

THE AMPHIPOD SUPERFAMILY EUSIROIDEA IN THE NORTH AMERICAN PACIFIC REGION.
I. FAMILY EUSIRIDAE: SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

by E. L. Bousfield¹ and E. A. Hendrycks²

ABSTRACT

The gammaridean amphipod family Eusiridae encompasses a group of marine epibenthic and pelagic carnivorous amphipods that prey mainly on other small crustaceans. The family is represented in the northeastern Pacific coastal marine region, from Alaska to central California, by fourteen species of the genus *Rhachotropis*, of which the following are fully described and figured here: *R. aculeata* (Lepechin, 1780), *R. oculata* (Hansen, 1882), *R. boreopacifica*, new species, *R. conlanae*, new species, *R. minuta*, new species, *R. calceolata*, new species, *R. americana*, new species, *R. distincta* (Holmes, 1908), and *R. natator* (Holmes, 1908). Taxonomic notes and commentary are provided on other regional sublittoral (eyed) species: *R. inflata* Sars, 1895, *R. helleri* (Boeck, 1871), and *R. macropus* Sars, 1895. *Rhachotropis clemens* Barnard, 1971 (eyed variant) from the coasts of Oregon to British Columbia, is redescribed as *R. barnardi*, new species. Based mainly on the literature, the study briefly treats sublittoral, bathyal, and abyssal species *R. luculenta* Barnard, 1969c, *R. ludificor* Barnard, 1967, *R. clemens* Barnard, 1967, *R. multesimus*, Barnard, 1967, and *R. gubilata* Barnard, 1964, mainly from other N. American Pacific regions, and *R. grimaldi* (Gurjanova form) from the western Pacific. *Eusirus longipes* (Boeck), figured by Hirayama from Japan, is redescribed here as *E. hirayamae*, new species. Also described and illustrated from the study region are *Eusirus cuspidatus* Kroyer, 1845, and *Eusirus columbianus*, new species, *Eusirella multicalceola* (Thorsteinson, 1941), and *Cleonardo moirae*, new species. Of the thirteen genera here comprising family Eusiridae, *Eusiroides* was found to be morphologically the most primitive, and *Eusirella* and *Rhachotropis* the most advanced genera. Within genus *Rhachotropis*, the holarctic benthic *R. aculeata* proved to be the most primitive, and the bathypelagic *R. natator* and *R. distincta* the most advanced species.

Biogeographically, the North Pacific region may be considered a major centre of eusirid evolution since it contains representatives of 10 of the 13 world genera, and its 35 species represent about 30% of the known world fauna. The eusirid fauna of the western (Asiatic) North Pacific appears more diverse at genus level and contains more primitive taxa. By contrast, the advanced genus *Rhachotropis* contains half the total North Pacific eusirid fauna and two-thirds of that fauna, including the most primitive and most advanced members, are recorded from the eastern (American) North Pacific region, here considered to be a major centre of origin and evolution of the group.

INTRODUCTION

Members of the amphipod family Eusiridae are medium to large epibenthic and pelagic marine carnivores that prey mainly on various benthic invertebrates or small fast moving crustaceans in the water column. The abdominal segments, pleopods, and tail fan of eusirids are typically large and powerfully developed, and function in rapid propulsion and change of direction. Eusirid sensory mechanisms include, typically, very large multi-faceted eyes, and antennal calceoli of a complex type that are presumed to detect acoustical or mechanical vibrations from prey organisms. Morphological adaptations for this life style consist of large raptorial gnathopods and maxillipeds by means of which prey organisms are rapidly captured, killed, and thrust towards the chewing mouthparts (Klages & Gutt, 1990). Deep-water eusirids employ their slender, long-dactylate peraeopods for standing on soft bottom sediments while awaiting benthic prey, or possibly as a raptorial "basket" in which prey organisms are entrapped when feeding pelagically (see also Enequist, 1950).

Eusirids tend to occur in deep coastal fiords and offshore waters, presumably where diurnal vertical migrations can be

effected in concert with movements of their prey. Many eusirid species are entirely abyssal, not captured in the euphotic zone at any time. The Eusiridae is one of several natantian gammaridean families (see Bousfield & Shih, 1994), including those among superfamilies Pardaliscoidea, Lysianassoidea, Stegocephaloidea, and Melphidippoidea, and among reptantian family Melitidae, whose members are specialized as pelagic predators. In size, functional morphology, and life style, members of these groups appear similar to hyperiid amphipods; all may be viewed, by 3-dimensional predatory analogy, as "dragonflies of the deep". However, eusirid species themselves serve as prey organisms of regional food fishes, either directly or indirectly, and thus are important in marine food energy cycles.

The history of development of systematic knowledge of eusirid amphipods on the North American Pacific coast is relatively limited. Nineteenth century regional records are not included in Stebbing (1906). The first confirmed records were those of *Gracilipes natator* and *G. distincta* by Holmes (1908), from off the coast of California. Thorsteinson (1941) included those species and her new species *G. multicalceola* from off the coast of Washington State. Shoemaker (1925) added *R. natator* from the Gulf of California, and *R. aculeata*

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

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

eata and *Eusirus cuspidatus* from the Pt. Barrow region of Alaska. J. L. Barnard published a number of important new records, commencing with redescription of *R. natator* from California (1954) followed by an extensive series on bathyal species (1957, 1964, 1967, 1971, etc.), and culminated in his most useful world compendium (with Gordan Karaman, 1991). A few records from the northwestern Pacific region had been summarized by Shoemaker (1955), Austin (1985), and Staude (1987).

The rich Asiatic Pacific eusirid fauna has been described and catalogued almost entirely within the last 50 years, mainly by Gurjanova (1951), Birstein & Vinogradov (1955, 1958, 1960), Hirayama (1985), and Ishimaru (1994).

The purpose of this investigation is to develop new taxonomic, ecological, and biogeographical information on the gammaridean amphipod family Eusiridae in the northeastern Pacific region, based mainly on recently collected material. This fauna, previously little studied, provides a connecting link between the relatively well known eusirid assemblages southward along the N. American Pacific coast, and those of the Asiatic Pacific region. The integrated results thereby facilitate analysis of the entire North Pacific fauna in the context of family Eusiridae on a world-wide basis.

ACKNOWLEDGEMENTS

Of the 18 species of family Eusiridae recorded authentically from the study region (Table III, zones 3-7), 8 species (5 new to science) were obtained from ~60 collections made by NMNS (CMN) expeditions to the study region during the period 1955-1980 (types deposited in the CMN), and an oceanographic survey in 1991. The station data and detailed acknowledgement of field assistance are provided in the published station lists of the senior author and collaborators (Bousfield, 1958, 1959, 1968; Bousfield & McAllister, 1963; Bousfield & Jarrett, 1981). Several lots of material of the Institute of Ocean Sciences (IOS), Sidney, B. C. (see Thomson et al, 1992), containing 3 regional oceanic species (1 new to science), were kindly made available to us by Moira Galbraith, Sy-Tech Research Ltd., Sidney, B. C. The authors are pleased to name (from this material) *Cleonardo moirae*, new species, in her honour (p. 15). Two large arctic and subarctic species were found in benthic material from the Bering Sea region kindly provided by Dr. Peter Slattery, Moss Landing, California. A single lot of specimens collected by Kathleen E. Conlan (CMN under grant DPP-2619394 to Dr. John Oliver, Moss Landing, CA, contained a distinctive new species of *Rhachotropis* (see p. 38). Collection abbreviations and plate legends are tabled on p. 56.

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SYSTEMATICS

Superfamily Eusiroidea

Eusiroidea Bousfield 1979: 255.—Bousfield, 1982: 263.—Schram, 1986: 178.—Staude 1987: 377.

Eusiridae: Barnard, 1969a: 213 (part).—Barnard & Karaman, 1991: 284 (part).—Ishimaru, 1994: 44.

Type family. Eusiridae Stebbing, 1888.

Families: Pontogeneiidae Stebbing, 1906 - type genus *Pontogeneia* Boeck, 1871; Bateidae Stebbing, 1906 - type genus *Batea* Muller, 1865; Calliopiidae Kroyer, 1845 - type genus *Calliopius* Liljeborg, 1865; Eusiridae Stebbing, 1888 - type genus *Eusirus* Kroyer, 1845; Gammarellidae Bousfield, 1977 - type genus *Gammarellus* Herbst, 1793; Amathillopsidae Heller, 1875 - type genus *Amathillopsis* Heller, 1875; Gammaracanthidae Bousfield, 1989 - type genus *Gammaracanthus* Bate, 1862; Paramphithoidae Stebbing, 1906 - type genus *Paramphithoe* Bruzelius, 1835.

Note: Southern continental freshwater eusiroidean genera, presently included in family Calliopiidae (e.g. *Paraleptamphopus* Stebbing, 1899; *Falklandella* Schellenberg, 1931; *Praefalklandella* Stock & Platvoet, 1993) may require separate family recognition.

Diagnosis (modified from Bousfield, 1982): Body medium to large, often dorsally, dorso-laterally, occasionally laterally processiferous. Rostrum often strong. Eyes usually large (often lacking in abyssal and hypogean forms). Antennae medium, not greatly elongate. Calceoli variously present, on distal peduncular and flagellar segments of both antennae, often in both sexes, or lacking; calceoli complex, often of sexual and asexual types, with receptacle, bulla, and modified distal elements. Antenna 1, callynophore weak or lacking; accessory flagellum short, vestigial or lacking. Antenna 2 (male): peduncular segments 4 & 5 often with brush setae; flagellum not greatly elongate.

Mouthparts basic, typically modified for carnivory. Upper lip, lower margin rounded. Lower lip, inner lobes lacking or weakly developed. Mandible, molar strong, triturative, or reduced; left lacinia 5-8+ dentate, right lacinia flabellate or trifold; spine row short; palp strong, segment 3 often falcate or elongate. Maxilla 1, outer plate with 11 (occ. fewer) apical spines, inner plate variously setose, palp 2-segmented. Maxilla 2, plates normal, inner plate, facial setae strong, less often few or lacking. Maxilliped normal, plates and palp strong, often raptorial.

Coxal plates 1-4 usually medium to large, occ. small, increasing in size posteriorly, usually lacking lower hind cusps. Gnathopods typically subsimilar in form and size, variously subchelate, not (or weakly) sexually dimorphic; carpus often shortened or modified, palms and dactyls smooth.

Peraeopods 3 and 4 regular, subsimilar, dactyls often strong or elongate. Peraeopods 5-7 basically homopodous or slightly heteropodous; 7 usually longest; coxae 5-7 postero-labate; segments 4-6 spinose, often elongate in abyssal

KEY TO FAMILIES OF SUPERFAMILY EUSIROIDEA

1. Telson distinctly bilobate or deeply cleft in most members 2.
—Telson plate-like or weakly notched apically 5.
2. Gnathopods large, strongly subchelate, often "eusiroidean" in form; peraeopods 5-7 generally elongate, slender; animals often large (10-40+ mm) 3.
—Gnathopods weakly or moderately subchelate (esp. in female); peraeopods 5-7 regular, stout, not elongate; animals small to medium (< 10 mm) 4.
3. Antenna usually calceolate (often in both sexes); accessory flagellum small, 1-2 segmented; telson large, cleft or notched distally; peraeopod 7 longer than 6 Eusiridae (p. 6)
—Antennae lacking calceoli; accessory flagellum prominent 3-7+ segments; telson very short, fully bilobate; peraeopod 7 not longer than 6 Gammaracanthidae
4. Gnathopods 1 and 2 normally subsimilar, subequal; peraeopods 5-7 generally homopodous in size and form Pontogeneiidae
—Gnathopod 1 (and coxa) vestigial; peraeopods 5-7 similar in size but distinctly heteropodous in form Bateidae
5. Coxae 1-4 acute or strongly toothed below; peraeon strongly dorsally carinate; peraeopod 7 not larger (longer) than peraeopod 6 6.
—Coxae 1-4 rounded or truncate below; peraeon smooth dorsally (except Gammarellidae); peraeopod 7 larger than peraeopod 6 7.
6. Body variously carinated or processiferous dorsolaterally and often laterally; gnathopods with weak carpal lobes; antenna 1, peduncular segments 1 & 2 each shorter than head Paramphithoidae
—Body mid-dorsally toothed only; carpal lobes of gnathopods deep; antenna 1, peduncular segments 1 and 2 each longer than head Amathillopsidae
7. Peraeon not (rarely) carinate; accessory flagellum minute (rarely 2-4 segmented); calceoli (when present) of a simple, single pontogeneiid type 8.
—Peraeon weakly mid-dorsally carinate; accessory flagellum distinct (4-6+ segments); calceoli of two types, complex, proximal and distal elements separate Gammarellidae
8. Pleon often dorsally carinate or toothed; gnathopods closely subequal in size (both sexes); coxal gills pleated, especially in male; sternal gills lacking; marine Calliopidae
—Pleon dorsally smooth; gnathopod 1 distinctly the larger; coxal gills simple; sternal gills often present; continental fresh waters of Australia, New Zealand, & Falkland Islands (potential new family)

forms; segment 4 little produced posterodistally, not strongly overhanging segment 5.

Pleon typically large, often dorsally carinate; pleopods powerful, sexually dimorphic in size, occasionally in form; pleon plates normal or toothed behind. Uropods 1 & 2 lanceolate, sublinear, serially spinose, apically spinose in littoral and freshwater groups. Uropod 3, rami typically lanceolate, margins serially spinose and/or setose; outer ramus 1-segmented, often reduced, spinose in freshwater groups. Telson large, bilobate, or lobes variously fused to entire plate, lacking ventral keel (e.g. of Pleustidae).

Coxal gills plate-like, often pleated (or double), especially in male, on peraeopods 2-7 (rarely lacking on 7),

secondarily simple (pleats lost); sternal gills often present in fresh-water members. Brood plates broad, marginal setae simple, numerous. Males typically smaller than females; usually mating freely in the water column.

Distributional Ecology. Essentially bipolar; dominant in coldwater marine regions, coastal and neritic to abyssal, occasionally estuarine and freshwater along continental coasts of Australia, New Zealand, the Falkland Islands, Japan, and Indo-Pacific Islands, but apparently not South America. A relatively ancient group, retaining many presumed ancestral gammaridean character states.

Taxonomic commentary: Following Bousfield & Shih (1994), the following families have been transferred to superfamily Leucothoidea: Acanthonotozomatidae Stebbing, 1906 - type genus *Acanthonotozoma* Boeck, 1875; Laphystiopsidae Stebbing, 1906 - type genus *Laphystiopsis* G. O. Sars, 1895; and Lafystiidae G. O. Sars, 1895 - type genus *Lafystius* Kroyer, 1842.

Eusiridae Stebbing

Eusiridae Stebbing, 1888: 953.—Stebbing, 1906: 327 (except *Rozinante*).—Gurjanova, 1951: 698 (except *Rozinante*).—Bousfield, 1973: 77.—Lincoln, 1979: 402.—Ledoyer, 1982: 233.—Bousfield, 1982a: 264.—Ishimaru, 1994: 44.—Bousfield & Shih, 1994: 128.
Eusiridae (partim) J. L. Barnard, 1969a: 213.—Barnard & Karaman, 1991: 284.

Type Genus. *Eusirus* Kroyer, 1845

Genera: *Eusiroides* Stebbing, 1888 (15 spp., mainly tropical, littoral and sublittoral); *Eusirella* Chevreux, 1908 (5 spp., mainly North Pacific, abyssal); *Eusirogenes* Stebbing, 1904 (5 spp., mainly northern oceans); *Eusiropsis* Stebbing 1897 (2 spp., North Pacific, Antarctic, abyssal); *Eusirus* Kroyer, 1845 (24 spp., cosmopolitan, littoral to abyssal); *Pareusirogenes* Birstein & Vinogradov, 1955 (1 species, Okhotsk Sea, bathyal); *Meteusiroides* Pirlot, 1934 (Indian ocean, mesopelagic); *Harclado* J. L. Barnard, 1964c (tropical Atlantic, Indian, & Pacific oceans, mesopelagic); *Cleonardo* Stebbing, 1888; (9 spp., 4 in North Pacific, bathy-pelagic); *Cleonardopsis* K. H. Barnard, 1916 (1 species, off S. Africa, bathypelagic); *Stenopleura* Stebbing 1888 (tropical Atlantic, North Pacific, mesopelagic); *Stenopleuroides* Birstein & Vinogradov 1964 (Indian Ocean, mesopelagic); *Rhachotropis* S. I. Smith 1883 (~50 species, mostly in northern oceans; some sublittoral, but mostly bathyal, and bathy-pelagic).

Diagnosis: Body medium small to medium large; processiferous dorsally and dorso-laterally on pleon, often on posterior segments of the peraeon, and on urosome 1. Peraeonal segments relatively short and compacted; pleonal segments large. Rostrum short to medium strong. Anterior head lobe broad, rounded or acutely produced (*Rhachotropis*). Eyes (when present) large, reniform to rhomboidal. Antennae 1 & 2 well developed, usually calceolate, usually on peduncle & flagellum, in both sexes. Antenna 1 usually shorter than 2; peduncular segment 3 short; flagellum of antenna 1 may be elongate in male; accessory flagellum small (1-2 segmented), scale-like, or lacking.

Mouthparts modified for carnivory. Upper lip rounded below, epistome not produced. Lower lip, inner lobes weakly developed. Mandible: molar conical, triturative; with short flagellum; blade row short; left lacinia 5-8+ dentate, right lacinia bifid; incisor strong, dentate; palp

elongate, slender, segment 3 often elongate. Maxilla 1, inner plate with 4-0 setae; outer plate with 11-9 apical spines; palp 2-segmented, proximal segment relatively long. Maxilla 2, inner plate broader than outer, facial setae reduced to single marginal seta or lacking. Maxilliped, palp strong, 4-segmented; outer plate slightly reduced; inner plate with 3+ apical spines.

Coxae 1-4 large to medium small, 4th largest, excavate behind; coxa 1 often produced anteriorly. Gnathopods 1 & 2 usually strongly subchelate, raptorial, subsimilar, 2 usually the larger; carpus usually shortened, hind lobe deep (rhachotropid form), or slender, elongate, lobe short, acute (eusirid form); basis often lined posteriorly with short spines.

Peraeopods 3 & 4 slender, bases extending beyond coxae; segment 4 usually longer than 5; dactyls strong. Peraeopods 5-7 slender, trending to dissimilarity in size and form, and elongation of distal segments and dactyls in abyssal forms.

Pleon plates regular, hind margin often serrate, hind corners not produced. Pleopods powerful, rami not sexually dimorphic. Uropods 1 & 2, rami lanceolate, serially spinose, usually lacking apical spines (except in *Eusiroides*), outer ramus distinctly the shorter. Uropod 3, rami subequal, margins serially spinose and/or weakly plumose setose. Telson usually elongate, lobes deeply and narrowly separated distally, apices acute; rarely short, and/or nearly totally fused at apex.

Coxal gills large, may be weakly pleated in male.

Taxonomic commentary. Component genera may be clustered into four main groups about the 65-70% similarity level (see Table I and Fig. 33) viz, the primitive littoral and sublittoral genus *Eusiroides*; an advanced littoral-pelagic abyssal *Rhachotropis-Eusirella* group, and two intermediate groups consisting of a relatively primitive *Cleonardo-Harclado-Stenopleura* complex, and a slightly more advanced sublittoral, bathyal, and bathypelagic *Eusirus-Eusirogenes* group. Within groups, component genera are separated at about the 80-85% level, not very far apart, and sharing some characters that may be convergent, but the bulk appear to be phyletic. Although the free-swimming deep-water genera entrain primitive reproductive and urosomal features, the mouthparts and peraeopods are advanced, suggesting specialization for capturing scarce, fast-moving prey organisms in the open ocean. The heavily plumose-setose peraeopods and uropod 3 of *Eusiropsis riisei*, and setose peraeopods 3 and 4 of *Eusirella multicalceola* may be flotation devices that assist in conserving energy in a food-deficient environment.

Birstein & Vinogradov (1958) have included *Stenopleura* in family Calliopidae on the basis of its fused telson lobes. In all other diagnostic features above, however, *Stenopleura* conforms most closely with family Eusiridae. *Rozinante* was earlier removed to Calliopidae (Bousfield, 1982). De Broyer and Jazdzewski (1993) have included *Atyloella*, Schellenberg, 1929, *Djerboa* Chevreux, 1906, *Liovillea*

KEY TO NORTH PACIFIC GENERA OF EUSIRIDAE

1. Gnathopods 1 and 2 distinctly eusiroidean in form (carpus slender, elongate, with narrow hind lobe, attached antero-distally to propod (Fig. 1) 2.
—Gnathopods 1 and 2, carpus short and deep or, if elongate, hind lobe broad, attached proximally to propod (Fig. 6) 5.
2. Gnathopod 1, propod distinctly larger than in gnathopod 2 *Eusirogenes* (p.21)
—Gnathopod 1, propod smaller than in gnathopod 2 3.
3. Coxal plates 1-4 deep, smooth below; accessory flagellum 1-segmented. *Eusirus* (p. 8)
—Coxae shallow, length > depth; accessory flagellum scale-like or lacking 4.
4. Peraeopods 3-7 distally plumose-setose; pleon dorsally smooth; mandibular molar reduced. *Eusiroopsis* (p. 21)
—Peraeopods 3-7 normally dactylate and spinose distally; pleon weakly toothed mid-dorsally; molar normal, triturative surface large *Pareusirogenes* (p. 21)
5. Peraeopods 3 and 4, segment 4 not longer (often distinctly shorter) than 5; coxa 1 usually produced anteriorly; anterior head lobe acute; pleon 1-3 usually dorsally toothed, mucronate . . . *Rhachotropis* (p. 22)
—Peraeopods 3 and 4, segment 5 > segment 4; coxa 1 little produced or rounded anteriorly; anterior head lobe normal, shallow; pleon dorsal teeth usually lacking 6.
6. Coxa 1 expanding distally; peraeopods 5-7 short, segments stout; uropods 1 and 2, rami linear, apically spinose; uropod 3, ramal margins setose. *Eusiroides* (p. 8)
—Coxae 1 parallel-sided; peraeopods 5-7 slender, often elongate; uropods 1 and 2, rami lanceolate, with single spine or none at apex; uropod 3, ramal margins spinose or smooth, not setose. 7.
7. Gnathopods 1 and 2, propod slender, carpus elongate; maxilla 1, palp short, segments 1 & 2 subequal; outer plate with 9 apical spines *Eusirella* (p. 17)
—Gnathopods 1 and 2, propod stout, deep, carpus short, deep; maxilla 1, palp normal, distal segment much the longer; outer plate with 11 apical spines 8.
8. Pigmented eyes lacking; coxae 1-4 normal; accessory flagellum 1-segmented *Cleonardo* (p. 14)
—Eyes pigmented; coxae 1-4 small, shallow; accessory flagellum lacking 9.
9. Telson elongate, deeply cleft; gnathopod propods, palm nearly horizontal *Harcledo* (p.21)
—Telson short, apex shallowly notched or entire; gnathopod palms usually oblique . . . *Stenopleura* (p. 21)

Chevreaux, 1911, and *Schraderia* Pfeffer, 1888 in family Eusiridae. These 4 genera are excluded here because of their weak gnathopods, facial row of setae on the inner plate of maxilla 2, and pontogeneioid telsons, among other features.

Within the North Pacific region, the genera *Eusirus*, *Eusiroides*, *Eusirella*, *Cleonardo*, and *Rhachotropis* are amphi-North Pacific. However, within the North Pacific broadly, the genera *Harcledo*, *Stenopleura*, *Pareusirogenes*, *Eusiroopsis*, and *Eusirogenes*, have been recorded only from western regional waters and only on the basis of one or two species each, all from bathyal and abyssal depths (Ishimaru, 1994; Birstein and Vinogradov, 1955, 1958, 1960). The monotypic genera *Cleonardopsis* and *Stenopleuroides* are known only from abyssal waters of the North and South Atlantic, and the Indian oceans respectively (Barnard & Karaman, 1991).

Barnard and Karaman (1991) have effectively elevated the family Eusiridae to superfamily level by submerging

within it virtually all families of the present superfamily Eusiroidea. However, the families of Eusiroidea are fairly readily separable on morphological, biogeographical, and to some extent ecological and behavioural grounds. For example, families Eusiridae and Pontogeneiidae, maintained separately by most authors (e.g. Ledoyer, 1982), have been fused as one family (e.g. Barnard, 1969a) on the basis of a superficially similar "deeply cleft telson". These two groups actually differ clearly in all categories. With few exceptions, members of family Eusiridae have carnivorous mouthparts, and elongate, raptorial "lentic water" appendages; the species are fully marine sublittoral, bathyal and bathypelagic, and almost exclusively predaceous in feeding behaviour. By contrast, the Pontogeneiidae have generalist feeding mouthparts and short sturdy "lotic water" appendages; the species are essentially marine littoral, but occur often in brackish and fresh water and are almost exclusively omnivorous or detritivorous, seldom carnivorous, in feeding style.

Eusiroides Stebbing

Eusiroides Stebbing, 1888: 969.—Barnard & Karaman, 1991: 319.

Type species. *Atylus monoculoides* Haswell, 1879.

Component North Pacific species: *Eusiroides japonica* Hirayama, 1985: 36, figs. 149-154; *Eusiroides diplonyx* Barnard, 1970a: (Hawaiian Islands); *Eusiroides monoculoides* (Haswell) in J. L. Barnard, 1964, and Barnard (1969b) (So. California).

Taxonomic and biogeographical commentary. The genus *Eusiroides* has been fully rediagnosed by Barnard & Karaman (1991). It entrains most of the plesiomorphic character states found in eusiroidean genera, and its unique character states (e.g. linear, apically spinose uropod rami, spinose propodal palmar margins of the gnathopods, and stout homopodous peraeopods) are mainly plesiomorphic and typical of littoral marine pontogeneiids with which family group it appears to form a connecting link. However, *Eusiroides* does exhibit combinations of character states such as reniform pigmented eyes, deep coxal plates (coxa 1 broadly expanded distally), broadly homopodous peraeopods 5-7, setose rami of uropod 3, and pencil-like, 1-segmented accessory flagellum that, in combination, relate it to the more advanced genus *Eusirus* whose members are mainly epibenthic and sublittoral.

The genus *Eusiroides* contains about 15 species that are mainly warm-temperate and tropical, in Atlantic, Indian, and austral Pacific coastal marine regions. The type species, *E. monoculoides* (Haswell, 1879) has been identified from depths of 0-20 m at Corona del Mar, S. California, by J. L. Barnard (1964; 1969b), but this identification has not been confirmed subsequently. The species is unrecorded on the N. American Pacific coast north of that point. It is distinguished from the Hawaiian and western Pacific species by characters of the text.

Eusirus Kroyer

Eusirus Kroyer, 1845: 511.—Stebbing, 1906: 338.—Gurjanova, 1951: 698.—Birstein & Vinogradov, 1960: 220.—Barnard, 1969a: 226.—Ledoyer, 1982: 235.—Barnard & Karaman, 1991: 320.

Type species. *Eusirus cuspidatus* Kroyer, 1845

Component North Pacific species: *Eusirus cuspidatus* Kroyer, 1845; *E. hirayamae*, new species; *E. columbianus*, new species; *E. fragilis* Birstein & Vinogradov, 1960; *E. bathybius* Schellenberg, 1955 (Birstein & Vinogradov, 1960) (see also Fig. 40, p. 59, but not treated in text).

Diagnosis: Pleon, occasionally posterior peraeonal segments, weakly toothed and/or ridged postero-dorsally; urosome smooth above. Rostrum short. Anterior head lobe broad, oblique, weakly incised. Pigmented eyes medium,

reniform, or lacking. Antennae well developed, peduncles strong; distal peduncular segments and flagella calceolate in most species, in both sexes. Calceoli complex, with separate cup-like proximal and rod-like distal elements. Antenna 1 longer than antenna 2; peduncles 1 and 2 often cusate, or pro-cusate distally; peduncle 3 short; accessory flagellum distinct, linear, 1-2 segmented.

Mouthparts modified for carnivory. Upper lip, apex rounded. Lower lip, inner lobes weakly developed. Mandible: molar columnar and triturative; left lacinia 6-8 dentate, right lacinia bifid; palp slender, segment 3 usually longer than 2. Maxilla 1, inner plate with 1 apical seta, outer plate with 11 apical spines (10 pectinate); palp slender, outer segment longest. Maxilla 2, inner plate lacking facial setae, broader than outer. Maxilliped, palp large, raptorial; inner plate short, apex with 2-3 spines; outer plate large.

Coxae 1-3 medium, deeper than wide; coxa 1 broadened distally, hind corner cusate; coxa 4 excavate behind. Gnathopods strongly subchelate, "eusiroidean" in form (carpus slender, elongate, posterior lobe small, narrow; propod short, very deep), subequal in size and form, palmar margins lacking stout spines; merus and ischium small.

Peraeopods 3 and 4 slender, elongate; segment 4 > segment 5; dactyls short to medium. Peraeopods 5-7 slender, homopodous, increasing posteriorly; bases broad, hind margins often serrate, narrowing distally, lobate below.

Pleon plates 2 and 3 deep, broad, hind margin of 3 rounded, usually serrate. Uropods 1 and 2 slender, rami narrowly lanceolate, serially spinose, apices lacking spines; uropod 1, peduncle usually armed with stout antero-distal spine. Uropod 3, rami lanceolate, subequal, margins spinose, occasionally weakly plumose-setose. Telson large, elongate, narrowing distally, apex narrowly and deeply cleft.

Coxal gills large, weakly pleated. Brood plates broad, margins simple-setose.

Taxonomic and distributional commentary. Of the 24 described species and forms of the genus *Eusirus*, two-thirds occur mainly in sublittoral coastal, or bathyal and abyssal offshore waters of the North Atlantic, Arctic, and Antarctic regions, and the remainder in the Indian and North Pacific oceans. In more detailed breakdown, 14 of the species have pigmented eyes and are sublittoral in depths of less than 500 m. All nine species that have been recorded from Arctic and Antarctic waters are essentially sublittoral, with pigmented eyes. Of the 7 Atlantic species, three are sublittoral, with pigmented eyes, whereas of the 8 species recorded from the Indian and North Pacific oceans, only two are sublittoral and fully eyed, and both occur in the North Pacific (p. 10). These limited data would suggest that the genus *Eusirus* is essentially bipolar, with relatively few members penetrating towards the tropics at bathyal and abyssal depths. As we shall see below (p. 22), this pattern contrasts with that of the relatively advanced genus *Rhachotropis* in which 2/3 of the ~50 species are bathyal and abyssal, and nearly all the sublittoral, eyed species occur in the northern hemisphere only.

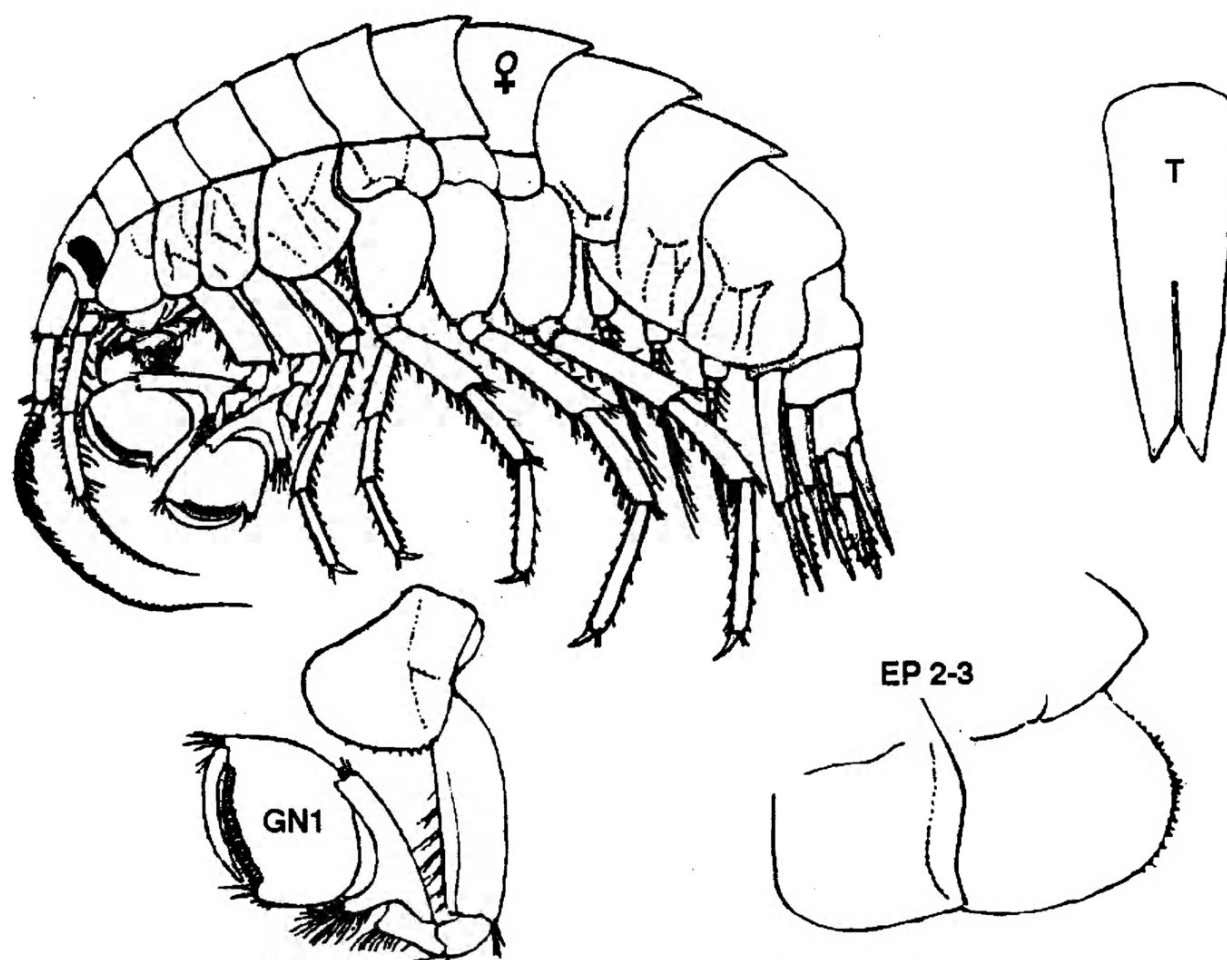


FIG. 1. *Eusirus cuspidatus* (Kroyer, 1845) Female (40 mm) Okhotsk Sea.
(modified from Sars, 1895)

Eusirus cuspidatus Kroyer
(Fig. 1)

Eusirus cuspidatus Kroyer, 1845: 501.—Sars, 1895: 416, pl. 146.—Gurjanova, 1951: 700, fig. 483.—Shoemaker, 1955: 46.—Barnard & Karaman, 1991: 321.

Material Examined: ALASKA: Amchitka I., 100 m, contour of "C" site, near Banjo Pt., trawl, G. Tutmark coll. Sept. 13/1971 - 1 female ov. (slide mt.); Bering Sea, near King I., P. Slattery coll., July 28, 1984 - 1 female br.II (IZ1989-002).

Diagnosis. Female (to 45 mm): The type species has been well described and diagnosed (loc. cit). The following character states have previously been little stressed or utilized in species comparisons:

Eye large, deep, narrowly reniform. Antenna 1 about 10% longer than antenna 2; flagellae weakly or not basally calceolate.

Mandible: molar with small triturating surface; spine row short; palp segment 3 longer than 2. Maxilla 1, inner plate with single apical seta. Maxilla 2, inner plate broad. Maxilliped, inner plate with 3 stout apical spines.

Gnathopods 1 & 2, posterior carpal lobes deeper than distal width of carpus; lobe apically strongly setose.

Peraeopods 3-7 dactyls very short, less than 1/6 length

of respective segment 6. Peraeopods 3 & 4, segment 4 slightly longer than segment 5. Peraeopods 5-7, bases medium broad, convex behind, weakly lobate below.

Uropod 1, peduncle with short distal process but lacking distal hood; rami subequal. Uropod 3, margins setose, spinose. Telson elongate (length ~ 3X basal width), cleft nearly 1/2, notch flared at apex.

Taxonomic and distributional commentary. Material from the southern Chukchi Sea and Bering regions differs in no significant manner from N. Atlantic material illustrated by Sars (1895). This very large species is similar to another large arctic regional species, *E. holmi* Hansen, 1887, in having a posteriorly toothed peraeon segment 7 and short peraeopod dactyls, but differs in its much larger pigmented eyes, much larger and deeper coxal plates, the larger gnathopod 1, shorter and stouter peraeopods, and more deeply cleft telson. Shoemaker (1955) gives regional records of *E. cuspidatus* from Pt. Barrow, Alaska to Kotzebue Sound, and Cook Island, Alaska, from the shallows to depths of 400 m. Like its counterpart species of the antarctic region, *E. perdentatus*, the species is probably an ambush predator that consumes small worms and crustaceans (including other amphipod species) that it seizes by means of its raptorial gnathopods (Klages & Gutt, 1990).

