67-68) except for minor differences in the shape of coxa 1, basis of peraeopod 6, form of the hind tooth on pleon 3, and spination of uropod 1. It is separable from *H. gurjanovae* by the very obvious difference in shape of the hind margin of the basis of peraeopod 7, by the very much longer distal segments of peraeopod 6, and by the presence of baso-facial setae on mandibular palp segment 3.

As noted below, this species is remarkably unlike *H. gurjanovae* diagnosed below. In many respects, especially the form of the mandibular palp, and uropod 3, it appears closer to species of the genus *Pseudharpinia*. A major revision of this deep-water genus is urgently needed.

Distributional Commentary: The species ranges from California north to British Columbia (but has not yet been taken in southeastern Alaska) in depths of 100-500+ metres, and to more than 2000 m. in the San Clemente Basin, California.

FIG. 33. *Harpiniopsis fulgens* J. L. Barnard.
FEMALE ov. (3.5 mm); MALE (3.5 mm)
(SEE PAGE 137 - OPPOSITE)



Harpiniopsis gurjanovae Bulycheva
(Fig. 34)

Harpiniopsis gurjanovae Bulycheva, 1936: 251, figs. 20-23 H.—Gurjanova, 1951: 368, fig. 217.

Material Examined: P. Slattery collns, Bering Sea region, 1980 1982, June-October, 8 lots, in depths of 20-25 m.: St. Lawrence I., July 10, 1980. 2 lots including 1 female ov. (3.5 mm), + slide mount, HOLOTYPE, CMN Cat. No. NMCC1992-1112. Additional lot from Unimak I. (no other data) - 1 specimen.

Diagnosis. Female ov. (3.5 mm): Inferior lateral head lobe short, straight, not upturned, acute. Antenna 1, peduncular segment 2 with fan of 5-6 postero-distal plumose setae; flagellum 5-segmented; accessory flagellum 4-segmented. Antenna 2, peduncular segment 4 little expanded, with 5-8 posterior marginal plumose setae and antero-distal fan of 9-10 slender spines; segment 5 shorter than 4; flagellum with 5 longish segments.

Mandible, molar with 3 stout apical blades; spine row short, with 4-5 large pectinate blades; left lacinia 4-5 dentate, right lacinia flabellate; palp elongate, segment 3 longer than segment 3, lacking "A" and "C" setae. Maxilla 1, outer plate with 7 apical spines, inner plate with 3 short apical setae; palp clavate, rounded apex with 3-4 slender spines. Maxilliped, inner plate broad, with 3 strong plumose spines; outer plate very short, not exceeding palp segment 1, inner margin with 5-6 pectinate marginal spines; palp segment 3 large, dactyl normal, unguis and body subequal in length.

Coxae 1-4 relatively narrow, coxa 1 not broadened distally, lower margins with few (<10) plumose setae. Coxa 4 enormous, broad and deep. Gnathopods subsimilar, but carpus of gnathopod 1 with distinct posterior border.

Peraeopods 3 & 4, segment 5 distinctly longer than deep; segment 6 spinose posteriorly only near apex; dactyl very long about equal to segment 6. Peraeopod 5, coxal hind lobe very deep, as long as basis; segments 5-6 short, 5 nearly as wide as long. Peraeopod 6 relatively short; basis expanded antero-distally, hind margin nearly straight; distal segments not elongate (atypical in this specimen? - segment 6 shorter than basis); dactyl nearly equal in length of segment 6. Peraeopod 7, basis, posterior margin irregular, postero-distally with two large acute teeth separated by a blunt tooth, and a fourth acute distal tooth; segments 4-6 with singly inserted anterior slender spines; dactyl very long, longer than segment 5 & 6 combined.

Pleon plate 3, hind corner with short, upturned tooth; lower margin distally with 4 short setae. Uropods 1 & 2, peduncles sparsely spinose; inner ramus smooth, outer medially with closely set paired posterior marginal spines. Uropod 3, rami medium, longer than peduncle, nearly bare, outer ramus slightly the longer, terminal segment short (<1/2 proximal segment).

Telson lobes relatively narrow, elongate, fused basally,

apices bluntly rounded, with subapical outer marginal seta; penicillate setae, short, inserted proximally.

Male: Unknown.

Taxonomic commentary: This species contrasts strongly, in several major character states, with *Harpiniopsis fulgens*. These differences include the number of apical teeth on the outer plate of maxilla 1, the much reduced maxilliped outer plate, the very different structure of the mandibular molar and lacinia, as well as obvious differences in the form of the basis of peraeopod 7. In any other taxonomic group, these differences would be considered to be of generic value. A major revision of this genus on a world basis appears urgently needed.

Distributional Commentary: ?The species is recorded from the Bering Sea and Sea of Okhotsk but is unknown further south on the North American coast.

Pseudharpinia Schellenberg

Pseudharpinia Schellenberg, 1931: 81.—J. L. Barnard, 1960: 342.—Barnard & Drummond, 1978: 533.—Barnard & Karaman, 1991: 628.

Type species. *Pseudharpinia dentata* Schellenberg 1931, monotypy.

Species (North American Pacific region): *Pseudharpinia sanpedroensis* Barnard, 1960 [329]; 1967 [423AB]; *P. cinca* Barnard, 1961 [735]; *P. productus* Barnard, 1964 [501A] (as *P. abyssalis productus*); *P. inexpectata*, new species. non *Pseudharpinia excavata* (Chevreux, 1887).

Diagnosis: (see Barnard & Karaman, *loc. cit.*). Rostrum full, nearly straight, inferior head lobe acute. Pigmented eyes lacking. Antennae short. Antenna 1, peduncle 2 very short. Antenna 2, segment 1 strongly ensiform; in male, peduncular segment 5 calceolate; flagellum elongate, possibly weakly calceolate.

