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(2) Mailing: Canadian Museum of Nature, Research Division, Ottawa, ON, Canada, K1P 6P4.

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# AMPHIPACIFICA

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# DEDICATION

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

This issue is dedicated to the memory of Norma Eleanor Jarrett, 1931 - 2001.

Cover design: Adapted from the title page of S. J. Holmes (1904). "Amphipod Crustaceans of the Expedition."

# Norma Eleanor Jarrett, 1931-2001: A Tribute

With the death of Norma Eleanor Jarrett, on April 25, 2001, the scientific community lost a major contributor to aquatic systematic research in Canada. Norma began her scientific career relatively late in life. Following her marriage to John W. Jarrett in 1952 in Ottawa, and the raising of three children to adulthood, in 1975 she answered a call for volunteer research assistance at the National Museum of Natural Sciences. She first worked with staff scientist Dr. Rita O'Clair on collections of marine polychaete worms and, during the following summer, Norma experienced her first marine field work on the Pacific coast of Canada. Following Dr. O'Clair's departure for the marine laboratory at Auke Bay, Alaska, Norma began systematic work on selected groups of marine amphipod crustaceans of the North American Pacific coast. museum staff scientist, Dr. E. L. Bousfield, she first published an extensive list of NMNS west coast field stations, followed by a revision of the lysianassid amphipod genus Hippomedon. In the meantime, at nearby Carleton University, she attended day courses in biology essential to a BSc degree, but not completed. Norma continued identification of Pacific amphipod collections, first at the museum's "Beamish building" laboratory on Carling Avenue and later at more commodious research quarters in the Holly Lane building in southeast Ottawa.

During the late 1980's, the museum's research publication series "Syllogeus" and "Bulletin" were terminated. These had offered important outlets for large copiously illustrated papers on the systematics of extensive Canadian Pacific aquatic inveretbrate faunas that traditional journals found difficult or impossible to accommodate. To fill this hiatus, creation of the privately funded research journal Amphipacifica in the early 1990's enabled Norma to continue meeting the



challenge of publishing upon these taxonomically difficult, biologially diverse, but mainly unknown "middlemen" of marine food energy cycles. She published, with help from line illustrator Susan Laurie-Bourque and in co-authorship with other scientists, 6 major lists and research papers. These treated more than 120 amphipod species, and included one new subfamily, 7 new genera, and 37 new species. Her final research paper, with Dr. Traudl Krapp-Schickel, Bonn, Germany, was published a few months before her death, and an additional three papers await publication.

This lovely, warm, and capable person was cherished by her husband, her family, and her grandchildren, and will be greatly missed by her many friends and museum colleagues.

The Editors

#### Research Publications of Norma E. Jarrett

- 1. Bousfield, E. L., & N. E. Jarrett 1981. Station lists of marine biological expeditions of the National Museum of Natural Sciences in the North American Pacific coastal region, 1966-1980. Syllogeus No. 34: 66 pp., 13 figs.
- 2. Jarrett, N. E., & E. L. Bousfield 1982. Studies on amphipod crustaceans of the northeastern Pacific region. I. 4. Family Lysianassidae, genus *Hippomedon*. Nat'l. Mus. Nat. Sci., Publ. Biol. Oceanogr. 10: 103-128, 9 figs.
- 3. Jarrett, N. E., & E. L. Bousfield 1994. The amphipod superfamily Phoxocephaloidea on the Pacific coast of North America. Family Phoxocephalidae. Part I. Metharpiniinae, new subfamily. Amphipacifica 1 (1): 58-140, 31 figs.
- 4. Jarrett, N. E., & E. L. Bousfield 1994. The amphipod superfamily Phoxocephaloidea on the Pacific coast of North America. Family Phoxocephalidae. Part II. Subfamilies Pontharpiniinae, Parharpiniinae, Brolginae, Phoxocephalinae and Harpiniinae. Systematics and distributional ecology. Amphipacifica 1 (2): 71-150, 36 figs.
- 5. Jarrett, N. E., & E. L. Bousfield 1996. The amphipod superfamily Hadzioidea on the Pacific coast of North America. Part 1. The *Melita* group: systematics and distributional ecology. Amphipacifica 2(2): 3-74, 41 figs.
- 6. Krapp-Schickel, T., & N. E. Jarrett 2000. The amphipod family Melitidae on the Pacific coast of North America. Part II. The *Maera-Ceradocus* complex. Amphipacifica **2** (4): 23-61, 14 figs.

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# THE AMPHIPOD SUPERFAMILY LEUCOTHOIDEA ON THE PACIFIC COAST OF NORTH AMERICA: FAMILY AMPHILOCHIDAE: SYSTEMATICS AND DISTRIBUTIONAL ECOLOGY.

# P. M. Hoover<sup>1</sup>, and E. L. Bousfield<sup>2</sup>

#### **ABSTRACT**

Previous definitions of component genera and their probable relationships within the gammaridean amphipod family Amphilochidae were found to be unsatisfactory, necessitating realignment of taxonomic groupings within the northern hemisphere. *Apolochus* n. g., encompassing the Mediterranean regional type species *A. neopolitanus* (Della Valle, 1893), and *A. litoralis* (Stout, 1912), *A. barnardi*, n. sp., and *A. staudei*, n. sp. from the North Pacific region, is separated from *Amphilochus* Bate, 1862, based on the North Atlantic type species *A. manudens* Bate, 1862. *Hourstonius*, n. g., based on the North Pacific type species *H. vilordes* (J. L. Barnard, 1962), is segregated from the Arctic and North Atlantic genus *Gitanopsis* Sars, 1895, based on *G. bispinosa* Boeck, 1871. Also redefined is *Gitana* Boeck, 1871, based on the Arctic type species *G. sarsi* Boeck, 1871, and including *Gitana ellisi*, n. sp., from the northeastern Pacific region.

Numerical analysis of 20 generic-level characters and character states suggests that *Hourstonius* and *Apolochus* are closely related, boreal and warm-temperate, North Pacific and North Atlantic generic complexes. By contrast, the primitive Arctic and North Atlantic genera *Gitana* Boeck, *Gitanopsis* Sars (sens. str.) and *Amphilochus* Bate (sens. str.) are closely related and possibly antecedent to the more advanced Mediterranean and "Pangean" genera *Amphilochoides* Sars, *Paramphilochoides* Lincoln, and *Amphilochella* Ledoyer. The diversity of eastern North Pacific species of Amphilochidae is below that of equivalent latitudes of the western North Pacific and eastern North Atlantic regions, but reasons for these differences are speculative.