KEY TO NORTH PACIFIC SPECIES OF *EUSIRUS*

1. Pigmented eyes present; pleon plate 3 strongly serrate behind; telson deeply cleft (coastal plain and fiord species) 2.
—Pigmented eyes lacking; pleon plate 3 smooth behind; telson, apex notched (offshore abyssal forms) . 4.
2. Peraeopods 3 and 4, segments 4 & 5 subequal in length; telson cleft ~ 1/2 from apex; animals very large to 40 mm) *E. cuspidatus* (p. 9)
—Peraeopods 3 and 4, segment 4 distinctly longer than 5; telson cleft ~ 1/3 from apex; animals small to medium (5 - 18 mm). 3.
3. Peraeon segment 7 with weak posterior dorsal tooth; peraeopod 7, hind margin of basis weakly incised; maxilliped, palp segment strongly broadened distally *E. hirayamae*, n. sp. (p. 10)
—Peraeon segment 7 lacking dorsal tooth; peraeopod 7, basis straight or slightly convex behind; maxilliped palp, segment 2 normal, much longer than broad *E. columbianus*, n. sp. (p. 10)
4. Peraeopod 5, basis much narrower than peraeopod 7; telson short, subtriangular *E. fragilis*
—Peraeopod 5, basis broad, convex behind; telson elongate *E. bathybius* (Fig. 40, p. 59)

Eusirus longipes Boeck
(Fig. 2)

Eusirus longipes Boeck, 1861: 665.—Sars, 1895: 420, pl. 148(1).—Gurjanova, 1951, 702, fig. 485.—Lincoln, 1979: 402, fig. 191.—Ledoyer, 1982: 235, fig. 159.—Barnard & Karaman, 1991: 321 (part).
non Hirayama 1985: 29.

Taxonomic and distributional commentary. This calceolate, medium-sized (to 18 mm) species occurs widely in the eastern North Atlantic, Mediterranean, and Black Sea regions, on muddy bottoms, in depths of 5-200 m, but not in arctic seas (Gurjanova, 1951; Lincoln, 1979; Ledoyer, 1982).

Hirayama (loc. cit.) identified as this species a 6.5 mm male specimen from the Ariake Sea, Japan. He noted differences between his western Pacific material and the type material from the North Atlantic region, in dorsal peraeonal carination and spination of coxae 2 and 3. These and other differences are here accepted as a basis for recognition of Hirayama's material as a distinct new species (below). The illustration provided by Sars (loc. cit.) is here reproduced for comparison with the new species from Japan.

Eusirus hirayamae, new species
(Fig. 3)

Eusirus longipes Hirayama, 1985: 29, figs. 142-147.—Ishimaru, 1994: 44.

Diagnosis. Male (6.5 mm), Holotype (Hirayama, loc. cit. here designated): Eye deep reniform, strongly pigmented. Antenna 1, flagellum calceolate. Antenna 2, peduncular segment 5 and flagellum calceolate.

Mandible, left lacinia 8-dentate. Maxilliped, palp segment 3 very broad (width ~ length), outer plate tall, columnar.

Gnathopods 1 and 2, carpus and propod broader (thicker) than in *E. longipes*. Peraeopods 3-7, segments 4-6 and dactyl relatively short, thick. Peraeopods 5 and 6, basis broad, rounded behind.

Uropod 1 with stout distal peduncular spine. Uropod 3, rami broadly lanceolate, inner ramus, margins strongly plumose-setose. Telson relatively short (length <2X basal width), cleft ~ 1/4, notch flared distally.

Etymology. The authors are very pleased to name this species in honour of Dr. Akira Hirayama, who first described it, and who has contributed very significantly to knowledge of the amphipod fauna of Japan.

Taxonomic commentary. *Eusirus hirayamae* differs from *E. longipes* Boeck principally in the shorter broader segments of the peraeopods, the short, thick peraeopod dactyls, the stout postero-distal spine of uropod 1, and the presence of a posterior marginal spine on coxal plates 2 and 3.

Eusirus columbianus, new species
(Fig. 5)

Eusirus leptocarpus Wailes, 1931: 41?—Fulton, 1968: 107?—Austin, 1985: 590?

Material Examined: S.E. ALASKA: Boca de Quadra, Head, KEC Sta: 89-2-44 (55° 19.2' N, 130° 27.4' W) 30 m dive, June 27, 1989 - 2 females (5.8 mm) (slide mount). BRITISH COLUMBIA: North-central coast: ELB Stn. H62, Rivers Inlet, 20-30 m, Aug. 10, 1964 - 2 females. C. Levings Stn. 51B-028 (53° 0.58' N, 128° 30.06' W), 52 m, April 4, 1973 - 1 female; Stn. 51B-001, Swanson Bay (52° 00' N, 128° 30' W), Aug. 18, 1975 - 1 female (5.1 mm) (slide mt.); Ibid. Stn. 51B-002, Nov. 18/75 - 1 female; Ibid., Stn. 51B-003, 51 m. - 1 male; Ibid., Stn. 51B-004, 47 m. - 1 female. N. Vancouver I. ELB Stn. P26, Quatsino Sd., Koprino Hbr., 12-16 m dredge, mud shell, woody debris, Aug. 14, 1975. -

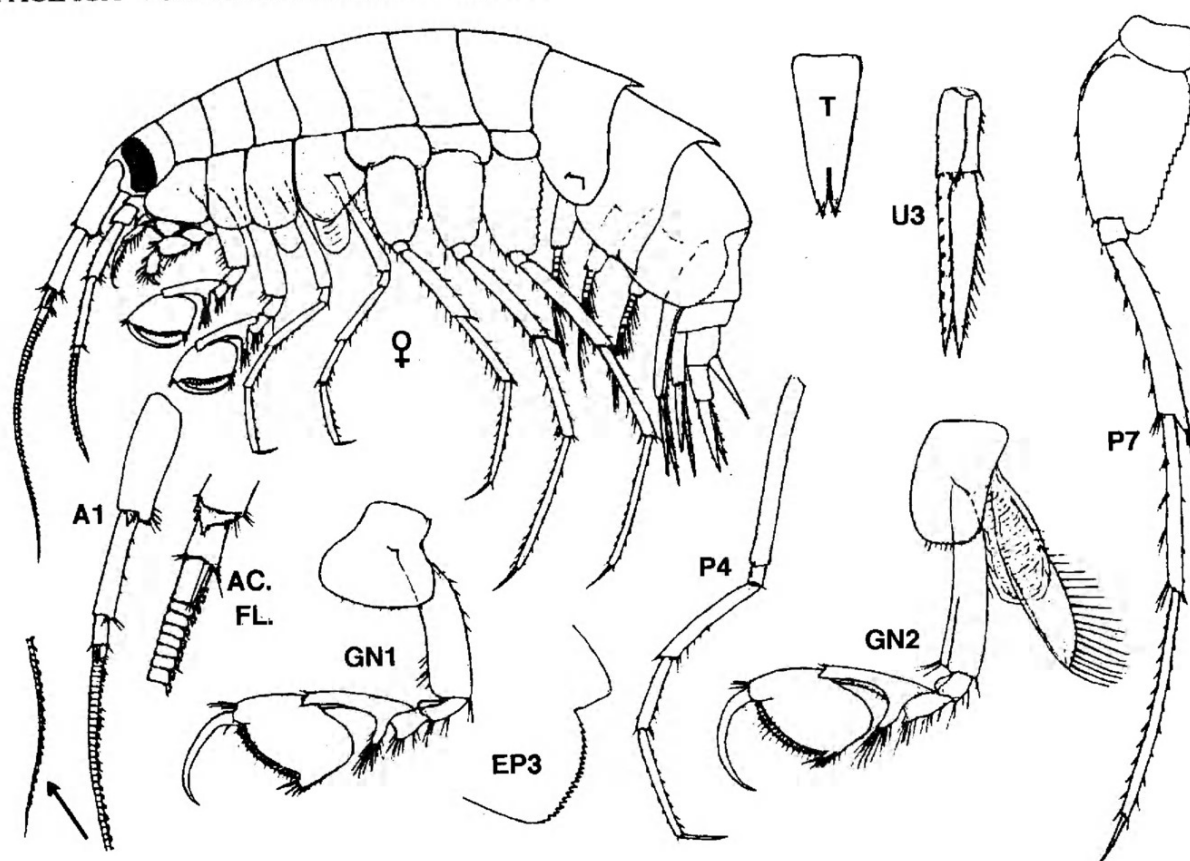


FIG. 2. *Eusirus longipes* Boeck, 1871 Female ov. (13.0 mm) NE Atlantic, to 225 m. (modified from Sars, 1895)

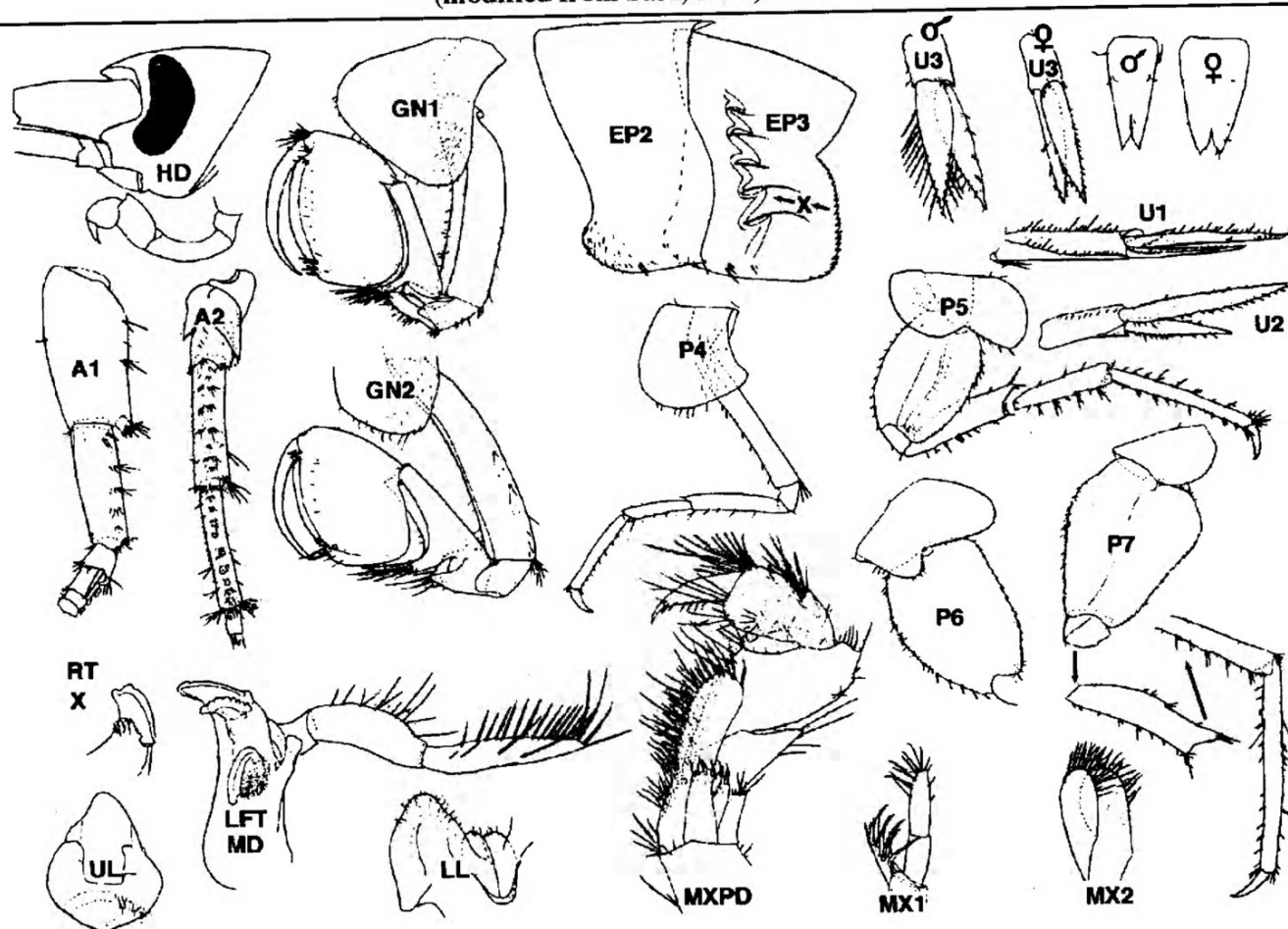


FIG. 3. *Eusirus hirayamae*, new species. Male (6.5 mm) Ariake Sea, Japan. (modified from Hirayama, 1985)

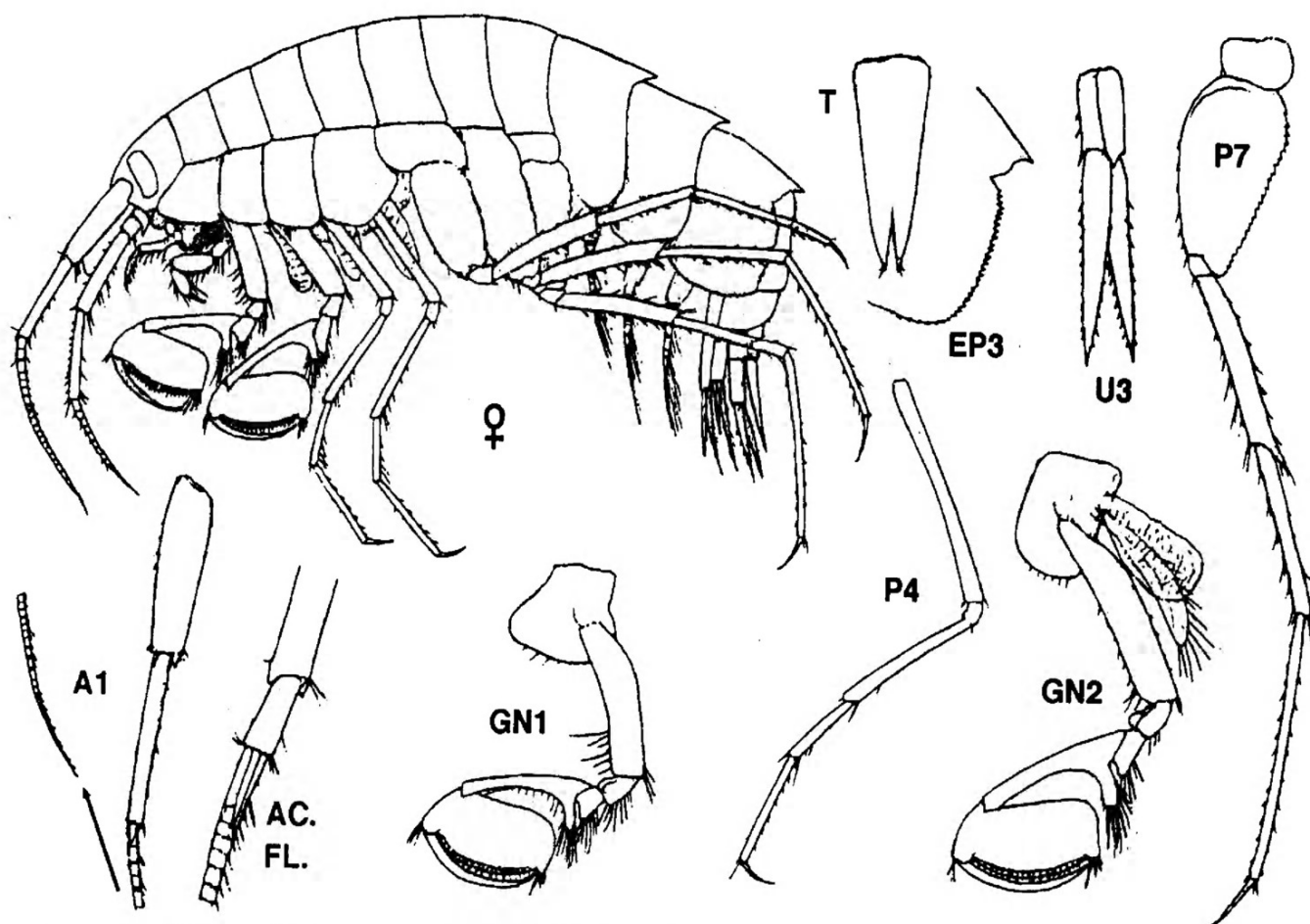


FIG. 4. *Eusirus leptocarpus* Sars, 1895. Female ov (7.5 mm). N.E. Atlantic, to 400 m. (modified from Sars, 1895)

HOLOTYPE female (5.2 mm), CMN Cat. No. pending. ELB Stn. P4, Mouth of Burrard Inlet, nat. dredge, 110 m Nov. 2/77 - 2 females; ELB Stn P6, Off Burrard Inlet, nat. dredge, 150 m., Nov. 3/77 - 1 male, 1 female; ELB Stn. P8, Queen Charlotte Channel, E. of Passage I., nat. dredge, 125 m, Nov. 3/77 - 1 female. S. Vancouver I.: GWO Stn. 153A, Victoria, off Clover Pt., 78 m. Aug. 27, 1976 - 1 female.

Diagnosis. Female (5.2 mm): Body small, slender. Pleon segments 1 and 2 each with low postero-dorsal tooth; peraeon and urosome smooth above. Eye medium, reniform. Antennae stout, relatively short. Antenna 1 little longer than antenna 2; peduncle 3 and flagellum calceolate; accessory flagellum slender, essentially 1-segmented, extending well beyond first flagellar segment. Antenna 2, peduncular segment 5 and basal flagellar segments with anterior marginal calceoli. Calceoli complex, distal element rod-like, elongate.

Mandible, molar weakly triturative, grinding surface with marginal incomplete ring of short spines; spine row of 4-5 blades; left lacinia 8-dentate; right lacinia bifid-flabellate; palp segment 3 slender, longer than 2 with proximal cluster of 3 longish "A" setae. Maxilla 1, outer plate, inner apical spine flagellate. Maxilla 2, inner plate slightly shorter and broader than outer. Maxilliped, palp segment 2 not broad-

ened distally; outer plate large; inner plate short, with 3 stout apical spines.

Coxae 1-4 medium deep, broad. Coxa 1 strongly broadened distally, hind corner with 2-3 cusps. Gnathopod 2 slightly larger than gnathopod 1; carpal lobes short, relatively broad; propods, postero-distal angle with cluster of 2-3 stout unequal spines.

Peraeopods 3 and 4 slender, 4 slightly the longer; segment 4 ~50% longer than segment 5; dactyls relatively long, slender, > 1/3 length of respective segment 6. Peraeopods 5-7 slender, closely homopodous, differing little in form and length, peraeopod 5 shortest; bases broad, hind margins gently convex or nearly straight, with medium strong serrations; dactyls slender, about 1/3 length of respective propods.

Pleon plate 2, hind corner acuminate. Pleon plate 3 broad, hind margin gently convex, with numerous strong serrations. Pleopods strong, rami about 15-segmented. Uropods 1 and 2 slender, rami strongly serially spinose. Uropod 1, distal peduncular spinose process lacking outer marginal "hood" (as in *E. longipes*); outer ramus slightly (~10%) shorter than inner. Uropod 2, outer ramus short, ~60% length of inner ramus. Uropod 3, rami narrowly lanceolate, outer ramus slightly the shorter, margins spinose.

Telson elongate, narrowing distally, cleft ~1/3. Coxal gills medium, slender sac-like, smallest on peraeopod 7.

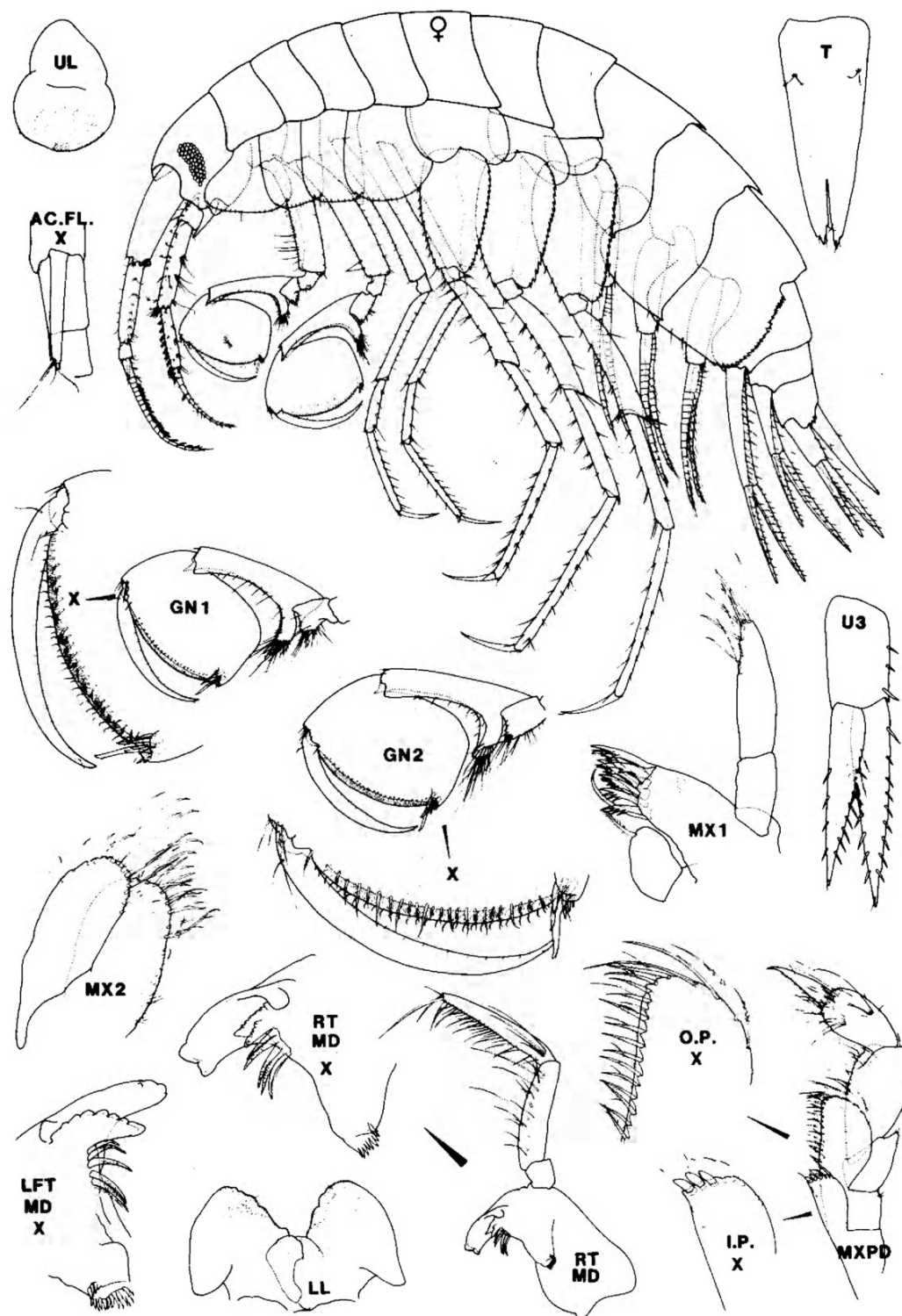


FIG. 5. *Eusirus columbianus*, n. sp. Female (5.2 mm). Koprino Harbour, V. I., British Columbia.

Taxonomic and distributional commentary. *Eusirus columbianus* is known from S. E. Alaska to S. British Columbia, in medium depths (to 125 m). It appears closest to *E. leptocarpus* Sars, 1895 (fig. 4) in the form of the gnathopods, and distinctive notch above the posterior margin of pleon plate 3. However, *E. columbianus* lacks a postero-dorsal

tooth on peraeon segment 3, the peraeopods are shorter and less slender, the dactyls stouter and, in gnathopod 1, the propod is relatively broad, and the carpal lobe broader and apically rounded, not subacute. Previous regional records of *E. leptocarpus* listed by Wailes (1931), (Fulton, 1968), and Austin (1985) are unconfirmed and may be this species.

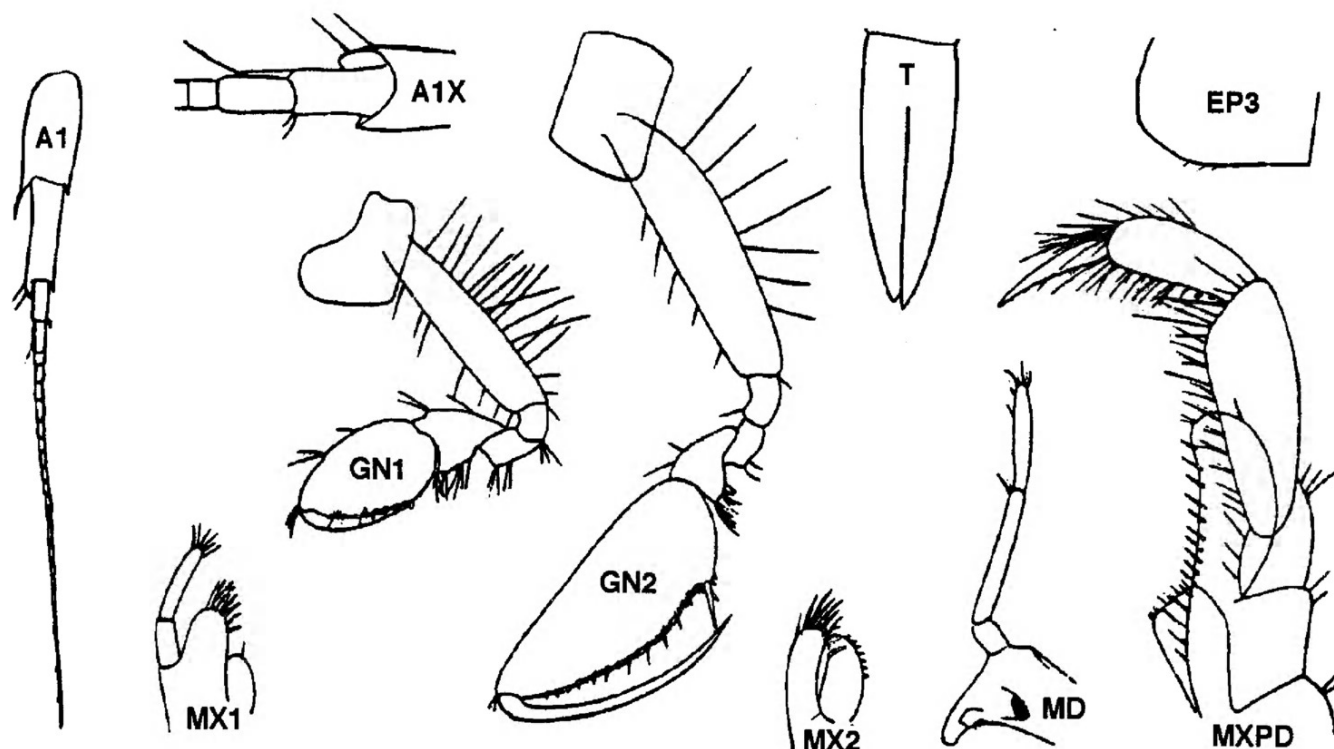


FIG. 6. *Cleonardo macrocephala* Birstein & Vinogradov, 1955. Male (8.0 mm)
Kurile-Kamchatka Trench (modified from Birstein & Vinogradov, 1955)

Cleonardo Stebbing

Cleonardo Stebbing, 1888: 959.—Stebbing, 1906: 345.—
Gurjanova, 1951: 704.—Birstein & Vinogradov, 1955: 272—
Barnard, 1969a: 222.—Barnard & Karaman, 1991: 315.

Type species. *Cleonardo longipes* Stebbing, 1888.

Component North Pacific species: *Cleonardo macrocephala* Birstein & Vinogradov, 1955; *C. longipes* Stebbing, 1888; *C. moirae*, new species (p. 15).

Diagnosis: Body not strongly compressed, dorsally smooth or nearly so. Rostrum short to medium. Anterior head lobe rounded to weakly produced. Pigmented eyes lacking. Antennae medium, peduncles and flagella usually calceolate in males and females; distal peduncular segments often lined with brush setae in male. Antenna 1 slightly longer than antenna 2, peduncle 2 usually shorter than 1, both usually with distal process or spine; basal flagellar callynophore weakly (or not) developed in male; accessory flagellum 1-segmented, linear. Antenna 2, peduncular segments 4 and 5 slender, flagellum not shortened.

Upper lip slightly incised below. Lower lip broad, inner lobes weak. Mandible, molar large, triturtative; left lacinia 6-8+ dentate, right lacinia bifid; spine row with 4-7 blades; incisor dentate; palp slender, segment 3 variable, occasionally longer than segment 2. Maxilla 1, inner plate with 1-2 apical setae; outer plate with 11 apical spines; palp slender, distal segment longest. Maxilla 2, inner plate broader and shorter than outer plate. Maxilliped palp, segments ordinary; outer plate large; inner plate with 2-3 apical teeth.

Coxae 1-4 regular, medium; coxa 1 broadly rounding, not produced; coxa 4 excavate behind. Coxae 5 and 6 posterolobate. Gnathopod 1 smaller than 2, both strongly subchelate; carpal lobes broad and shallow, or deep and narrow; propods large, posterior margin short, palms oblique, margin spinose, especially near postero-distal angle, having 1-3 clusters of spines into which the tip of the dactyl closes.

Peraeopods 3 and 4 slender, segment 4 distinctly longer than 5, dactyls elongate and simple, or shorter, plumose-setose. Peraeopods 5-7 homopodous, subequal in form and size, not greatly elongate; bases broad, variously lobate; dactyls long.

Pleon plates 1-3 large, regular, not serrate behind. Uropods 1 and 2, rami broadly lanceolate, outer ramus little (10-20%) shorter than inner ramus. Uropod 3, rami broadly lanceolate, outer ramus slightly the shorter, inner margin of inner ramus may be setose. Telson elongate, deeply cleft.

Coxal gills sac-like or plate like, smallest on peraeopod 7. Brood plates on peraeopod 2-4 broad, strap-like on peraeopod 5.

Taxonomic and distributional commentary. The ten described species of *Cleonardo* are bathypelagic (1880-3000+ m), mainly in the North Atlantic, Indian, and North Pacific oceans. The *C. macrocephala* group is distinctive and endemic to the North Pacific region. *Cleonardo longirostris* Chevreux, 1908, an Atlantic species, has been recorded from the northwestern Pacific region by Birstein & Vinogradov (1955, 1960), but is unknown from the North American Pacific study region.

KEY TO NORTH PACIFIC SPECIES OF *CLEONARDO*

1. Gnathopods 1 & 2 subsimilar in size; antenna 1, peduncular segment 1 ordinary *C. longirostris*
—Gnathopod 1 distinctly smaller than 2; antenna 1, peduncular segment 1 with distal hood-like process 2.
2. Coxa 1 strongly expanded antero-distally; antenna 1, peduncular segment 3 regular, length 1/3-1/2 segment 2; telson lobes narrowing distally *C. macrocephala* (p. 15)
—Coxa 1 slightly expanded antero-distally; antenna 1, peduncular segment 3 very short, ~1/4 length of segment 2; telson lobes narrowing regularly towards apex *C. moirae* (p. 15)

From the standpoint of overall morphology, the 10 world species appear separable into 4 main groups, viz: (1) a relatively primitive, essentially North Atlantic group of *C. appendiculata* (Sars, 1879), *C. microdactyla* Stephensen, 1912, *C. neuvillei* Chevreux, 1908, and *C. longipes* Stebbing, 1888, with the related but more advanced *C. biscayensis* Chevreux, 1908, and *C. maxima*, Birstein & Vinogradov, 1964, occurring also in the Indian Ocean; (2) the single species, *C. spinicornis* Chevreux, 1908, with apomorphic modifications of antenna 1, gnathopods 1 and 2, and bases of pereopod 5-7, also from the Atlantic and Indian oceans; (3) the uniquely deep-plated and setose *C. brevipes* Ledoyer, 1982, known only from the Indian Ocean near Madagascar; and (4) the advanced, globose-headed *macrocephala*-*moirae* species pair, endemic to the North Pacific region.

The two sibling North Pacific species are very similar to each other but differ widely from the other 8 described species of the genus. Unique to the North Pacific pair is the globose form of the head, the antero-distal hood-like process of peduncular segment 1 of antenna 1, the weakly calceolate flagellae of both antennae, the relatively small size of coxa 1, the markedly unequal size of gnathopods 1 and 2, and the short segment 3 of the mandibular palp. They also differ from all but *C. spinicornis* in the relatively long shallow carpal lobes of the gnathopods. Such large and numerous morphological differences are generally recognized at generic (and certainly subgeneric) level in virtually all other gammaridean amphipod families. A revision of the genus *Cleonardo* would therefore seem urgently needed, but is beyond the scope of this limited study.

Cleonardo macrocephala Birstein & Vinogradov
(Fig. 6)

Cleonardo macrocephala Birstein & Vinogradov, 1955: 273, fig. 31.—Birstein & Vinogradov, 1958: 247.—Barnard & Karaman, 1991: 315.

Distributional and taxonomic commentary. This species is a member of the bathypelagic gammaridean amphipod community, sampled in deep closing tows (0-7200 m) over the Kurile-Kamchatka Trench in the northwestern Pacific ocean (Birstein & Vinogradov, loc cit). In most taxonomic features it closely resembles the sibling species *C. moirae* that is described (below) from comparable depths in the eastern North Pacific region.

In addition to the differences provided in the key, *C. macrocephala* may be distinguished from *C. moirae* by:

coxa 1 moderately expanded and strongly rounded anteriorly; propod of gnathopod 2 elongate (length fully twice its depth vs. 1.5 X its depth in *C. moirae*); maxilliped, outer plate large and relatively slender, extending fully half the length of palp segment 2; maxilla 2, inner plate less broadly expanded, width less than twice that of the outer plate; pleon plate 3, hind corner sharply obtuse (vs. sharply rounded in *moirae*); and telson lobes narrowing distally rather than continuously from their basal fusion.

As noted above (p. 15), the *macrocephala* complex stands in considerable morphological isolation from the 3 other major world-wide morphotypes recognized here. Such differences may simply reflect major differences in the kinds of prey organisms or food resources that can be utilized through specialized morphologies. The near-total lack of information on the diets of these species renders such consideration highly speculative. However, the morphological differences might also reflect discontinuities in the deep-water circulation of the world's oceans, non-overlaps that would tend to isolate the North Pacific gene pool and prevent significant genetic influx from adjacent species complexes. Speculatively also, the degree of morphological difference between adjacent populations might also be a measure of the geological time frame or duration of genetic isolation.

Cleonardo moirae, new species
(Fig. 7)

Material Examined: Institute of Ocean Sciences: Off Vancouver Island, over Endeavour Ridge, (47° 58'N., 129° 06' W), June 19-21, 1990: IOS Stn. LC 90-3, tow 006, net 2 1870-1900 m. - 1 female ov. (7.0 mm) Holotype (slide mount), 2 females ov. (7.0 mm) Paratypes, Cat. Nos. pending; IOS Stn. LC 90-3, tow 008, net 2, 1950-1935 m. - 1 male (5.0 mm) Allotype (slide mount), 1 other male (5.0 mm), 1 subadult female (6.0 mm). Ibid, (48° 01'N., 129° 06'W'), July 17-19, 1991: IOS Stn. 91-12, VT1, net 1, 0-1888 m - 3 females; Ibid, VT3, net 3, 1985-1787 m. - 1 female. (see also Thomson et al, 1992).