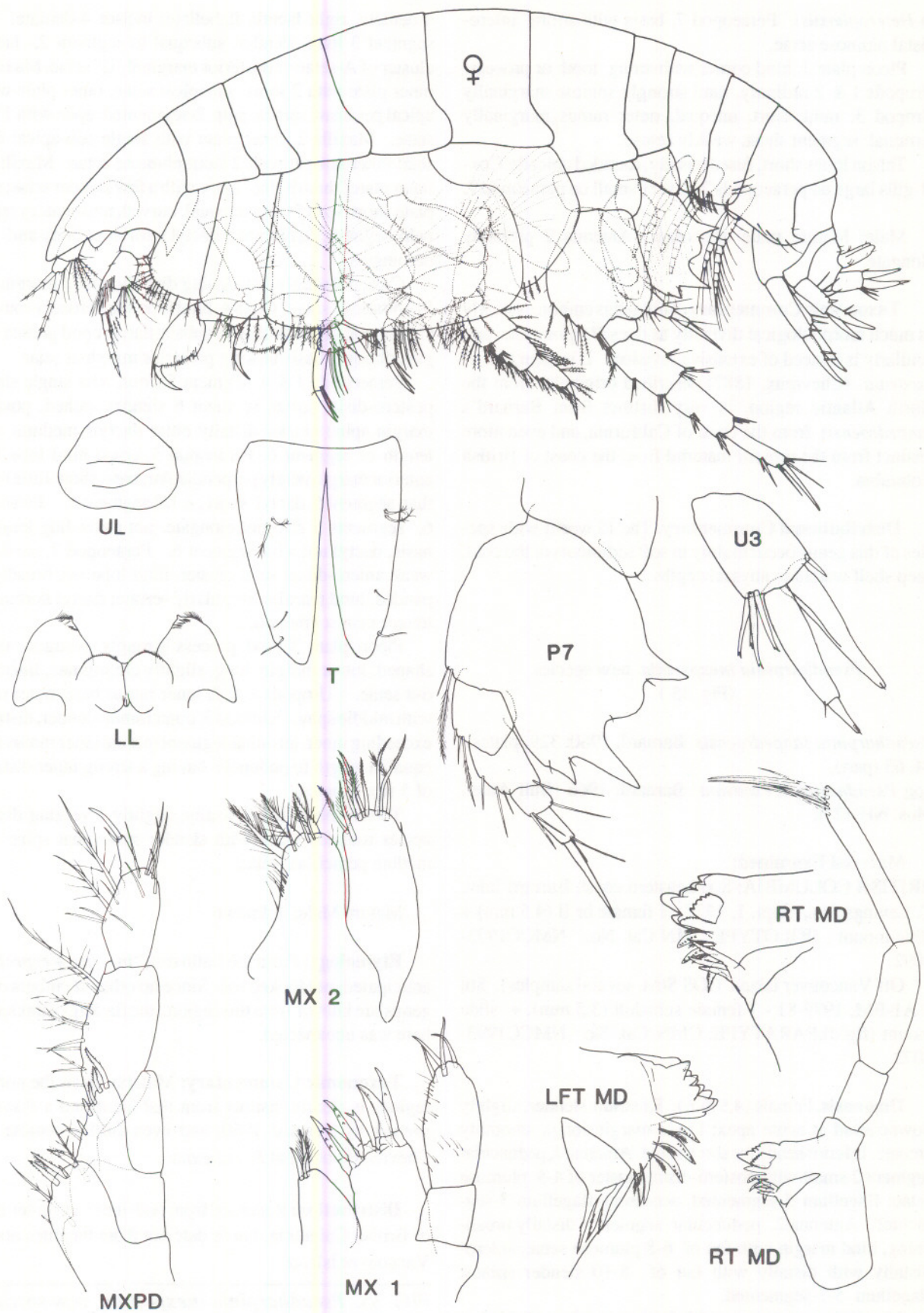
Mouthparts: mandibular molar small, apex with 2-4 blades; raker blades short, thick; palp slender, weakly setose. Maxilla 1, outer plate with 9 apical spines; palp 1 or 2-segmented. Maxilliped reduced; palp, dactyl small, with long apical spine.

Coxae 1-4 very broad, 1 expanded distally, lower margins with spaced plumose setae. Coxa 4, lobe rounded behind. Gnathopods 1 & 2 relatively strong, propods obliquely subchelate, subsimilar, carpus of both short. Peraeopod 5 strong, coxal hind lobe deep, dactyl short. Peraeopod 6, distal segments with anterior slender spines (as

FIG. 34. *Harpiniopsis gurjanovae* Bulycheva

FEMALE ov. (3.5 mm).

(SEE PAGE 139 - OPPOSITE).



in *Heterophoxus*). Peraeopod 7, basis with strong antero-distal plumose setae.

Pleon plate 3, hind corner with strong tooth or process. Uropods 1 & 2 ordinary, rami strongly spinose marginally. Uropod 3, rami short, unequal, outer ramus marginally terminal segment short, weakly setose.

Telson lobes short, fused basally, rounded apically. Coxal gills large on peraeopods 2-6, very small on peraeopod 7.

Male: Mature male unknown. Antenna 2 probably elongate.

Taxonomic Commentary. This genus embraces nearly as much morphological diversity as does *Harpiniopsis*, and similarly is in need of extensive revision. It is clear that *P. excavata* (Chevreux, 1887) described originally from the North Atlantic region, is very distinct from Barnard's *sanpedroensis* from the coast of California, and even more distinct from the present material from the coast of British Columbia.

Distributional Commentary. The 12 world-wide species of this genus occur mainly in soft sediments of the cold, deep shelf waters to abyssal depths.

Pseudharpinia inexpectata, new species
(Fig. 35)

Pseudharpinia sanpedroensis Barnard, 1960: 329, plates 64, 65 (part).

non *Pseudharpinia excavata* Barnard, 1966 (Bull. Amer. Mus. Nat. Hist. 127).

Material Examined:

BRITISH COLUMBIA: Southeastern coast, Burrard Inlet, C. Levings Stn., Sept. 1, 1977 - 1 female br II (4.5 mm) + slide mount, HOLOTYPE CMN Cat. No. NMCC1993-0092.

Off Vancouver Island (IOS Stns. several samples). Stn 2 A1-BM, 1979-81 - 1 female subadult (3.5 mm), + slide mount (fig'd), PARATYPE, CMN Cat. No. NMCC1993-0073.

Diagnosis. Female (4.5 mm): Rostrum slender, slightly downcurved at acute apex; lower margin long, smoothly arcuate. Inferior head lobe short, acute. Antenna 1, peduncular segment 2 small, with postero-distal cluster of 4-5 plumose setae; flagellum 5-segmented, accessory flagellum 3-segmented. Antenna 2, peduncular segment 4 distally broadening, hind margin with fan of 6-8 plumose setae, antero-distally with distally with fan of 8-10 slender spines; flagellum 5-7-segmented.

Mandible, molar, apex with 2 stout and 2 weak blades; spine row short, with 4-5 heavy pectinate blades; left lacinia

4-dentate, right lacinia flabellate; incisor 4-dentate; palp segment 3 long, slender, subequal to segment 2, lacking cluster of A-setae or posterior marginal "C" setae. Maxilla 1, inner plate with 2 short subapical setae, outer plate with 9 apical pectinate spines; palp 2-segmented, apex with 3 stout setae. Maxilla 2, inner plate with single sub-apical facial seta; inner margin with 2 stout plumose setae. Maxilliped, inner plate "thumb-like" apex with a few slender setae; outer plate short, with 5 very unequal, curved, masticatory spines; palp segment 2 columnar; dactyl with short body and slender unguis.

Coxa 1 strongly broadening distally, lower margin with 8-9 plumose setae. Coxa 4, hind lobe very broadly rounded. Gnathopod propods closely subsimilar, propod palmar margins oblique; basis lacking posterior marginal setae.

Peraeopods 3 & 4, segment 5 stout, with single slender postero-distal spine; segment 6 slender arched, posterior margin spine cluster distally only; dactyls medium > 1/2 length of segment 6. Peraeopod 5, coxal hind lobe deep, anterior margin nearly perpendicular; basis short, little longer than segment 5, dactyl short, < 1/2 segment 6. Peraeopod 6, segments 5 & 6 not elongate, not exceeding length of basis, dactyl not > 1/2 segment 6. Peraeopod 7, basis with weak antero-distal setal cluster, hind lobe not broadly expanded, hind margin irregularly serrate; dactyl normal, not longer than segment 6.

Pleon plate 3 hind process strongly produce, sickle-shaped, lower margin long, slightly emarginate, lined with 6-8 setae. Uropods 1 & 2, inner ramus bare, outer ramus with middle spines. Uropod 3, outer ramus slender, distinctly exceeding inner, terminal segment minute inner ramus about equal in length to peduncle having a strong inner distal fan of 5 stout spines.

Telson lobes fused basally, slightly diverging distally, apices rounded, each with slender sub-apical spine, sand median penicillate setae.