## INTRODUCTION

Amphilochids are small, colourful, benthic leucothoidean amphipods commensal with sea fans, hydroids and other sessile marine invertebrates. During the past century and half of faunistic explorations of the Pacific coast of North America, only three species had previously been recorded, none prior to the turn of the century (Stimpson 1857; Stebbing 1906).

The first regional species was described from southern California by Vimy Stout in 1912. Three additional new species were described from California by J. L. Barnard (1962, 1969b). He also listed species from deeper waters and submarine canyons (1966), and described the ecological occurrence of species in the rocky intertidal of south-central California (1969b; 1975).

Among semi-popular accounts, Ricketts & Calvin (1968) included only "Amphilochus neopolitanus" among "common intertidal amphipod species" of the North American Pacific coast. Staude (1987) included four amphilochid species in lists and keys from the northwestern Pacific region, and Austin (1985) listed the same species from this general region, but none actually from the coast of British Columbia.

Gurjanova (1951) had listed amphilochids from the

North Atlantic, Black Sea, and Arctic (Barents Sea) regions, and Shoemaker (1955) recorded *Gitanopsis arctica* from Pt. Barrow, Alaska. Barnard (1970) described several new taxa from the Hawaian archipelago. However, few amphilochid species had been recorded elsewhere in the North Pacific until the extensive work on Japanese coastal marine species by Hirayama (1983). These, and more recent records from Japan, were summarized in phyletic classification by Ishimaru (1994).

The present study encompasses the previously untreated amphilochid fauna of the Canadian Pacific and adjacent coastal marine regions and places it in the context of systematic concepts developed elsewhere.

# **ACKNOWLEDGEMENTS**

Completion of field work, 1955-1980, was greatly assisted by several marine research agencies and their staffs, and were acknowledged in published stations lists (Bousfield 1958, 1963, 1968; Bousfield & Mc-Allister 1962; Bousfield & Jarrett 1981). The authors are indebted to the Pacific Biological Station, Nanaimo, the Bamfield Marine Station, and the Friday Harbor Laboratories, WA, with special thanks to bi-

- 1. Assistant Curator, Marine Invertebrates, Natural History Museum of L. A. County, Los Angeles, CA, USA, 90007.
- 2. Research Associate, Royal Ontario Museum, Toronto, ON, CAN M5S 2C6.

ologist Dr. Craig P. Staude. Dr. D. V. Ellis kindly provided laboratory facilities at the University of Victoria for much of the identification work. Dr. Pierre Brunel, Université de Montréal, provided illustrations and helpful commentary on a proposed new amphilochid taxon from the St. Lawrence estuary.

The authors are grateful for facilities at the Holly Lane laboratory provided by the Canadian Museum of Nature, Ottawa, during 1992-1995, and to the collections management staff of the CMN, especially Judith Price, for more recent help in cataloguing and labelling type material. The original line illustrations were prepared with the capable assistance of artist Floy E. Zittin, Cupertino, CA.

# **SYSTEMATICS**

# AMPHILOCHIDAE Boeck

Amphilochidae Boeck, 1871: 107;—Stebbing 1906: 149;—Barnard 1962: 116;—Barnard 1969a: 132;—Lincoln1979:146;—Krapp-Schickel1982:70;—Bousfield 1982: 266.—Barnard & Karaman 1991: 92.

Type Genus: Amphilochus Bate, 1862 (N. Atlantic).

#### Genera:

North Pacific: Gitana Boeck, 1871; Hourstonius, n. g. (p. 11); Apolochus n. g. (p. 15); Paramphilochus Ishimaru & Ikehara, 1986; Afrogitanopsis Karaman,

1980 (Indian Ocean-Japan).

Extralimital: Gitanopsis Sars, 1895 (Arctic-N. Atlantic); Amphilochoides Sars, 1895 (N. Atlantic-Mediterranean); Gitanogeiton Stebbing, 1910 (Southwestern Pacific); Amphilochopsis Stephensen, 1925 (Arctic); Amphilochella Schellenberg, 1926 (Antarctic-Indian); Rostrogitanopsis Karaman, 1980 (S. African); Cyclotelson Potts, 1915 (Indo-Pacific). An undescribed genus is listed from the St. Lawrence estuary by Brunel et al. (1998).

Diagnosis: Body small, smooth; abdominal segments separate, generally unornamented. Anterior head lobe acute or rounded; rostrum distinct; eyes rounded. Antennae short; accessory flagellum minute or lacking. Flagellum of antenna 1 longer and more richly armed with aesthetascs in male.

Mouthparts modified: upper lip apically notched, lobes often asymmetrical; lower lip tall, inner margins often "notched", inner lobes essentially lacking. Mandible: molar various, often much reduced; spine-row strong; palp slender. Maxilla 1, inner plate small, outer plate strongly spined and/or toothed, palp 1- or 2-segmented. Maxilla 2 small, weakly setose. Maxilliped inner plate slender; outer plate broad; palp medium, dactyl not falciform.

Coxae 2-4deep, increasing posteriorly; coxa 1 small, partly hidden by coxa 2. Gnathopods usually subchelate, often dissimilar in form and size, not sexually dimorphic. Gnathopod 2 usually the larger; posterior

# KEY TO NORTH PACIFIC GENERA OF AMPHILOCHIDAE (see also Fig. 1)

Peraeopods 3-7 ordinary, ambulatory; gnathopod 2 similar in both sexes . . . . . . . . . . . . . . . . . 2. 2. Telson elongate, sharply acute, apex minutely dentate; coxae 2-4, lower margin serrate; accessory Telson apex smoothly and sharply rounded, rarely acute; coxae 2-4, lower margin smooth; accessory 3. Gnathopod 2 distinctly parachelate, propod large; maxilla 1, palp 2-segmented; mandibular molar not triturative ...... Paramphilochus (Japan) Gnathopods 1 & 2, propods small, nearly simple, palm weakly (or not) distinct from hind margin; maxilla 1, palp 1-segmented; mandibular molar normally large, triturative (Fig. 1B).... Gitana (p. 6) 4. Mandibular molar large, triturative, with marginal fringe of slender spines (Fig. 1c); gnathopod 1, propod broadening distally, sub-triangular; peraeopod 5, brood lamella longer than basis, with 8+ Mandibular molar vestigial, triturating surface weak or lacking; gnathopod 1, propod slightly (or not) broadening distally, anterior margin convex; peraeopod 5, brood lamella small, with 5-6 marginal 