Diagnosis: Holotype female (7.0 mm): Head medium large, somewhat globose. Rostrum short, strongly deflexed. Antennae 1 & 2 subequal, finely calceolate (in males only). Antenna 1, peduncular segment 1 produced antero-distally hoodlike over base of shorter segment 2; segment 2 with 2 sharp antero-distal cusps; peduncle 3 short; accessory flagellum very short; flagellum 20+ segmented. Antenna 2, peduncular segment 5 is 2/3 length of peduncular segment 4;

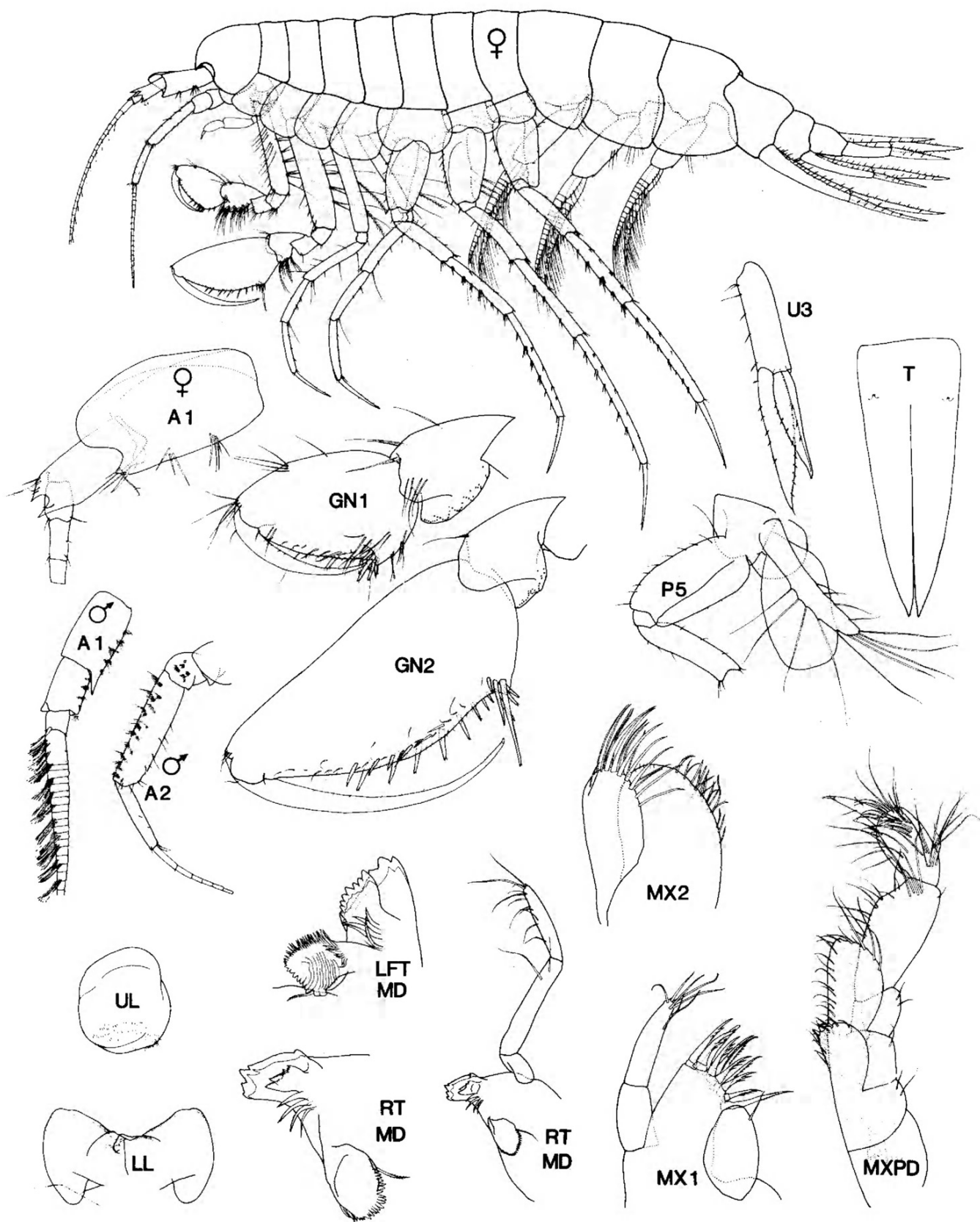


FIG. 7. *Cleonardo moirae*, n. sp. Female ov. (7.0 mm). Off Vancouver I., above Endeavour Ridge. IOC Stn. 90-3 (1900 m); Male (5.0 mm) Stn. 90-3 (1950 m).

flagellum ~ 20-segmented, proximal segment elongate.

Mandible, molar grinding surface ringed by short blades; spine row with 4-5 blades; left lacinia 8-9 dentate; palp not elongate, segment 3 weakly setose, shorter than segment 2. Maxilla 1, inner plate with 1 apical seta. Maxilla 2, inner

plate as long as outer, apex nearly devoid of short setae. Maxilliped ordinary; inner plate with 3 stout apical spines.

Coxal plates 1-4 medium, about as deep as broad; coxa 4 little excavate behind; coxa 5 nearly aequilobate. Gnathopod 1 distinctly smaller than gnathopod 2; posterior margin of

basis lined with setae; carpus shallow, medium, broadly rounded below; propod ovate, palm 2X length of hind margin, outer palmar margin with 2-3 spines proximally and a cluster of 6 spines at palmar angle. Gnathopod 2, carpus shallow, shorter (narrower) than in gnathopod 1; propod slender subovate, palmar margin nearly 3X length of hind margin, proximal 2/3 of inner and outer margins lined with stout spines and a cluster of 6 spines (one spine elongate) at the posterior angle.

Peraeopods 3 and 4 ordinary; segment 4 slightly longer than segment 5; dactyls long, simple. Peraeopods 5-7 homopodous, 6 slightly the longest; bases, hind margins nearly straight, not serrate.

Pleon plates 1-3 broad, hind corners subquadrate, lower margins weakly setose. Uropods 1 and 2, rami medium; inner ramus broadly lanceolate. Uropod 3, rami little longer than peduncle, inner ramus broader and longer than outer ramus, margins weakly spinose. Telson elongate, slender, cleft 3/4 to base; apices sharply acute.

Coxal gills simple, subquadrate. Brood plate on peraeopod 5 strap-like, as long as basis, margins with long setae. Allotype male (5.0 mm): Antennae lacking calceoli; distal peduncular segments of both antennae armed with clusters of brush setae. Antenna 1, peduncular segment 1 with acute postero-distal process; flagellum with weak basal calynophore; distal segments with numerous aesthetascs.

Etymology: This new species is named in honour of Moira Galbraith, Victoria, B. C. who has facilitated examination of much new Pacific pelagic amphipod material.

Taxonomic and distributional commentary. *Cleonardo moirae* is recorded from the IOS stations above, some 300+ km off the outer coast of Vancouver I., B. C., at depths between 1750 and 1950 m. This species is a member of the *macrocephala* group having a large subglobular head, antenna 1, peduncular segment 1 produced anterodistally, and gnathopod propods very unequal in size, with strongly spinose palmar margins. It is distinguished from *C. macrocephala* by the relatively long and shallow carpal lobe of gnathopod 1, the relatively short peduncular segment 2 of antenna 1, and less strongly anteriorly produced margin of

Eusirella Chevreux

Eusirella Chevreux 1908:12.—Birstein & Vinogradov, 1955: 271.—Birstein & Vinogradov, 1960: 224.—Barnard & Karaman, 1991: 317.

Type species. *Eusirella elegans* Chevreux, 1908.

Component North Pacific species: *E. longisetosa* Birstein & Vinogradov, 1960 (tropical western N. Pacific); *E. multicalceola* (Thorsteinson, 1941) (eastern and western North Pacific). A third species, or female morphotype, may be present in material from the eastern North Pacific.

Diagnosis: Body broad and somewhat depressed, as in

physosomatid hyperiids, smooth above. Rostrum short; anterior head lobe rounded, not produced. Pigmented eyes lacking. Antennae medium, calceolate on peduncles and flagella (both sexes), peduncles elongate. Antenna 1 longer than antenna 2; peduncle 2 longer than 1, calceolate; accessory flagellum very short or scale like. Antenna 2, peduncle 4 calceolate, subequal to 5 (shorter than 5 in males); flagellum short, variously longer in males).

Upper lip broadly rounded below. Lower lip, inner lobes distinct. Mandible, molar conical, grinding surface small; spine row with 1-5 blades; left lacinia 6-7 dentate; right lacinia bifid?; palp segments 2 and 3, length subequal. Maxilla 1, inner plate lacking apical setae; outer plate with 9 apical spines; palp short, proximal segment the longer. Maxilliped, palp large, segments 2 and 3 sublinear, not broadened; outer plate large, arcuate; inner plate with minute apical spines.

Coxae 1-4 small, short; coxa 1 weakly produced anteriorly; coxa 4 not excavate behind. Gnathopod 2 larger than 1, both slender, not eusirid in form; propod and carpus variously elongate; palm of propod elongate, margin variously spinose; anterior and posterior margins of bases setose.

Peraeopod 3 and 4 slender, segment 5 shorter than 4, segment 6 and dactyl short, bearing long plumose setae. Peraeopods 5-7 slender, elongate; coxae shallow, aequilobate; bases ovate or sublinear; segments 6 and 7 (dactyl) elongate.

Pleon plates 1-3 rounded below, hind margins not serrate. Pleopods normal, stronger in males. Uropods 1 and 2, rami narrowly lanceolate, outer ramus distinctly (40-50%) shorter than inner ramus; peduncle of uropod 1 lacking antero-distal inter-ramal process. Uropod 3, rami narrowly lanceolate, margins spinose, outer ramus shorter than inner. Telson elongate, deeply cleft, narrowing distally.

Coxal gills medium, sac-like anteriorly, reverse L-shaped, posteriorly smallest on peraeopod 7. Brood plates long, strap-like.

Taxonomic commentary. Two species of *Eusirella* have been recorded from the N. Pacific region but only *E. multicalceola* is known from offshore waters of the North American Pacific coast. The genus is plesiomorphic in the calceolate antennae, slender gnathopods, and deeply cleft telson, but in most character states of the mouthparts and appendages it is strongly apomorphic (see also Fig. 33).

Five species have been described, three of which (*E. elegans* Chevreux, 1908; *E. heterochela* Birstein and Vinogradov 1964, and *E. flagella* Andres, 1982, have been recorded from Atlantic and Antarctic regions. Barnard (1964) suggested that *E. elegans* Shoemaker, 1945, exhibits several character states distinct from those of *E. elegans* Chevreux, and may be a full species of its own.

Eusirella longisetosa Birstein & Vinogradov (Fig. 8)

Eusirella longisetosa Birstein & Vinogradov, 1960: 224, fig. 30.—Barnard & Karaman, 1991: 318.

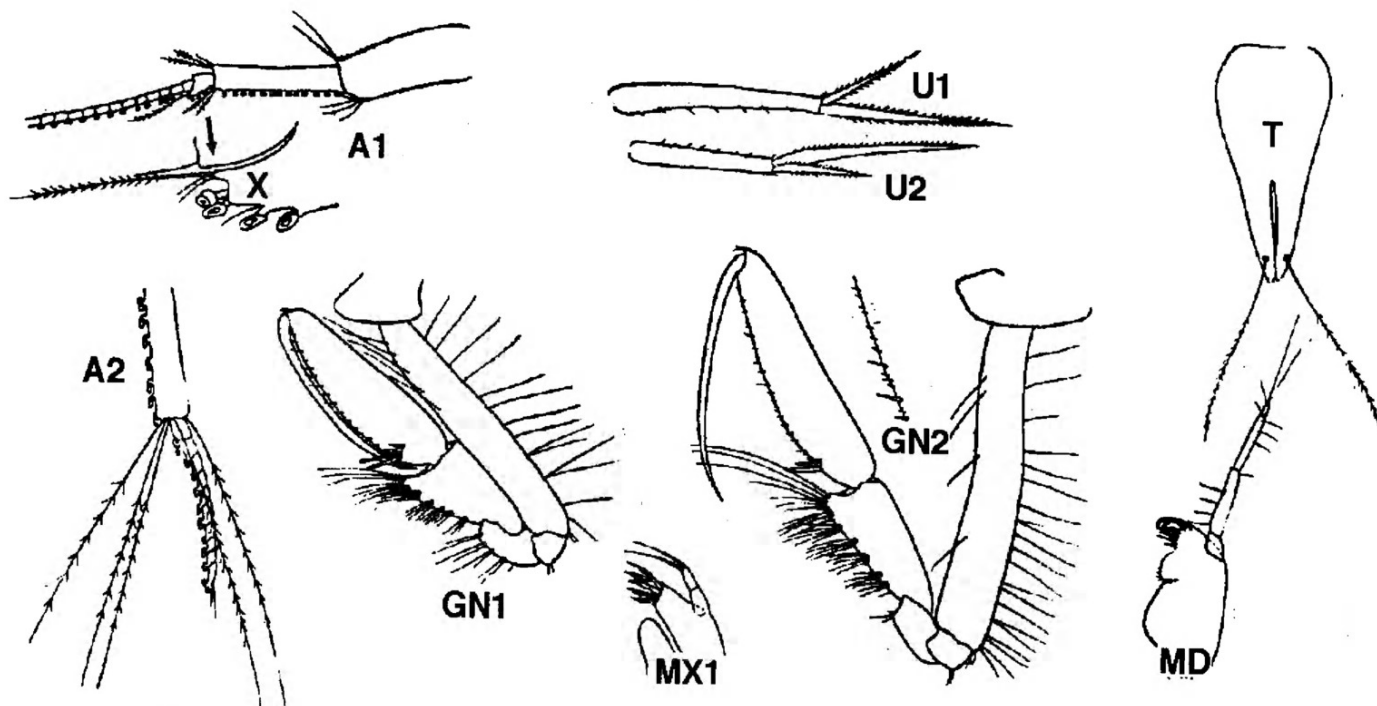


FIG. 8. *Eusirella longisetosa* Birstein & Vinogradov, 1960. Male (7.3 mm). Warm-temperate N. Pacific, off S. E. Japan (After Birstein & Vinogradov, 1960)

KEY TO NORTH PACIFIC SPECIES OF *EUSIRELLA*

1. Antennal peduncles with dense masses of calceoli; antenna 1, peduncular segment 3 regular, short; gnathopod 2, propod much longer than in gnathopod 1; dactyl extending little more than half total lower margin of propod; telson cleft 3/4 length, apices normal *E. multicalceola* (p. 18)

—Antennal peduncles with ordinary numbers of calceoli; antenna 1, peduncular segment 3 produced under first flagellar segment; gnathopod 2, propod little longer than in gnathopod 1; dactyl extending very nearly along the entire lower margin; telson cleft 1/3, apices each with single long seta . . . *E. longisetosa* (p. 17)

Taxonomic and distributional commentary. The partial description and illustration of this species is based on a single male specimen (7.3 mm) taken in a vertical tow (0-8500 m) off the southeastern coast of Japan (Birstein & Vinogradov, loc. cit.). *E. longisetosa* has not yet been taken in North American Pacific waters. It differs markedly from the female of *E. multicalceola* Thorsteinson in character states of the antennae, gnathopods, and telson, as outlined in the key (above). Additional differences are as follows:

Antenna 1, peduncular segment 3 produced posterodistally behind flagellar segment 1, hind margin with 4 calceoli.

Gnathopod 1, coxa, anterodistal corner slightly produced, rounded; basis slender, elongate; propod, palmar margin lined with evenly spaced short slender spines; postero-distal angle with cluster of 4 stout spines. Gnathopod 2, basis posteriorly lined throughout with longish setae; propod, palmar margin lined with slender spines of irregular length; postero-distal angle with cluster of 3 stout spines.

Mandible, spine row with 5-6 blades; palp segment 3 slightly longer than segment 2. Maxilla 1, palp segments 1 and 2 subequal in length; outer plate with 9 apical spines; inner plate apically bare.

Uropods 1 and 2, outer ramus short, < 1/2 length of inner ramus, margins with numerous serial pairs of short spines.

Eusirella multicalceola (Thorsteinson) (Figs. 9, 10, 11)

Gracilipes multicalceolus Thorsteinson, 1941: 85, pl. 7, figs. 71-77.—Birstein & Vinogradov, 1955: 271, fig. 30.

Eusirella multicalceola—Birstein & Vinogradov, 1958: 247.—Birstein & Vinogradov, 1960: 224.—J. L. Barnard, 1964: 321, figs. 6, 7.—Kamenskaya, 1981a: 101.—Barnard & Karaman, 1991: 318.

Material Examined: BRITISH COLUMBIA: Queen Charlotte Islands: off Kunghit I. (52°00.39'N, 131°23.97'W to 52°00.55'N, 131°30.90'W) IKMT, 0-510m, RBCM/CMN Stn 91-1-03, Mar. 19/91 - 2 females; off Tasu Sd (52°38.72'N, 132°05.79'W to 52°38.31'N, 132°09.90'W) IKMT 0-520m, RBCM/CMN Stn. 91-1-09, Mar. 20, 1991 - 1 male, 1 female. Ibid., over Barkley Canyon, J. P. Tully Cruise, #1990-12, IKMT 450-525m, December, 1990 - 2 females. off Hippa I. (53°30.39'N, 133°26.35'W 53°34.55'N, 133°30.20'W) IKMT 0-660m, RBCM/CMN Stn. 91-1-12, Mar. 22/91. - 3 females.

Off outer Coast of Vancouver I., over Endeavour Ridge, (48°01'N, 129°06'W) IOS Stn 91-12, Tow 3, net 3, 1985-1787 m. - 1 female ov. (11.0) mm. 1 br. young; Stn. 91-12,

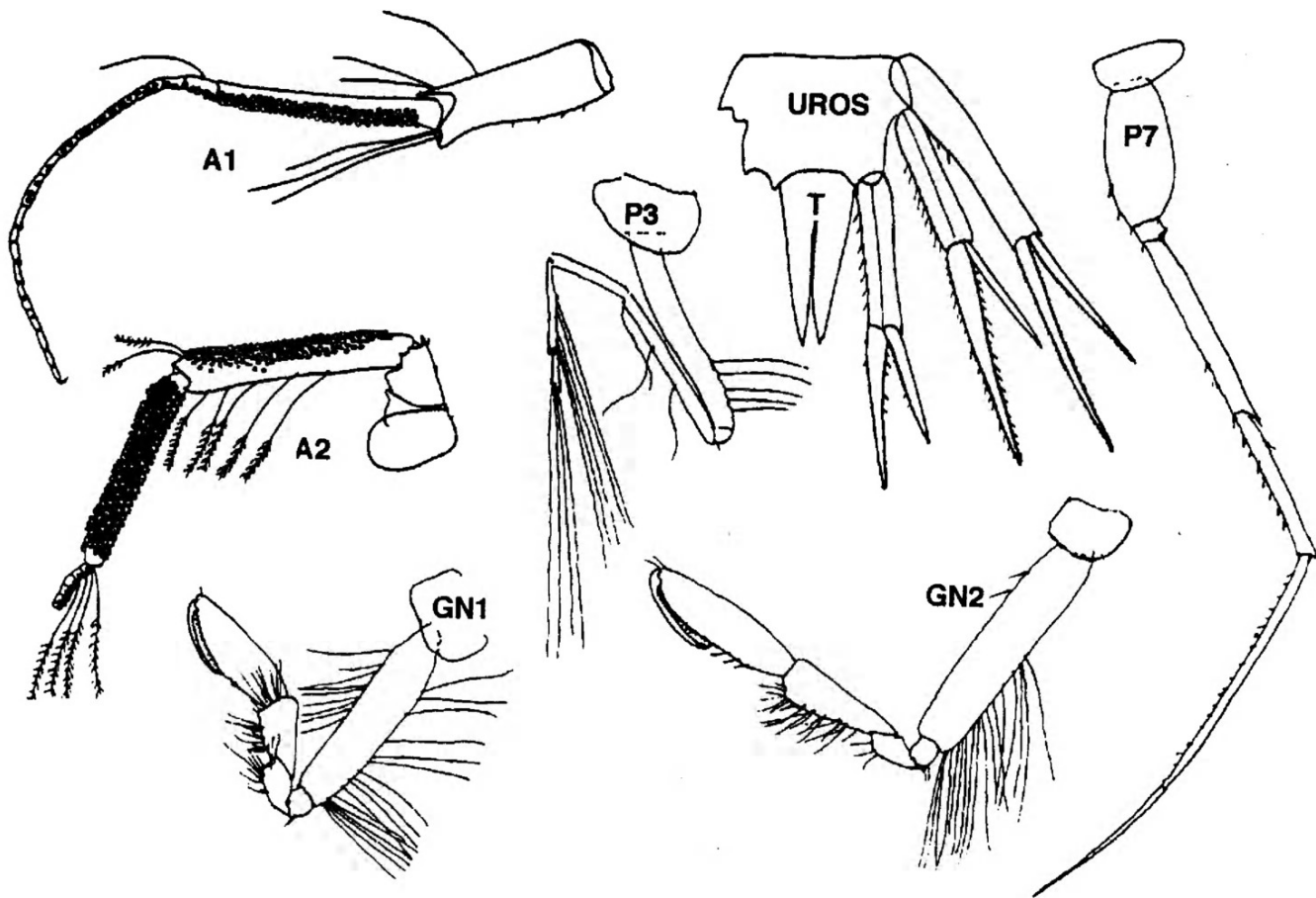


FIG. 9. *Eusirella multicalceola* (Thorsteinson, 1941) Male (11.0 mm)
Gulf of Alaska, 1000-1200 m. (modified from Thorsteinson, 1941).

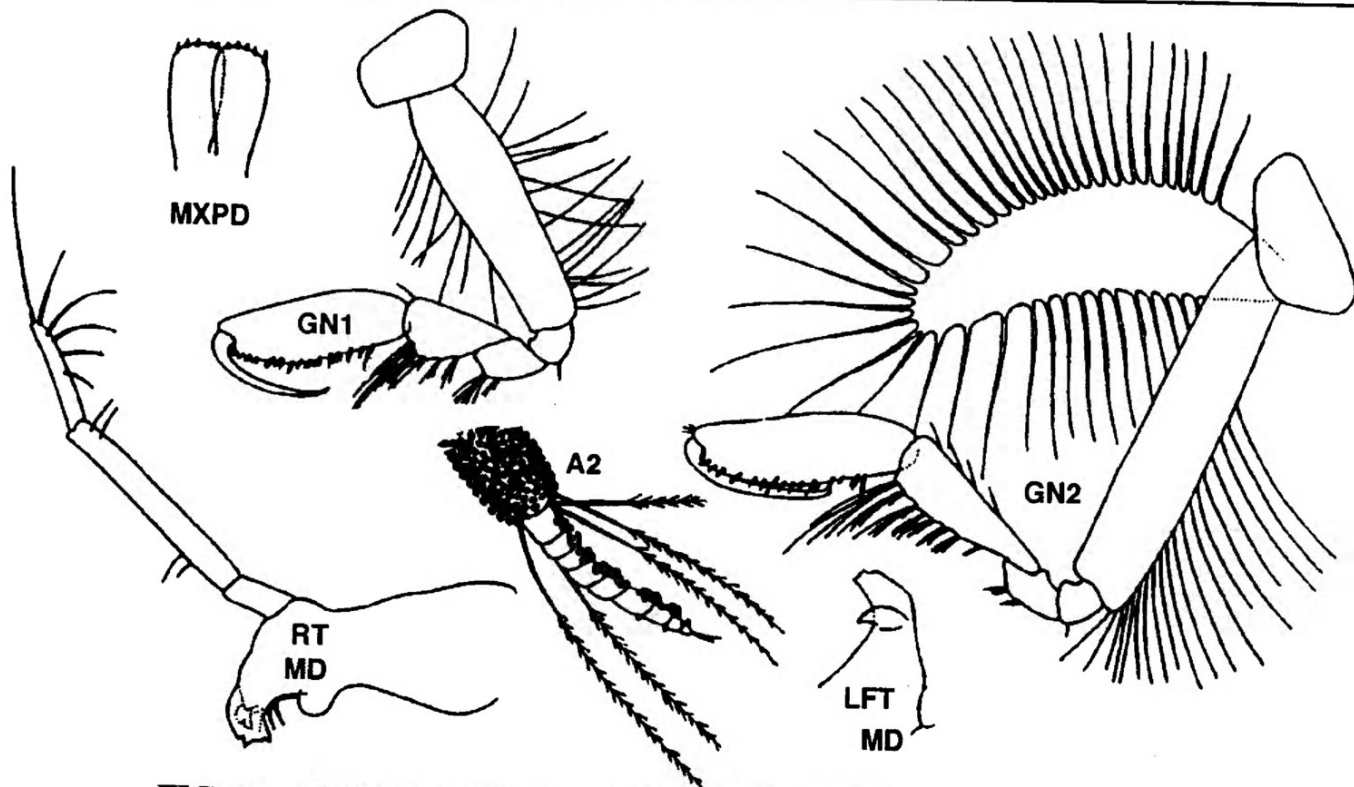


FIG. 10. *Eusirella multicalceola* (Thorsteinson, 1941). Female (9.0 mm)
Kurile-Kamchatka Trench (modified from Birstein & Vinogradov, 1955)

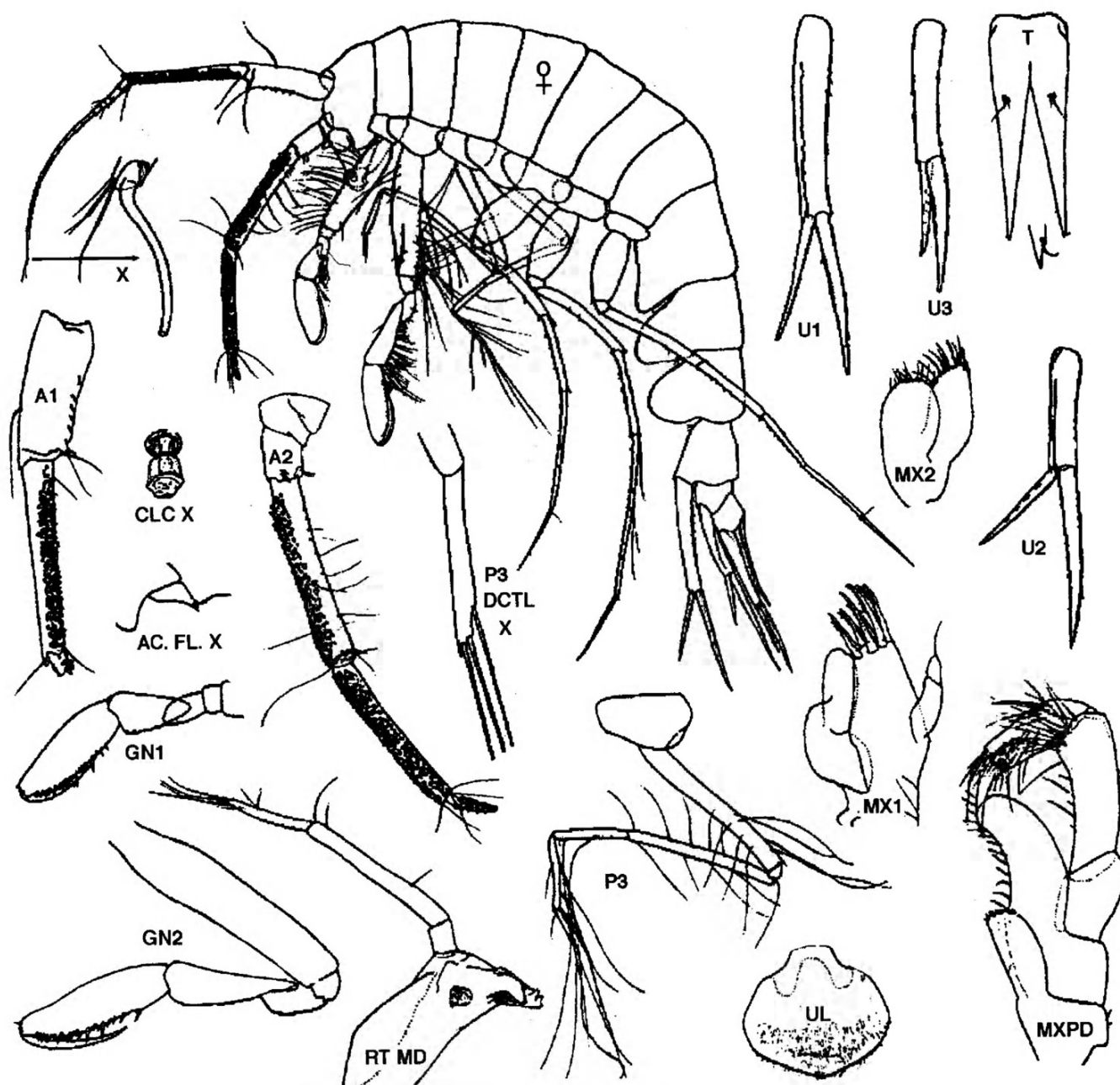


FIG. 11. *Eusirella multicalceola* (Thorsteinson). Female? (8.0 mm)
Off Queen Charlotte Islands, 3200 m. (modified from Barnard, 1964)

Tow 4, Net 3, 2306-1925 m. - fem. br. III (10.2 mm); Stn. 91-12, Tow 2, Net 1, 0-1900 m. - 1 male (7.2 mm).

Diagnosis. Male (8.0 mm): The male of the species has been described and figured by Thorsteinson, 1941. No female-defining characters were treated by Barnard, 1964, or by Birstein & Vinogradov (1955) and in our view a bone fide female has yet to be treated clearly as such.

Female (10.0 mm): Differs from the male in its larger size, broader body, longer and less calceolate antennae, more elongate gnathopod propods and dactyls, more elongate pereopods, and presence of strap-like brood plates on pereopod segments 2-5.

Antenna 1, peduncle 3 slender, elongate (2 X segment 1) Antenna 2, peduncular segments 4 and 5 slender, subequal, anterior margins moderately heavily but not densely calceolate (as in male); flagellum with 8 short segments (remainder

broken off), proximal 3 each with single calceolus; accessory flagellum as illustrated by Barnard, 1964 (see Fig. 11).

Coxa 1 truncated. Gnathopod propods very slender, elongate; gnathopod 1 smaller than gnathopod 2, propod of gnathopod 1 about 2/3 length of 2, dactyls long, closing along almost entire lower margin, bordered by spine cluster at the postero-distal angle, near carpus.

Coxal gills present on pereopods 2-7, slender sac-like on 2-4, reverse L-shaped on 5 and 6, small, on pereopod 7. Brood plates medium; long, strap-like on pereopod 5.

Taxonomic and distributional commentary. Birstein & Vinogradov (1958) include this species (along with *Rhachotropis natator*) in a northern group of pelagic gammarids from collection localities of the Institute of Oceanography from off eastern Japan to the Kamchatka peninsula (north of 37-40°), in depths ranging from 100 - 2000+ m.

Western Pacific Genera and Species

Of the ten genera of family Eusiridae represented in the North Pacific ocean, five of these (*Harcledo*, *Stenopleura*, *Pareusirogenes*, *Eusiropsis*, and *Eusirogenes*) are known to date only from Asiatic offshore localities, well outside the present study region. One of these (*Pareusirogenes*) has not yet been recorded elsewhere in the world (see also Table III, p. 52). However, in view of the limited amount of collecting and/or analysis of meso- and bathypelagic gammaridean amphipods from North American Pacific waters, published upon to date (p. 4), and the broad distributions of some species, most (if not all) of these genera may yet be recorded from the eastern North Pacific region. These genera are therefore included in the key (p. 7) and annotated briefly (below), and morphological features of representative western Pacific species are shown in the Appendix (pp. 57-59, Figs. 35-39).

Harcledo J. L. Barnard
(see Fig. 35, p. 57)

Harcledo J. L. Barnard, 1964: 60.—Barnard & Karaman, 1991: 323.

Meteusiroides Pirlot, 1934: 602.—Birstein & Vinogradov, 1955: 269, fig. 29.

Taxonomic commentary. *Harcledo curvidactyla* (Pirlot) was first described from the North Pacific as *Meteusiroides plumipes* Birstein & Vinogradov (loc. cit.) from mesopelagic waters of the Kurile-Kamchatka Trench. The genus *Harcledo* is primitive in that the single known species possesses pigmented eyes, relatively unmodified mouthparts, broad but unproduced coxal plates; regular (non-eusirid) gnathopod carpi; broad, lobate bases of peraeopods 5-7; subacute, unserrated pleon plate 3; marginally setose rami of uropod 3; and long, deeply cleft telson. The dorsally smooth body, and distally narrowing gnathopod propods with palmar margins nearly horizontal are distinctive, more apomorphic features of the genus.

Stenopleura Stebbing
(see Fig. 36, p. 57)

Stenopleura Stebbing, 1888: 949.—Birstein & Vinogradov, 1958: 243.—Ibid, 1960: 220.—Barnard & Karaman, 1991: 340.

Taxonomic commentary. *Stenopleura atlantica* Stebbing, 1888, has been recorded from the North Pacific region by Birstein and Vinogradov (loc. cit.) from warmer mesopelagic waters southeast of Japan. Whereas the genus entrains some plesiomorphic character states such as pigmented eyes, regular (non-eusirid) gnathopod carpi, and unmodified pleon plates, it is more advanced than *Harcledo* in its smaller coxal plates (coxa 1 sharply produced); more specialized mouthparts; spinose (not setose) margins of the rami of uropod 3; and short, apically notched telson.

Pareusirogenes Birstein & Vinogradov
(see Fig. 37, p. 58)

Pareusirogenes Birstein & Vinogradov, 1955: 266, fig. 27.—Ibid, 1958: 246.—Barnard & Karaman, 1991: 333.

Taxonomic commentary. *Pareusirogenes carinatus* was described by Birstein and Vinogradov (1955, 1958) from deep net hauls (0-3000 m) over the Kurile-Kamchatka Trench and in the Sea of Okhotsk. The genus is characterized by weakly eusirid gnathopods 1 and 2 in which the posterior margin of the carpus is elongate, shallow and heavily fringed with setae, the propod palmar margins are strongly oblique, and uropod 3 has a single large marginally serrate ramus. Many of the body parts (including the antennae, distal segments of the peraeopods, uropods 1 and 2, and telson) have not yet been described or figured. The genus is the most primitive of *Eusirus*-like genera in the relatively unmodified mouthparts and broad posteriorly convex bases of peraeopods 5-7.

Eusiropsis Stebbing
(see Fig. 38, p. 58)

Eusiropsis Stebbing 1897: 39.—Stebbing 1906: 343, figs. 80, 81.—Birstein & Vinogradov, 1958: 246.—Ibid, 1960: 223.—Barnard & Karaman, 1991: 319.

Taxonomic commentary. Birstein & Vinogradov (loc. cit.) recorded *E. riisei* Stebbing, 1897, on the basis of 20 specimens (7-12 mm) from closing tows, mostly of less than 1000 m. in depth, at a dozen oceanographic stations off southeastern Japan. The genus differs from all others (with eusirid gnathopods), in having a combination of nearly smooth dorsum, elongate strongly calceolate antennae, shallow coxal plates, short cryptic gnathopod carpi, slender distally plumose-setose peraeopods, heavily setose rami of uropod 3, and relatively short, shallowly cleft telson.

Eusirogenes Stebbing
(see Fig. 39, p. 59)

Eusirogenes Stebbing 1904: 15.—Stebbing, 1906: 728.—Birstein & Vinogradov, 1955: 259, fig. 26.—Ibid, 1958: 246.—Barnard & Karaman, 1991: 318.

Taxonomic commentary. The genus is superficially similar to *Eusirus* but the propod of gnathopod 1 is distinctly larger than in gnathopod 2, the mouthparts are more specialized, coxae 1-4 are markedly unequal in size and depth, the bases of peraeopods 5-7 are markedly heteropodous, and the telson is usually less deeply cleft. The northerly records of *Eusirogenes homocarpus* Birstein & Vinogradov (loc. cit.) in the western North Pacific, indicate that this species, or a sibling counterpart, is likely to occur in deep offshore waters of the North American Pacific coast.

Rhachotropis Smith

Rhachotropis Smith, 1883: 222.—Stebbing, 1906: 847.—Shoemaker, 1930: 317.—Gurjanova, 1951: 706.—Barnard, 1969a: 229.—Ledoyer, 1982a: 235.—Barnard & Karaman, 1991: 337.
Gracilipes Holmes, 1908: 526.

Type Species. *Oniscus aculeatus* Lepechin, 1780.

Component North Pacific species. (Alaska to Baja California): *Rhachotropis aculeata* (Lepechin, 1780); *R. inflata* (G. O. Sars, 1892), *R. oculata* (Hansen, 1888), *R. minuta*, new species; *R. helleri* (Boeck, 1871); *R. macropus* Sars, 1895; *R. boreopacifica*, new species, *R. conlanae*, new species; *R. calceolata*, new species; *R. ludificor*, J. L. Barnard, 1967a; *R. clemens* J. L. Barnard, 1967a; *R. barnardi*, new species; *R. multesimus* J. L. Barnard, 1967; *R. americana*, new species; *R. grimaldi* (per Gurjanova, 1955); *R. inflata* Sars, 1883; *R. natator* (Holmes, 1908), and *R. distincta* (Holmes, 1908). *R. gubilata* J. L. Barnard, 1964, a relatively primitive bathyal species originally described from the Gulf of Panama, is recorded from the Cascadia abyssal plain off Oregon and is therefore included in the morphological analysis (pp. 51-52) and phenogram (Fig. 34). The identity of *R. cervus* Barnard, 1964, in the Baja California region is uncertain, and not included in the analysis or keys of this study.

Diagnosis: Body usually carinate-mucronate on pleon mid-dorsally and laterally, often also on posterior peraeonal and first urosomal segments. Rostrum medium, strong to short; anterior head process usually acutely produced. Pigmented eyes present in neritic species, large, often nearly meeting mid-dorsally, lacking in bathyal species. Antennae medium, stout, subequal, peduncles strong, often calceolate, distal ends often armed with longish "bottlebrush" sensory setae. Antenna 1, accessory flagellum very short, 1-segmented, apex spinose and/or setose, or scalelike, or lacking. Antenna 2 often calceolate on peduncle and flagellum in female.

Upper lip rounded below, epistome not produced. Lower lip, outer lobes broad, inner lobes strong. Mandible: molar columnar, grinding surface reduced; spine row with 3-8 blades; left lacinia 6-7 dentate; palp strong, segment 3 usually longer than segment 2. Maxilla 1, outer plate 9-dentate; inner plate with 1-4 apical setae; palp stout, normally 2-segmented. Maxilla 2, inner plate broader, facial setae reduced to single strong inner marginal plume, or lacking. Maxilliped, palp powerful; plates reduced, inner plate, apical spines present.

Coxal plates small, shallow, slightly increasing in size posteriorly. Coxa 1 strongly and narrowly produced anteriorly; coxa 4 weakly (or not) excavate behind. Gnathopods powerfully subchelate, subequal, raptorial; propod broadly ovate, palmar margin smoothly convex, lined on either side with closely set stiff setae, but with stout spines only at posterior angle; carpus short, posterior lobe deep.