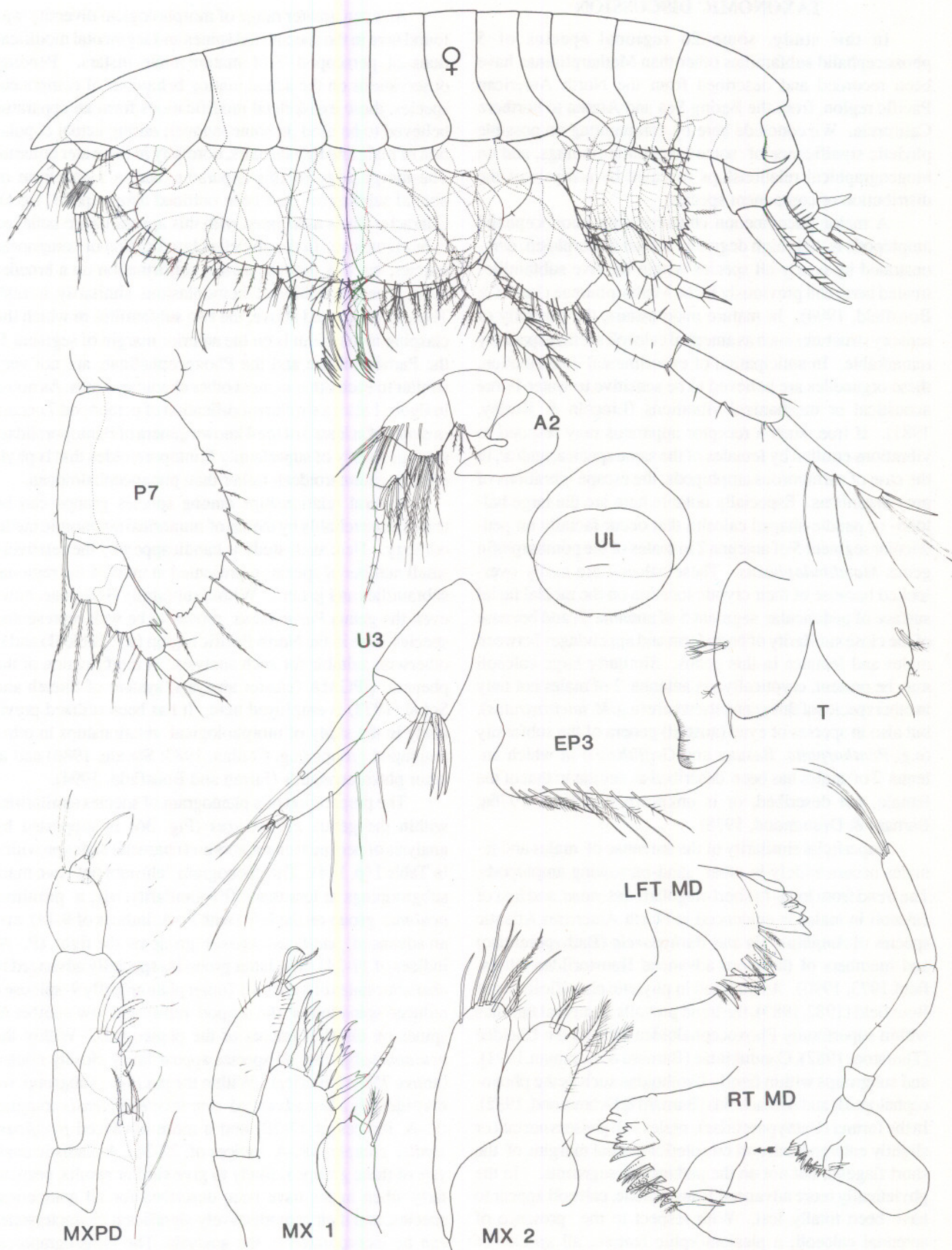
Mature Male: unknown.

Etymology: From the Latin root "*in - not + expectata*" - anticipated, not looked for. Since no other members of this genus are known from this region, the finding of this species here was unexpected.

Taxonomic Commentary: Material from the northern regions is clearly distinct from that identified as *P. sanpedroensis* by Barnard 1960, and even further remote from Chevreux's original *P. excavata*.

Distribution: Recorded from both inner and outer coasts of British Columbia, but to date not from localities north of Vancouver Island.

FIG. 35. *Pseudharpinia inexpectata*, new species.
FEMALE ov. (4.5 mm) HOLOTYPE.
(SEE PAGE 141 - OPPOSITE)



TAXONOMIC DISCUSSION

In this study, some 20 regional species of 5 phoxocephalid subfamilies other than Metharpiniinae have been recorded and described from the North American Pacific region, from the Bering Sea and Alaska to northern California. We conclude here by commenting on possible phyletic significance of some taxonomic findings, and on biogeographical relationships revealed by analysis of the distribution of component species.

A major phenomenon characterizing phoxocephalid amphipods is their high degree of sexual dimorphism, demonstrated by nearly all species within the five subfamilies treated here, and previously in the Metharpiniinae (Jarrett & Bousfield, 1994). In mature male instars, the diversity of sensory structures such as antennal calceoli seems especially remarkable. In anticipation of experimental confirmation, these organelles are believed to be sensitive to water-borne acoustical or mechanical vibrations (Lincoln & Hurley, 1981). If true, such a receptor apparatus may respond to vibrations emitted by females of the same species, and/or, in the case of carnivorous amphipods, the escape vibrations of prey organisms. Especially notable here are the large balloon- or paddle-shaped calceoli that occur facially on peduncular segment 5 of antenna 2 in males of the pontarpariniin genus *Mandibulophoxus*. These calceoli are easily overlooked because of their cryptic location on the medial facial surface of peduncular segment 5 of antenna 2, and because of the close similarity of body form and appendages between males and females in this genus. Similarly large calceoli may be present, cryptically, on antenna 2 of males not only in other species of this genus elsewhere (e.g. *M. uncirostratus*), but also in species of eyed (austral) genera of the subfamily (e.g. *Pontharpinia*, *Basuto*, and *Griffithsius*) in which antenna 2 of males has been described as similar to that of the female, not described, or is unknown (Griffiths, 1976a; Barnard & Drummond, 1978).