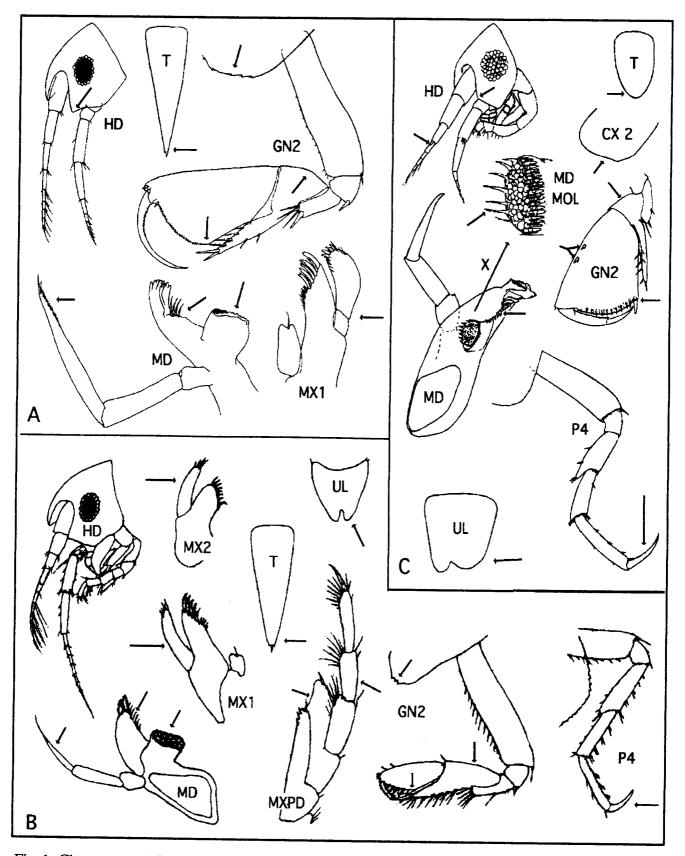


Fig. 1. Characters and Characters states of *Gitanopsis*, *Gitana*, and *Hourstonius*. A. *Gitanopsis inermis* (modified from Lincoln (1979). B. *Gitana sarsi* (modified from Sars (1895); C. *Hourstonius laguna* (after McKinney 1978). [see p. 28 for figures legend]

lobe of carpus typically extended forward behind propod. Coxae 5-7 deep, regularly postero-lobate. Peraeopods slender. Peraeopods 5-7 usually subsimilar in size and form; segment 4, posterodistal process not strongly overhanging segment 5.

Uropods slender, rami narrowly lanceolate. Uropod 2 small, rami unequal, rarely exceeding elongate peduncle of biramous uropod 3. Telson longer than wide, distally (sub)acute, minutely tridentate, or rounded, weakly (or not) keeled below,

Brood plates broad, decreasing posteriorly, margins long-setose. Coxal gills simple, on pereopods 2-6.

Remarks: Family Amphilochidae is a member of superfamily Leucothoidea, closely related to family Pleustidae (see Bousfield 1983; Bousfield & Shih 1994). Character states of coxal plates and uropods are also superficially similar to those of family Stenothoidae near which it often closely positioned (e.g., Stebbing 1906; Barnard 1962). Barnard & Karaman (1991) include family Amphilochidae within an amphilocoid group that encompasses families Cyproideidae, Pseudamphilochidae, and Bolttsiidae.

Family Amphilochidae presently encompasses 13 genera and about 70 species world-wide. A further yet undescribed genus, based on an undescribed Gitanopsis-like species, is listed tentatively from the St. Lawrence estuary by Brunel et al. (1998, p. 187). All but 5 essentially monotypic genera and about 85% of the species are endemic to the northern hemisphere. On this basis, and cognizant of the need for more realistic recognition of natural relationships, the partial realignment of North Pacific and North Atlantic species of Amphilochus Bate, sens. lat. and Gitanopsis Sars, sens. lat. would appear justified at this time [see Discussion and figs. 8-10].

## Gitana Boeck

Gitana Boeck, 1871: 132;—Stebbing 1906: 155;—Chevreux & Fage 1925: 118;—Gurjanova 1951: 302;—Lincoln 1979: 162;—Krapp-Schickel 1982: 82, key;—Barnard & Karaman 1991: 96.

**Type species.** Gitana sarsi Boeck, 1871, designated by Sars 1895; 229.

Pacific Species: Gitana abyssicola Sars, 1895 (N. Atlantic); G. calitemplado Barnard, 1962 (California); G. liliuokalaniae Barnard, 1970 (Hawaii); G. bilobata Myers, 1985 (Fiji); G. gracilis Myers, 1985 (Fiji); G. ellisi, n. sp., (British Columbia).

Extralimital species: G. sarsi Boeck, 1871 (N. Atlantic); G. rostrata Boeck, 1871 (N. Atlantic); G. longicarpa Ledoyer, 1977 (Mediterranean); G. dominica Thomas & Barnard, 1990 (Caribbean).

**Diagnosis:** Anterior head lobe acute or rounded. Antennae unequal in length; accessory flagellum lacking or very minute.

Upper lip, lobes symmetrical. Lower lip, inner shoulders with sharp notch. Mandibular molar large, cushion-shaped, triturative; spine row moderate, 5-9 blades; palp segment 3 not elongate. Maxilla 1, palp 1-segmented. Maxilla 2, inner plate stout. Maxilliped, inner plate with two stout medially curved spines; inner margin of outer plate weakly excavate; palp segment 1 equal to segment 2.

Coxae 2 weakly serrate posterodistally. Gnathopods 1-2 small, weakly subchelate or simple; palm very oblique, dactyl often pectinate posteriorly. Peraeopods slender; dactyls relatively long.

Pleome side plate 2, hind corner squared or obtuse. Uropod 3, ram short, margins bare or nearly so. Telson long, tapering, apex acute, usually minutely tridentate.

Coxal gills small. Brood plates variable, usually large on peraeopods 2 and 3.

**Distribution:** Pan arctic-boreal, N. Atlantic and N. Pacific, extending southwards into warm-temperate and tropical regions, in depths of 0-578 m.

Remarks: Gitana as presently defined, exhibits considerable morphological variation, especially in gnath-opods, mouthparts and brood plates. Tropical species (e.g., G. dominica) show mouthpart character states similar to Hourstonius but a full revisionary analysis is outside the scope of the present study.

# Gitana ellisi new species (Fig. 2)

#### Material examined.

British Columbia, Southern Vancouver Island: ELB Stn. B21b, off Brady's Beach, Vancouver I. (48°,50′N, 125°,09′W), on sand, algae, 10-20 m, dredge, June 1, 1977. - Q ov. holotype, slide mount; 2 QQ paratypes; slide mount, NMCC1992-0242. Ibid. - 2 QQ paratypes, NMCC1992-0243.