Peraeopods large, stout, spinose, raptorial, dactyls medium to elongate, nails short. Peraeopods 3-4, segment 4 variously shorter than segment 5 (subequal in type species), usually markedly shorter in peraeopod 3. Peraeopods 5-7 elongate. Peraeopods 5 and 6 often subequal in length, but bases subsimilar in form. Peraeopod 7 distinctly largest, basis usually larger and differing in form from that of peraeopods 5 and 6.

Pleon plate 3 rounded and usually strongly serrated behind. Uropods 1 and 2, rami slender, lanceolate (apices lacking terminal spines); outer ramus the shorter. Uropod 3, rami subequal, broadly lanceolate, inner margins spinose, also setose in primitive species. Telson elongate, narrowing distally; apex variously cleft; lobes often slightly asymmetrical, rarely fused to entire plate; basally with pair of elongate "bottle-brush" sensory setae.

Coxal gills large, weakly pleated, smallest on peraeopod 7. Brood plates broad, margins setose.

Taxonomic and distributional commentary. On a world-wide basis, about 60% of the ~50 described species of *Rhachotropis* occur in northern oceans, including the Mediterranean Sea, and the remainder in Indian, Australian and Antarctic waters. Only about one-third of the species are sublittoral and have pigmented eyes; most are epibenthic bathyal and abyssal, lacking pigmented eyes, and a few are bathypelagic. Most of the sublittoral (eyed) species have been found in arctic and arctic-boreal regions of the North Atlantic and North Pacific oceans. In the North Atlantic, the species occur variously southward to the Mediterranean region in the east, and to the Cape Cod region in the west. In the North Pacific they are dominant along the North American coastal plain south to Baja California, and penetrate the western Pacific south to the Sea of Japan. Although the genus *Rhachotropis* may be considered cosmopolitan, most bathyal and abyssal species are recorded from the northern hemisphere; their distributions are based on very few records, perhaps suggesting a significant degree of regional endemism within the deep-water forms.

Morphologically, the sublittoral forms tend to retain plesiomorphic character states, whereas the bathyal species trend to apomorphies such as total fusion of telson lobes and loss of antennal calceoli. The bathypelagic species are most apomorphic in extreme elongation of peraeopods and dactyls, reduction of coxal plates, and elongation of antennae.

The *Rhachotropis* fauna of the North Pacific region contains a mixture of sublittoral, bathyal, and bathypelagic species of which 19 species are included in the regional key and species analysis (p. 23). Of these, 8 are fully described and/or figured, based mainly on material at hand. Descriptive remarks and/or figures of the other species, based on the literature, are provided in several instances.

These 19 North Pacific species of *Rhachotropis* may be grouped on a phyletic-ecological basis, as follows: (1) a primitive, strongly rostrate and dorsally toothed group that includes the monotypic *R. aculeata* (Lepechin) of arctic

KEY TO NORTH PACIFIC SPECIES OF *RHACHOTROPIS*

1. Pigmented eyes present 2.
—Pigmented eyes lacking 11.
2. Peraeon segments 6 and 7 with dorsal and dorso-lateral teeth; urosome 1 with 2 dorsal teeth; peraeopods 5 and 6, hind margin of basis with strong posterior tooth *R. aculeata* (p. 24)
—Peraeon segments 6 and 7 with distinct tooth mid-dorsally only, or all teeth lacking; urosome 1 with single dorsal tooth (or none); peraeopods 5 and 6, basis convex behind, without strong posterior tooth 3.
3. Pleon segment 3 with mid-dorsal tooth; telson elongate ($> 2X$ basal width) 4.
—Pleon segment 3 lacking mid-dorsal tooth; telson relatively short ($\sim 2X$ basal width, or less) 7.
4. Peraeopods 3 and 4, dactyls ordinary (length $< 2/3$ segment 6); telson deeply cleft ($> 1/3$ its length) . . . 5.
—Peraeopods 3 and 4, dactyls elongate (\sim segment 6); telson with short apical cleft 6.
5. Peraeopod 7 elongate ($>>$ peraeopod 6); telson deeply cleft ($\sim 1/2$ length) *R. macropus* (p. 26)
—Peraeopod 5 regular (slightly $>$ peraeopod 6); telson cleft $\sim 40\%$ of its length *R. helleri* (p. 26)
6. Pleon segment 3 with strong dorsal and dorso-lateral mucronations *R. boreopacifica* (p. 29)
—Pleon segment 3 lacking dorsal and dorso-lateral mucronations *R. barnardi* (p. 29)
7. Peraeon segment 7 with mid-dorsal tooth 8.
—Peraeon segment 7 lacking mid-dorsal tooth 9.
8. Peraeopods 3 and 4, dactyls long (\sim segment 6); rami of uropod 3, inner margins setose *R. oculata* (p. 33)
—Peraeopods 3 and 4, dactyls short ($\sim 1/2$ segment 6); uropod 3 rami, inner margins spinose *R. minuta* (p. 35)
9. Pleon segments 1 and 3 each with strong dorso-lateral tooth and ridge *R. inflata* (p. 33)
—Pleon segments 1 and 3 lacking dorso-lateral tooth and ridge 10.
10. Peraeopods 3 and 4, dactyls short, thick, $< 1/2$ segment 6; S. E. Alaska *R. conlanae* (p. 37)
—Peraeopods 3 and 4, dactyls elongate, length \sim segment 6; Gulf California *R. luculenta* (p. 37)
11. Urosome 1 with mid-dorsal tooth or mucronation 12.
—Urosome 1 lacking mid-dorsal tooth 14.
12. Pleon segment 3 with dorsal tooth; coxa 1 weak; antenna 1, ped. segment 3 long . . . *R. distincta* (p. 43)
—Pleon segment 3 lacking dorsal tooth; coxa 1 produced; antenna 1, peduncular segment 3 short . . . 13.
13. Antennae strongly calceolate; telson deeply cleft; gnathopod carpal lobes broad . . *R. calceolata* (p. 26)
—Antennae not calceolate; telson notched at apex; gnathopod carpal lobes narrow . . . *R. clemens* (p. 32)
14. Coxa 1 small, short; telson elongate, shallowly notched apically 15.
—Coxa 1 strongly produced anteriorly; telson deeply cleft ($> 1/3$) 16.
15. Peraeopods 5-7, basis with posterior cusp; pleon 3 strongly toothed, dorso-laterally . . *R. gubilata* (p. 24)
—Peraeopods 5-7, basis smooth behind; pleon 3 weakly cusped, mid-dorsally only . . . *R. natator* (p. 46)
16. Pleon segment 3 lacking dorsal tooth; peraeopod 6, basis broad; rostrum large . . . *R. ludificor* (p. 37)
—Pleon segment 3 with mid-dorsal tooth; peraeopod 6, basis narrow; rostrum short, small 17.
17. Peraeopod 7, basis narrow, straight; pleon plate 3 smooth behind *R. multesimis* (p. 40)
—Peraeopod 7, basis medium broad, hind margin convex; pleon plate 3 serrate behind 18.
18. Head and peraeon with low dorsal tubercles; pleon 3, dorso-lateral tooth strong . . . *R. grimaldi* (p. 40)
—Head and peraeon segments smooth above; pleon 3, dorso-lateral cusp weak . . . *R. americana* (p. 40)

waters and possibly the abyssal *R. gubilata*; (2) a more advanced northern sublittoral *macropus* group that includes *R. boreopacifica*, n. sp., *R. barnardi*, n. sp., and *R. clemens* Barnard, 1967 along the North American coast, and *R. helleri* (Boeck) and *R. macropus* Sars in the western North Pacific; (3) a further advanced sublittoral subarctic *oculata-inflata* group that includes *R. conlanae*, n. sp., and *R. minuta* n. sp. of the North American coast; (4) a bathyal complex apparently endemic to the eastern North Pacific region, that includes *R. ludificor*, *R. calceolata*, a group in which the sublittoral *R. luculenta* from the Gulf of California may also be placed; (5) a bathyl *R. grimaldi* group (Gurjanova type) that includes *R. americana* and *R. multesimus* of the North American coast; and (6) a bathypelagic offshore group that comprises *R. natator* and *R. distincta*, with specialized character states, formerly recognized in the genus *Gracilipes* Holmes, 1908. *Gracilipes* may yet prove to be a valid genus, but its determination requires detailed study of the entire range of deep sea species and materials not available to us here.

***Rhachotropis aculeata* (Lepechin)**
(Fig. 12)

Rhachotropis aculeata Sars, 1895: 424, pl. 149.—Shoemaker, 1920: 14E.—Gurjanova, 1951: 707, fig. 491.—Shoemaker, 1955: 46.—Barnard & Karaman, 1991: 339.

Material Examined. CHUKCHI SEA: Stn AHPR -off Wainwright, Alaska, otter trawl, 35 m., gravel, P. Slattery coll. 1984 - 1 female ov (31 mm) (fig'd), 9 other females. CMN Acc. No.; Ibid. 25 m dive, P. slattery coll. Aug. 1984. 1 male; Off Cape Thompson, 26 m. S.E. Point Hope 35 m trawl, P. Slattery coll., August, 1984 - 1 female (br. I).

Diagnosis. Female (to 40 mm): Body large, broadest in mid peraeon. Peraeon segments 1-5 mid-dorsally rugose, segment 6 and 7 with acute dorsal, dorso-lateral, and lateral processes. Pleon segments 1-3 each with strong mid-dorsal tooth, and small anterior cusp and strong dorsolateral tooth. Urosome 1 with bidentate mid-dorsal ridge and postero-lateral marginal tooth. Urosome 3 weakly toothed above base of telson.

Head with raised crown; rostrum strong, attaining end of antennal peduncular segment 1; anterior head lobe acute. Pigmented eyes very large, subrhomboidal, nearly meeting mid-dorsally. Antenna 1 shorter than 2; peduncular segment 2 shorter than 1, 3 very short; flagellum of about 50 short segments; accessory flagellum, short, rod-like. Antenna 2, peduncular segment 4 stout, margins with numerous plumose and simple setae; peduncle 5, posterior margin with a few plumose setae, anterior margin finely calceolate; flagellum of more than 50 short calceolate segments.

Upper lip rounded below. Lower lip broad, inner lobes weak, fused medially. Mandible, molar large, triturating surface squarish, edges lined with short blades; spine row

with 6-7 slender blades; left lacinia 5-6 dentate, right lacinia bifid; incisor with short cutting edge, toothed distally; palp large, segment 3 longer than 2, narrowing apically. Maxilla 1 inner plate with 2 apical setae; palp slender, acute. Maxilla 2, inner plate very broadly rounding apically, marginal setae short. Maxilliped, palp powerfully raptorial, segments 2 and 3 broadened; outer plate ordinary, inner plate broad, with 16 short apical spines.

Coxal 1 strongly produced anteriorly, tip acute, deflexed. Coxae 2-4 medium, about as deep as wide. Coxa 4 distinctly excavate behind. Gnathopod 2 slightly larger than 1; bases stout, hind margin lined with short spines; carpal lobes medium; propods broadly ovate; palmar margins oblique; dactyl-tip depression at posterior angle large, lined behind and medially with 3-4 groups of short spines, and 3 stouter outer marginal spines.

Peraeopods 3 and 4 stout, margins thickly short-setose; segments 4 and 5 subequal; dactyls regular (about 2/3 length of segment 6). Coxa 5 shallowly aequilobate. Peraeopods 5 and 6 stout, subsimilar in form and size; bases acutely produced posteriorly; segments 4-6, hind margins highly setose; dactyls strong. Peraeopod 7 larger than 5 and 6, basis broad, lower hind lobe acute; segment 4-6 setose behind. dactyl straight.

Pleon plates 2 and 3 wide, deep, hind margins nearly straight; lower and posterior margins of pleon 3 finely serrate. Uropods 1 and 2 elongate, rami narrowly lanceolate, margins serially lined with numerous short spines, outer ramus distinctly the shorter. Uropod 3, rami long, lanceolate, inner margins setose and spinose. Telson elongate, narrow, nearly reaching tip of uropod 3, narrowly cleft about 30% of its length.

Coxal gills large, broad. Brood plates broad, margins strongly simple-setose.

Taxonomic and distributional commentary. Shoemaker (1955) recorded the species from off Pt. Barrow, Alaska, in depths of 35 - 50 m. On the Asiatic coast it occurs southward to the Sea of Japan (Gurjanova, 1951).

The type species, *R. aculeata*, entrains more plesiomorphic characters states than any of the ~50 world-wide species to date. It stands in isolation from its nearest relatives at the 50% similarity level (Fig. 34, p. 51).

***Rhachotropis gubilata* J. L. Barnard**
(Fig. 13)

Rhachotropis gubilata J. L. Barnard, 1964: 34, fig. 28. Barnard & Karaman, 1991: 338.

Material Examined: USA: R/V Yaquina, Stn BMT 281, Off Oregon, Cascadia Abyssal Plain (44°38.55'N, 127°39.05'W) OSU Dept. Oceanogr., 2816 m, May 19, 1971 - 1 female br. II (slide mt.)

Taxonomic and distributional commentary. This species, originally described from the Panama Basin, evinces a number of plesiomorphic character states, and does not

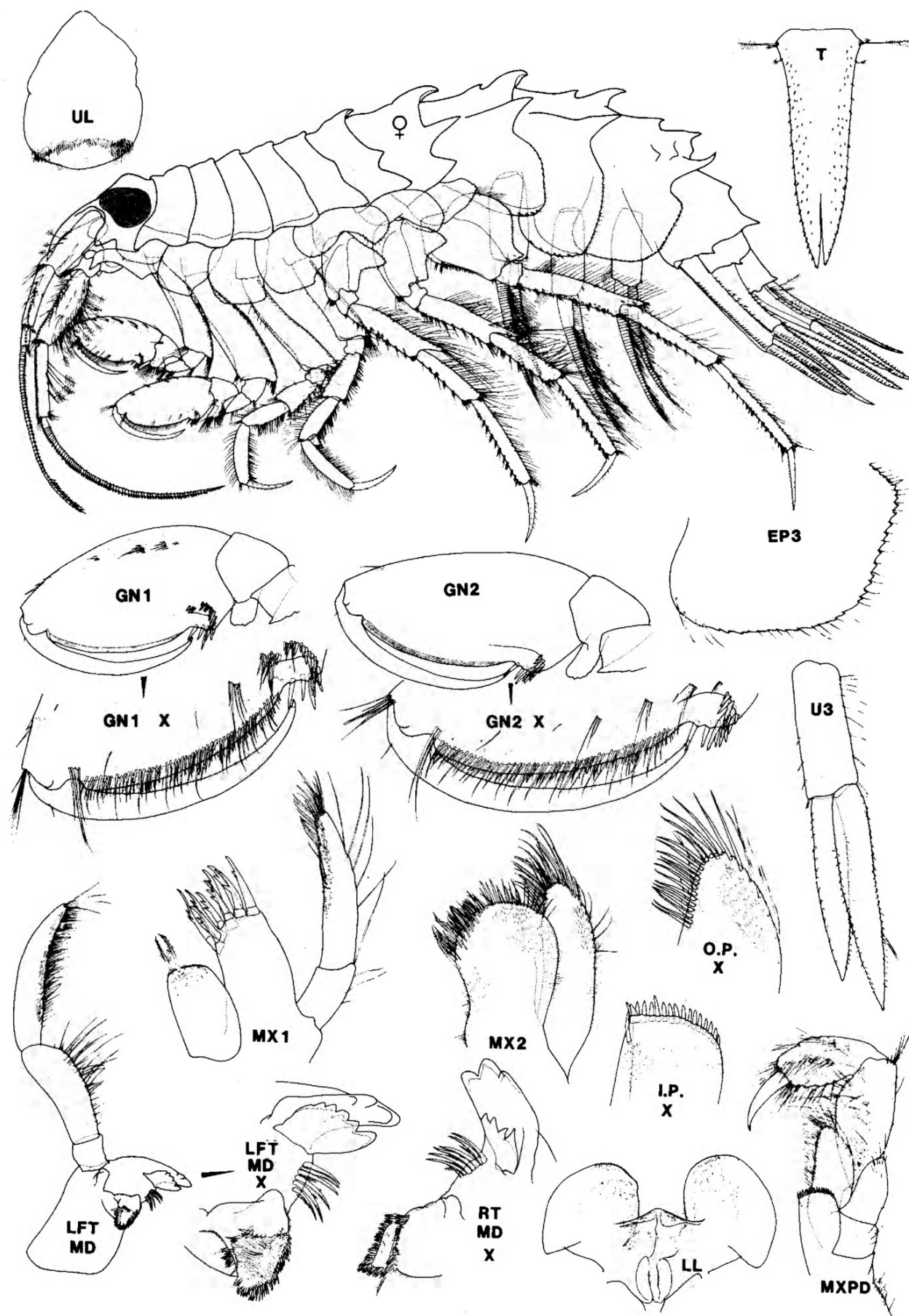


FIG. 12. *Rhachotropis aculeata* (Lepechin) Female ov. (31 mm). Off Wainwright, Alaska.

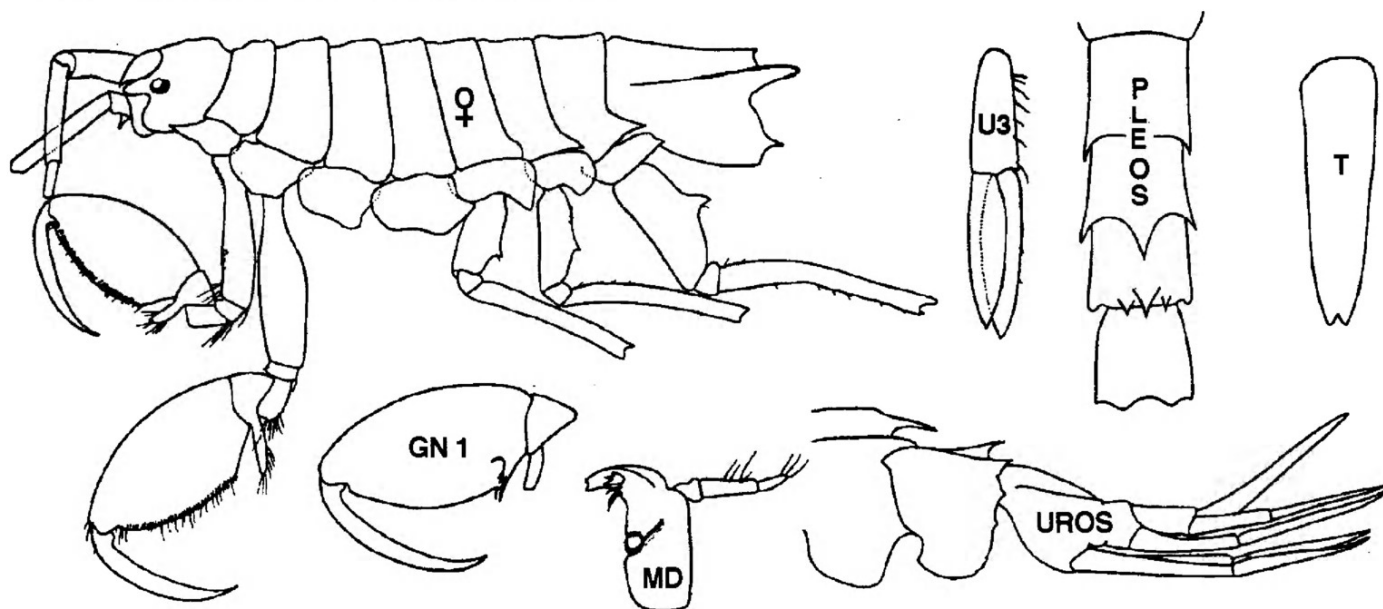


FIG. 13. *Rhachotropis gubilata* Barnard, 1964. Female (17.0 mm). Panama Basin.

compare closely to any of the known N. Pacific deep-water species. The plesiomorphic character states includes the eye remnants, the anteriorly acutely toothed coxa 1, the acutely toothed posterior margins of the bases of pereopods 5-7 (reminiscent of *R. aculeata*?), and the broad rami of uropod 3. Apomorphic character states include the relatively short rostrum, narrower form of the bases of pereopods 5-7, and nearly totally fused telson lobes.

Rhachotropis helleri (Boeck)

(Fig. 14)

Rhachotropis helleri Sars, 1895: 426, pl. 150.—Gurjanova, 1951: 708, fig. 492.—Barnard & Karaman, 1991: 339.

Taxonomic and distributional commentary. This wide-ranging holarctic species is included here because of the records of Gurjanova (loc. cit.) from the Chukchi and Bering Sea regions. The B. C. records of Wailes (1931), Fulton (1968), and Austin (1985) are unconfirmed. *R. helleri* is closely related to *R. macropus* Sars, but less closely similar to the bathyal N. American Pacific species *R. calceolata* n. sp. (below), and *R. boreopacifica*, n. sp. (p. 29).

Rhachotropis macropus G. O. Sars

(Fig. 15)

Rhachotropis macropus G. O. Sars, 1895: 428, pl. 15(1).—Gurjanova, 1951: 709, fig. 493.—Barnard & Karman, 1991: 339.

Taxonomic and distributional commentary. Gurjanova (loc. cit.) includes an early record by Derzhavin (1930) from the Sea of Japan. This 16 mm. eyed species occurs in depths of 100-800 m. and may be expected to occur in North American offshore waters of the Chukchi Sea. In its elongate antennal peduncles, strongly produced coxa 1, slender dactylate pereopods 3 and 4, elongate pereopod 7 and subovate gnathopod propods, *R. macropus* resembles

the *boreopacifica* group (p. 29), but the deeply cleft telson may link it more closely to *R. calceolata*, n. sp. (below).

Rhachotropis calceolata, new species

(Fig. 16)

Material Examined: BRITISH COLUMBIA: Queen Charlotte Islands, northwest of Englefield Bay (53°05.08'N, 133°00.08'W to 53°06.58'N, 133°01.22'W), RBCM/CMN Deepwater II Stn. 91-1-11, 0-1227 otter trawl, March 21, 1991. - 1 female (8.7 mm) Holotype (slide mount), CMN-Cat. No. pending.

Diagnosis. Female ov. (8.7 mm): Body medium, compressed. Pereon segments 1-7 and pleon segment 3 lack dorsal teeth or mucronations. Pleon 1 and urosome 1 with short postero-dorsal tooth; pleon segment 2 with postero-dorsal and dorsolateral mucronations. Rostrum slender, produced; anterior head lobe, apex blunt. Pigmented eyes lacking. Antenna 1, peduncle 1 stout, peduncle 2 slender, subequal; segment 3 medium (1/3 length of segment 2), calceolate; flagellum 14-segmented, proximally calceolate; accessory flagellum very short, subconical. Antenna 2 slightly the longer; peduncular segment 5 slender, longer than segment 4, both calceolate; flagellum ~12-segmented, proximal 5 segments calceolate; calceolate relatively large, receptacle broad, orbicular (tympanic - Barnard, 1967), distal elements forming a short narrow central cone.

Mandible, molar narrowing distally to small grinding surface; spine row with 4-5 blades and accessory setae; left lacinia irregularly 8-9 dentate; right lacinia essentially bifid, 1 cusp bifid; cutting edge of incisor long, nearly smooth; palp segment 3 slender slightly longer than segment 2, apex acuminate. Maxilla 1, inner plate with 2 apical setae, palp slender. Maxilla 2, inner plate broad, inner margin proximally with 2 longer plumose setae. Maxilliped, palp large, powerful, segment 2 somewhat broadened; outer plate broad; inner plate with 4 apical spines.

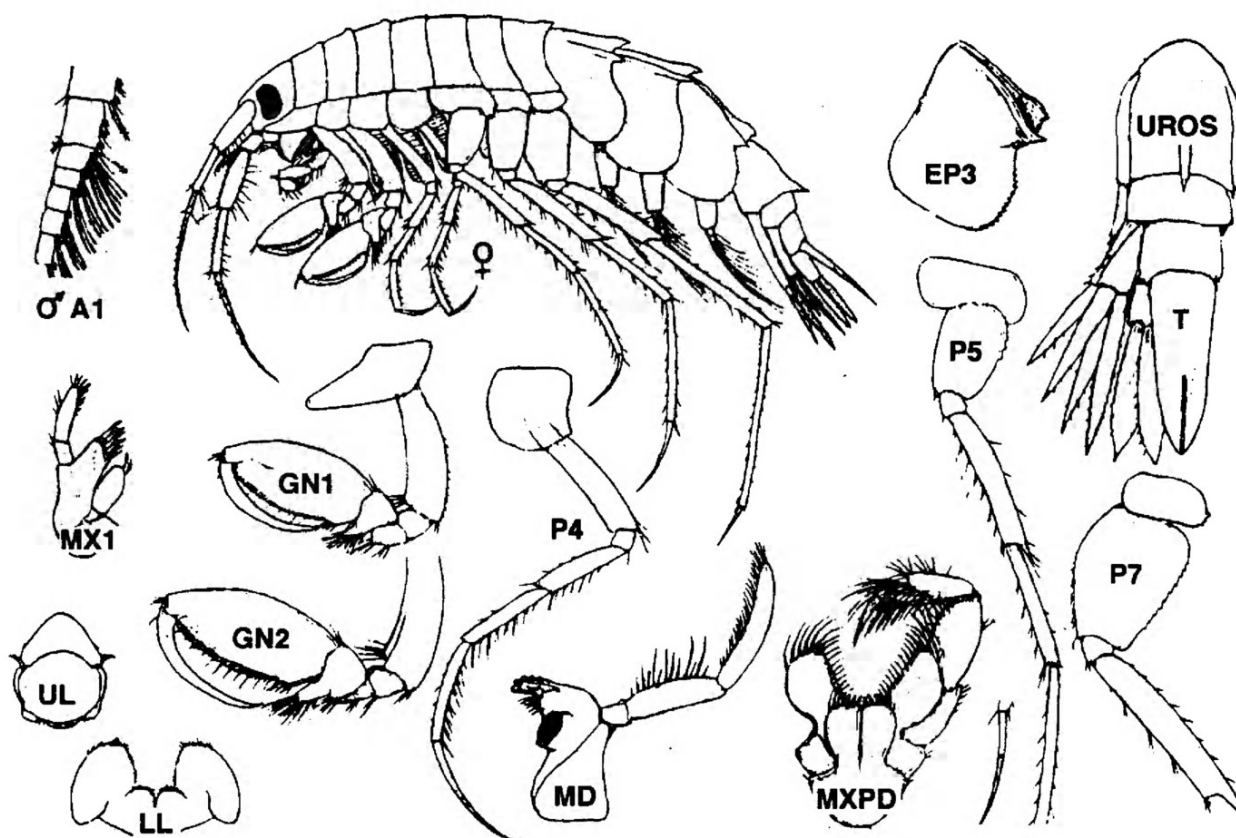


FIG. 14. *Rhachotropis helleri* Boeck Female, Male Norwegian Sea 400 m. (modified from Sars, 1895)

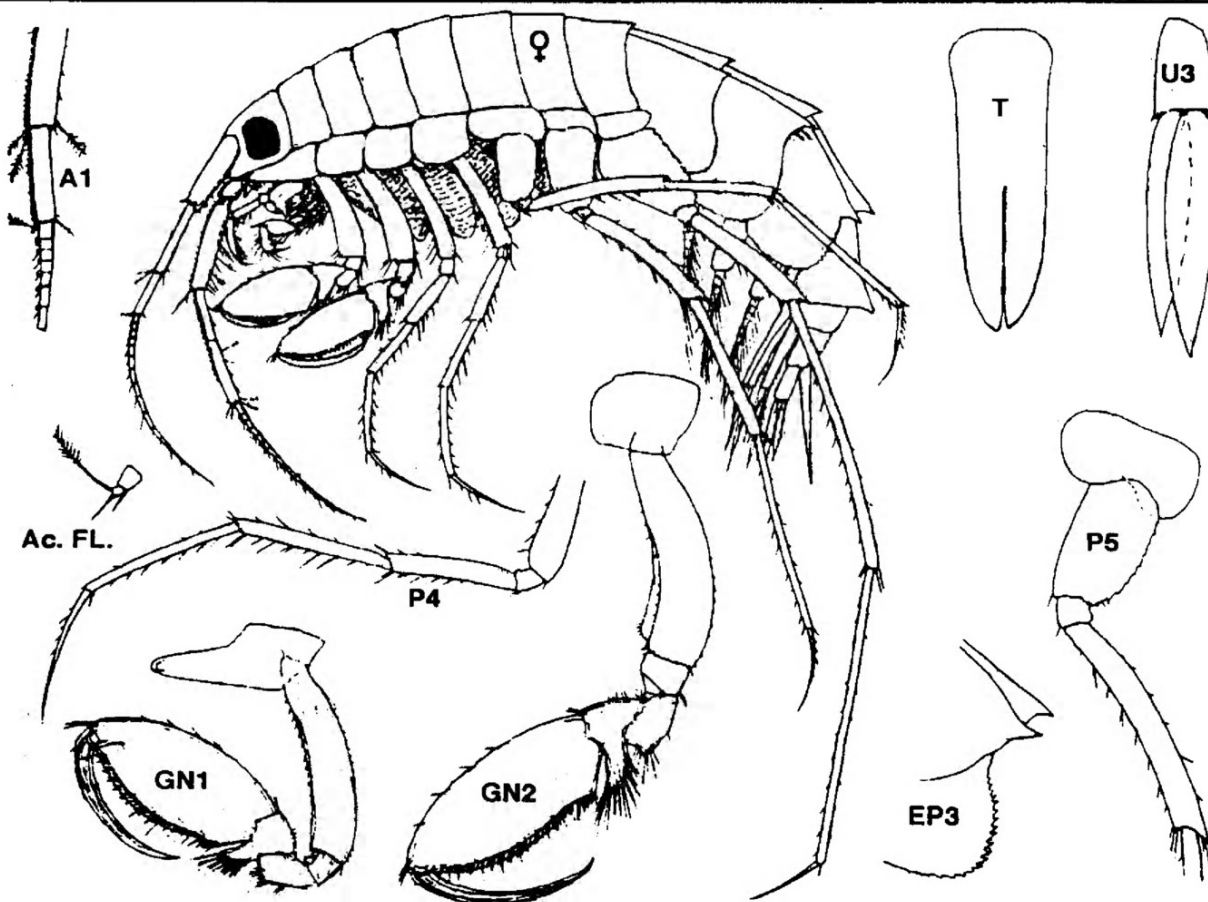


FIG. 15. *Rhachotropis macropus* G. O. Sars, 1895 Female (16.0 mm) Northeastern Atlantic to Japan Sea, 100 to 800 m. (modified from Sars, 1895)

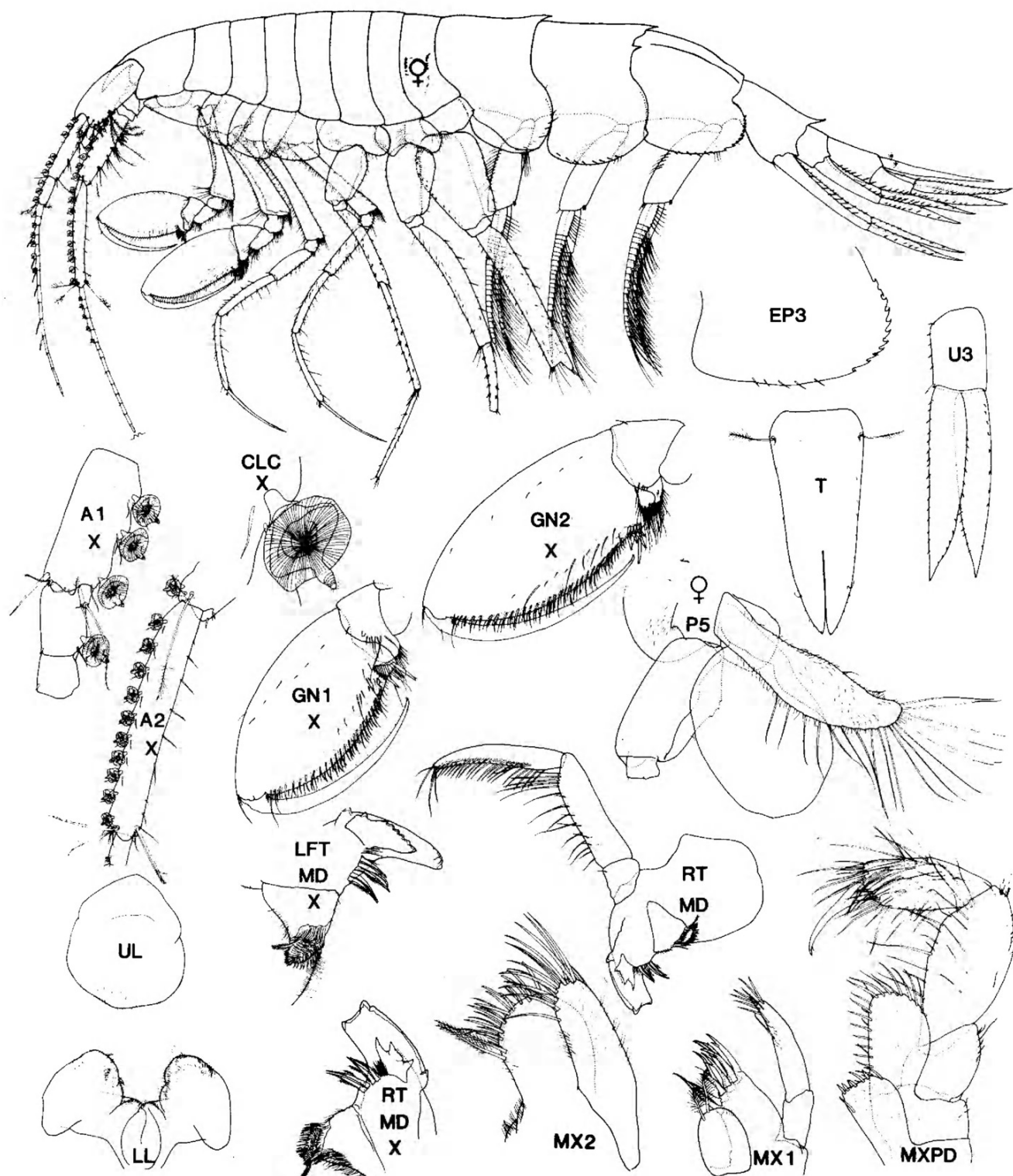


FIG. 16. *Rhachotropis calceolata*, new species. Female (8.7 mm). Northwest of Englefield Bay, Queen Charlotte Islands, B. C., 0-1227 m.

Coxa 1 produced anteriorly, apex subacute; coxae 2-4 wider than deep; coxa 4 shallowly excavate behind. Gnathopod 2 larger than gnathopod 1; bases broadening distally; carpus, posterior lobe relatively short; propods shallowly ovate, hind margin very short, palmar margin very long, postero-distal angle with outer and inner clusters of closing spines.

Peraeopods 3 and 4 slender, segment 4 slightly shorter than 5; dactyls elongate (about = segment 6). Coxae 5 and 6 shallowly anterolobate. Peraeopods 5-7 unequal in form and

size, peraeopod 5 shortest, 7 longest (distal segments missing in type); bases medium broad, narrowing distally, weakly lobate below.

Pleon plates 1-3 broad, lower margins rounded, spinose; hind margin of 3 strongly convex, serrate. Uropods 1 and 2, rami narrowly lanceolate, subequal, not reaching tip of uropod 3. Uropod 3, rami medium broad, subequal, margins finely spinose. Telson medium, narrowing, cleft ~1/3 length, apex not attaining tips of uropod 3.

Coxal gills large, orbicular, smallest on peraeopod 7.

Broods plates broad, narrower and strap-like on peraeopod 5, marginal setae long. Male: unknown.

Etymology. The Latin name "calceolata" alludes to the large and conspicuous calceoli of the female antennae

Taxonomic commentary. *Rhachotropis calceolata* is known only from a single specimen at the type locality. Phyletically, it appears most closely related to *R. helleri* (Boeck) and *R. macropus* Sars in its strongly dissimilar peraeopods 5-7, strong antennal calceolation, medium deep coxae 1-4, and deeply cleft telson. However, its weak pleonal mucronation, short carpal lobes of the gnathopods, and slender, elongate peraeopods 3 and 4 are specifically distinctive.

***Rhachotropis boreopacifica*, new species**
(Fig. 17)

Material Examined: BRITISH COLUMBIA: Off Vancouver I., G. B. Reed Stn. 68-32 (48°21'N 126°08'W) Agassiz trawl, 549 m. - 1 female br. I (10.5 mm), Holotype (slide mount), CMN Acc. No. 68-211. 1 female Paratype. (CMN Cat. Nos. pending).

Diagnosis. Female br I (10.5 mm): Body slender, somewhat elongate. Mid-dorsal mucronations on peraeon segments 6 and 7, pleon segments 1-3, and urosome segment 1; dorso-lateral ridge and mucronation on pleon segments 1-3. Rostrum medium, extending beyond sharply rounded head lobe. Pigmented eyes broadly reniform. Antennae slender, sub-equal, finely calceolate on peduncles and proximal flagellar segments. Antenna 1, peduncular segments 1 and 2 subequal, 3 medium (1/3 length of segment 2); flagellum 19-segmented; accessory flagellum minute, with long apical seta. Antenna 2, peduncular segments 4 and 5 slender, hind margins setose, anterior margins calceolate; flagellum 17-segmented.