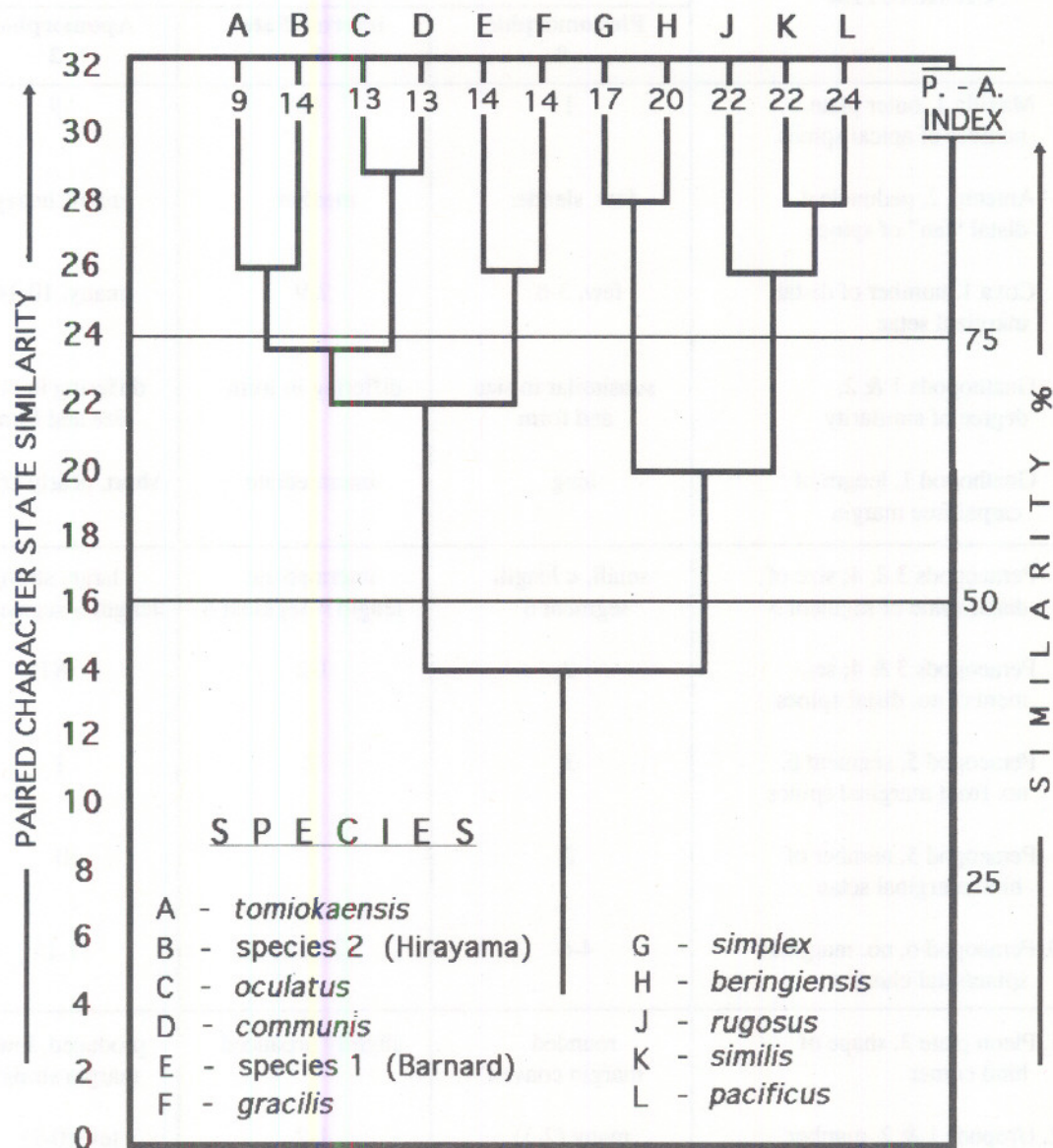
Superficial similarity of the antennae of males and females occurs widely in other sand-burrowing amphipods. The trend from long- to short-flagellate antennae, and loss of calceoli in males is evidenced in North American Atlantic species of *Amphiporeia* and *Bathyporeia* (Bathyporeiidae) and members of the more advanced Haustoriidae (Bousfield, 1973, 1990). As outlined in phyletic classifications of Bousfield (1982, 1983), the trend prevails in austral families within superfamily Phoxocephaloidea such as the Cheidae (Thurston, 1982), Condukiidae (Barnard & Karaman, 1991), and subgroups within family Urothoidae such as the phoxocephalopsids and zobrachoids (Barnard & Drummond, 1982). In the former (Bathyporeiidae), males still possess normal or slightly enlarged calceoli on anterior medial margins of the short flagella, but not on the peduncular segments. In the phyletically more advanced Haustoriidae, calceoli appear to have been totally lost. With respect to the presence of antennal calceoli, a plesiomorphic feature, all species of North American Pacific phoxid subfamilies are relatively primitive, and close to the subfamily ancestral morphotype.

An even greater range of morphological diversity was found here in the specialized spines and segmental modifications of pereopod 7 of mature male instars. Pending observations on the actual mating behaviour of component species, these exoskeletal modifications form an apparatus believed to be used, in some manner, during actual copulation of male and female pairs, normally in the water column. The morphology of this apparatus, across a spectrum of phoxid subfamilies, has been outlined above (p. 73, fig. 1). Character states associated with this apparatus are believed to be significant in the phyletic classification of component species, but this premise awaits confirmation on a broader basis. The possibility of homoplasious similarity is real. Thus, as diagnosed above, the two subfamilies in which the clasping mechanism is on the anterior margin of segment 5, the Parharpariniinae and the Phoxocephalinae, are not very similar to each other in most other character states. As noted in figure 1 also, a similar modification of pereopod 7 occurs in males of at least 3 of the 4 known genera of Pontoporeiidae, the type family of superfamily Pontoporeioidea that is phyletically gammaroidean rather than phoxocephaloidean.

Natural relationships among species groups can be tested more reliably by means of numerical taxonomic methodology. Here such study is handicapped by the relatively small number of species represented in most of the regional subfamilies and genera. Within subfamily Brologinae, however, the genus *Paraphoxus* proves to be well represented species-wise in the North Pacific region (see Table II) and is otherwise suitable for such analysis. A modification of the phenetic UPGMA (cluster analysis) system of Sneath and Sokal (1973) is employed here. It has been utilized previously in the study of morphological relationships in other amphipod groups (e.g. Conlan, 1983; Staude, 1986) and in other phoxocephalids (Jarrett and Bousfield, 1994).

The preparation of a phenogram of species similarities within the genus *Paraphoxus* (Fig. 36) is supported by analysis of pertinent characters and character states provided in Table I (p. 144). The phenogram "clusters out" two main subgroupings at less than 50% similarity, viz, a primitive *oculatus* group on the left (with P.-A. indices of 9-14), and an advanced *pacificus-rugosus* group on the right, (P.-A. indices of 17-24). The latter group is especially advanced in character states of maxilla 1 (outer plate apically 9-spinose), reduced spination of the uropod rami, and low number of spines on distal segments of the pereopods. Within the *oculatus* subgroup, all species appear fairly closely related (above 75% similarity). Within the *pacificus* subgroup, we may identify a less advanced *simplex-beringensis* complex (P.-A. indices of 17-20) and a more advanced *pacificus-similis* complex (P.-A. indices of 22-24). A cladistic analysis of these groups is likely to give similar results, particularly when males have been described for all component species, and their reproductively significant character states can be incorporated in the analysis. The biogeographical significance of these morphological relationships is noted below (p. 146).

FIG. 36. PHENOGRAM OF SPECIES OF *PARAPHOXUS*



BIOGEOGRAPHICAL DISCUSSION

This study analyses species distributions within five subfamilies of Phoxocephalidae that occur in littoral marine (shelf) waters of the North American Pacific region. The subregional occurrence of species and genera is provided in Table II. More than 30 species of these five subfamilies are listed here. Of the five subfamilies, four are pan-Pacific; only members of the Ponharpiiniinae (*Mandibulophoxus*) do not occur on both sides of this northern ocean.

Treating the North Pacific fauna of 30+ listed species as a whole (pan-Pacific), 20 species have been identified from the region of study material, from the Bering Sea to northern California. The number is increased to 26 species if those of central and southern California are included. A similar

north-south species trend on the Asiatic coast, is indicated in existing records, mostly provided in the works of Gurjanova, 1951, 1977, 1980, etc.) and may be more broadly confirmed through the on-going studies of adjacent regional faunas, especially by Hirayama (1992). If we examine the totals for each subregion we find that high numbers (> 10 species) occur in zone 1 (Asiatic Pacific) and in zones 4, 5, 6 and 8 (North American Pacific). This feature contrasts with that of species of subfamily Metharpiiniinae (Jarrett & Bousfield, 1994) wherein the numbers show an overall gradual increase from very few on the Asiatic and Bering Sea coasts to greatest species representation in southern California. The significance of these results with respect to present studies are tempered by limitations in geographical coverage and bathymetrical sampling at subtidal depths (>25 m.) where compo-