Victoria region, Saanich Peninsula (48<sup>O</sup>N, 123<sup>O</sup>W) (KEC Stn.?, no other data), 1981 - 2 QQ, NMCC1992-0252.

Diagnosis: Female ov (3.0 mm) holotype: Rostrum medium, apex slightly down curved. Eye large, black,

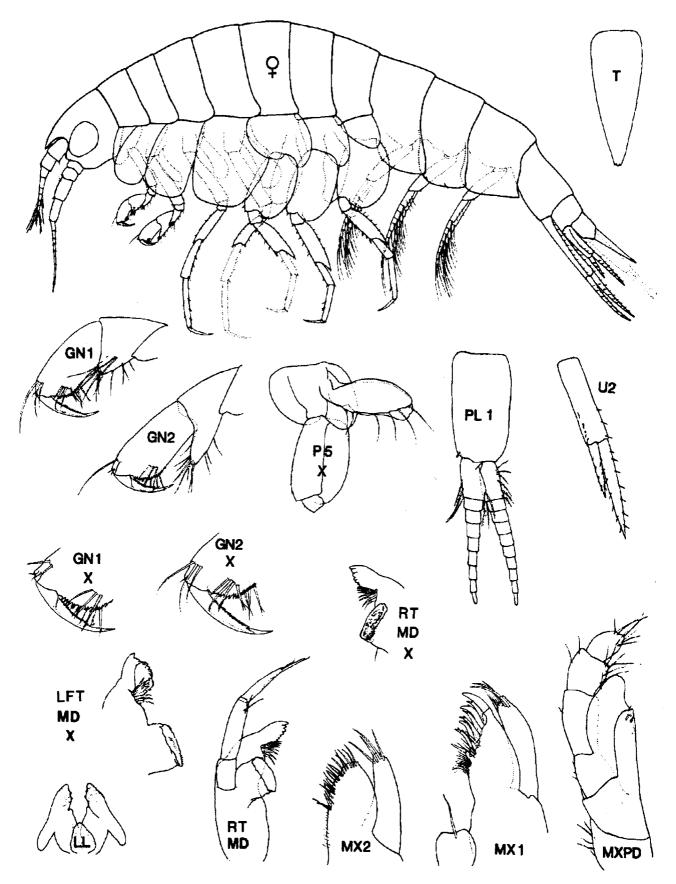


Fig. 2. Gitana ellisi, n. sp.. Q ov. (3.0 mm). Off Brady's Beach, Vancouver I., B. C.

# Key to North Pacific and some North Atlantic species of Gitana.

- 1. Head lobe acute; coxa 2, lower margin sharply rounded, serrate medially; brood plates large . . . 2. Head lobe rounded; coxa 2 smooth below or serrration postero-distally; brood plates small . . . . . 3.
- 2. Gnathopod 2, carpal lobe < 1/4 propod); peraeopod 7, basis widest medially . . . . G. abyssicola Sars Gnathopod 2, carpal lobe, length >1/2 propod; peraeopod 7 basis widest distally . . G. sarsi Boeck

almond-shaped, outer row of facets largest. Antenna 1 shorter than antenna 2, lacking accessory flagellum; peduncular segments short, flagellum 6-segmented. Antenna 2, flagellum 9-10 segmented.

Mandibular molar stout triturative; spine row with 7-8 slender blades; left lacinia ~8-dentate; palp segment 3 slender, shorter than segment 2, apex narrowly truncate, with 2-3 longish simple setae. Maxilla 1, outer plate oblique apex with 8 stout spine-teeth and proximal tuft of fine setae; palp stout, 1-segmented, with several apical setae. Maxilla 2, inner distal margin with several slender setae; outer plate stout, with 4 apical setae. Maxilliped, inner plate narrow, apex subtruncate; outer plate medium broad, with inner marginal subapical incision; palp segment 2 exceeding outer plate; segment 3 shorter than 2.

Coxa 1 narrow, rounded below; coxae medium deep, increasing posteriorly, smooth below. Gnathopods 1 & 2, propods small, subrectangular; palms short, oblique, convex, denticulate, not sharply demarcated at posterior angle; dactyls stout, pectinate behind, unguis overlapping palm. Gnathopod 1, carpal lobe very short, little produced. Gnathopod 2 larger, carpus shorter than propod, posterior lobe short, stiff-setose, extending about half length of propod.

Peraeopods 3 & 4 very slender, weakly armed; dactyls slender, medium long. Coxae 5-7 deeply posterolobate, margins unarmed. Peraeopods 5-7 regularly and subequally homopodous; bases regularly expanded, posteriorly slightly increasing in size; segment 4 long, 5 short; dactyls slender, medium long.

Pleon side plate 3, lower margin straight, hind corner slightly produced. Pleopod rami 9-10 segmented, slightly longer than thick peduncle. Uropod 1 slender, rami subequal, margins spinose. Uropod 2, rami marginally short-spinose; outer ramus >1/2 inner. Uropod 3, rami much shorter than slender peduncle,

marginally smooth, distinctly exceeding telson.

Telson narrowly subtriangular, apex tridentate

Brood plates 2-4 large; 5 small with 3-4 distal marginal setae.

Etymology: The species name recognizes the extensive contributions of Dr. Derek V. Ellis, University of Victoria, in the development and teaching of coastal marine ecological and environmental concepts.

**Distribution:** Only 7 specimens known; from shallow-sublittoral depths off southern Vancouver Island, B. C.

Remarks: Gitana ellisi is closest to G. sarsii Boeck; however, its larger eyes, more distinctly subchelate gnathopods with less produced carpal lobes, smaller coxal plates, and much less markedly reduced mandibular palp are more plesiomorphic character states than in G. sarsi.

# Gitanopsis Sars (restricted)

Gitanopsis Sars, 1895: 223;—Stebbing 1906: 153;—Gurjanova 1951: 302.

Gitanopsis Lincoln 1979: 164 (part);—Barnard 1962: 130 key (part);—Barnard & Karaman 1991: 97 (part). non: Gitanopsis McKinney 1978: 140.—Karaman 1980: 44;—Hirayama 1983: 124.

**Type species:** Amphilochus bispinosa Boeck, 1871, original designation by G. O. Sars.

Species: Gitanopsis inermis Sars, 1883; G. arctica Sars, 1895;—Shoemaker 1955; G. abyssicola Sars, 1895; Gitanopsis sp. A, Just, 1980; Gitanopsis sp. B, Just, 1980.