Mandible, molar large, triturating surface reduced; spine row with 3-4 blades; left lacinia 6-7 dentate, right lacinia appearing trifid; main cutting edge of incisor denticulate; palp stout, segment 3 elongate, narrowing apically. Maxilla 1, inner plate with 2 apical setae; palp ordinary. Maxilla 2, inner plate broad, apical marginal setae not differentiated. Maxilliped, palp strong, segments little broadened; outer plate regular, inner plate with 4-5 apical spines.

Coxa 1 strongly produced anteriorly, apex acute. Coxae 2-4 shallow, broader than deep; coxa 4 weakly excavate behind. Gnathopod 2 slightly larger than 1; bases ordinary. Carpal lobes relatively short and broad; propods subsimilar in form, subovate, hind margin short, palmar margin with large dactyl-tip depression at palmar angle, with 3-4 inner marginal spines (1 elongate), and 3 stout outer marginal spines.

Peraeopods 3 and 4 slender; segment 4 slightly shorter than 5; dactyls elongate (~= segment 6). Coxa 5 shallowly aequilobate. Peraeopods 5 and 6 slender, subequal; bases narrowing distally, weakly lobate behind; dactyls elongate (> 1/2 segment 6). Peraeopod 7 distinctly the longest; basis

narrowing and weakly lobate distally; dactyl slender, straight.

Pleon plates 1 and 2 rounded below, nearly straight behind; pleon plate 3 nearly straight below, strongly convex and serrated behind. Uropods 1 and 2 very long, rami extending to tip of uropod 3; uropod 2, outer ramus distinctly shorter than inner ramus. Uropod 3, rami medium, lanceolate, subequal, inner margin of inner ramus weakly setose. Telson very long, slender, reaching nearly to tip of uropod 3, basally with elongate lateral plumose setae, apex shallowly cleft. Coxal gills plate-like, not pleated

Etymology: The species name alludes to its known occurrence in the North Pacific marine region.

Taxonomic and distributional commentary. *Rhachotropis boreopacifica* is known only from the type locality. Its general affinities are with *R. helleri* (Boeck) and *R. macropus* G. O. Sars, circumpolar species that have been recorded previously from the Bering and Chukchi Sea regions of the western North Pacific (Gurjanova, 1951). However, it appears similar in many points of detail to *R. barnardi*, new species, from the Oregon coast, as detailed below.

***Rhachotropis barnardi*, new species**
(Fig. 18)

Rhachotropis clemens J. L. Barnard, 1971: 10, figs 6, 7 (eyed material). (Selection of type specimen pending).

Material Examined. BRITISH COLUMBIA: 34 specimens in 15 lots at 10 stations, as follows: Off Queen's Beach, Jervis Inlet, ELB Stn. J1, 350 m. dredge, May 12, 1977 - 4 females, 2 males (slide mounts); Burrard Inlet and offing, Nov. 2-3, 1977: ELB Stns. P4 (6 females); P6 (1 female); P7 (1 female (slide mount), 3 males); P8 (5 females, 1 male). Burrard Inlet and offing, July 5, 1978: ELB Stns. V5, 150 m. dredge - 1 male; V6, 150 m. nat. dredge - 4 females, 3 males (slide mounts). Off Hammond Beach, Departure Bay, ELB Stn. B1, 17.5 m. nat. dredge, May 14, 1977 - 1 male. Nukumis Bay, Vancouver I., B. C., PF and MB colls. - 1 female. English Bay, B. C., N McD coll., 1977 - 1 female.

Diagnosis. Male (3.3 mm) (amplifies significant features not fully treated in the original description, based on Barnard's original 2 lots from off the coast of Oregon):

Body mid-dorsally smooth on peraeon, mid-dorsally and dorso-laterally ridged and mucronate on pleon segments 1 and 2, dorso-laterally ridged on pleon 3, and strongly toothed mid-dorsally on urosome 1, and laterally above base of uropod 1. Rostrum strong, apex acute, not deflexed; anterior head lobe blunt, almost rounded. Eye broadly subreniform, consisting of a loose aggregation of 40-50 weakly pigmented facets. Antenna 1, peduncle 1 with strong distomedial cusp (both sexes). Antennae calceolate in female.

Mouthparts not treated by Barnard (1971), but relatively plesiomorphic in B. C. material, as in *R. boreopacifica*.

Coxae 1-4 shallow, little deeper than wide; coxa 1 produced, broadly rounded, hind corner with small notch and

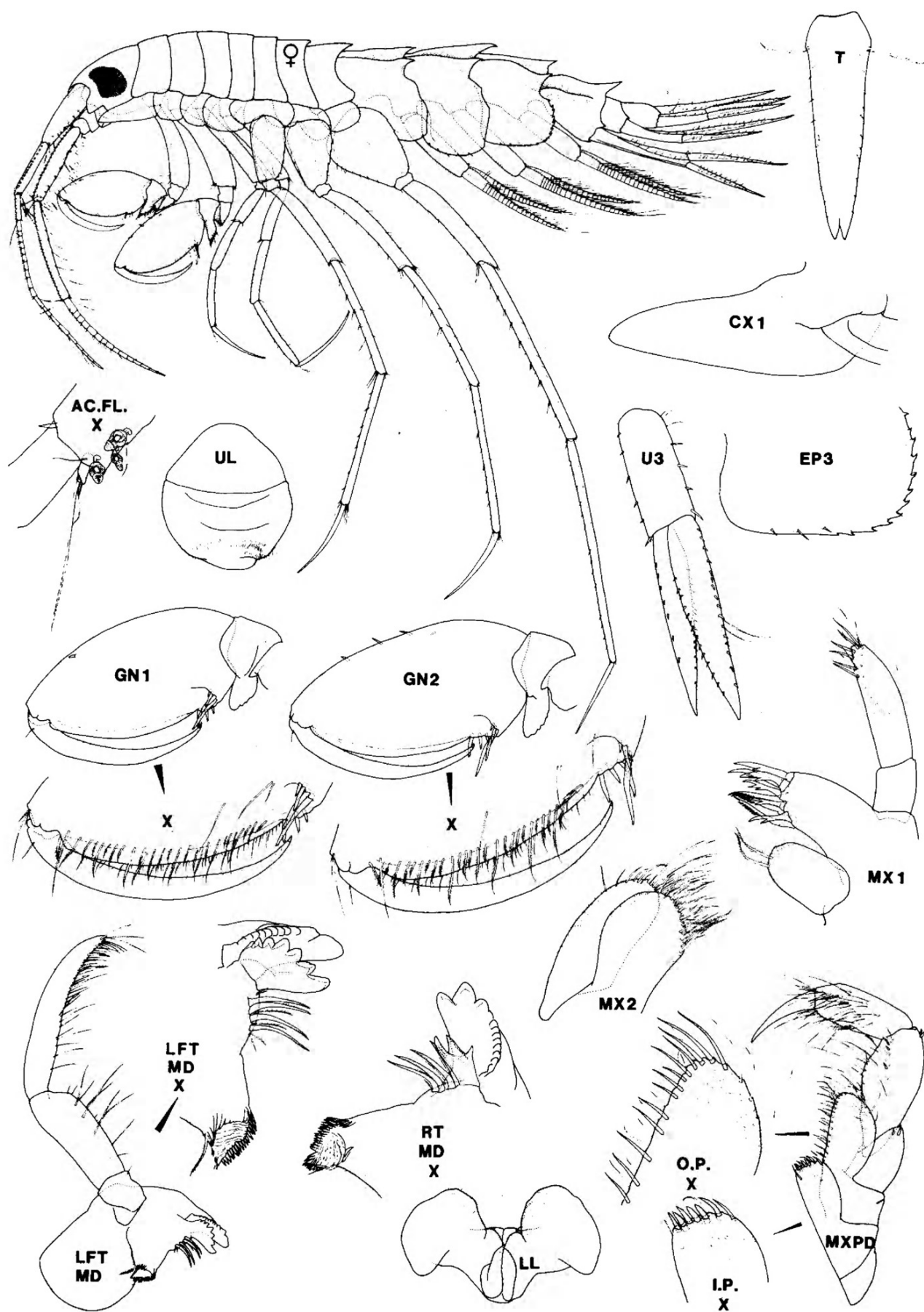


Fig. 17. *Rhachotropis boreopacifica*, n. sp. Female br. I (10.5 mm). Off Vancouver I., B. C., 549 m.

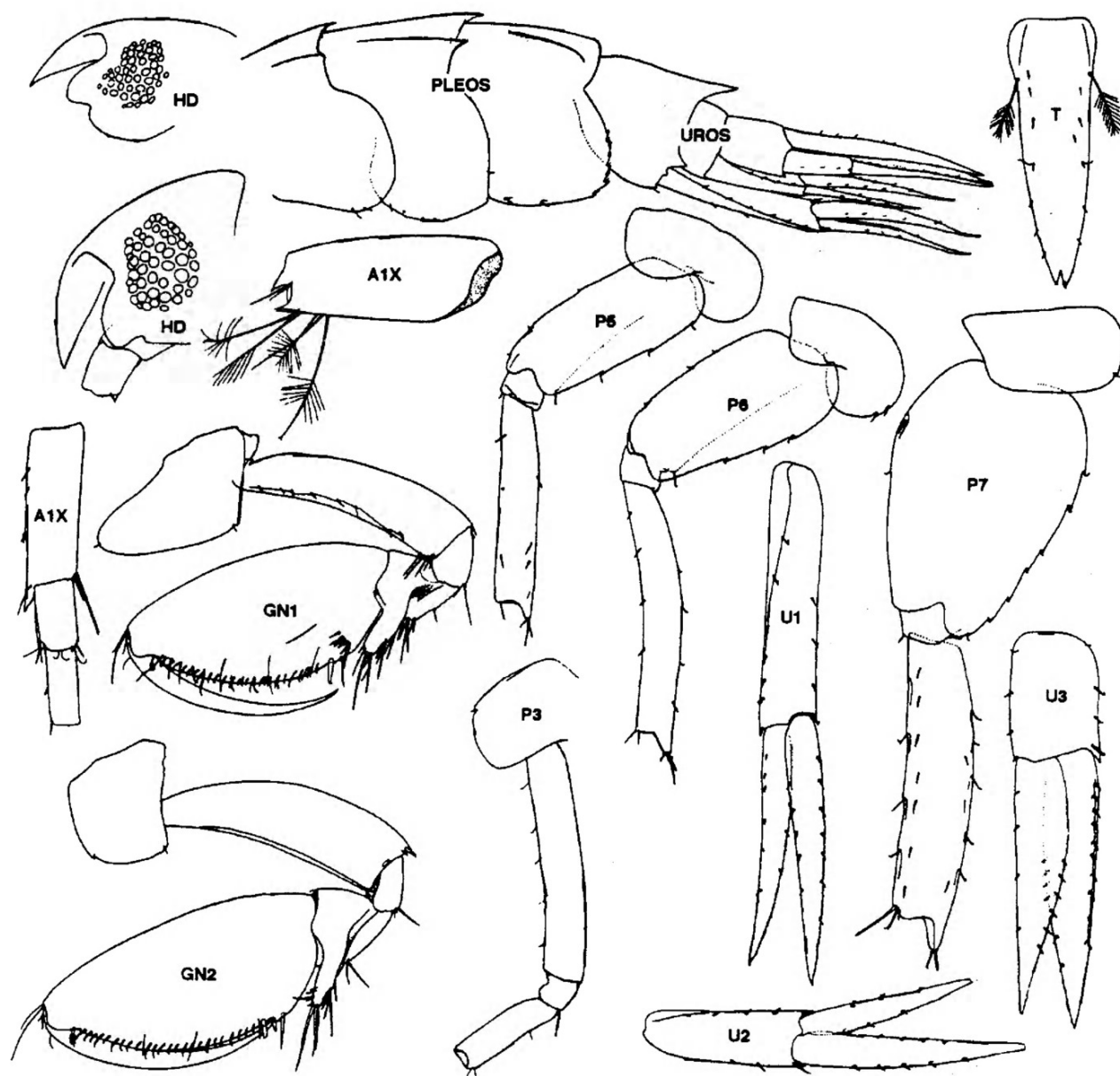


FIG. 18. *Rhachotropis barnardi* new species. Male (3.3 mm).
(modified from Barnard, 1971). Off Oregon, 200 m.

seta. Gnathopods 1 and 2, propods subovate, closely similar in size and form; carpal lobes narrow, 2 the longer, apices with 2-3 slender spines; palmar margins with few long setae; posterior angle with 2 outer marginal spines at dactyl tip depression.

Peraeopods 3 and 4 slender, segment 4 short (dactyls missing, presumably slender). Peraeopods 5-6, coxae postero-lobate; bases medium, narrowing distally, lobate below. Peraeopod 7 stouter and longer than 5 and 6; basis convex and weakly serrate behind, narrowing distally, lobate below. Pleon plate 2, hind corner weakly obtuse; pleon plate 3, hind corner rounded, lower hind margin irregularly serrate. Uropod 1, rami narrow, elongate, subequal, tips extending to tips of uropod 3. Uropod 3, rami subequal, margins spinose. Telson elongate, length > 3X basal width, basally with pair of large lateral plumose setae; apex sharply notched, nearly attaining tips of rami of uropod 3.

Coxal gills and brood plates not described.

Etymology. The species is named in honour of the late J. L. Barnard who first described and figured the Oregon material.

Taxonomic and distributional commentary. Barnard (loc. cit.) concluded that this form was an eyed variant of *R. clemens*, a bathyal species that he had earlier described from the Cedros Trench (p. 32). However, as noted in the key, and above, several external features of *R. barnardi* differ specifically from those of *R. clemens*, and some are closer to those of *R. boreopacifica* (above). These include not only the pigmented eyes, but the more elongate propod, stronger carpal lobe, and less spinose basis of gnathopod 1; the broader and distinctly more lobate bases of peraeopods 5-7, the more rounded pleon plate 3, the broader rami of uropods 1-3, the more elongate telson, and lack of dorso-lateral mucronation on pleon 3. The last feature, long sharply acute rostrum, and aetose rami of uropod 3 readily separate *R. barnardi* from *R. boreopacifica*.

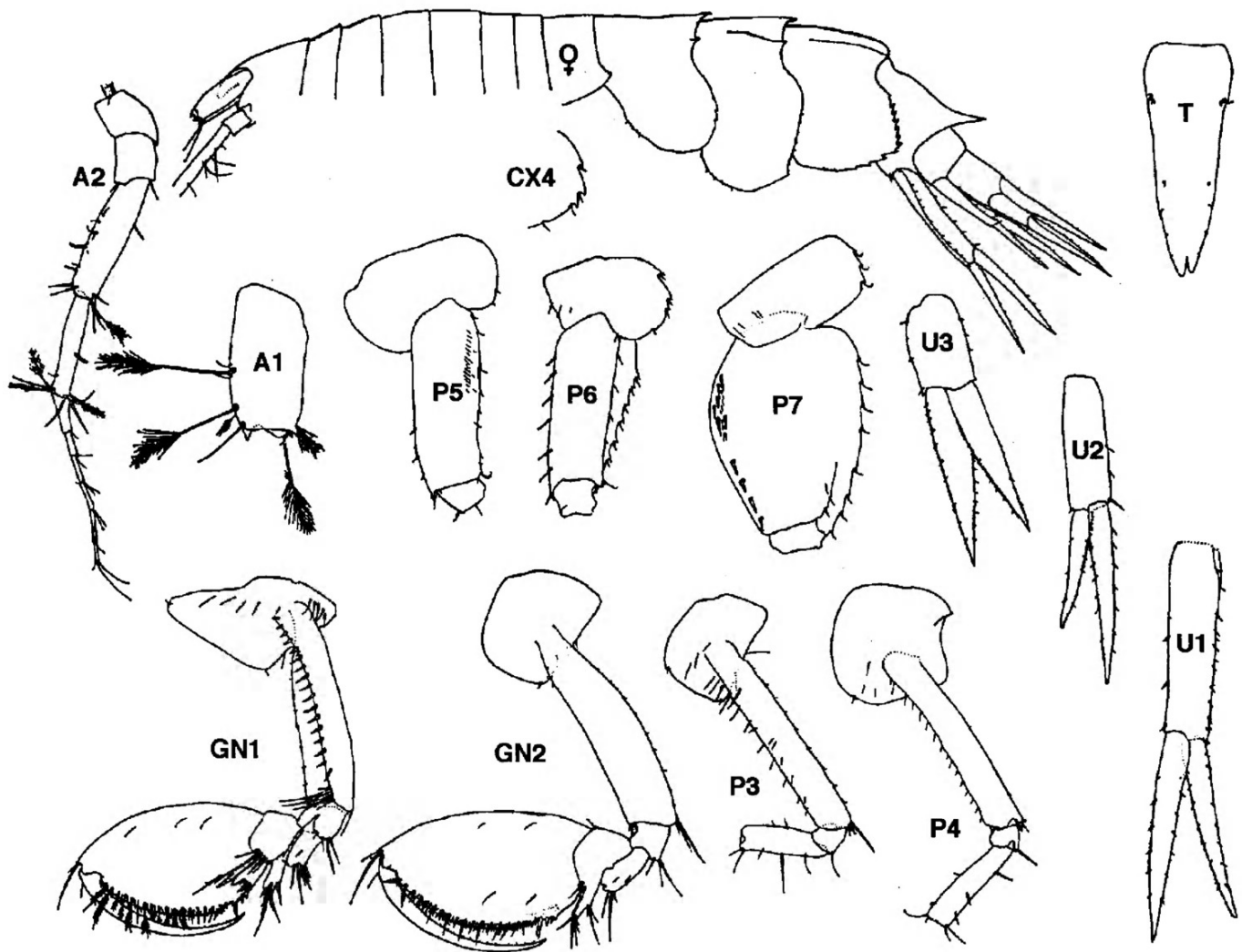


FIG. 19. *Rhachotropis clemens* Barnard, 1967. Female (4.5 mm)
Off S. California, ~800 m. (modified from Barnard, 1967)

Rhachotropis clemens J. L. Barnard
(Figs. 19)

Rhachotropis clemens J. L. Barnard, 1967: 16, fig. 5.—J. L. Barnard, 1971:10, figs. 6, 7.

Taxonomic and distributional commentary. The original description of this species (Barnard, 1967a) was based on anoculate material (female- 4.5 mm) from depths of 791-842 m. in the Cedros Trench, off Baja California. Barnard did not include details of the mouthparts, coxal gills, and brood plates, character states of which are proving phylogenetically significant. Description of these features would require re-examination of the 3 specimens from the type locality, not performed in the present study.

However, in comparing *R. clemens* with other N. American Pacific species, the overall form of its pereopods 3-7, uropods and telson, and mucronate urosome 1, would relate it more closely to the northern sublittoral eyed species, *R. barnardi* and *R. boreopacifica* than to other bathyal species of the Cedros Trench, or to the sublittoral eyed *R. luculenta*

of the Gulf of California.

The smaller Oregon material to which Barnard referred this name (1971, and p. 29) has generally fewer spines, the telson is relatively longer and its apex is less deeply notched than in the larger Californian specimens. Such differences between sizes and between male and female specimens of the same species would not be unexpected. However, transcending differences in sex and size, *R. clemens* is distinctive not only in its total lack of pigmented eyes, but also in its short anterior head lobe, relatively short antennae 1 and 2, the strong plumose setal armature of antennal ped-uncular segments, the deep gnathopod propods with relatively strongly setose palmar margins, the narrow, nearly alobate bases of pereopods 5 and 6, the squarish hind corner of pleon plate 3, the short, slender uropod rami, the relatively short telson (length <3X basal width), with asymmetrical apical lobes of which do not nearly attain the tips of uropod 3. In some features (e.g., form of antennae and gnathopods), *R. clemens* somewhat resembles the northern sublittoral species complex of *R. inflata* (G. O. Sars), *R. minuta*, and *R. conlanae*, but differs significantly otherwise.

***Rhachotropis oculata* (Hansen)**
(Fig. 20)

Tritropis oculata H. J. Hansen 1888: 140.

Rhachotropis oculata G. O. Sars 1895: 424, pl. 153.—Stebbing, 1906: 350.—Gurjanova, 1951: 712, fig. 496.—Bousfield, 1973: 78, pl. XI.—Austin, 1985: 590.—Staude, 1987: 378.

Material Examined. BRITISH COLUMBIA: 125 specimens, in 15 lots, mainly from the north central coast of British Columbia, south to Burrard Inlet:

ELB Stn. H37, Open Bight, mouth of Rivers Inlet, 50-60 m. dredge, fine sand and shell, July 22, 1964. - 1 female ov. (10.1 mm), (slide mount). Off Spanish Banks, Burrard Inlet, Stn. EB7, muddy sand, 26 m. dredge, June 16, 1976 - 2 imm. specimens; West Bay, 3/4 mile south, ELB Stn. P3, 30 m. dredge, Nov. 2, 1977 - 1 female, 1 imm. Trevor Channel, off Brady's Beach, V. I., ELB Stn. B13, 6-24 m dredge, May 25, 1977 - 1 male.

Diagnosis. Female ov. (10.1 mm): Body medium broadest in peraeon. Peraeon segment 7 and pleon segments 1-3 with postero-dorsal mucronation, very short and deflexed on 3; pleon segments 1-3 each with dorso-lateral ridge and tooth. Urosome segment 1 lacking dorsal process. Rostrum medium, exceeding short acute lateral head lobe. Pigmented eyes large, rhomboidal, nearly meeting mid-dorsally. Antenna 1, peduncular segment 1 and 2 stout, 2 short, 3 very short; flagellum 20-segmented, weakly calceolate; accessory flagellum rod-like, 1-segmented. Antenna 2 slightly longer than 1; peduncular segment 4 strongly setose behind, segment 5 more strongly calceolate anteriorly; flagellum calceolate, 25-segmented.

Mandible, molar large, conical, grinding surface large; spine row with 3-4 narrow blades; left lacinia 6-dentate; right lacinia trifid; incisor, cutting margin relatively short; palp stout, segment 3 slender, distinctly longer than segment 2, narrowing distally. Maxilla 1, inner plate with 2 apical setae, palp stout. Maxilla 2, inner plate shorter and broader than outer, inner margin proximally with single stout plumose seta. Maxilliped, palp strong, segment 2 broadened; outer plate tall; inner plate with 7 apical short spines.

Coxa 1 produced anteriorly, apex sharply rounded; coxae 2-4 shallow broader than deep; coxa 4 weakly excavate behind. Gnathopod 2 larger than 1; bases, anterior and posterior margins lined with short spines; carpal lobes narrow, not strongly produced; propods subsimilar, regularly ovate; hind margin medium; palmar margin with large dactyl-tip depression lined by interior cluster of 4-6 spines (1 elongate), and short outer row of 3 spines.

Peraeopods 3 and 4 medium, strong, segment 4 shorter than 5; dactyls strong (length ~ segment 6). Coxae 5 and 6 shallow, nearly aequilobate. Peraeopods 5 and 6 subsimilar in form and size; bases short, broad, weakly lobate below; hind margins of segments 4-6 of peraeopod 6 bearing spines and setae; dactyls elongate. Peraeopod 7 more elongate;

basis broad, hind lobe acute below; distal segments spinose and weakly setose; dactyl sublinear.

Pleon plate 2, hind corner squarish, slightly acuminate; pleon plate 3, hind margin convex, strongly serrated. Uropods 1 and 2, rami narrow lanceolate, margins strongly serially spinose; uropod 2, outer ramus distinctly shorter than inner ramus. Uropod 3, rami broadly lanceolate, subequal, inner margins setose and spinose. Telson basally broad, medium long, not reaching tip of uropod 3, cleft 40% of its length.

Coxal plates large, subovate.

Taxonomic and distributional commentary. The present material differs little from that described and figured from the North Atlantic coast by the senior author (Bousfield 1973). *Rhachotropis oculata* is amphiboreal and subarctic, ranging southward on both sides of the North Atlantic and North Pacific oceans. On the coast of British Columbia, it is the shallowest ranging species, taken mainly at depths of less than 100 m.

***Rhachotropis inflata* (G. O. Sars)**
(Fig. 21)

Tritropis inflata G. O. Sars, 1882.

Rhachotropis inflata Sars, 1895: 430, pl. 152.—Waiiles, 1931: 41.—Gurjanova, 1951: 713, fig. 497.—Fulton, 1968: 107.—J. L. Barnard, 1971: 12.—Austin, 1985: 590.—Barnard & Karaman, 1991: 338.

Taxonomic and distributional commentary. This relatively small species (female to 8.0 mm) has been well described and figured by Sars (loc. cit) on the basis of material taken at depths to ~100 m. in Norwegian coastal fiords. Although Gurjanova (1951) lists this species from the Bering Sea and Sea of Japan, it was not identified in material of the present North American Pacific study region.

The species is recorded, but not authentically, from the B. C. coast by Waiiles (1931) and Fulton (1968), and from off the coast of Oregon by Barnard (1971), records repeated by Austin (loc. cit). However, its moderately close similarity to *R. conlanae*, and to lesser extent to *R. minuta*, both newly described herein, indicates that a re-examination of the earlier materials is advisable, if possible. *R. inflata* is similar to both *R. minuta* and *R. conlanae* in lacking a dorsal tooth on pleon 3 and urosome 1, in the short antennae, relatively short, weak peraeopods 3 and 4, and the relatively short deeply cleft telson.

However, *R. inflata* differs from both in the relatively slender form of the propod of gnathopod 2, and more uniform length of the palmar setae. Although *R. inflata* is similar to *R. minuta* in having distinct dorso-lateral ridges and mucronations on pleon segments 1-3, it differs further from *R. minuta* in lacking a dorsal tooth on peraeon 7, in its broader less reniform eye, and in its broader and more posteriorly convex basis of peraeopod 7.

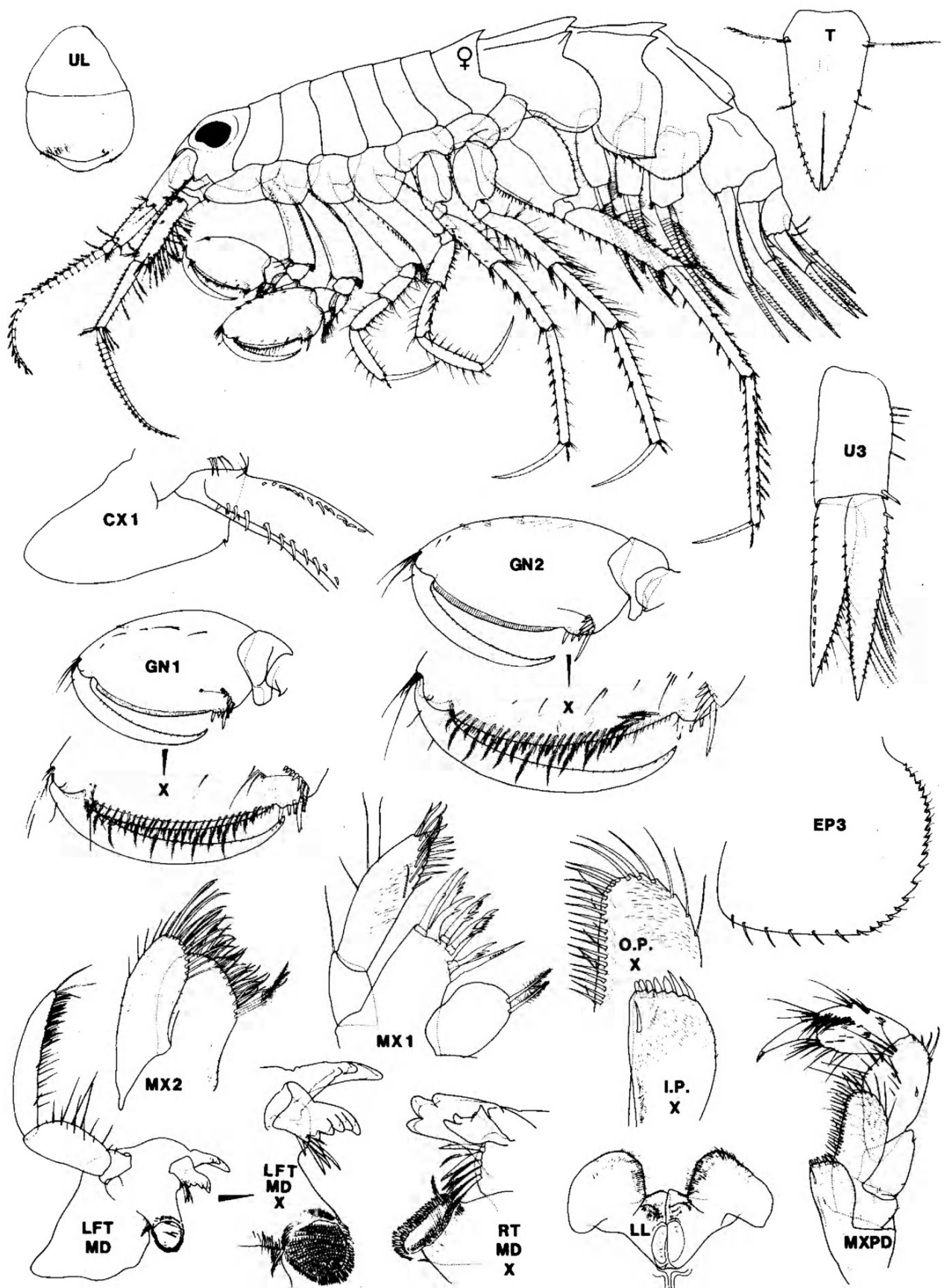


FIG. 20. *Rhachotropis oculata* (Hansen). Female ov. (10.1 mm). Open Bight, B. C., 50-60 m.

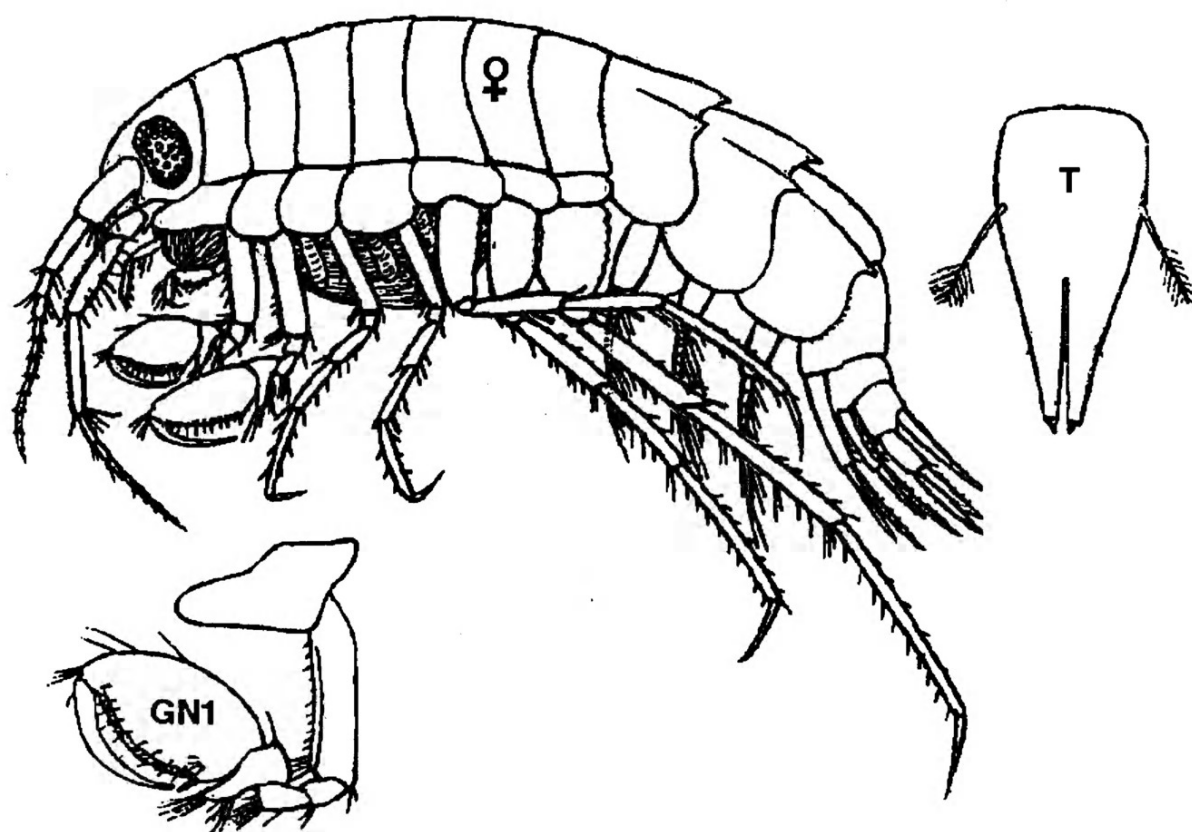


FIG. 21. *Rhachotropis inflata* (G. O. Sars, 1883). Female (8.0 mm)
Off Norway, 200 m. (modified from Sars, 1895)

Rhachotropis minuta, new species
(Fig. 22)

Material Examined: BRITISH COLUMBIA: ELB Stn. P3, West Bay, 3/4 miles south, 60 m. dredge, Nov. 2, 1977 - 1 female ov (3.8 mm) Holotype (slide mount), 2 other female, Paratypes (slide mount), CMN Acc. No. 1977-327.

Diagnosis. Female (3.8 mm): Body small, slender. Peraeon segment 7 with small dorsal and dorso-lateral teeth. Pleon segments 1 and 2 toothed dorsally and dorso-laterally, but pleon segment 3 very weakly so. Urosome 1 with very weak posterior marginal cusps and tooth above junction of uropod 1. Rostrum medium; lateral head lobe short, acute. Eye large, broadly reniform. Antenna 1, peduncular segments short, flagellum 7-segment, not calceolate; accessory flagellum minute, with strong apical spine. Antenna 2, peduncular segments 4 and 5 subequal, 4 setose behind, 5 calceolate anteriorly; flagellum 6-segmented, calceolate basally.

Mandible, molar conical, grinding surface small, surrounded by blade spines; spine row with 3-4 blades; left lacinia 6-dentate; incisor main cutting edge nearly smooth; palp stout, segment 3 longer than 2. Maxilla 1, inner plate with 2 apical setae; palp slender. Maxilla 2, inner plate little broadened, with stout inner marginal seta. Maxilliped ordinary; outer plate not broadened; inner plate with 3 apical spines.

Coxa 1 very strongly produced anteriorly, apex sharply rounded.; coxae 2-4 shallow, wider than deep, coxa 4 shallowly excavate behind. Gnathopod 2 distinctly larger than gnathopod 1; bases with antero-distal cluster of setae; carpus narrowly lobate; propod medium, ovate, posterior angle with inner marginal group of 2 spines and a single stout outer marginal spine; palmar setae longest near hinge.

Peraeopods 3 and 4 ordinary; segment 4 little shorter than 5, dactyls medium (~50% length of segment 6). Peraeopods 5-7 regular 7 distinctly longest; bases of 5 and 6 narrowly lobate, of 7 broader and more strongly lobate below; dactyls regular.

Pleon plate 2, hind corner acuminate; pleon plate 3 strongly rounded and strongly serrated behind. Uropods 1 & 2, rami slender, uropod 2 extending beyond uropod 3. Uropod 3, rami narrowly lanceolate, subequal, margins sparsely spinose. Telson short, extending little beyond peduncle of uropod 3; cleft about 40% of its length, apices spreading slightly.

Coxal gills plate-like, unpleated.

Etymology. From the Latin "minuta" referring to the very small size of the adult animal.

Taxonomic and distributional commentary. *Rhachotropis minuta* is closely similar to *R. conlanae*, n. sp. but differs in the stronger dorsal armature of the pleon, and the normal dactyls. Both species are closest in form to *R. inflata*, (Sars) and to lesser extent to *R. oculata* (Hansen).