TABLE 1. SPECIES OF *PARAPHOXUS*: CHARACTERS AND CHARACTER STATES

CHARACTER	CHARACTER STATE VALUE		
	Plesiomorphic 0	Intermediate 1	Apomorphic 2
1. Maxilla 1, outer plate, number of apical spines	11	10	9
2. Antenna 2, peduncle 4, distal "fan" of spines	few, slender	medium	many, heavy
3. Coxa 1, number of distal marginal setae	few, 3-6	7-9	many, 10-14
4. Gnathopods 1 & 2, degree of similarity	subsimilar in size and form	differing in form	differing in both size and form
5. Gnathopod 1, length of carpal free margin	long	intermediate	short, nearly cryptic
6. Peraeopods 3 & 4; size of distal spine of segment 5	small, < length segment 6	intermediate length = segment 6	large, strong, length > segment 6
7. Peraeopods 3 & 4; segment 6, no. distal spines	3	1-2	0(1)
8. Peraeopod 5, segment 6, no. front marginal spines	3	2	1
9. Peraeopod 5, number of hind marginal setae	2	1	0
10. Peraeopod 6, no. marginal spine/setal clusters	4-6	7 - 10	11-15
11. Pleon plate 3, shape of hind corner	rounded margin convex	slightly produced	produced, lower margin straight
12. Uropods 1 & 2, number of marginal ramal spines	many (2-3)	1-2	few (0-1)
13. Uropod 3, strength of peduncular fan of spines	few (2-3)	4-7	many (8-10)
14. Uropod 3, outer ramus, size terminal segment	short; 1/4-1/3 proximal segment	~1/3 proximal segment	long, ~1/2 prox. segment
15. Telson, L/W ratio of of each lobe	long, slender >2:1	medium ~2:1	short, broad <2:1

nent species are numerically most abundant, and ecologically dominant.

Regional endemism is expected to be high in sediment-dwelling amphipods, especially those that occur in shallow shelf waters (Jarrett & Bousfield, 1994). It is true that all five phoxid subfamilies and their 11 genera (of this study) are

well represented elsewhere, mostly in the southern hemisphere and some in the north Atlantic region. However, endemism of species in the North American Pacific region appears to be extraordinarily high. Thus, when the taxonomy of certain broad-ranging species such as "*Paraphoxus oculatus*" and "*Metaphoxus fultoni*" has been

**TABLE III. DISTRIBUTION OF SELECTED PHOXID SUBFAMILIES,
GENERA, AND SPECIES IN THE NORTH PACIFIC REGION**

TAXON	BIOGEOGRAPHICAL ZONE (legend on page 146)							
	1	2	3	4	5	6	7	8
PONTOHARPINIINAE								
1. <i>Mandibulophus alaskensis</i>			X	X	X			
2. <i>M. mayi</i>				X	X			
3. <i>M. gilesi</i>					X	X	X	x?
PARHARPINIINAE								
1. <i>Eyakia subuncigera</i>	X							
2. <i>E. uncigera</i>	X							
3. <i>E. calcarata</i>	X							
4. <i>E. ochotica</i>	X							
5. <i>Eyakia</i> sp. 1 (Barnard)	X							
6. <i>Eyakia robusta</i> Holmes				X	X	X	X	X
7. <i>Eyakia</i> sp. 2 (Barnard)								X
BROLGINAE								
1. <i>Eobrolgus pontarpioides</i>	X							
2. <i>Eobrolgus chumashi</i>			X	X	X	X	X	X
3. <i>Paraphoxus oculatus</i> Sars	(Authentically North Atlantic)							
4. <i>P. tomiokaensis</i>	X							
5. <i>P. species 2</i>	X							
6. <i>P. communis</i>				X				
7. <i>P. gracilis</i>					X			
8. <i>Paraphoxus</i> species 1 (Bnd)								X
9. <i>P. simplex</i> Gurj.	X	?						
10. <i>P. beringiensis</i>		X						
11. <i>P. rugosus</i>		X						
12. <i>P. pacificus</i>			X	X	x?			
13. <i>P. similis</i>					X			
PHOXOCEPHALINAE								
1. <i>Cephalophoxoides prolixus</i>	X							
2. <i>C. homilis</i>				X	X	X	X	x?
3. <i>Metaphoxus frequens</i>			X	X	X	X	X	X
4. <i>Parametaphoxus asiaensis</i>	X							
5. <i>P. quaylei</i>				X	X	X		
HARPINIINAE								
1. <i>Harpinia</i> spp.	X	X						
2. <i>Heterophoxus affinis</i>			X	X	X	X	X	X
3. <i>H. conlanae</i>			X	X	X	X		
4. <i>H. ellisi</i>				X	X	X		
5. <i>H. ellisi</i> var.				X	X			
6. <i>H. oculatus</i>								X
7. <i>Heterophoxus</i> spp. (S. Cal.)								X
8. <i>Harpiniopsis gurjanovae</i>		X						
9. <i>H. fulgens</i>				X	X	?	?	X
10. <i>Pseudharpinia inexpectata</i>				X	X			

Legend for Biogeographical Zones of Table II.

I. Occurrence

- X - abundant in subregion (or presumed so)
- x - marginally occurring in subregion

II. Coastal SubRegions (Progression: Northwest to Southeast)

1. Japan and Western Pacific
2. Bering Sea and Aleutian Chain
3. Prince William Sound & southeastern Alaska (north of Dixon Entrance)
4. North-central coast of British Columbia and Queen Charlotte Islands
5. Southern British Columbia and Vancouver Island
6. Washington & Oregon
7. Northern and central California
8. Southern & Baja California

critically sorted out, none of the 20 study-region species is found to occur elsewhere. Of the ten genera represented in study collections here, all but one subgroup of *Paraphoxus* occur amphi-Pacifically in temperate-cold-temperate waters. They range northward only slightly into southeastern Alaska, and not at all into the Bering Sea region. Only in the deep-water Harpiniinae and one subgroup of Brolginae were member species found in the Bering Sea region or along the Alaska coast (subregions 2 & 3 of Table II, above). Species of all other genera show high regional endemism or range southward into central and southern California. These southward-ranging groups appear to be matched to some extent on the Asiatic Pacific coast. Corresponding species pairs may be noted in at least four genera; viz., *Eyakia calcarata* and *Eyakia* spp. 1 & 2 of J. L. Barnard; *Eobrolgus pontarpioides* and *E. chumashi*, *Cephalophoxoides prolixus* and *C. homilus*; and *Parametaphoxus asiaensis* and *P. quaylei*. Within the genus *Paraphoxus*, we have noted (above) two distinct taxonomic subgroups which here show corresponding biogeographical differences. The primitive *oculatus* subgroup is cool-temperate and southward ranging, on both the North American and Asiatic Pacific coasts, and occurs elsewhere in warm temperate waters of the eastern Atlantic and Mediterranean region. By contrast, the advanced *pacificus-rugosus* taxonomic subgroup of *Paraphoxus* is endemic to cold-temperate Pacific waters and ranges north into the Bering Sea. A similar phenomenon may be detected elsewhere, within subfamily Metharpiniinae. Thus, only the genus *Grandifoxus* exhibits a similar cold-temperate N. American Pacific endemism, whereas all four other genera of the subfamily range mainly southward into California.

The studies on the Metharpiniinae showed also that primitive members of shallow-water faunas tend to occur in colder northern biogeographic regions, and advanced members in warmer southern regions, with phylogenetically intermediate members mainly in the middle part of the range (Jarrett & Bousfield, 1994). This trend or pattern is the not clearly evidenced within the genera of subfamilies treated here,

probably because numbers of species are small, and the sampling was limited in scope. However, such a trend is suggested within the pontarpiiniin genus *Mandibulophoxus*. There the northern species, *M. alaskensis* is phylogenetically more primitive than the southern species *M. gilesi*. Also, in the *pacificus* subgroup within genus *Paraphoxus*, the most northern species, *P. simplex* has the lowest A.-P. index, whereas the most southerly species, *P. similis* and *P. pacificus* have highest P.-A. ratings, and are therefore most advanced.