# KEY TO NORTH PACIFIC SPECIES OF HOURSTONIUS

(Gitanopsis iseebi Yamato transferred to Afrogitanopsis)

1. Gnathopods 1 & 2, propods subsimilar in size and shape, palmar angle squared, defined by small tooth and spine; carpus, posterior lobe short, little produced
2. Gnathopods 1 & 2, posterior angle of propod defined by single spine; maxilliped, outer plate markedly incised mediodistally; Hawaiian islands
3. Telson apically acute, minutely bifid; maxilliped palp, segment 2 distinctly longer than segment 3; mandibular spine row short, ~6-bladed
4. Gnathopod 2, propod with two prominent anterior submarginal spines; gnathopod 1, anterior margin of basis setose throughout; maxilla 2, inner plate weak, little broader than outer 5. Gnathopod 2 lacking anterior submarginal spines; gnathopod 1, anterior margin of basis nearly bare; maxilla 2, inner plate normal, setose, broader than outer plate 6.
5. Gnathopod 2, carpal lobe elongate, extending almost to palmar angle; telson elongate, length >2X maximum width; N. American Pacific
6. Telson narrow, elongate, length > 2X maximum width; gnathopod 2, carpal lobe extending beyond posterior palmar angle
7. Abdominal (epimeral) side plate 3, hind corner slightly produced; uropod 2, outer ramus normal, >1/2 length of inner ramus

**Diagnosis:** Rostrum medium; anterior head margin usually acute; eye round. Antennae usually subequal in length; accessory flagellum lacking or very minute.

Upper lip shallowly notched, lobes subsymmetrical. Lower lip, inner margins strongly notched. Mandible: molar process large, triturating surface without raised marginal spines; spine row with few blades; palp segment 3 elongate, setulose near apex. Maxilla 1 normal, palp 2-segmented. Maxilla 2 normal, inner plate narrow. Maxilliped palp slender, segment 2 often short.

Coxae 2-4 large, lower margin weakly serrate. Gnathopods 1 & 2 medium to weakly subchelate; prododal palm not demarcated from posterior margin; carpus of medium length, lobe produced. Peraepods 3 & 4,

dactyls slender, medium. Coxae 5-7 regularly posterolobate. Peraeopods 5-7, dactyls slender, medium long.

Epimeral plate 3, hind corner subquadrate. Uropod 3 relatively short, little exceeding uropod 1. Telson elongate, narrowing, apex acute, minutely tridentate.

**Distribution:** Holarctic and northern North Atlantic, 0-875 m. in depth.

Remarks: Gitanopsis sens. lat. (e.g., Barnard & Karaman, loc. cit.) here consists of three groups: Gitanopsis Boeck sens. str. (Arctic and northern North Atlantic in distribution); and Hourstonius new genus, mainly in

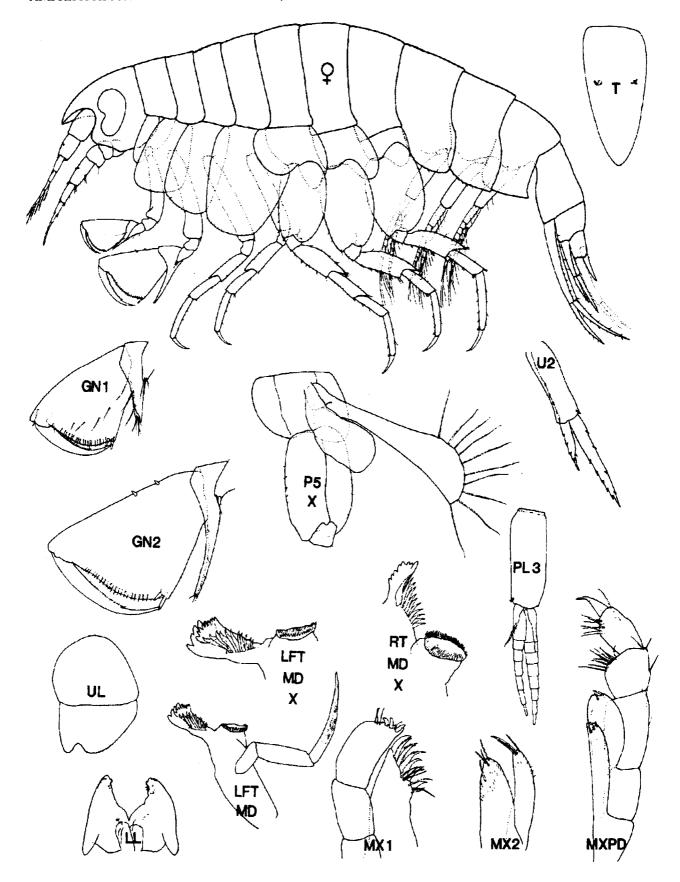


Fig. 3. Hourstonius vilordes (Barnard). Q ov. (3.9 mm). Hinks I., N. end Aristazabel I., B.C.

the North Pacific region, with some species in the Gulf of Mexico, and possibly coastal waters of the African South Atlantic region. A third generic group, informally recognizable and yet unnamed within Gitanopsis (sens. lat.), may be represented by G. marionis (Stebbing, 1888), as figured by Bellan-Santini & Ledoyer (1974), G. tai Myers, 1985, and several other largely Indo-Pacific and southern hemispheric species (except G. squamosa (Thompson, 1880) as listed by Barnard & Karaman (1991).

Principal characters and character states utilized in keys, diagnoses, and numerical analyses pertaining to the genus *Gitanopsis* (sens. lat.) are represented in Fig. 1 (p. 55).

# Hourstonius, new genus

Gitanopsis Sars, 1895: 224 (part);— Barnard 1962: 130 (key, part);—Hirayama 1983: 124 (key);—Barnard & Karaman 1991: 97 (part);—Ishimaru, 1994: 52 (species list).

non Gitanopsis Gurjanova 1951: 302;—Lincoln 1979: 164.

Type species: Gitanopsis vilordes J. L. Barnard, 1962

Species: Hourstonius breviculus (Hirayama, 1983); H. japonica (Hirayama, 1983); H. longus (Hirayama, 1983); H. robastodentes (Hirayama, 1983) (Japan); H. laguna (McKinney, 1978); H. tortugae (Shoemaker 1942) (Florida); H. pusilloides (Shoemaker, 1933; H. pusilla (K. H. Barnard, 1916) (S. Africa); H. pele (J. L. Barnard, 1970); H. baciroa (J. L. Barnard, 1979) (Galapagos); H. magdai (Reid, 1951) (Trop. Atlantic) non: Afrogitanopsis paguri (Myers, 1974) (W. Indian); A. iseebi (Yamato, 1993) (Japan).