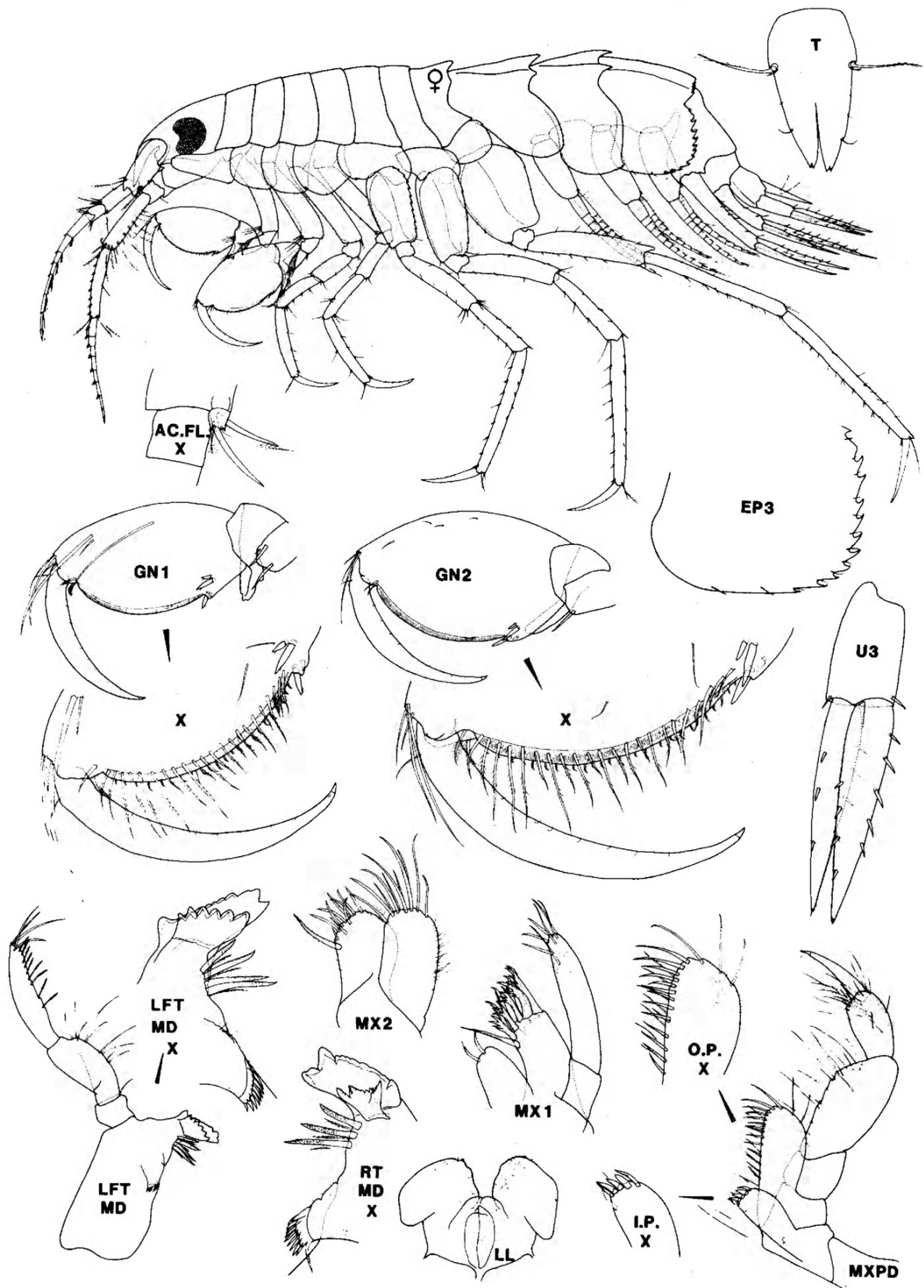


FIG. 22. *Rhachotropis minuta*, n. sp. Female ov. (3.8 mm). West Bay, B. C. 60 m. dredge.

***Rhachotropis conlanae*, new species**
(Fig. 23)

Rhachotropis inflata Austin, 1985, partim?

Material Examined: S.E. ALASKA: Boca de Quadra, across from Bactrian Point (55° 07.9'N, 130° 43.5'W.), 29 m. dive, in sponge bed, K. E. Conlan Stn. 89-2-45, June 27, 1989 - 1 female ov (4.5 mm) Holotype (slide mount); female (4.1 mm) Paratype; about 100 other specimens (no mature males), CMN Acc. No IZ1989-066.

Diagnosis. Female ov. (4.5 mm): Body small, compressed. Peraeon pleon 3 and urosome dorsally unarmed. Pleon 1 with small mid-dorsal cusp, and pleon 2 with very short mid-dorsal and dorso-lateral mucronations. Rostrum medium; anterior head lobe short, acute. Eye very large, round. Antenna 1, peduncular segments short; flagellum 6-7 segmented, lacking calceoli; accessory flagellum very short, apex with stout spine and plumose seta. Antenna 2, peduncular segment 5 longer than 4, both anteriorly marginally calceolate; flagellum calceolate, 7-8 segmented.

Mandible molar columnar, triturating surface small; spine row with 3-4 blades and accessory setae; left lacinia 7-dentate; incisor multidentate; palp stout, segment 3 slightly longer than segment 2. Maxilla 1 inner plate with 1 apical seta; palp large. Maxilla 2, inner plate little expanded, shorter than outer plate. Maxilliped regular; outer plate relatively narrow, inner plate with 4-5 apical spines.

Coxa 1 strongly produced anteriorly, apex subacute. Coxae 2-4 broader than deep, 4 scarcely excavate behind. Gnathopod 2 slightly larger than gnathopod 1; bases, with cluster of antero-distal setae; carpus narrowly produced; propods deeply ovate; posterior angle with a medial group of 3 short spines and a single exterior stout spine.

Peraeopods 3 and 4, segment 4 slightly shorter than 5; dactyls relatively short, stout, unguis short. Peraeopods 5-7 not elongate, increasing posteriorly; bases medium broad and lobate; dactyls short, thick, as in peraeopods 3 and 4.

Pleon plate 2, hind corner acuminate; pleon plate 3 rounded behind with about 10 medium strong serrations. Uropods 1 and 2 rami elongate extending to tips of uropod 3. Uropod 3, rami narrowly lanceolate, subequal, margins spinose. Telson relatively short, extending little beyond peduncle of uropod 3, cleft about 40%, apices slightly spreading.

Coxal gills plate-like, unpleated.

Etymology. The species is named in honour of Dr. Kathleen E. Conlan in recognition of her continuing major contributions to knowledge of amphipod crustaceans.

Taxonomic and distributional commentary. The species is closest to *R. inflata*, but differs in the characters of the key (p. 23). *R. conlanae* is remarkably similar to *R. luculenta* Barnard from sublittoral depths of the Gulf of California. However, it is unique among species of the N. American Pacific coast in its relatively short peraeopods 3 and 4, and short stout dactyls of peraeopods 3-7.

***Rhachotropis luculenta* Barnard**
(Fig. 24)

Rhachotropis luculenta J. L. Barnard, 1969c: 203, Fig. 16.

Taxonomic and distributional commentary. Barnard (loc. cit.) described this small, eyed, calceolate species (male - 4.6 mm) from Bahia de Los Angeles, Gulf of California, at depths of 38-46 m. He compared it most closely with *R. inflata* Sars but noted differences in the dorsal pleon mucronation, rostral shape, length of peraeopod dactyls, and other features. He also compared it with *R. oculata* (Hansen) but noted a greater range of differences in dorsal mucronation and peraeopod features.

R. luculenta differs from all other known eyed species of the northern hemisphere that lack a tooth on urosome 1, including the Mediterranean region, in the combination of the very short flagellum of antenna 1, the very different size and form of the propods of gnathopods 1 and 2, the short segment 4 of peraeopod 3, the double- or triple-toothed posterior margins of the bases of peraeopods 5 and 6, and the much smaller eyes of the female. Regrettably, of the mouthparts, only the mandibular palp was figured and mentioned briefly in Barnard's text. In the present study, the balance of character states was found to be relatively advanced (Fig. 34) and least different from the bathyal species, *R. ludificor*, that Barnard described earlier (1967) from bathyal depths of the outer coast of Baja California (see below). *R. luculenta* may be a warm-water species that is unlikely to be found north of Pt. Conception on the N. American Pacific coast.

***Rhachotropis ludificor* Barnard**
(Fig. 25)

Rhachotropis ludificor J. L. Barnard, 1967: 18, fig. 6.

Taxonomic and distributional commentary. The species is based on a male specimen (4.5 mm) taken at a depth of 1720-1748 m in Cedros Trench, Baja California. Barnard (loc. cit.) had readily distinguished it from all eyeless world species described at that time but linked it most closely with *R. distincta* Holmes (1908). *R. ludificor* is here grouped with the eyed, calceolate species *R. luculenta* and *R. conlanae* in sharing the following features: medium strong rostrum; weakly mucronate pleon; dorsal mucronation on urosome 1 minute or lacking; coxa 1 strongly produced anteriorly, with broadly rounded apex; large deep gnathopod propods; lobate bases of peraeopods 5-7; non-setose margins of uropod 3 rami, and relatively short, deeply cleft telson. *R. ludificor* more closely resembles *R. luculenta* in the slender distal segments and dactyls of peraeopods 3 and 4 and triple micro-cusping of the postero-dorsal margin of pleon segment 3. It differs, however, in the more elongate antennal peduncular segments, apparent lack of antennal calceoli, and total lack of pigmented eyes.

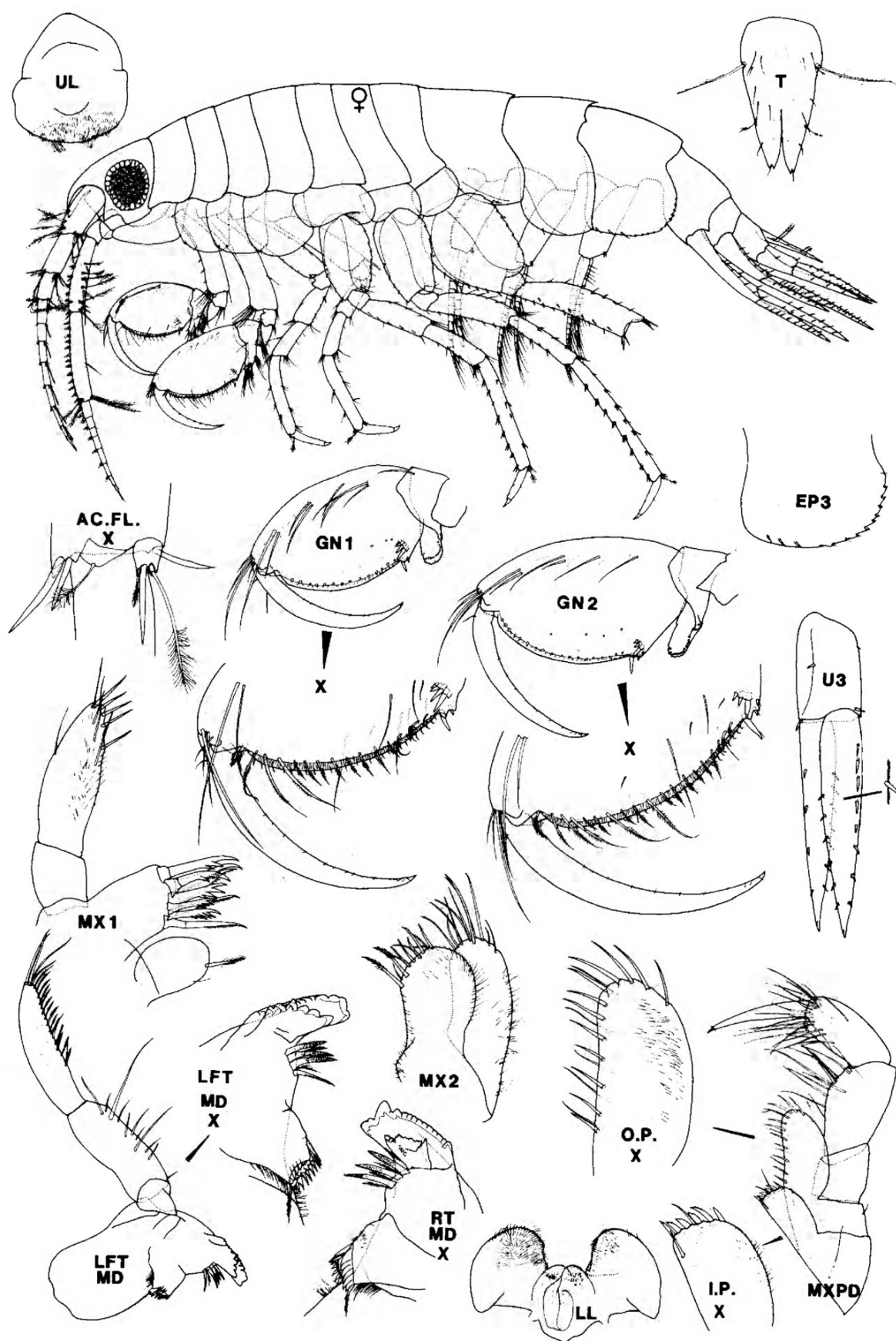


FIG. 23. *Rhachotropis conlanae*, n. sp. Female (4.5 mm). Boca de Quadra, Alaska, 29 m.

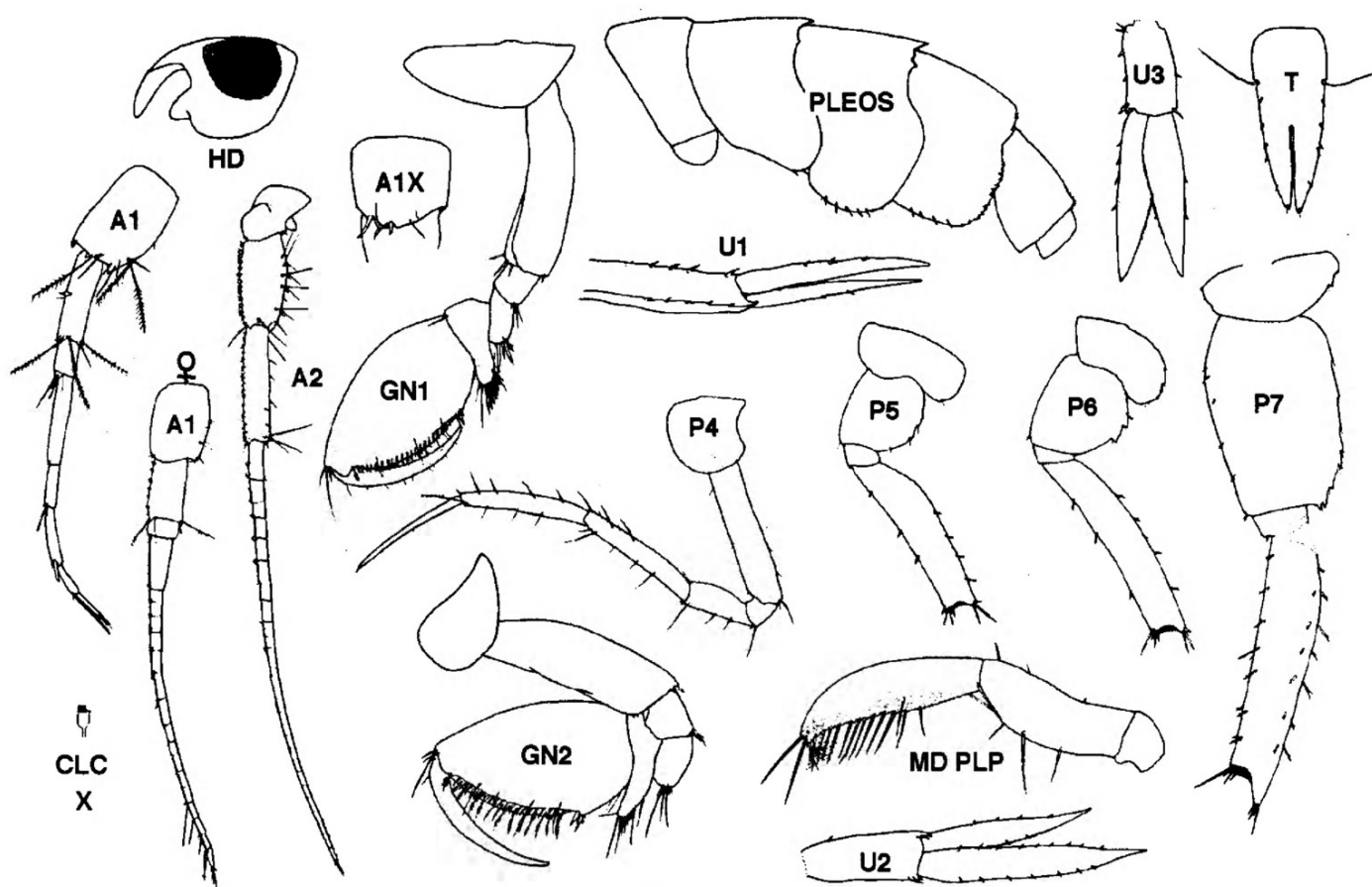


FIG. 24. *Rhachotropis luculenta* J. L. Barnard, 1969c. Male (4.6 mm)
Gulf of California. (modified from Barnard, 1969c)

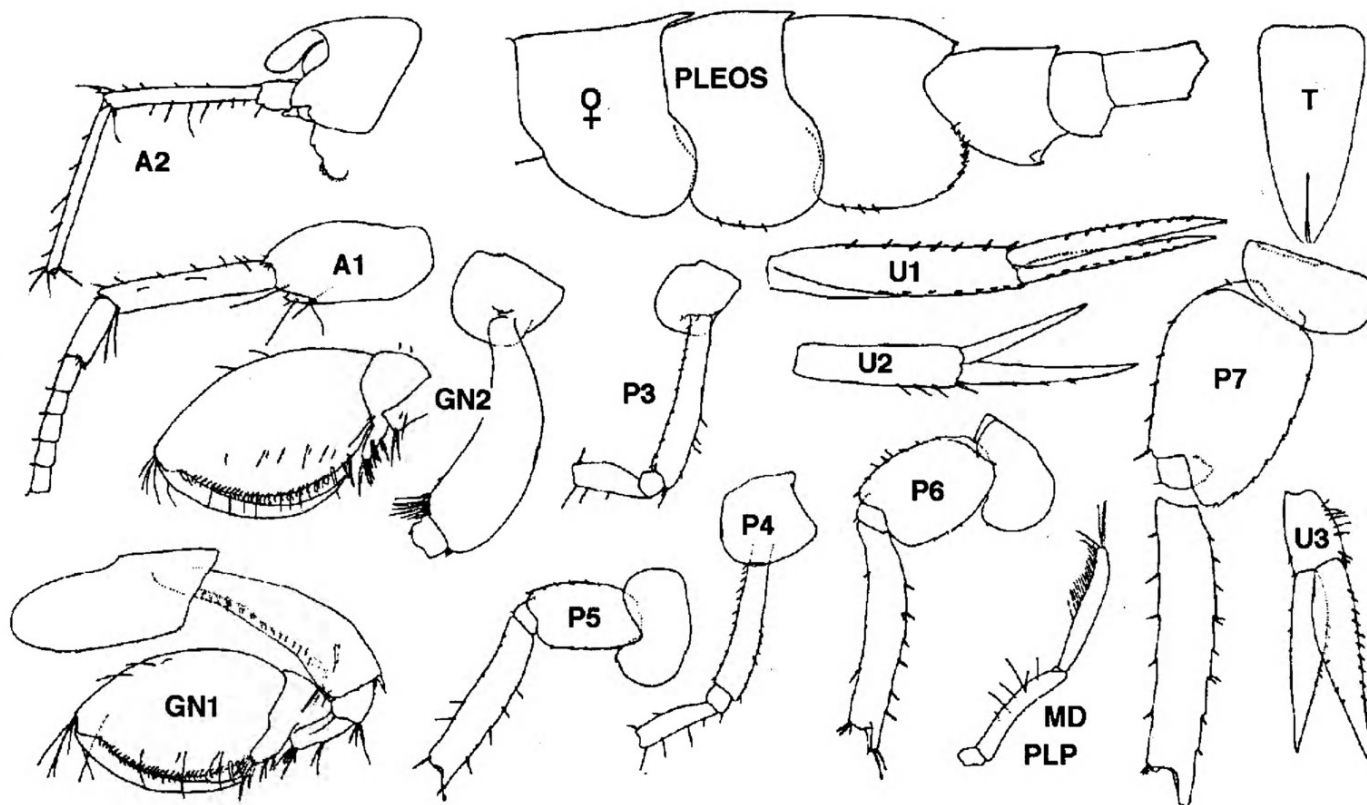


FIG 25. *Rhachotropis ludificor* J. L. Barnard, 1967. Male? (4.5 mm).
Off southern California, 1700+ m. (modified from Barnard, 1967)

Rhachotropis americana new species
(Fig. 26)

Material Examined:

BRITISH COLUMBIA: CMN Collections: NW of Englefield Bay, Queen Charlotte Ids., RBCM/CMN Stn 91-1-119, Deep water II, otter trawl, 0-1227 m, Mar. 21, 1991 - 1 female ov (11.3 mm), Holotype (slide mount); male (9.5 mm), Allotype (slide mount), 5 females, 1 MALE Paratypes; Off Frederick I., Q. C. I., Stn. 91-1-14 (53°57.00'N, 133°52.86'W to 53°57.63'N, 133°54.30'W) 0-1150 m otter trawl, Mar. 22/91 - 1 female.

Diagnosis. Female (11.3 mm) Holotype: Peraeon and urosome 1 smooth above. Pleon segments 1-3 with medium strong dorsal and dorso-lateral teeth, 2 largest. Rostrum short; anterior head lobe prominent, acute. Pigmented eyes lacking. Antenna 1 shorter than antenna 2, lacking calceolae; peduncular segments 1 and 2 medium, subequal, 3 elongate ($>1/2$ segment 2); flagellum 12-segmented; accessory flagellum very short, apex with plumose seta. Antenna 2 lacking calceoli; peduncular segments 4 and 5 slender, subequal, segment 4 with proximal posterior cluster of plumose setae; flagellum 16-segmented.

Mandible, molar small, subconical, grinding surface evanescent, replaced by several slender blades; spine row with 5-6 slender blades; left lacinia unevenly 5-dentate; right lacinia bifid; main cutting edge of incisor nearly smooth; palp slender, apically narrowing, segments 2 and 3 subequal in length. Maxilla 1, inner plate with 2 apical setae; palp slender, apex acute. Maxilla 2, inner plate broad, rounded, inner margin proximally with 2 longer plumose setae. Maxilliped palp strong, segment 2 little broadened; outer plate large, inner plate with 4-5 slender apical spines.

Coxa 1 strongly produced anteriorly, reaching tip of anterior head lobe, apex subacute, lower hind corner with single cusp. Coxae 2-4 shallow, broader than deep; coxa 4 excavate behind. Gnathopod 2 larger than gnathopod 1; basis heavier, lined with short spines; carpal lobes slender apices sparsely setose; propods slender ovate, hind margins short; palmar margins nearly horizontal, dactyl tip depression broad, with 2-3 inner marginal and 1 stouter outer marginal spine.

Peraeopods 3 and 4 slender, segment 4 distinctly shorter than segment 5; dactyls elongate ($>$ segment 6). Coxae 5 and 6, hind lobes acute below. Peraeopods 5 and 6 slender, subsimilar in form and presumably length; bases slender, not lobate behind; dactyls slender. Peraeopod 7 very much larger and presumably longer (distal segments missing); basis medium broad, not lobed below.

Pleon plates 1-3 broad rounded and weakly spinose below; hind margin of plate 3 convex, with numerous medium serrations. Uropods 1 and 2, rami slender, not reaching tip of uropod 3; outer ramus of uropod 2 distinctly shorter than inner ramus. Uropod 3, outer ramus slightly the shorter; peduncle with acute inner marginal distal process. Telson elongate, nearly attaining tip of uropod 3, narrowly cleft

1/3 of length.

Coxal gills large, plate-like, not pleated. Brood plates on peraeopods 2-4 broad, on 5 broadly strap-like.

Male (9.5 mm): Antenna 1 not calceolate, peduncular segments 1 and 2 with strong posterior marginal clusters of brush setae; flagellum basally weakly callynophorate. Antenna 2 not calceolate; peduncular segments 3 and 4 with strong anterior marginal clusters of brush setae. Mandible, left lacinia 6-dentate; palp segment 3 slightly longer than 2, apex rounded.

Etymology. The species name alludes to its occurrence in coastal waters of Pacific North America.

Taxonomic and distributional commentary. *Rhachotropis americana* is known only from two localities off the Queen Charlotte Islands, B. C. It closely resembles *R. grimaldi* (Chevreux), previously recorded from the Sea of Okhotsk (Gurjanova, 1951), in characters of the key (p. 23), and in the strong postero-distal notch of coxa 1, but differs in the less rugose dorsum of head and anterior peraeonal segments, and the button-like (rather than linear) form of the accessory flagellum, among other differences. It is also similar to *R. multesimus* Barnard from Los Cedros Trench off central Baja California (below), but differs in characters outlined in the key.

Rhachotropis grimaldi Gurjanova
(Fig. 27)

?*Rhachotropis grimaldi* Gurjanova, 1955: 180, fig. 11.

~~non~~ *Tritopsis grimaldi* Chevreux, 1887: 571.

~~non~~ *Rhachotropis grimaldi* Ledoyer, 1982a: 239, fig. 162.—
Barnard & Karaman, 1991: 338.

Taxonomic and distributional commentary. Gurjanova (loc. cit.) has figured a medium large (15 mm) deep-water species from the Okhotsk Sea that lacks the pigmented eyes of the Mediterranean type regional species illustrated by Ledoyer (1982a). Although the two populations are obviously closely related, they appear to differ significantly in the form of the telson, dorsal armature of the pleon, and in a number of other features that would suggest that two distinct species are involved.

Rhachotropis multesimus Barnard
(Fig. 28)

Rhachotropis multesimus J. L. Barnard, 1967: 119, fig. 7.

Taxonomic commentary. This very small (3.8 mm) blind species from bathyal depths off Baja California, resembles *R. grimaldi* as illustrated by Gurjanova 1955 (above) except for the much less strongly developed teeth and spines of the body and appendages. The enigmatic *R. cervus* Barnard, 1957, from the same location, may be phylogenetically closest to *R. grimaldi* (Gurjanova) and to *R. multesimus*.

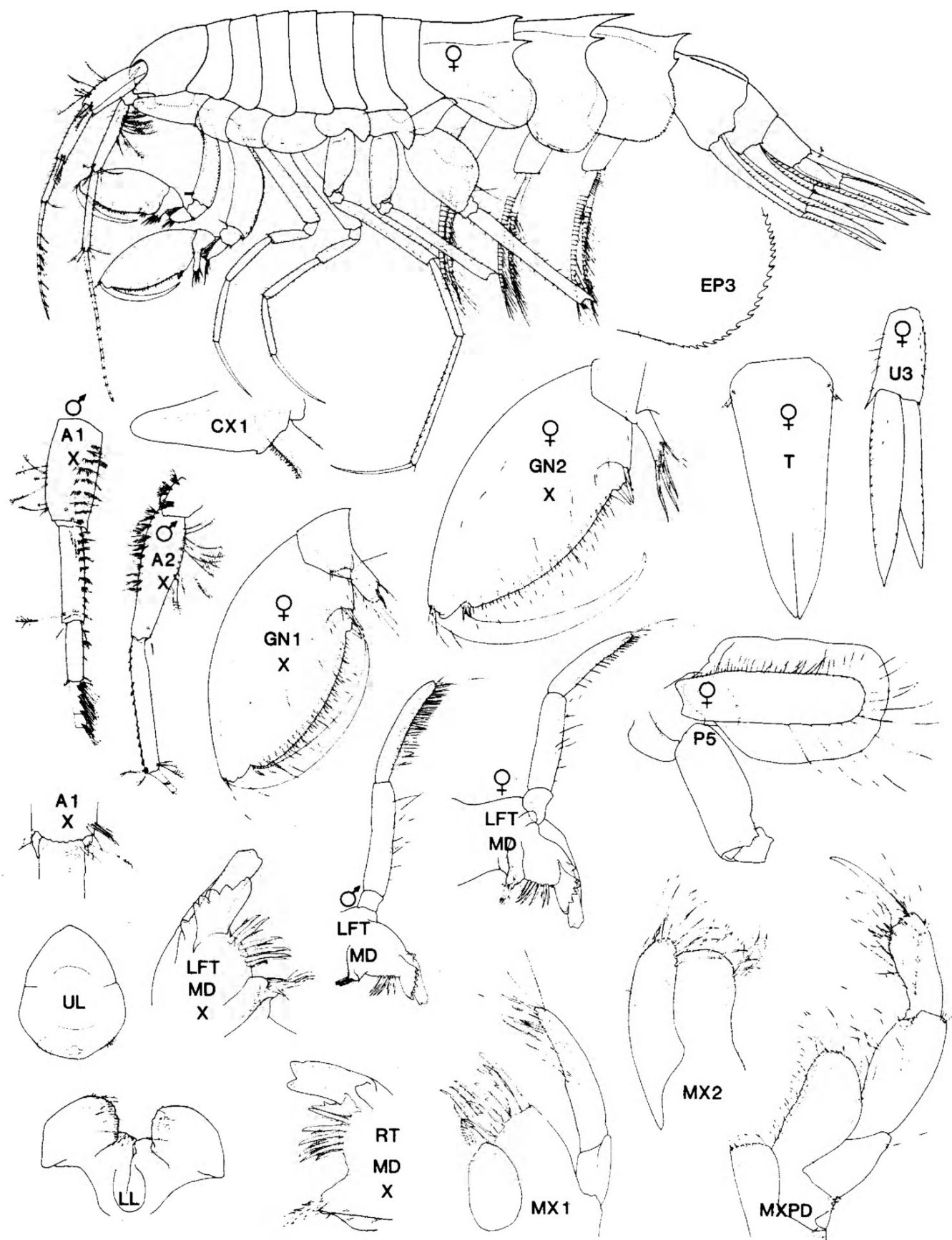


FIG. 26. *Rhachotropis americana*, n. sp. Female (11.3 mm); male (9.5 mm). NW of Englefield Bay B.C.

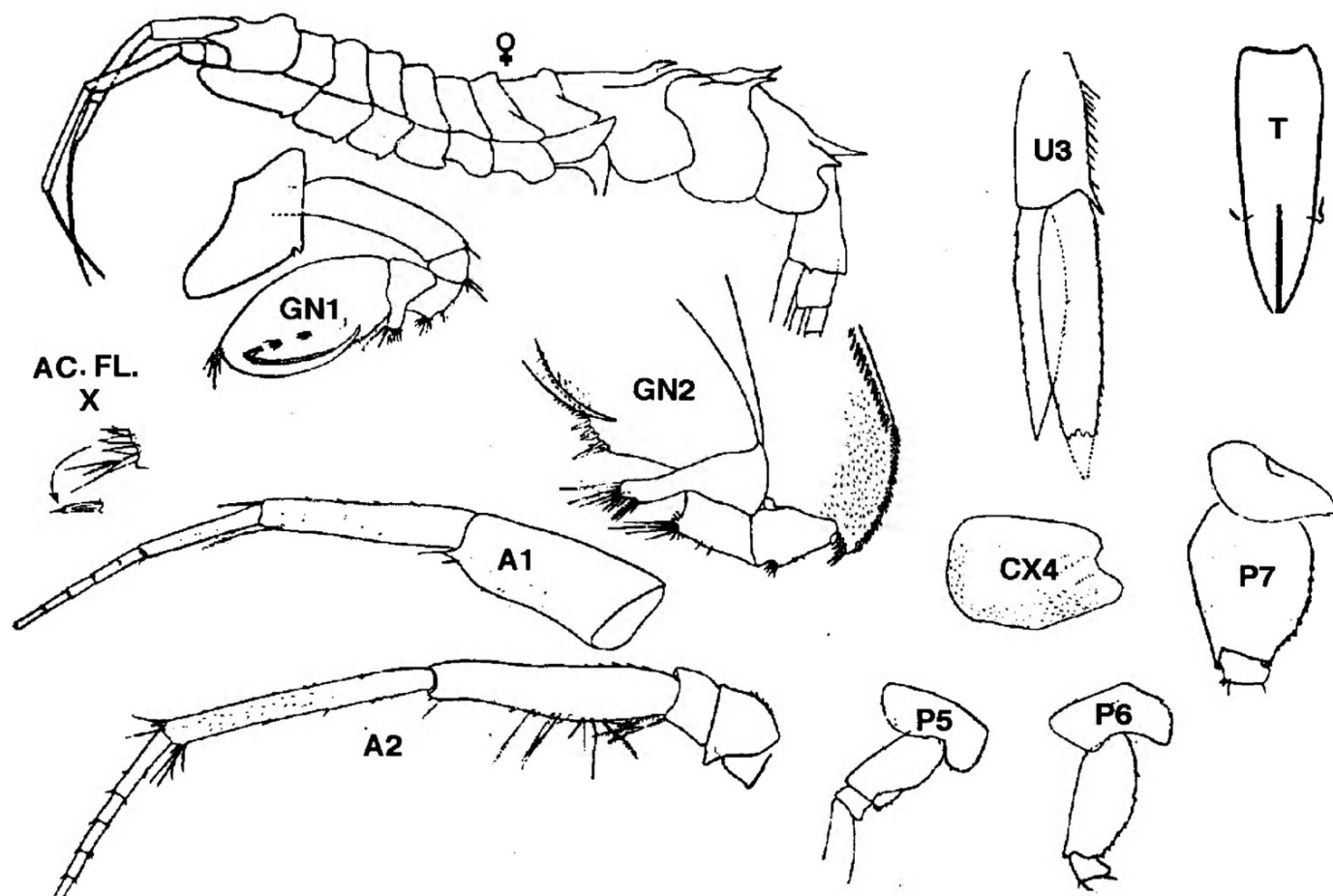


Fig. 27. *Rhachotropis grimaldi* (Chevr) Gurj. 1955. Female (15.0 mm)
Okhotsk Sea and N. Pacific (to 3000 m) (modified from Gurjanova, 1955)

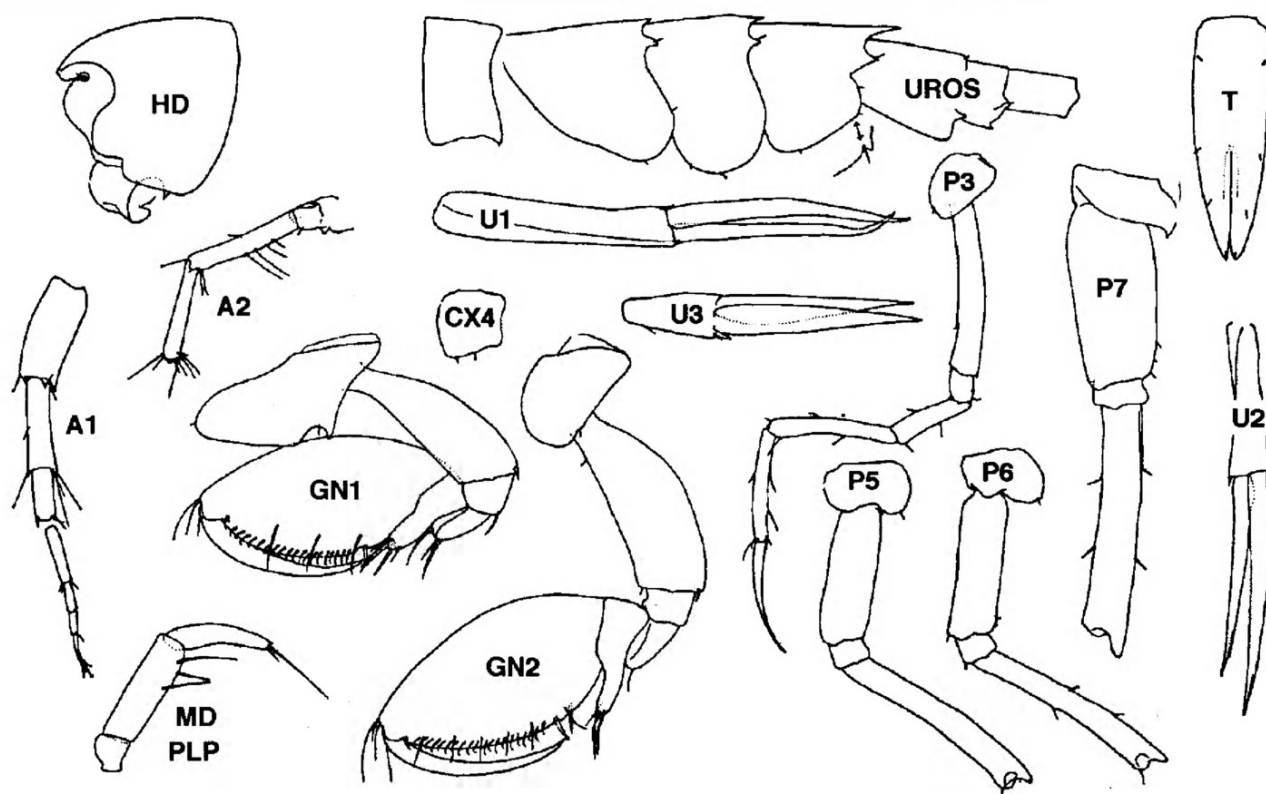


FIG. 28. *Rhachotropis multesimus* Barnard, 1967. Female? (3.8 mm)
off S. California, 1700+ m) (modified from Barnard, 1967)

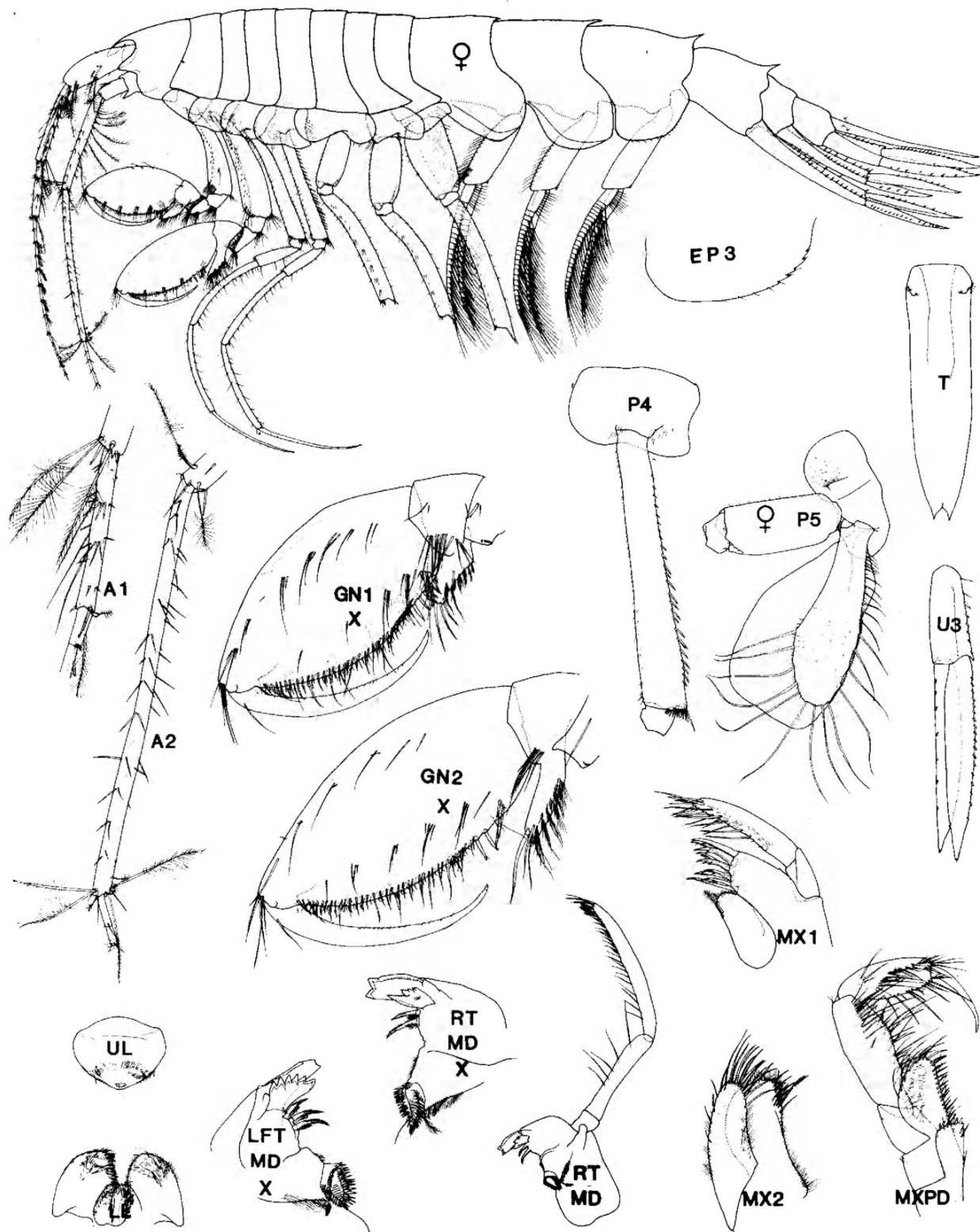


FIG. 29. *Rhachotropis distincta* (Holmes, 1908). Female ov. (9.0 mm). NW Englefield Bay, Q.C. I., B. C.