Although the species numbers presented here are modest compared to those of other well-studied regions such as southeastern Australia (Barnard & Drummond, 1978), we may conclude that the faunistic affinities of at least four of these five subfamily groups is temperate and cold-temperate, and the principal range is southward in American Pacific coastal waters. We may conclude also that, in these same groups, endemism at the genus level is moderate (three of 11 genera and one generic subgroup occur nowhere else in the North Pacific). However, at the species level, endemism is extremely high since none of the North American Pacific species occurs elsewhere.

The results of this study suggests a possible relationship between phylogeny and biogeography of component subfamilies. Thus, subfamily Pontarpiiniinae (whose genus is entirely North American endemic) matches distributionally subfamily Metharpiniinae in which only two species (of more than 30 subfamily members) have apparently penetrated to the Asiatic Pacific coast (Jarrett & Bousfield, 1994). According to that study (*loc. cit.*, Table I), families Metharpiniinae and Pontarpiiniinae are the two most primitive regional subfamilies, with phyletic indices little above their close austral relative, the most primitive phoxid subfamily, Tipimeginae. The other four sub-families of this study are more strongly represented on the Asiatic Pacific coast, possibly because (in the case of the the most advanced Phoxocephalinae and Harpiniinae) the member species are better adapted to deep-water conditions. According to the standard vicariance model, the deeper-water groups presumably would be less affected by short-term (intra-epochal) geographical and climatic fluctuations, and show greater long-term stability, at all taxonomic levels, over a broader geographic area.

The general applicability of such theory appears to be validated by the high degree of endemic speciation within the two primitive North American Pacific phoxid sub-families. These also contain the highest percentage of member species that occur intertidally or in shallow-water habitats, above the summer thermocline, and subject to widest annual thermal fluctuations. It would seem therefore, that the North American Pacific phoxocephalid fauna retains a major component of phylogenetically primitive or relict groups, early derived from southern austral regions, along with more modern groups that have spread from the edaphically rigorous shallows into physically more stable but less nutrient-rich environments of fiords and deeper off-shore waters.

REFERENCES

- Austin, W. C., 1985. An Annotated Checklist of Marine Invertebrates of the Cold Temperate Northeast Pacific. Khyotan Marine Laboratory, Cowichan Bay, B. C. Vols. I-III: 682 pp.
- , 1957. A new genus of phoxocephali Amphipoda (Crustacea) from Africa, India, and California. *Ann. Mag. Nat. Hist.*, ser. 12, 10: 432-438, 4 figs.
- , 1958. Revisionary notes on the Phoxocephalidae (Amphipoda), with a key to the genera. *Pacif. Sci.* 12: 146-151.
- , 1960. The amphipod family Phoxocephalidae in the eastern Pacific Ocean, with analysis of other species and notes for revision of the family. *Allan Hancock Pacific Expeditions*, 18(3): 175-368, 75 pls., 1 chart.
- , 1961. Gammaridean Amphipoda from depths of 400 to 6000 meters. *Galathea Report* 5: 23-128, 83 figs.
- , 1963. Relationship of benthic Amphipoda to invertebrate communities of inshore sublittoral sands of southern California. *Pacif. Nat.* 3: 437-467, 7 figs.
- , 1964. Marine Amphipoda of Bahia de San Quintin, Baja California. *Pacif. Nat.* 4: 55-139, 21 figs, 17 charts, 13 tables.
- , 1966. Submarine canyons of southern California. part V. Systematics: Amphipoda. *Allan Hancock Pacific Expeditions* 27(5): 1-166, 46 figs.
- , 1969. The Families and Genera of Marine Gammaridean Amphipoda. *Bull. U. S. Natl. Museum*, 271, 535 pp., 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 edition, 716 pp. Univ. California Press, Berkeley, California.
- , 1979a. Revision of American species of the marine amphipod genus *Paraphoxus* (Gammaridea: Phoxocephalidae). *Proc. Biol. Soc. Wash.* 92: 368-379.
- , 1979b. Littoral gammaridean Amphipoda from the Gulf of California and the Galapagos Islands. *Smiths. Contr. Zool.* 271: vi + 149 pp. 74 figs.
- , 1980a. Revision of *Metharpinia* and *Microphoxus* (Marine phoxocephalid Amphipoda from the Americas). *Proc. Biol. Soc. Wash.* 93(1): 104-135, 5 figs.
- , 1980b. The Genus *Grandifoxus* (Crustacea: Amphipoda: Phoxocephalidae) from the northern Pacific Ocean. *Proc. Biol. Soc. Wash.* 93 (2): 490-514. 2 figs.
- , & C. M. Barnard, 1980. Two new phoxocephalid genera, *Fuegiphoxus* and *Phoxorgia* from magellanic South America (Amphipoda: Crustacea). *Proc. Biol. Soc. Wash.* 93: 849-874, 7 figs.
- , 1981. The amphipod genera *Eobrolgus* and *Eyakia* (Crustacea: Phoxocephalidae) in the Pacific Ocean. *Proc. Biol. Soc. Wash.* 94: 295-313, 1 fig.
- , 1982a. Revision of *Foxiphalus* and *Eobrolgus* (Crustacea: Amphipoda: Phoxocephalidae) from American oceans. *Smiths. Contr. to Zool.* 372: 1-35, 5 figs.
- , 1982b. The Genus *Rhepoxynius* (Crustacea: Amphipoda: Phoxocephalidae) in American Seas. *Smiths. Contr. Zool.* 357: 1-49, 6 figs.
- , & M. M. Drummond, 1976. Clarification of five genera of the Phoxocephalidae (marine Amphipoda). *Proc. Biol. Soc. Wash.* 88: 515-547, 4 figs.
- , 1978. Gammaridean Amphipoda of Australia. Part III: The Phoxocephalidae. *Smiths. Contr. Zool.* 245: 1-551, 269 figs.
- , 1979. Gammaridean Amphipoda of Australia, part IV. *Smiths. Contr. Zool.* 269: 1-69, 38 figs.
- , 1982. Gammaridean Amphipoda of Australia, part V. Superfamily Haustorioidae. *Smiths. Contr. Zool.* 360: 1-148, 58 figs.
- , & G. S. Karaman, 1982. Classificatory revisions in gammaridean Amphipoda Crustacea, part 2. *Proc. Biol. Soc. Wash.* 95: 167-187, fig. 1.
- , 1991. The Families and Genera of Marine gammaridean Amphipoda (Except Marine Gammaroids). *Rec. Austral. Mus. Suppl.* 13, Parts 1 & 2: 1-866, 133 figs.
- Barnard, K. H., 1930. Amphipoda. British Antarctic ("Terra Nova") Expedition, 1910. *Natur. Hist. Repts, Zool.* 8: 307-454, 63 figs.
- , 1932. Amphipoda. *Discovery Reports* 5: 1-326, 174 figs., 1 pl.
- Bate, C. S., 1857. A Synopsis of the British edriophthalmous Crustacea. *Ann. Mag. Nat. Hist.*, ser. 2, 19: 135-152, 2 figs.
- Birstein, J. A. & M. E. Vinogradov, (1955). Pelagicheskie Gammaridy (Amphipoda: Gammaridea) Kurilo, Kamchatskoi Vradiny. *Akad. Nauk., SSSR Inst. Okeanol. Trud.* 12: 210-287, 35 figs.
- Boeck, A., 1872. Die Skandinaviske og Artisk Amphipoder Christiania: A.W. Brogger. 1: 160 pp., 7 pls.
- , 1876. *Ibid.* iv. + 712 pp., 32 pl. Christiania.
- Bonnier, J., 1896. Edriophthalmes. Resultats scientifiques de la campagne du "Caudan" dans le Golfe de Gascogne. *Ann. Univ. Lyon* 26: 527-689, pls. 28-40.
- Bousfield, E. L., 1958. Ecological investigations on shore invertebrates of the Pacific coast of Canada. *Natl. Mus. Can. Bull.* 147: 104-115.
- , 1963. Investigations on sea-shore invertebrates of the Pacific coast of Canada, 1957 and 1959. I. Station List. *Natl. Mus. Can. Bull.* 185: 72-89.
- , 1968. Studies on littoral marine invertebrates of the Pacific coast of Canada, 1964. I. Station List. *Natl. Mus. Can. Bull.* 223: 49-57.
- , 1973. Shallow-water gammaridean Amphipoda