**Diagnosis:** Anterior head lobe generally rounded. Accessory flagellum 1-segmented or minute.

Upper lip notched, lobes asymmetrical; lower lip, inner marginal "notch" weak or lacking; mandible, molar distinct, outer triturating ridge with raised spines; maxilla 1, palp slightly modified; maxilliped, palp segment 3 short; coxa 2, lower margin smooth (not serrate); gnathopods 1 & 2 strongly subchelate, propod with paired spines at posterodistal angle demarcating palm; gnathopod 2, carpus narrow, posterior lobe elongate;

Epimeral plate 3, hind corner squared or rounded; telson linguiform, medium to long, apex broadly or sharply rounded (acute in *H. japonica*).

**Distribution:** Mainly North Pacific, with some species in the Gulf of Mexico, and possibly coastal waters of the African South Atlantic region.

Etymology: The genus is named in honour of the late Alan S. Hourston, fisheries scientist with the Pacific Biological Station, Nanaimo, British Columbia. Dr. Hourston, his wife Barbara, and their family provided much help and encouragement to the senior author and his family during the 25-year period of field work for the Pacific amphipod program, 1955-1980.

Remarks: Members of this genus are readily distinguished from species of *Gitanopsis* Sars (sens. str.) in possessing an accessory flagellum, more strongly subchelate gnathopods with shorter carpus; weakly (or not) serrated lower margin of coxa 2; and linguiform telson with rounded apex. Moreover, species of *Gitanopsis* (sens. str.) are mainly Arctic and North Atlantic in distribution.

Members of the third generic group (G. marionis, G. squamosa, G. tai, and several others (see Gitanopsis above). Members appear superficially more closely similar in some character states (e.g., of accessory flagellum, upper lip) to Hourstonius than to Gitanopsis sens. str., but detailed analysis is beyond the scope of the present study.

# Hourstonius vilordes (J. L. Barnard, 1962) (Fig. 3)

Gitanopsisvilordes Barnard, 1962: 131, fig. 6; — 1969b: 82; — 1975: 344, fig. 190; — Austin, 1985: 593; — Staude, 1987: 379.

#### **Material Examined:**

**ALASKA** 

SE Alaska, ELB Stns., 1961:

A3, Little Daykoo, Dall I. (54°42'N, 132° 42' W); MW-LW, May 31 - 2 QQ, NMCC1992-0215.

#### BRITISH COLUMBIA.

# Queen Charlotte Islands, ELB Stns., 1957:

W4b, Small bay, north shore Hippa Passage (53°27'N, 132°58'W), 6-10 m dredge, gravel, stones, shells, Aug. 10. - 1 Q, NMCC1992-0204.

# North Central coast, ELB Stns., 1964:

H3, Cockle Bay, Lady Douglas I. (52°21'N, 128°23'W), sand, Zostera, kelp, LW, July 9. - 4 QQ, NMCC1992-0219. H5, Hinks I., north end Aristazabal I. (52°38'N, 129°05' W), stones, Phyllosp[adix, kelp LW, July 10.- Q (ov.) (Fig'd specimen), 2 QQ; 3 &C, 57 imm.; slide mounts: QQ (1.8mm,

2.2 mm, 2.3 mm, 2.4 mm, 2.6 mm, 2.7 mm, 2.9 mm), NMCC1992-0220. H26, Cox Pt., inlet at mouth (53°08'N, 129°45'W), shelly sand, kelp, LW, July 19. - 2 QQ, NMCC1992-0225. H65, Christie Pass, cove on south side Hurst I. (50°50'N, 127°35'W), shelly gravel, kelp, MW-LW, Aug. 11. - 8 QQ, NMCC1992-0232.

# Northern Vancouver I., ELB Stns., 1959:

O4, Browning Inlet (50°30'N, 128°06'W), shelly sand, eel grass, LW, July 19. - 1 Q, NMCC1992-0213? V5, Lemon Pt., Nigei I. (50°51'N, 127°46'W), *Phyllospadix, Corallina*, fucoids, LW, Aug. 7. - 1 Q, NMCC1992-0210. V7, Lady Ellen Pt.,Broughton Str. (50°36'N, 127°07'W) - 1 Q, NMCC1992-0211. V10, AlertBay, Broughton Str. (50°35'N, 126°56'W) muddy sand, kelp, LW, Aug. 1-1 Q, NMCC1992-0212. V17, Boat Bay, Cracroft I. (50°31'N, 126°34'W), coarse sand, eelgrass, LW, Aug. 5. - 3 QQ, NMCC1992-0217. V20, Brown Bay (50°10'N, 125°22'W), coarse sand, kelp, LW, June 22. - 1 6°, 2 QQ, NMCC1992-0214. N11, Port Progress, Queen Charlotte Str. (50°55'N, 127°16' W), sandy mud, *Zostera*, LW, Aug. 4 - 3QQ, NMCC1992-0205.

# Southern Vancouver Island, ELB Stns., 1955:

F6, Telegraph Bay (48°27'N, 123°17'W) - 1 Q NMCC1992-0202. Victoria region (48°N, 123°W), KEC Stn.?, 1981. - 1 Q, NMCC1992-0249; Ibid., - 3 & , 1 Q ov. (2.5 mm), slide mount, 10 females, NMCC1992-0250; Ibid., - 1Q, NMCC1992-0251.

Diagnosis: Female ov. (3.9 mm) (fig'd specimen).

Rostrum medium. Eye large, subreniform. Antennae short, subequal. Antenna 1, flagellum 5-6 segmented; accessory flagellum minute. Antenna 2, flagellum 6-segmented.

Upper lip, apex distinctly asymmetrical. Lower lip with weak inner "shoulders". Left mandible, lacinia 8-9 cuspate; spine row with 10-12 slender blades; palp segment 3 distinctly longer than 2, inner distal margin finely pectinate, apex sharply acute. Maxilla 1, inner plate with 7 apical spine teeth and 4-5 inner apical seta; palp and segments stout. Maxilla 2, plate medium, weakly armed. Maxilliped, plates narrow; palp segment 1 large, length nearly equal to 2 & 3 combined.

Coxa 1 narrow elongate; coxae 2 -4 large deep, smooth below. Gnathopods 1 & 2 propods large, palms smoothly convex, nearly vertical, sharply demarcated at posterior angle by paired spines; dactyls slender, finely pectinate behind except on unguis. Gnathopod 1, carpal lobe spinose, produced 2/3 length of posterior margin of propod. Gnathopod 2, carpus narrow, lobe extending almost to posterior angle of propod.

Peraeopods 3 & 4 slender, weakly armed; dactyls slender. Coxae 5-7 normally posterolobate, margins unarmed. Peraeopods 5-7 regularly and subequally

homopodous; bases regularly expanded, posteriorly slightly increasing in size; dactyls slender, medium long.