Rhachotropis distincta (Holmes)
(Figs. 29, 30)

Gracilipes distincta Holmes, 1908: 529, fig. 35.—Thorsteinson, 1941: 85 (key only).

Rhachotropis distincta Shoemaker, 1930: 316, figs. 41-44.
—Birstein & Vinogradov, 1955: 276.—Birstein & Vinogradov, 1958: 248.—Barnard & Karaman, 1991: 338.

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands, northwest of Englefield Bay (53° 05.08'N, 133° 00.08'W to 53° 06.58'N, 133° 01.22'W), RBCM/CMN Deepwater II Stn. 91-1-11, 0-1227 otter trawl, March 21, 1991. - 1 female (9.0 mm) (slide mount).

Diagnosis. Female (9.0 mm): Peraeon smooth above. Pleon segments 1-3 and urosome 1 each with posterior dorsal

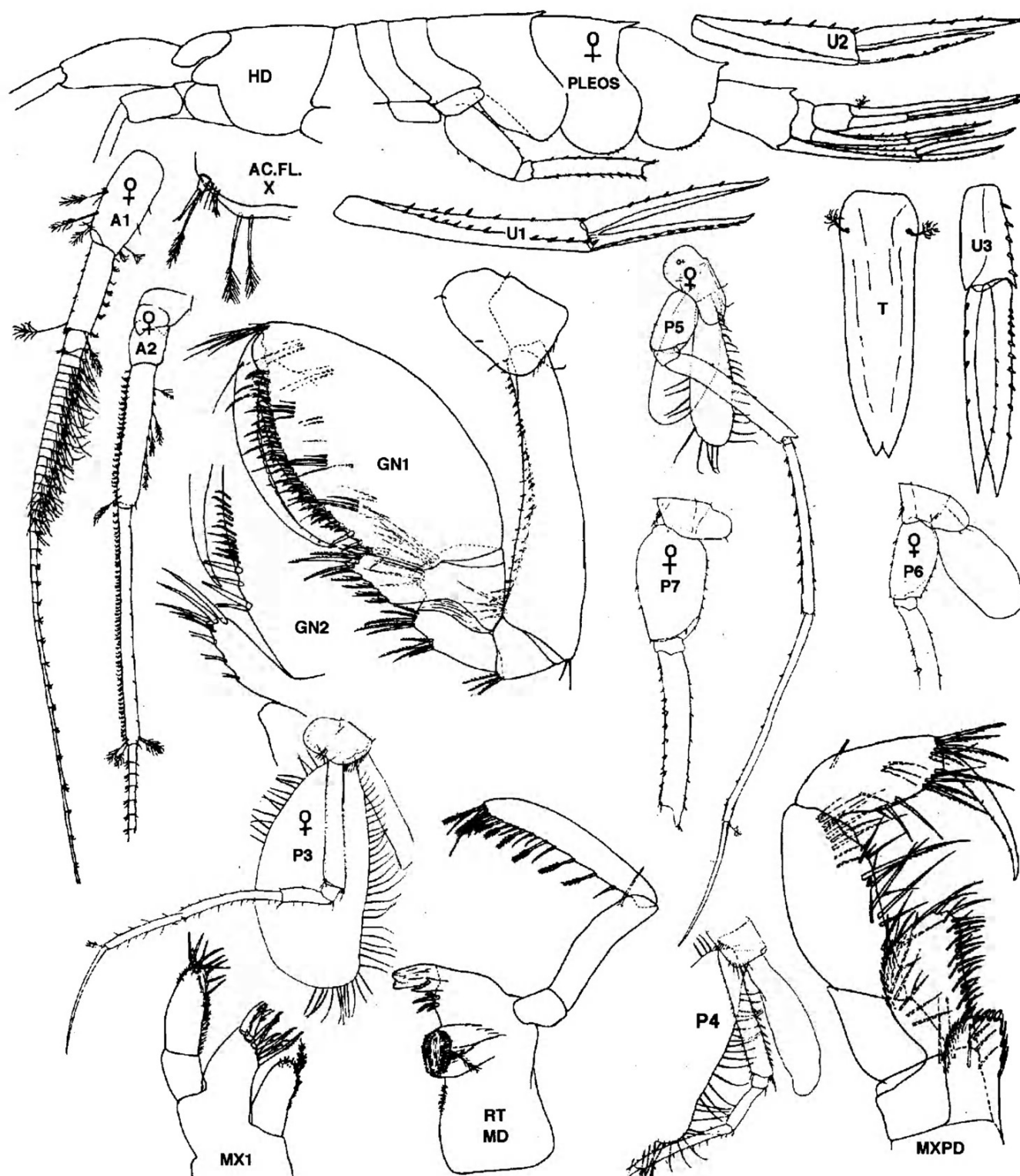


FIG. 30. *Rhachotropis distincta* (Holmes, 1908) Female ov (9.0 mm) Male (8.0 mm)
Cabot Strait. 378m (modified from Shoemaker, 1930)

mucronation. Rostrum medium strong, extending beyond acute anterior head lobe. Pigmented eyes lacking. Antenna slender, not calceolate in female. Antenna 1, peduncular segments 1 and 2 subequal in length, segment 3 elongate ($>1/2$ segment 2); flagellum 10-12 segmented; accessory flagellum minute, apex with spine and plumose seta. Antenna 2 longer than 1; peduncle 4 shorter than 5, hind margin lined with plumose setae; flagellum 12-14 segmented.

Lower lip tall, inner lobes distinct. Mandible, molar

narrowing to small grinding surface, margins lined with blades; spine row with 2-3 blades; left lacinia 6-dentate, right lacinia bifid; incisor cutting edge thickened; palp slender, segment 3 longer than 2. Maxilla 1, inner plate with long and short apical setae; palp slender. Maxilla 2, inner plate broader than outer, inner margin with longer plumose seta. Maxilliped strong, segment 3=2 and 3, slightly broadened; outer plate ordinary, inner plate with 5 apical short spines.

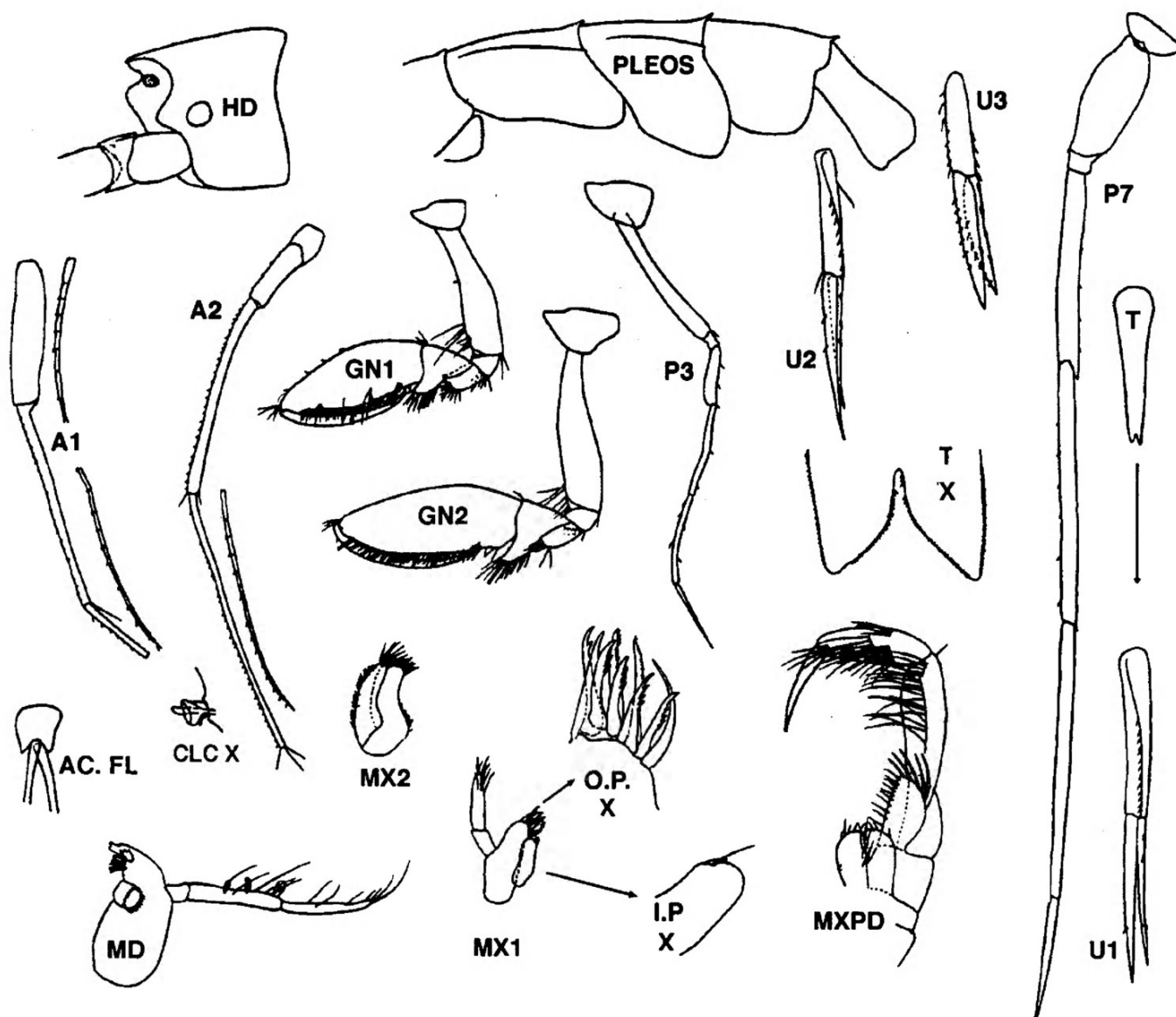


FIG. 31 *Rhachotropis natator* (Holmes, 1908). Female (13.0 mm) off S. California (1000+ m.) (modified from Barnard, 1954)

Coxae 1-4 shallow, broader than deep, not produced anteriorly; coxa 4 weakly excavate behind. Coxa 5 shallowly aequilobate. Gnathopod 2 larger than gnathopod 1; bases with antero-distal setal group and short-spinose anterior face; carpal lobes well developed, directed forwards under short posterior margin of propod; propods ovate, palmar margins oblique, dactyl tip depression with inner posterior group of 3-4 spines and 2-3 larger outer marginal spines.

Peraeopods 3 and 4 slender, elongate; segment 4 much shorter than segment 5; dactyls slender, longer than segment 6; basis of peraeopod 4 lined posteriorly with medium spines. Peraeopods 5-7 extremely elongate, increasing in size posteriorly; bases medium, not lobed below; dactyls very long, slender.

Pleon plates 1-3 broad rounded and weakly spined below; posterior margin of plate 3 weakly serrate. Uropods 1 and 2, peduncles longer than narrowly lanceolate rami, tips reaching to end of uropod 3; outer ramus shorter than inner. Uropod 3, rami somewhat broadly lanceolate, subequal,

margins weakly spinose. Telson elongate, parallel-sided, narrowing relatively abruptly, apex notched.

Coxal gills sac-like, broadest on peraeopods 5 and 6. Brood plates very large and broad on peraeopods 2-4, medium broad on peraeopod 5, margins strongly setose. Male (8.0 mm): Antenna 1, peduncular segment 2, hind margins with a few brush setal clusters; flagellum elongate, basal 20 segments forming a weak callynophore, distal segments calceolate. Antenna 2, anterior margins of peduncular segments 4 and 5 lined with brush setae; flagellum elongate, segments calceolate.

Taxonomic and distributional commentary. *Rhachotropis distincta* occurs broadly across the boreal North Pacific and North Atlantic oceans but is apparently less frequently encountered in the Pacific than is *R. natator*. The present material compares closely with that figured by Holmes (loc. cit.) from southern California, and the detailed figures of material from the western North Atlantic region provided by Shoemaker (loc. cit.).

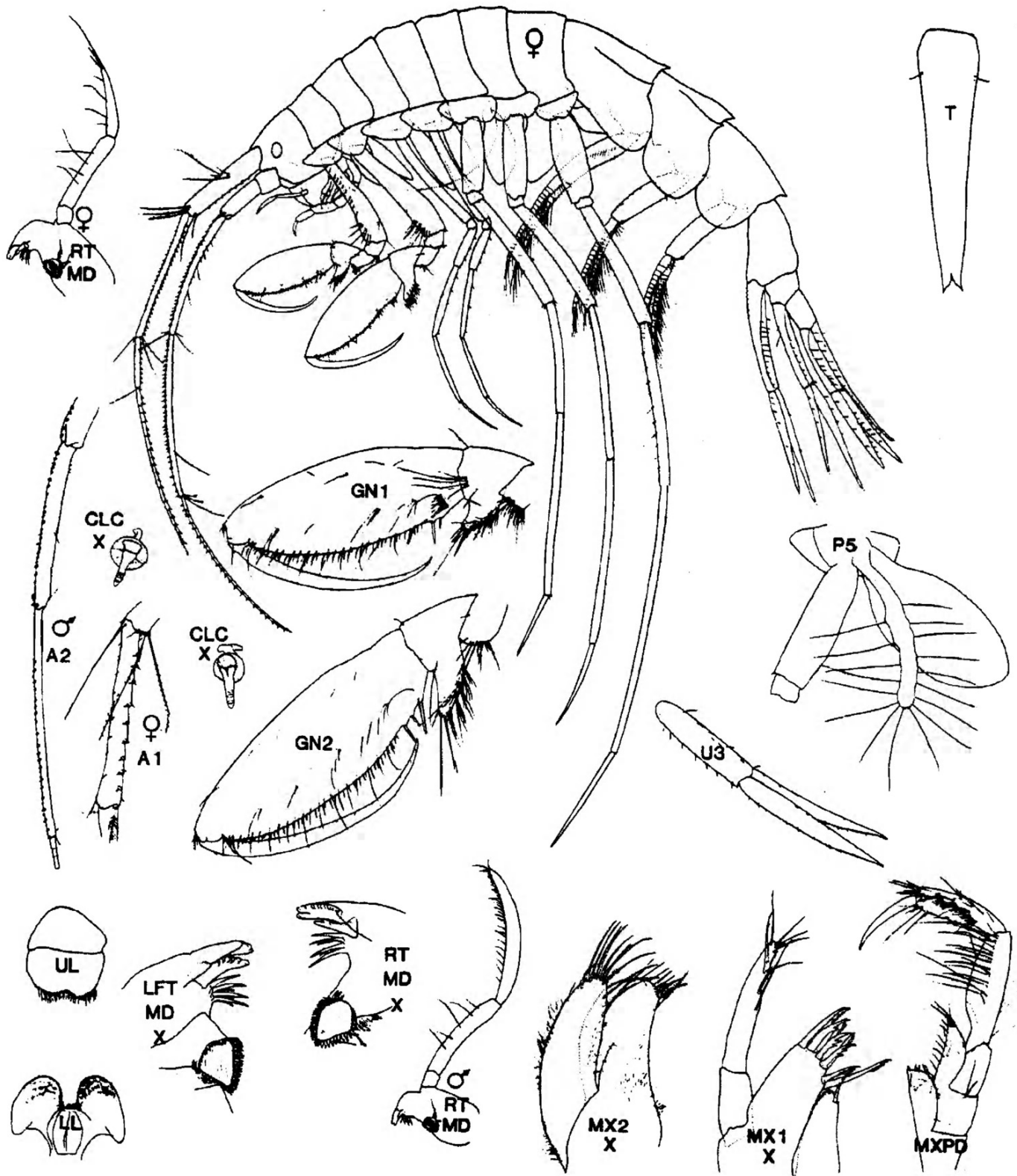


FIG. 32. *Rhachotropis natator* (Holmes, 1908). Female ov. (13.0 mm). Off Vancouver I., B. C. 1800 m

***Rhachotropis natator* (Holmes)**
(Figs. 31, 32)

Gracilipes natator Holmes, 1908: 527, figs. 32-34.—Thorsteinson, 1941: 85, figs. 67-70.

Rhachotropis natator Barnard, 1954: 54, pl. 6.—Birstein & Vinogradov, 1955: 275.—Birstein & Vinogradov, 1958: 247.—Birstein & Vinogradov, 1960: 225. Barnard & Karaman, 1991: 338.

Material Examined:

BRITISH COLUMBIA: Queen Charlotte Islands: Off Tasu Sd ($52^{\circ}38.72'N$, $132^{\circ}05.79'W$ to $52^{\circ}38.31'N$, $132^{\circ}07.90'W$) IKMT 0-520 m., RBCM/CMN Stn. 91-1-09 - 1 male, 1 female; Off Kughit I., ($52^{\circ}00.39'N$, $131^{\circ}23.97'W$ to $52^{\circ}00.55'N$, $131^{\circ}30.90'W$) IKMT 0-510 m, RBCM/CMN Stn. 91-1-03, Mar. 19, 1991 - 6 females; off Hippa I. ($53^{\circ}30.39'N$, $133^{\circ}26.35'W$ to $53^{\circ}34.5'N$, $133^{\circ}30.20'W$) IKMT 0-660m, RBCM/CMN Stn 91-1-12, Mar. 21, 1991-4 males.

,6 females (1 male, 1 female slide mts).

Off Vancouver I., above Endeavour Ridge (47° 58'N., 129° 06' W), IOS Stns, June 18-19, 1990: LC 90-3 Tow 006 Net 2, 1870-1900 m - 1 male (12.0 mm) (slide mount). Ibid, July 17-19, 1991. IOS Stn. 91-12: tow 1, net 5, 1706-704 m. - 2 males; tow 2, Net 1, 0-1900 m. - 1 female ov (13.0 mm) (slide mount), 1 female br. I (11.5 mm); tow 3, net 3, 1985-1787, 2 females, 1 male; Tow 4, net 3, 2306-1925 m - 1 female; tow 4, net 6, 713-560 m - 1 male. Collections of the Institute of Oceanography, Sidney, B. C.

Diagnosis. Female (13.0 mm): Peraeon segments 1-7 and urosome segment 1 generally smooth dorsally. Pleon segments 1 & 2 with low mid-dorsal and dorso-lateral mucronations; pleon 3 with small dorsal tooth. Rostrum very short, extending little beyond short anterior head lobe. Pigmented eyes lacking. Antennae very slender and elongate, calceolate on peduncles only; calceoli with broad orbicular receptacle and distal elements in a rod-like central column. Antenna 1, peduncular segment 2 elongate, 1.5X segment 1; segment 3 long, ~ 1/3 segment 2; flagellum 15-segmented; accessory flagellum minute, with apical spine and setae. Antenna 2 longer than 1, peduncle 3 elongate, segment 5 > 4; flagellum 25-segmented, basally calceolate.

Upper lip slightly incised below. Lower lip, inner lobes narrow, distinct. Mandible, molar stout, grinding surface large, diamond shaped, margins lined with short blades; spine row with 4 slender blades; left lacinia 6-dentate; right lacinia bifid; incisor denticulate; palp slender, segment 3 shorter than 2. Maxilla 1, inner plate tall, with 1 apical seta; outer plate with 9 apical slender spines; palp slender. Maxilla 2, plates slender, setae apical. Maxilliped, palp large, segments 2 & 3 not broadened; outer plate slender; inner plate with 1-2 short apical spines.

Coxae 1-4 very small, shallow, anterior margin somewhat produced; coxae 5 and 6 shallowly aequilobate. Gnathopod 2 larger than 1; bases stout, with antero-distal setae; carpus produced below and under short hind margin of palp; propods elongate-ovate, palmar margins elongate, nearly horizontal, dactyl-tip depressions broad, with 1-2 outer marginal spines.

Peraeopods 3 and 4 very slender, segment 4 much shorter than 5; dactyls shorter than segment 6. Peraeopod 5-7 very slender and elongate, increasing in length posteriorly; bases narrow, not lobate behind.

Pleon plates 1-3 broad, differing in form, 2 deepest; 3 rounded; hind margin not serrated. Uropods 1 and 2, rami narrowly lanceolate, margins weakly spinose, outer ramus shorter than inner. Uropod 3, rami subequal, margins very weakly spinose. Telson very elongate, narrowing distally, reaching nearly to tip of uropod 3, apex broadly notched.

Coxal gills sac-like, broadest on peraeopod 6, smallest on peraeopod 7. Brood plates broad, narrow on peraeopod 5.

Male (12.0 mm): Similar to female but differing in the flagellum of antenna 1 that is proximally weakly

callynophorate, and distally weakly calceolate. Mandibular palp, segment 3 elongate, not reduced.

Taxonomic and distributional commentary. *Rhachotropis natator* is apparently widespread in offshore waters of the boreal North Pacific Ocean, in depths of 1000-5000 m. The present material compares closely with the 14 mm male figured by Thorsteinson (loc. cit) from off the coast of Washington State, and the 13.0 mm female illustrated by Barnard (loc. cit.) from waters off southern California. Material from the western Pacific region, for which numerous offshore collection stations are provided by Birstein and Vinogradov (loc. cit.) has not been sufficiently well figured to facilitate detailed comparison with eastern Pacific material.

DISCUSSION AND CONCLUSIONS

This systematic study has examined material of 14 species (in 5 genera) of amphipod crustacean of the family Eusiridae that occur in shelf and offshore waters of the North American Pacific region, from the Bering Sea to central California. The taxonomy and distributional ecology of this limited assemblage can now be analyzed in relation to an overall amphipod North Pacific eusirid fauna of some 35 species (in 10 genera), a number that represents about 30% of the species of family Eusiridae world-wide. As noted in station lists of the previous descriptive accounts, species of Eusiridae tend to occur in relatively deep benthic and offshore bathyal and bathypelagic environments, and are thus not well represented in present regional amphipod collections that were obtained mainly from shallow water and littoral marine habitats.

However, despite the limited nature of the material at hand, the possible broader phyletic and biogeographic significance of these morphological and distributional findings may be analyzed on a numerical basis. A modification of the phenetic UPGMA (cluster analysis) system of Sneath and Sokal (1973) has been employed reasonably effectively in earlier studies of this type (e.g. Bousfield and Jarrett, 1994; Bousfield & Hendrycks, 1994) and is utilized here. In this system, the character states are ordered on a presumed phyletic basis, and from this can be developed an overall criterion of phyletic similarity termed the Plesio-Apomorphic (P.-A) Index in which low numbers signify phyletically primitive, and high numbers relatively advanced, species or taxonomic groups.

Within the family Eusiridae, analysis of morphological similarities is based on 20 characters, and corresponding 40 paired character states, of the 13 component genera world-wide (Table I, p. 48). The characters selected include a mixture of conspicuous body features, well described and illustrated in the literature, as well as more cryptic, but possibly more phyletically significant features such as those of the mouthparts. The latter have been summarized especially helpfully by Barnard and Karaman (1991), although

TABLE I. GENERA OF EUSIRIDAE: CHARACTERS AND CHARACTER STATES

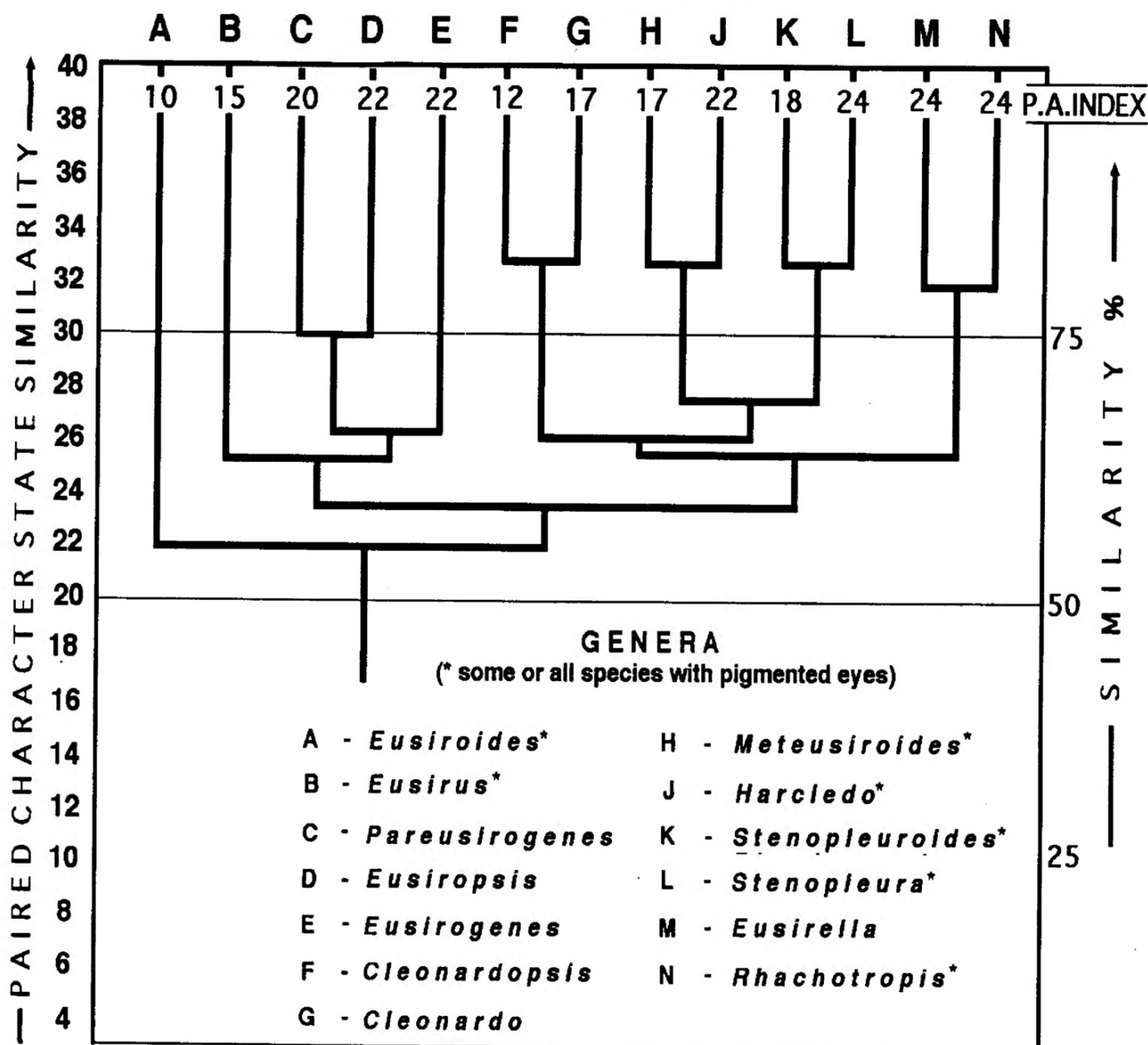
| CHARACTER | CHARACTER STATE VALUE | | |
|---|-----------------------------|-------------------|-------------------------------|
| | Plesiomorphic 0 | Intermediate 1 | Apomorphic 2 |
| 1. Rostrum, length | long (~ length of head) | | short (<anterior head lobe) |
| 2. Pigmented eyes | present | | absent |
| 3. Antenna calceolate | calceolate | weakly calceolate | calceoli lacking |
| 4. Accessory flagellum | present, 1-2-segmented | scale-like | lacking |
| 5. Peraeon 5-7 dorsally toothed | strongly | weakly | smooth |
| 6. Pleon dorsally toothed | strongly | weakly | smooth |
| 7. Lower lip, inner lobes | weak | | strong |
| 8. Mandibular molar, triturating surface | large | | small |
| 9. Mandibular palp, segment 3 | ordinary (< segment 2) | | slender (> segment 2) |
| 10. Maxilla 1, number of inner plate setae | 4+ | 2-3 | 0-1 |
| 11. Maxilla 1, number of outer plate spines | 11 | | 9 |
| 12. Maxilla 2, width of inner plate | ~ outer plate | | >> outer plate |
| 13. Coxae 1-4, depth | deeper than wide | squarish | shallow, depth < width |
| 14. Gnathopods 1 & 2 propod & carpus, form | ordinary, carpus thick | | "eusiroidean", carpus slender |
| 15. Gnathopods, armature of palmar margin | heavy spines | few spines | setae only |
| 16. Peraeopods 3-4, length of dactyls | short, (< 1/3 segment 6) | | elongate (~ segment 6) |
| 17. Peraeopods 5-7 form and length | homopodous in form & length | | heteropodous in form & length |
| 18. Uropods 1 & 2, armature, apex of rami | lanceolate, no spines | | spinose |
| 19. Uropod 3 rami, inner margins | setose & spinose | | spinose only or unarmed |
| 20. Telson, length | elongate, length >3X width | | short, length < 2X width |

the basic pertinent references have been consulted wherever possible. In evaluating some character states, an intermediate character state did not exist, and was therefore not given in the table.

Within the resulting phenogram of genera (Fig. 33), three main groups may be recognized that cluster between the 50 and 60% similarity levels. These comprise the primitive relatively isolated genus *Eusiroides* on the left (P.

A. Index of 10), a relatively advanced *Cleonardo-Rhachotropis* group on the right (P. A. Indices mainly of 17-24, excluding the monotypic genus *Cleonardopsis*), and an intermediate *Eusirus* group on the left centre (P. A. Indices of 15-22). Species of the genus *Eusiroides* are characterized by pigmented eyes, distinct accessory flagellum, deep coxae, subsimilar spiny-palmed gnathopods, short stout short-dactylate peraeopods, and setose rami of uropod 3, among

FIG. 33. PHENOGRAM OF GENERA: FAMILY EUSIRIDAE



other plesiomorphic character states. With few exceptions the 16 described species are littoral, along tropical and warm-temperate, high salinity coasts of the Atlantic, Indian, and Pacific oceans. These character states are similar to those of members of families Pontogeneiidae and Calliopiidae within superfamily Eusiroidea.

The *Eusirus* group is characterized mainly by the "eusirid" form of the gnathopod propods, in which the deep, smooth-palmed propod is subtended from the tip of the long slender narrow-lobed carpus. Of the 32 described world species, two-thirds are species of *Eusirus*, whose members are relatively large bodied, eyed, and sublittoral and epibenthic. The remaining eight species, within *Pareusirogenes*, *Eusiropsis*, and *Eusirogenes*, are relatively small, eyeless, more slender bodied and uncarinated, that are meso- or bathypelagic in life style. The *Cleonardo-Rhachotropis* group encompasses 8 genera and about 70

world species whose members are mostly meso- and bathypelagic. The gnathopods are subsimilar but non-eusirid in form, the carpus simple and lobate behind, and the propodus usually with an elongate, marginally spinose, and very oblique palm. The group encompasses 4 sets of genera: (1) a primitive *Cleonardo* subgroup of about 10 eyeless, homopodous, bathypelagic world species, (2) a more advanced *Harcledo-Stenopleura* complex of 4 monotypic generic whose members are mesopelagic, and have small bodies, with shallow coxae, pigmented eyes, and short telsons, but the antennae lack calceoli and accessory flagellum., and (3) an advanced but amorphous *Eusirella* complex of about 55 world species of which 9/10 are species of *Rhachotropis* (analyzed below). "Classical" morphological analysis of *Eusirella* and *Rhachotropis* would suggest rather different basic morphologies between the two genera, although similarities in mouthpart structure such as the

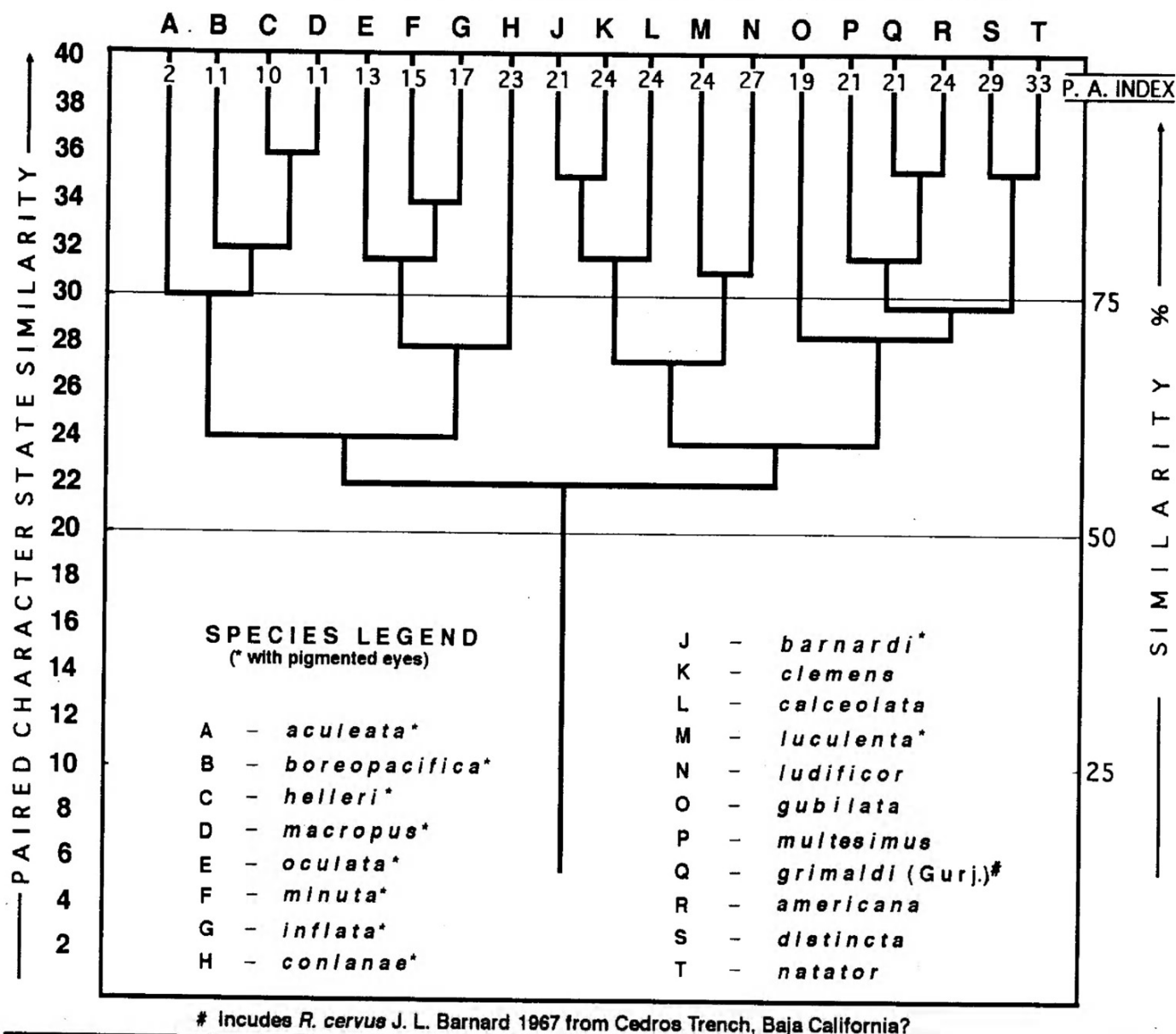
TABLE II. SPECIES OF *RHACHOTROPIS*: CHARACTERS AND CHARACTER STATES

| CHARACTER | CHARACTER STATE VALUE | | |
|--|-------------------------------|-------------------|-----------------------------|
| | Plesiomorphic 0 | Intermediate 1 | Apomorphic 2 |
| 1. Rostrum, length | long (~ length of head) | | short (<anterior head lobe) |
| 2. Pigmented eyes | present | | absent |
| 3. Peraeon 5-7 dorsally toothed | strongly | weakly | lacking |
| 4. Pleon 1-2, mid-dorsal mucronation | strong | weak | lacking |
| 5. Pleon 1-2, dorso-lateral mucronation | strong | weak | lacking |
| 6. Pleon 3, mid-dorsal mucronation | strong | weak | lacking |
| 7. Pleon 3, dorso-lateral mucronation | strong | weak | lacking |
| 8. Urosome 1, mid-dorsal tooth | strong | weak | lacking |
| 9. Antenna 1, length of peduncular segment 3 | very short (<1/4 segment 2) | | long (~1/3 segment 2) |
| 10. Gnathopods 1 & 2, propods | subequal | | unequal in size and form |
| 11. Peraeopods 3 & 4 segment 4: segment 5 | subequal | | segment 4 << 5 |
| 12. Peraeopods 3-4, length of dactyls | short, (< 1/3 segment 6) | | elongate (~= segment 6) |
| 13. Coxae 1-4, depth | deeper than wide | squarish | shallow, depth < width |
| 14. Peraeopod 7, width of basis | broad, lobate below | | narrow, not lobate below |
| 15. Pleon plate 3 hind corner | squarish | | strongly rounded |
| 16. Uropod 1, length peduncle | >>inner ramus | | ~inner ramus |
| 17. Uropod 2, length inner ramus | long, attains tip of uropod 3 | | short, << tip of uropod 3 |
| 18. Uropod 3 rami, inner margins | setose & spinose | | spinose only or unarmed |
| 19. Telson, length | elongate, length >3X width | | short, length ~2X width |

relatively well developed inner lobes of the labium, and the 9-dentate outer plate of maxilla 1, would seem basic. However, basic differences (in peraeopods 3 and 4) may well have been masked in this analysis by instances of convergence and superficial similarity in body form and structure of the posterior peraeopods, uropods, and telson, etc, in various bathypelagic members of *Rhachotropis* resulting from convergent similarities in life style. More extensive conclusions would depend on more detailed morphological examination,

involving all members of both generic groups, well beyond the scope of this limited regional study.