- of New England. Cornell Univ. Press, Ithaca, N.Y. 312 pp, 13 figs., 69 pls.
- , 1979. A revised classification and phylogeny of amphipod crustaceans. *Trans. Roy. Soc. Canada* 4: 343-390, 6 figs.
- , 1982. Amphipoda. Gammaridea. in *Synopsis and Classification of Living Organisms*. McGraw-Hill, New York., vol. 2: 254-285.
- , 1983. An updated phyletic classification and palaeohistory of the Amphipoda. *Crustacean Issues* 1: 257-278.
- , 1990. Convergent morphologies in sand-burrowing members of phyletically unrelated gammaridean superfamilies. *Proc. VII Intern. Colloquium on Amphipoda*, Walpole, Maine, Sept. 14-16, 1989. Oral presentation, Abstract.
- , & C. P. Staude, 1994. The Impact of J. L. Barnard on North American Pacific Amphipod Research: A Tribute. *Amphipacifica* I (1): 3-16.
- , & D. E. McAllister, 1962. Station list of the National Museum marine biological expedition to south-eastern Alaska and Prince William Sound. *Natl. Mus. Can. Bull* 183: 76-103.
- Bousfield, E. L. 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.
- Bulycheva, A. I., 1936. New species of Amphipoda from the Japan Sea. *Ann. Mag. Nat. Hist. ser. 10*, 18: 242-256, 35 figs.
- Calman, 1896. On species of *Phoxocephalus* and *Apherusa*. *Trans. Roy. Irish Acad.* 30: 743-754, pls. 31, 32.
- Cadien, D. B., 1991. List of the marine amphipod faunas 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 Tech. Publ.*, Los Angeles, California., Sept., 1991, 21 pp. list.
- Chevreaux, 1887. Crustacés amphipodes nouveaux dragués par l'*Hirondelle*, pendant sa campagne de 1886. *Bull. Soc. Zool. France* 12: 566-580.
- Conlan, K. E., 1977. Effects of log dumping and booming on the sand beach benthos of Saanich Inlet, British Columbia.. MSc thesis, Univ. Victoria. ~250 pp.
- , 1983. The amphipod superfamily Corophioidea in the northeastern Pacific Region 3. Family Isaeidae: systematics and distributional ecology. *Natl. Mus. Nat. Sci., Publ. Nat. Sci.*, No. 4: 1-75.
- Coyle, K. O., 1982. The amphipod genus *Grandifoxus* Barnard (Gammaridea, Phoxocephalidae) in Alaska. *Jour. Crust. Biol.* 2(3): 430-450, 10 figs.
- Dickinson, J. J., 1982. Studies on amphipod crustaceans of the northeastern Pacific Region. I. 1. Family Ampeliscaidae, Genus *Ampelisca*. *Natl. Mus. Can., Publ. Biol. Oceanog.* No. 10: 1-39, 21 figs. 3 Tbls.
- Giles, G. M., 1890. Descriptions of seven additional new Indian amphipods. *Natural History notes from H. M.'s Indian marine survey steamer 'Investigator'*. No 15. *Jour. Asiat. Soc. Bengal* 59: 63-74, pl. 2.
- Gray, W. S. Jr., & J. C. McCain, 1969. The taxonomic status of *Mandibulophoxus gilesi* Barnard, 1957 (Crustacea: Amphipoda). *Proc. Biol. Soc. Wash.* 82: 189-192, 1 fig.
- Griffiths, C. L., 1975. The Amphipoda of southern Africa.. Part I. The Gammaridea and Caprellidea of southern Mocambique. *Ann. S. Afr. Mus.* 60: 265-306, figs. 4-11.
- , 1974a.. The Amphipoda of southern Africa. Part 2. The Gammaridea and Caprellidea of S. W. Africa. *Ann. S. Afr. Mus.* 62: 169-208, 7 figs.
- , 1974b. The Amphipoda of southern Africa. Part 3. The Gammaridea and Caprellidea of Natal. *Ann. S. Afr. Mus.* 62: 209-264, 8 figs.
- , 1975. The Amphipoda of southern Africa. Part 5. The Gammaridea and Caprellidea of the Cape Province west of Cape Agulhas. *Ann. S. Afr. Mus.* 67: 91-181, 21 figs.
- , 1976a. Some new and notable Amphipoda from southern Africa. *Ann. S. Afr. Mus.* 72: 11-35, 12 figs.
- , 1976b. Guide to the benthic marine Amphipoda of South Africa. South Africa Museum, Cape Town. 106 pp., 60 figs.
- Gurjanova, E. F., 1936. Neue Beiträge zur Fauna der Crustacea-Malacostraca des arktischen Gebietes. *Zool. Anz.* 113: 245-255.
- , 1938. Amphipoda Gammaroidea of Siau ku Bay and Sudzukhe Bay (Japan Sea). Reports of the Japan Sea Hydrobiological Expedition of Zoological Institute of the Academy of Sciences USSR in 1934, 1: 241-404, 59 figs. {in Russian}.
- , 1946. New species of Amphipoda and Isopoda from the Arctic Ocean. *Works of Drifting Ice Expedition in the Central Arctic Ocean in Icebreaking Steamer G. Sedov*: 272-297, 26 figs. (In Russian).
- , 1951. *Bokoplavny morei SSSR i sopred el'nykh Vod* (Amphipoda: Gammaridea). *Akad. Nauk SSSR pred. po Faune SSSR* 41: 1-1029, illustr.
- , 1953. *Novye dopolneniya k dal'nevostochnoi faune morskikh bokoplavov*. *Akad. Nauk. SSSR. Trud. Zoolog. Inst.* 13: 216-241, 19 figs.
- , 1977. Some new data in taxonomy of family Phoxocephalidae *sensu lato* (Amphipoda, Gammaridae). *Rept. Akad. Nauk SSSR., Zool. Inst. Issled. Faun. Morei.* 21(29): 67-87, 9 figs.
- , 1980a. *Novoe v sistematike semeistva Phoxocephalidae sensu lato* (Amphipoda: Gammaridea) *Soobshchenie II*. *Akad. Nauk SSSR Issl. fauny morei* 25: 89-97.
- , 1980b. Some New data in taxonomy of family Phoxocephalidae *sensu lato*. Report III. *Akad. Nauk SSSR, Zool. Inst., Issled. Fauny Morei* 25: 98-100.
- Haswell, W. A., 1879. On some additional new genera