Pleon side plates 2 &3, hind corners weakly acuminate. Pleopod rami slightly longer than peduncle, 7-8 segmented. Uropod 1, rami markedly unequal, margins weakly spinose. Uropod 2, ramus marginally short-spinose; outer ramus ~= 1/2 inner. Uropod 3, rami short, broad, marginally smooth, slightly exceeding telson.

Telson elongate, smooth, apex narrowly rounded. Brood plates medium broad; plate 5 with 10-12 distal marginal setae.

Distribution: Shallow littoral depths from SE Alaska to southern Vancouver Island, south to central and southern California.

Remarks: In character state similarity, Hourstonius vilordes appears somewhat closer to species of Hourstonius from the Gulf of Mexico than to species of "Gitanopsis" (sens. lat.) described by Hirayama (1983) from Japanese coastal marine waters (see key to species, p. 9). H. vilordes differs from the Hawaiian species, H. pele (Barnard, 1970), in its larger coxal plate 2, larger mandibular palp, and narrower telson, as well as character states of the gnathopods given in the key.

## Amphilochus Bate (restricted)

Amphilochus Bate, 1862: 107.—Stebbing 1906: 149 (part);—Lincoln 1979: 148 (part);—Krapp-Schickel 1982: 74 (part);—Barnard & Karaman 1991: 96 (part).

**Type species.** Amphilochus manudens Bate, 1862, monotypy.

Species: Amphilochus tenuimanus Boeck, 1871; A. planierensis Ledoyer, 1977.

**Diagnosis:** Rostrum medium; anterior head lobe acute; eyes rounded. Antennae subequal in length; accessory flagellum lacking or minute.

Upper lip, apical incision shallow, lobes sub-symmetrical. Lower lip, inner margins smooth. Mandible: molar very reduced, knob-like, lacking triturating ridges; spine-row medium; palp segment 3 elongate. Maxilla 1 normal, palp 2-segmented. Maxilla 2 regular, outer plate slender. Maxilliped palp slender.

Coxal plates 2-4 large, lower margins serrate. Gnathopods 1 & 2 medium to strongly subchelate, palmar

# KEY TO NORTHERN PACIFIC AND ATLANTIC SPECIES OF APOLOCHUS (see character states of subgroups 1 & 2 of Fig. 4, p. 64)

1	Mandibular molar small, knob-like, lacking triturating ridges; maxilla 2, plates reduced, weakly armed; peraeopods 3 & 4, dactyls short, thick (North American Pacific subgroup) 2. Mandibular molar distinct, apex acute with few triturating ridges, or flat, with several ridges; maxilla 2, inner plate broad; peraeopods 3 & 4, dactyls usually slender, medium (Atlantic-Mediterranean regional subgroup) 4.
2	. Gnathopod 2, carpal lobe short, <1/2 propod margin; mandibular spine-row 10-12 bladed; uropod 2, rami nearly bare; telson elongate, 2 1/2X width
3	Antenna 1 shorter than 2; gnathopod 2, palm shallowly convex, nearly perpendicular; maxilliped outer plate wide, little longer than broad
4	Mandibular molar elongate, apex subacute, with few (or no) triturating ridges; gnathopod 2, carpus short, < 1/3 anterior margin of propod
5	Gnathopod 2, propod large, carpal lobe extending almost to palmar angle; accessory flagellum very minute or lacking
6	Uropod 3, rami subequal; maxilliped, outer plate broader than long
7.	Antennae subequal in length; coxa 1 serrate below; mandibular spine-row with 8-10 blades 8. Antenna 1 short flagellum little beyond peduncle of A2; coxa 2 smooth below; mandibular spine row with ~14 blades
8.	Gnathopod 2, propod with 4 stout antero-marginal spines
9.	Uropod 2, ramal margins spinose; coxa 1 subrectangular, lower margin smooth; telson short, length 1.5 X maximum width

margin not demarcated from posterior margin by paired spines; carpus medium, lobe variously produced; dactyls finely denticulate. Peraeopods 3-4, dactyls slender, medium long. Coxae 5-7 deep, shallowly posterolobate. Peraeopods 5-7, dactyls slender, medium long.

Pleon segment 3, hind corner with small cusp. Pleopods regular. Uropod 3, inner ramus slightly broadened. Telson elongate, narrowing distally, apex acute, minutely dentate.

<sup>\* &</sup>quot;Amphilochus" neopolitanus of Lincoln (1979) differs from that of Krapp-Schickel (1982)

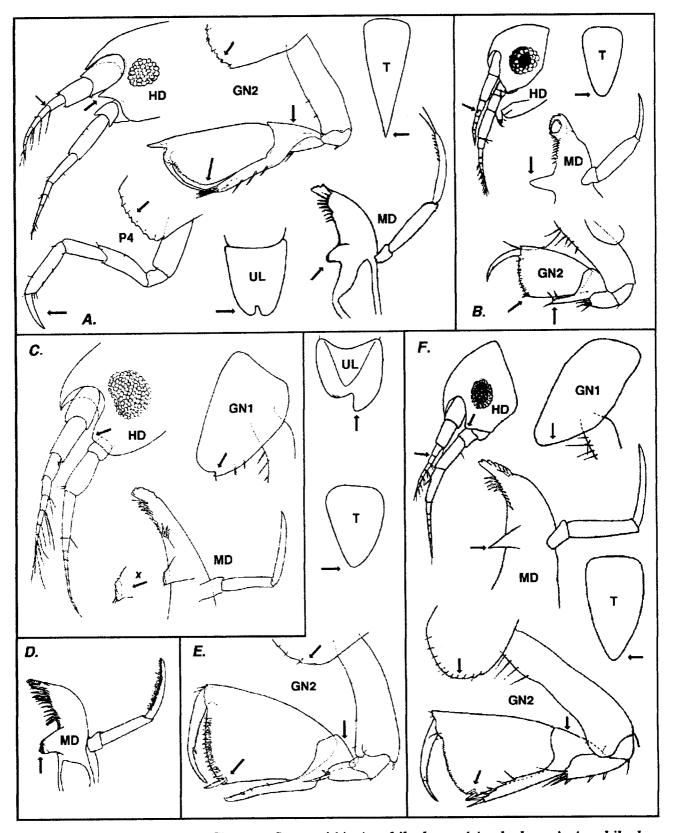


Fig. 4. Selected Characters and Character States within Amphilochus and Apolochus. A. Amphilochus manudens Bate [modifed from Lincoln (1979), Sars (1895)]; B. Apolochus borealis (Enequist, 1950); C. Apolochus sp. [= A. picadurus (Krapp-Schickel (1982)]; D. Apolochus delacaya (McKinney, 1978). E. Apolochus neopolitanus Della Valle (after Krapp-Schickel (1982)]; F. Apolochus picadurus (Barnard, 1962). [see p. 28 for figure legend]

**Distribution:** Northern North Atlantic, N. American [Brunel et al. 1998) and boreal European-Mediterranean region.

Habitat: On scleractinian and horny corals, 0-600 m.