The morphological relationships of North Pacific species within the relatively advanced genus *Rhachotropis* may be analyzed numerically on the basis of 20 characters and corresponding character states outlined in Table II (above). The characters selected are mainly superficial and conspicuous features of the body and appendages rather than mouthparts and reproductive features that may actually

FIG. 34. PHENOGRAM OF NORTH PACIFIC SPECIES OF *RHACHOTROPIS*

prove more significant phylogenetically. However, the "high profile" characters tend to be described and illustrated more consistently and more completely in the available reference works and thus provide a more reliable basis for comparison between all species analyzed numerically here.

The resulting semi-phyletic phenogram is shown in Fig. 34 (above). As noted below, the 20 regional species (including the problematical *R. cervus*) represent about 40% of the known world species. This "breakout" also includes equal numbers having, or lacking, pigmented eyes, a feature that corresponds essentially with "shelf" or coastal species, and "bathyal" or deep-water species, respectively. Clustering between the 55 and 75% similarity levels are two main groups, a relatively primitive "*aculeata*" assemblage of 8 species on the left (P. A. indices of 2-23) and a relatively advanced "*natator*" assemblage of 11 species on the right (P. A. Indices of 19-33). The *aculeata* group tends to be of larger body size and more strongly toothed dorsally, and have pigmented eyes and more strongly calceolate antennae.

Species of the *natator* group are of smaller body size and weaker dorsal mucronation (peraeon generally smooth), the antennae are more frequently acalceolate and, with few exceptions, lack pigmented eyes.

The "*aculeata*" subgroup contains two distinct subclusters, a primitive *aculeata-macropus* group on the left (P. A. indices of 2-11) and a more advanced *oculata-inflata* group on the right (P. A. Indices of 13-23). The former species tend to be of larger size (10.5 - 40 mm in body length) are strongly toothed on pleon and urosome, and the telson is elongate. The latter species are typically small (3.8 - 12 mm in body length), the urosome lacks a dorsal tooth, and the telson is relatively short.

The "*natator*" group similarly contains two distinct subclusters, a slightly more primitive *clemens-ludificor* group on the left (P. A. indices of 21-27) and a more advanced *grimaldi-distincta* group on the right (P. A. Indices of 19-33). The former species tend to be of smaller size (3.8-8.7 mm in body length), are more weakly carinate on the pleon,

TABLE III. DISTRIBUTION OF NORTH AMERICAN PACIFIC EUSIRIDAE

| SPECIES | NORTH PACIFIC SUBREGION | | | | | | | | |
|-------------------------------------|-------------------------|----|----|---|----|----|----|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
| I. Eusiroides | | | | | | | | | |
| <i>japonica</i> Hirayama, 1985 | X | | | | | | | | |
| <i>monoculoides</i> (B'n'd, 1969) | | | | | | | | | X |
| II. Eusirus | | | | | | | | | |
| <i>hirayamae</i> , n. sp. | X | | | | | | | | |
| <i>columbianus</i> , n. sp. | | | | X | X | X | | | |
| <i>cuspidatus</i> Koyer, 1845 | | x? | X | | | | | | |
| <i>bathybius</i> B. & V., 1960 | X | | | | | | | | |
| <i>fragilis</i> B. & V., 1960 | X | | | | | | | | |
| III. Pareusirogenes | | | | | | | | | |
| <i>carinatus</i> B. & V., 1955 | | X | | | | | | | |
| V. Eusiropsis | | | | | | | | | |
| <i>riisei</i> Stebbing, 1897 | X | | | | | | | | |
| IV. Eusirogenes | | | | | | | | | |
| <i>homocarpus</i> B. & V., 1955 | X | | | | | | | | |
| VI. Cleonardo | | | | | | | | | |
| <i>longisetosa</i> Chevreux, 1908 | | X | | | | | | | |
| <i>macrocephala</i> B. & V., 1955 | | X | | | | | | | |
| <i>moirae</i> , n. sp. | | | | | x | | | | |
| VII. Harcledo | | | | | | | | | |
| <i>curvidactyla</i> (Pirlot, 1934) | | X | | | | | | | |
| VIII. Stenopleura | | | | | | | | | |
| <i>atlantica</i> Stebbing, 1888 | X | | | | | | | | |
| IX. Eusirella | | | | | | | | | |
| <i>multicalceola</i> (Thorst, 1941) | X | X | | | X | X | | | X |
| <i>longisetosa</i> B. & V., 1960 | X | | | | | | | | |
| X. Rhachotropis | | | | | | | | | |
| <i>aculeata</i> (Lepechin) | | X | X | | | | | | |
| <i>americana</i> , n. sp. | | | | | X | | | | |
| <i>barnardi</i> , n. sp. | | | | | X? | X | X | | |
| <i>boreopacifica</i> , n. sp. | | | | | x? | X | | | |
| <i>helleri</i> (Boeck) | | X | X? | | | | | | |
| <i>macropus</i> Sars | | X | X? | | | | | | |
| <i>oculata</i> (Hansen, 1888) | | X? | X | | x? | X | ? | X | |
| <i>minuta</i> , n. sp. | | | | | | X | | | |
| <i>inflata</i> (Sars, 1883) | | X | | | x? | x? | X? | | |
| <i>conlanae</i> , n. sp. | | | | X | | | | | |
| <i>clemens</i> Barnard, 1967 | | | | | | | | | X |
| <i>calceolata</i> , n. sp. | | | | | | | | | X |
| <i>luculenta</i> Barnard, 1969 | | | | | | | | | X |
| <i>ludificor</i> Barnard, 1967 | | | | | | | | | X |
| <i>gubilata</i> Barnard, 1964 | | | | | | | x? | | |
| <i>grimaldi</i> (Gurjanova, 1951) | | X | | | | | | | ? |
| <i>multesimus</i> Barnard, 1967 | | | | | | | | | X |
| <i>distincta</i> (Holmes, 1908) | | X | | | X | X | | | X |
| <i>natator</i> (Holmes, 1908) | X | X | | | X | X | x? | | X |

LEGEND: 1 - Southern Japan; 2 - Okhotsk, N. Japan; 3 - S. Chukchi & Bering Seas; 4 - S.E. Alaska; 5 - N. Brit. Columbia; 6 - S. Brit. Columbia; 7 - Wash.-Oregon; 8 -N. Calif.; 9. - S. and Baja Calif.

have relatively short rami of uropods 1 & 2, short peduncular segment 3 of antenna 1, some members are oculate, and all are taken almost exclusively in benthic samples. Members of the latter group (except for the small benthic *R. multesimus*), however, tend to be of medium size (11-17 mm), are more strongly toothed on the pleon, have longer uropod rami, and longer segment 3 of antenna 1, are exclusively eyeless, and are usually taken planktonically in the open water column.

This limited semi-phyletic analysis suggests a direct relationship between morphology and life style within N. Pacific members of the genus *Rhachotropis*. The coastal shelf, benthic and epibenthic species tend to be relatively large, oculate, processiferous, and spiny-limbed animals that become smaller, more weakly spinose, and anoculate in the most abyssal members. Bathypelagic members are of intermediate size and body armature but more slender-bodied and slender-limbed, exclusively anoculate, and generally most advanced phylogenetically. Such trends might indicate that the fully planktonic life style is a secondary development, and a possible basis for further formal subdivision within the genus *Rhachotropis*.

Biogeographic Analysis

The distribution of 36 species of family Eusiridae across the North Pacific region is represented in Table III (p. 52). The data were derived mainly from the literature, and the balance from the records of present material. A total of 22 species in 5 genera are now known from the North American Pacific region (sub regions 3-9) and about half the North Pacific total (18 species) have actually been recorded from the present study region (sub regions 3-7) from which specimens have actually been collected and examined.

The primitive benthic genus *Eusiroides* is represented on both Asiatic and N. American shores by single species that are restricted to the warmest and most southerly fringes (sub regions 1 and 9). Along more northerly and colder shores of both coasts, their ecological niches are presumably filled by hosts of "swash zone" pontogeneiid and calliopiid eusiroidean counterparts.

The genus *Eusirus*, containing about 24 described world species, is moderately speciose in Arctic and eastern North Atlantic (including Mediterranean) sublittoral habitats. In the North Pacific, however, it is apparently restricted to single shelf species on each of the Asiatic and North American coasts, and two bathyal species along the Asiatic coast. The large arctic species, *E. cuspidatus*, penetrates only into the Bering Sea region.

With respect to the occurrence of offshore meso- and bathypelagic eusirids, a rich fauna of monotypic and near-monotypic eusirid genera has been discovered off the Asiatic coast, especially over the Kurile-Kamtschatka Trench, and off the southeastern coast of Japan (genera III to XI, sub

regions 1 and 2). The studies of Birstein and Vinogradov (1955, 1958, 1960, 1964) have been instrumental in describing and analyzing this rich fauna both systematically and biogeographical. However, the paucity of counterpart records from the northeastern Pacific region (sub regions 4-8) poses limits to the present biogeographical analysis. The hiatus may reflect, at least in part, a deficiency in deep-sea biological sampling off the Pacific coast of the United States and Canada to date, or a delay in working up and publishing upon collections already at hand.

With respect to overall distribution, however, analysis of Table III reveals that the genus *Rhachotropis* dominates the North Pacific fauna of eusirid amphipods, both benthically and pelagically. In the northeastern Pacific region, the 15 species of *Rhachotropis*, from all habitats and life styles, represents more than two-thirds of the North American eusirid species total, and is nearly double the number (8) recorded to date from the Asiatic Pacific coast. Many of these North American species are regionally endemic, some newly described (above). Furthermore, in the eastern North Pacific, benthic species of *Rhachotropis* extend well down the coast, from Alaska to Baja California, whereas in the western North Pacific, the six sublittoral coastal species penetrate from the arctic to the Bering Sea and Sea of Okhotsk, barely reaching the northern Sea of Japan, and none are considered endemic.

Phylogenetically, *Rhachotropis* is here concluded to be the morphologically most advanced of the 13 described genera within family Eusiridae. *Rhachotropis* is autapomorphic in several character states (e.g. the shortened segment 4 of pereopods 3 and 4) and stands apart from the other genera. On the other hand, the body form, size relationships of the posterior pereopods (subequal pereopods 5 and 6 and elongate pereopod 7) and lanceolate uropods, renders the primitive "*aculeata*" subgroup of possible ancestral "outgroup" significance to the Oedicerotidae. The latter family comprises regional counterpart carnivorous amphipods that burrow into soft bottom sediments, from the shoreline to the abyss. Within the genus *Rhachotropis*, both the most primitive and most advanced species are found among the North American complex of species (Fig. 34, p. 51). By contrast, few but the most primitive species of *Rhachotropis* occur on the Asiatic Pacific coast.

We might tentatively conclude, therefore, that the North Pacific region represents a major centre of origin and evolution of eusirid amphipods in general, and the North American Pacific sub region represents a major centre of evolution within the advanced genus *Rhachotropis*. Within *Rhachotropis*, evolutionary thrust appears to have involved morphological reductions on the one hand (e.g. loss of pigmented eyes, body armature, and decrease in body size) and functional specializations on the other (e.g. elongation of appendages and dactyls) for penetration and exploitation of food resources of both epibenthic abyssal, and meso- and abyssal pelagic marine niches.

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TABLE IV. Collection Abbreviations

ELB = senior author
 EAH = junior author
 KEC = K. E. Conlan, CMN, Ottawa, Canada
 PS = Peter Slattery, Moss Landing, California
 IOS = Institute of Ocean Sciences, Sidney, B. C.
 CMN = Canadian Museum of Nature, Ottawa, Canada
 GWO = G. W. O'Connell
 JLB = J. L. Barnard (deceased)
 NMCD = Neil McDaniel, Vancouver, B. C.
 NMNS = National Museum of Natural Sciences, Ottawa.
 OSU = Oregon State University
 PF = Peter Frank, CMN, Ottawa.
 RBCM = Royal British Columbia Museum, Victoria, B. C.
 USNM = U. S. National Museum (Natural History)

TABLE V. Abbreviations in figures

| | |
|-------------------------------|------------------------|
| A1 - antenna 1 | MX1 - maxilla 1 |
| A2 - antenna 2 | MX2 - maxilla 2 |
| AC. FL. - accessory flagellum | O. P. - outer plate |
| CIC -- calceolus | P3-P7 - peraeopods 3-7 |
| CX - coxa | PER - peraeon |
| DCTL - dactyl | PL1-3 - pleopods 1-3 |
| EP1-3 - pleon plates 1-3 | PLEOS - pleosome |
| GN1 - gnathopod 1 | PLP - palp |
| GN2 - gnathopod 2 | RT - right |
| I. P. - inner plate | T - telson |
| LFT - left | U1-3 - uropods 1-3 |
| LL - lower lip | UL - upper lip |
| MD - mandible | UROS - urosome |
| | MXPD - maxilliped |
| | ov. - ovigerous |

APPENDIX.

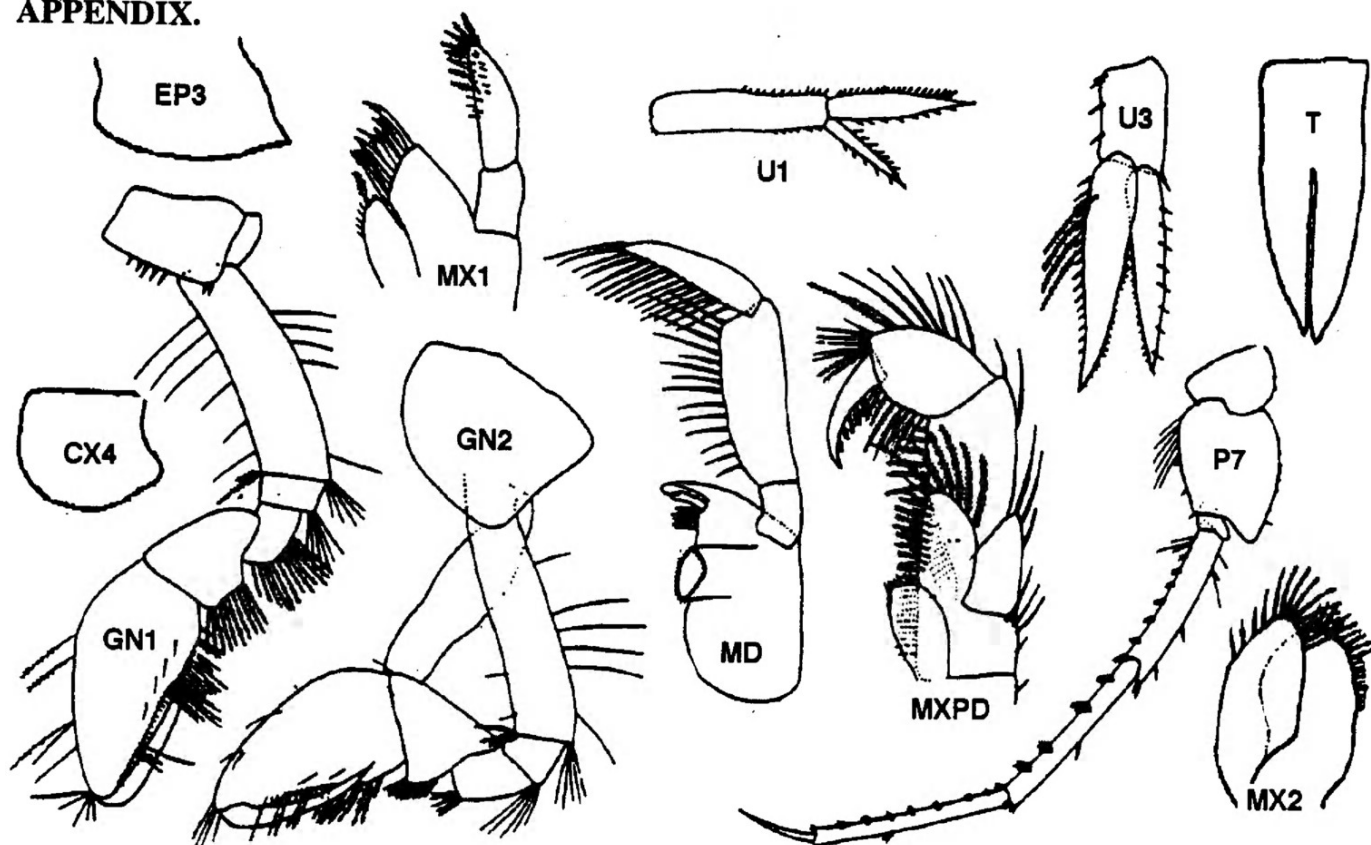


FIG. 35. *Harcledo curvidactyla* (Pirlot, 1929). Female ov. (21 mm)
Kurile-Kamchatka Trench. (modified from Birstein & Vinogradov, 1955)

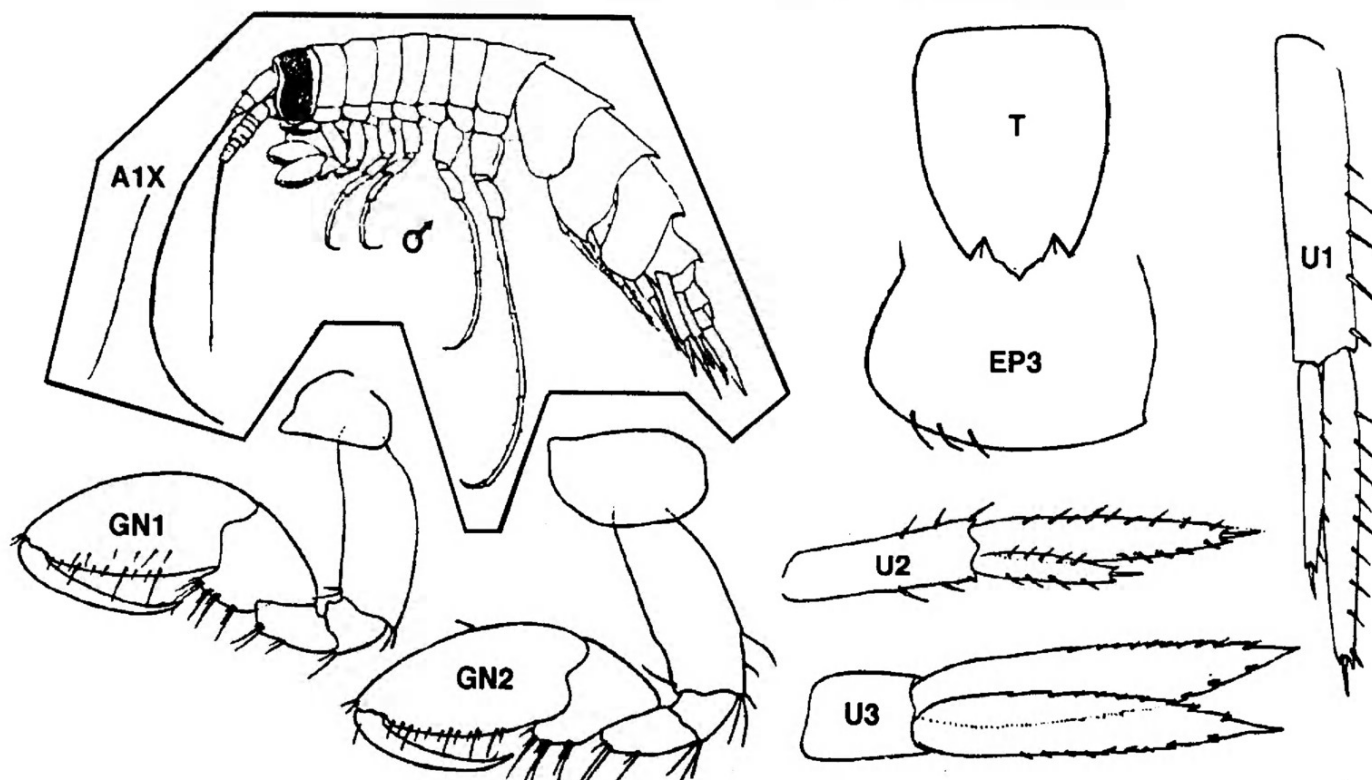


FIG. 36. *Stenopleura atlantica* Stebbing, 1888. Northwestern Pacific (0-600 m tow)
Male (7.5 mm). (after Birstein & Vinogradov, 1960)
INSET: *Stenopleuroides macrops* Birstein & Vinogradov, 1964) Indian Ocean.

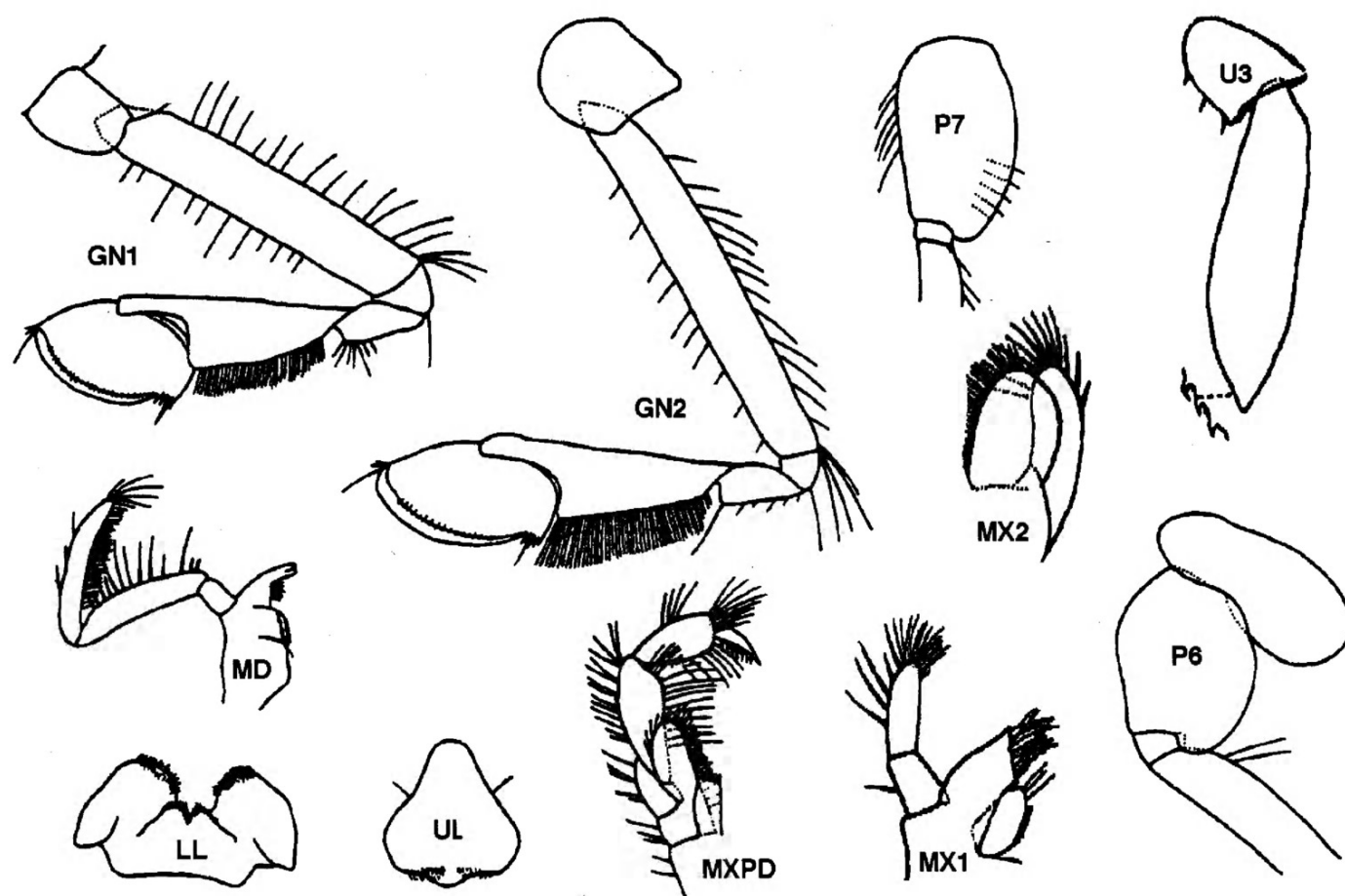


FIG. 37. *Pareusirogenes carinatus* Birstein & Vinogradov, 1955. Female (19.0 mm)
Kurile-Kamchatka Trench (modified from B. & V. 1955)

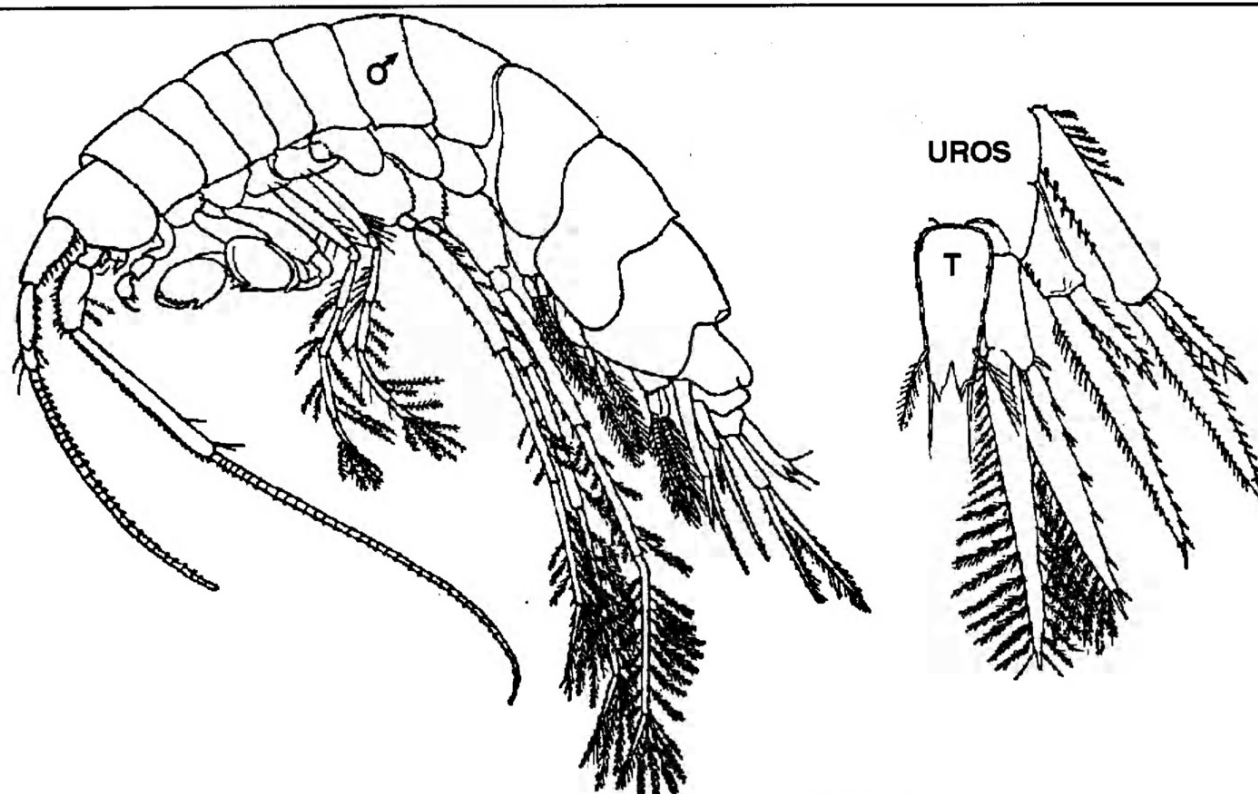


FIG. 38. *Eusiropsis riisei* Stebbing, 1897. Male (10.0 mm)
North Atlantic Ridge (modified from Stebbing, 1906)

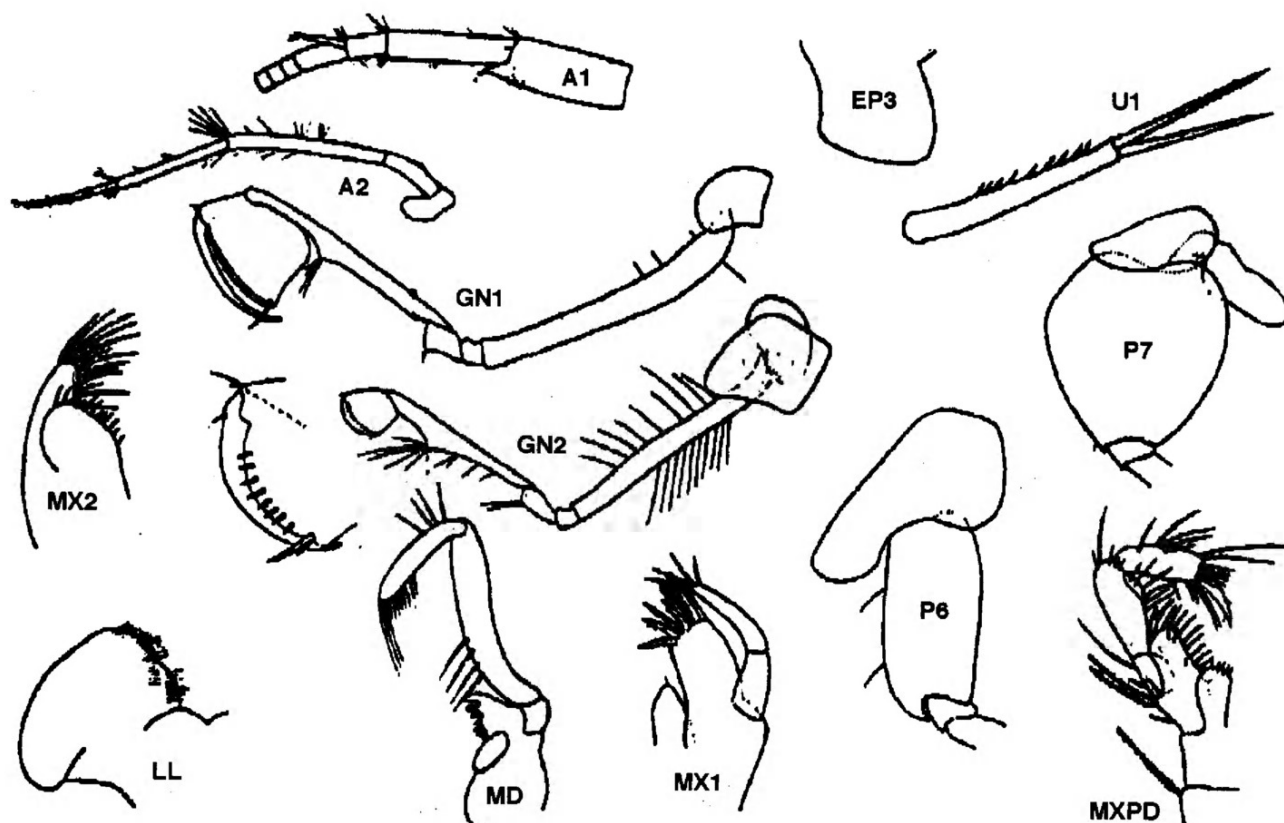


FIG. 36. *Eusirogenes homocarpus* Birstein & Vinogradov, 1955. Kurile-Kamchatka Trench (modified from B. & V., 1955)

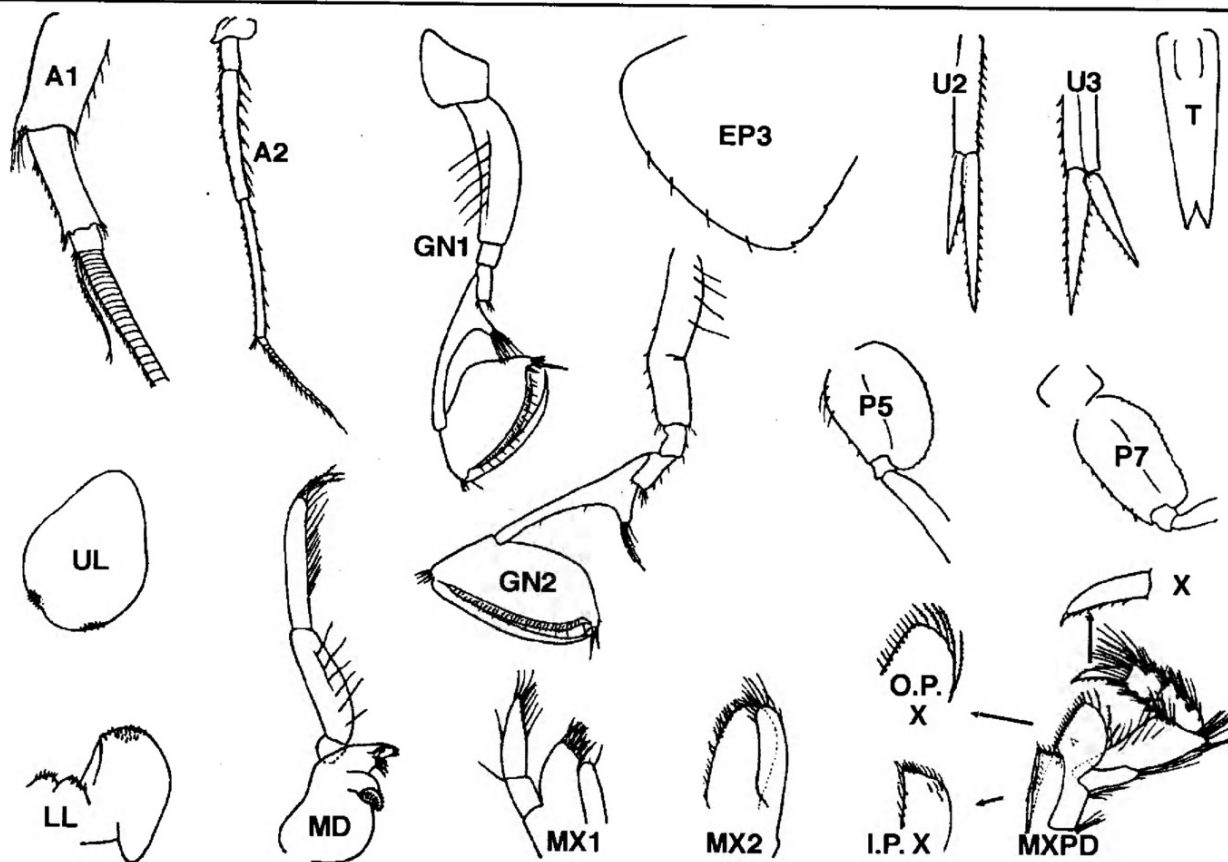


FIG. 40. *Eusirus bathybius* Schellenberg, 1955. Male? (17.0 mm)
N. Pacific, off Japan, 0-7500 m (modified from Birstein & Vinogradov, 1960)



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