- and species of amphipodous crustaceans. Proc. Linn., Soc. N. S. Wales 4: 319-350, pls. 18-24.
- Hirayama, A., 1987. Taxonomic Studies on the Shallow Water Gammaridean Amphipoda of West Kyushu, Japan. VII. Melita, Melphidippidae, Oedicerotidae, Phliantidae, and Phoxocephalidae. Publ. Seto Mar. Bi. Biol. Laboratory 32 (1/3): 1-62.
- , 1992. Phoxocephalidae and Urothoidae (Crustacea: Amphipoda: Phoxocephaloidea) from Hong Kong. Asian Mar. Biol. 9 (1992): 117-138, 18 figs.
- , 1908. The Amphipoda collected by the United States Bureau of Fisheries Steamer "Albatross" off the west coast of North America in 1903 and 1904, with descriptions of a new family and several new genera and species. Proc. U. S. Nat. Mus. 35: 489-543., 46 figs.
- 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.
- , E. A. Hendrycks, & E. L. Bousfield, 1989. Progress report on research on phoxocephalid and calliopiid amphipods of the Pacific coast of Canada. 2nd CMN Staff Symposium, October, 1989, 55 MS pp., sev. figs.
- Karaman, G. S., 1972. The Phoxocephalidae family of the Adriatic Sea. Glasnik Republ. Zavoda za Zastitu Pirode, Titograd 5: 47-101, 28 figs.
- , 1980. *Cocoharpinia iliffei*, new genus and species from Bermuda, with remarks to other genera and species (fam. Phoxocephalidae). Inst. Biol. Medic. Res., Montenegro, Titograd 9-10: 149-175, 10 figs.
- , 1993. Phoxocephalidae. in Ruffo, S., ed. The Amphipoda of the Mediterranean. Mem. Inst. Oceanogr. Monaco. Part 3: 639-665.
- Kroyer, H. 1842. Une nordiske Slaegter og Arter af Amphipodernes Orden, henhørende til Familien Gammarina. (Forl. Ud. storcv. Arb.) Naturh. Tidskr. 4: 141-146.
- Ledoyer, M., 1986. Crustacés amphipodes gammariens. Faune de Madagascar 59 (2): 599-1112, figs. 227-415.
- Lincoln, R. J., 1979. British Marine Amphipoda: Gammaridea. London: British Museum (Natural History). 658 pp, 280 figs., 3 pls.
- , & D. E. Hurley, 1981. The calceolus, a sensory structure of gammaridean amphipods (Amphipoda: Gammaridea). Bull. Brit. Mus. Nat. Hist. (Zool) 40: 103-116, 4 figs.
- Lowry, J. K., The callynophore, a eucaridan/peracaridan sensory organ prevalent among the Amphipoda (Crustacea) Zool. Scripta 15: 333-349, 14 figs.
- Meinert, F., Crustacea Malacostraca. Det Vidensk. Udb. Kanonb. Hauchs Togt. Danske Have Idenf. Skag. Aarene 1883-86. Copenhagen, pp. 147-232, 2 pls.
- Nagata, K., 1960. Preliminary notes on benthic gammaridean Amphipoda from the *Zostera* region of Mihara Bay, Seto Inland Sea, Japan. Publ. Seto Mar. Biol. Lab. 8: 163-182. 2 figs., pls. 13-18.
- Reid, D. M., 1951. Report on the Amphipoda (Gammaridea and Caprellidea) of the coast of tropical West Africa. Atlante Report 2: 189-291, 58 figs. W. African amphipods
- Sars, G. O., 1879. Crustacea et Pycnogonida nova in itinere 2do et 3tio expeditionis Norvegicae anno 1877 & 78 collecta. (Prodromus descriptionis). Arch. Mathem. Naturvid. 4: 427-476.
- , 1895. An Account of the Crustacea of Norway. I. Amphipoda. Christiana & Copenhagen. 711 pp., 240 pls., 8 suppl.
- Schellenberg, A., 1925. Die Gammariden Spitzbergens nebst einer Uebersicht der von Romer & Schaudinn 1898 im nördlichen Eismeer gesammelten Arten. Mitteilungen aus dem Zoologischen Museum in Berlin 11: 195-231, 10 figs.
- , 1931. Gammariden und Caprelliden des Magellangebietes, Sudgeorgiens unter der westantarktischen. Further Zoological Results of the Swedish Antarctic Expedition 1901-1903, 2(6): 290 pp., 1 pl., 136 figs.
- Schram, F. R., 1986. Crustacea. Oxford University Press, New York. 606 pp.
- Scott, T., 1890. Additions to the fauna of the Firth of Forth. Ann. Rept. Fish. Bd. Scotland 8: 312-333, pls. 12, 13.
- , 1909. On new and rare Crustacea from Scottish waters. Ann. Mag. Nat. Hist. ser. 8, 4: 31-36, pls. 2-3.
- Shoemaker, C. R. 1925. The Amphipoda collected by the United States Fisheries Steamer "Albatross" in 1911, chiefly in the Gulf of California. Bull. Amer. Mus. Nat. Hist. 52: 21-61, 26 figs.
- Slattery, P. N., 1985. Life histories of infaunal amphipods from subtidal sands of Monterey Bay, California. Jour. Crust. Biol. 5(4): 635-649, 8 figs.
- Sneath, P. H. A. and R. R. Sokal, 1973. Numerical Taxonomy. W. H. Freeman, San Francisco. 573 pp.
- Staude, C. P., 1986. Systematics and Behavioural Ecology of the Amphipod Genus *Paramoera* Miers (Gammaridea: Eusiroidea: Pontogeneiidae) in the eastern North Pacific. PhD Thesis, University of Washington, Seattle, 324 pp. *Heterophoxus ellisi* part??
- , 1987. Amphipoda: Gammaridea. pp. 346-391. in E. Kozloff (ed). Marine Invertebrates of the Pacific Northwest. Univ. Wash. Press., Seattle. 511 pp.
- Stebbing, T. R. R., 1888. Report on the Amphipoda collected by H.M.S. Challenger during the years 1873-1876. Report on the Scientific Results of the Voyage of H.M.S. Challenger During the Years 1873-1876. Zoology 29: 1737 pp., 210 pls., London.
- , 1897. Amphipoda from the Copenhagen Museum and other Sources. Trans. Linn. Soc. London, (2, Zoology) 7: 25-45, pls. 6-14.
- , 1899. Revisions of Amphipoda (continued). Ann. Mag. Nat. Hist., ser. 7, 4: 205-211.
- , 1906. Amphipoda: Gammaridea. Das

Tierreich. I. Berlin. 806 pp.

_____, 1908. South African Crustacea (Part IV).

Ann. S. Afr. Mus. 6: 1-96. 40 pls.

Stimpson, W., 1857. The Crustacea and Echinodermata of the Pacific shores of North America. Jour. Bost. Soc. Nat.

Hist. 6: 444-532, pls. 18-23.

Thurston, M. H., 1982. *Cheus annae*, new genus, new species (Cheidae, new family), a fossorial amphipod from the Falkland Islands, Journal Crustacean Biology 2: 410-419, 3 figs.

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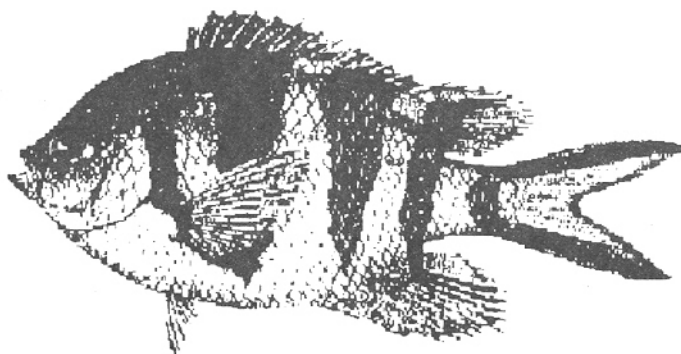
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