Remarks: Amphilochus Bate (sens. str.) is defined by: anterior head lobe acute; accessory flagellum lacking; upper lip apical lobes subsymmetrical; gnathopod propods lacking posterodistal palmar spines; coxae 2-4 with serrate lower margins; peraeopod dactyls elongate; and telson apically acute, minutely tridentate.

The form of the gnathopods, mouthparts, and telson suggest that Amphilochus sens. str. may have been para-ancestral to regionally more advanced genera such as Amphilochoides Sars, 1895, and Paramphilochoides Lincoln, 1979. However, these latter two genera may themselves require redefinition. Thus, the type species of Amphilochoides [A. boecki Sars (= A. odontonyx Sars, 1895)] possesses a unique combination of generic-level character states: upper lip, apical lobes subsymmetrical; maxilla 2 plates small, partly fused; dactyls of both gnathopod 1 & gnathopod 2 with proximal nodiform process; and epimeral plate 3, hind corner toothed. At least three species with normally reduced mandibular molar, presently included in the genus Amphilochoides by Barnard & Karaman (1991), differ in the above character states. Thus, "Amphilochoides" longimanus Chevreux, 1888, A. serratipes Norman, 1869, and a distinctive Mediterranean species figured as A. serratipes by Krapp-Schickel (1982) might justify separate generic recognition.

Despite aberrencies in the form of the gnathopods, in overall character-state similarity the genus *Paramphilochus* Ishimaru & Ikehara, 1986, appears more closely similar to Pacific members of *Apolochus* and *Hourstonius* than to *Amphilochus* (sens. str.).

# Apolochus, new genus

Amphilochus Sars 1895: 215 (part); Stebbing 1906: 149(part);—Barnard1969a:136(part);—Lincoln1979: 148 (part);—Krapp-Schickel 1982: 74 (part); Barnard & Karaman 1991: 96 (part).

non: Amphilochus Bate, 1862: 107.

**Type species**: Amphilochus neopolitanus Della Valle, 1893.

Species: 1. Nominate subgroup: Apolochus picadurus (Barnard, 1962) (California); Apolochus species (= A.

picadurus Krapp-Schickel, 1982) (Mediterranean); A. borealis (Enequist, 1950) (NW Europe); A. pillaii (Barnard & Thomas, 1983) (Florida); A. casahoya (McKinney, 1978) (Gulf of Mexico); A. delacaya (McKinney, 1978) (Gulf of Mexico); A. kailua Barnard, 1970 (Hawaii); A. likelike Barnard, 1970 (Hawaii); A. menehune Barnard, 1970 (Hawaii).

- 2. <u>Fastern Pacific subgroup</u>: Apolochus litoralis (Stout, 1912) (p. 16); A. barnardi, new species (p. 18); A. staudei, new species (p. 19).
- 3. Mediterranean "southern" subgroup: Apolochus brunneus (Della Valle, 1893), A. spencebatei (Stebbing, 1876), and two species described from the Indian Ocean region as Amphilochus neopolitanus by Ledoyer 1978, 1979.

**Diagnosis:** Anterior head lobe rounded. Antenna 1 short to medium, peduncular segments 1 & 2 slightly broadened posteriorly; accessory flagellum 1-segmented, rarely lacking.

Upper lip, apical lobes asymmetrical. Lower lip, inner margins variously "notched". Mandible, molar reduced, apically with few triturating ridges, setae, or none; spine-row well developed; palp segment 3 little longer than segment 2. Maxilla 1, outer plate spines regular; palp segment 1 enlarged. Maxilla 2, setation of plates tending to reduction. Maxilliped outer plate broad, palp regular.

Coxae 2-4 weakly or not serrate below. Gnathopod 2, carpus short to medium in length, posterior lobe well developed; palmar margin of propod distinct, steeply oblique or nearly vertical, palmar angle defined by 1-2 spines. Peraeopods 3 & 4, dactyls short to medium, shorter than those of peraeopods 5-7.

Telson linguiform, apex sharply rounded or sub-acute. Brood plate (P5) short, with 5-6 marginal setae.

Etymology: A combining form of "apo" and "lochus", referring to the generally advanced nature of the character states of the genus.

Remarks: The genus Amphilochus Bate, 1862 (sens. lat.), previously encompassed a heterogeneous group of amphilochid species characterized by stoutly subchelate gnathopods and reduced, essentially nontriturative, mandibular molar process. Characters and character states previously utilized in diagnoses and keys (above) have been limited in number and kind, and apparently not previously ordered or subject to numerical analysis.

A semi-phyletic phenogram of northern hemisphere

species of Amphilochus (sens. lat.) (see p. 9, supporting data supplied on request) suggests that the name Amphilochus is more realistically confined to the type species Amphilochus manudens Bate, 1862, A. tenuimanus Boeck, 1871, and (less closely) A. planierensis Ledoyer, 1977.

# Apolochus litoralis (Stout) (Fig . 5)

Amphilochus litoralis Stout, 1912: 136, fig. 78;—Barnard 1962: 82;—Barnard 1969b: 124, fig.2;—Barnard 1975: 358, fig. 327;—Staude 1987: 379;—Barnard & Karaman 1991: 96.

Material Examined: 32 lots of specimens containing about 80 specimens (mostly ovig. females but also incl. 6 males and a few imm.), mostly from high salinity outer coast stations, from about Sitka, SE Alaska. south ward through the Queen Charlottes Islands, the north-central B. C. coast, Vancouver I., Washington state, to southern California.

# ALASKA SE Alaska, ELB Stns., 1961:

A168, Klokachef I., Chickagof I. (57°25'N, 135°52'W), kelp over boulders, LW, July 24. - Q ov. (damaged), NMCC-1992-0217. A175, West Eugenia Pt., San Juan Batista I. (55°26.44'N, 133°17.18'W), *Zostera*, algae, sand, rock, LW, July 26. - 10°, 1 Q, NMCC1992-0218.

#### 1980:

S5B1, N.W. end Hogan I., west cove (57°43'N, 136°15.5'W) prganic debris, slatey gravel, LW July 28. - 1 Q, NMCC1992-0245. S23F1, Taigud I., south beach, Baranof I. (56°54.5'N, 135°24'W), kelp, sand, LW, Aug. 4. - 3 QQ + 2 QQ (damaged), NMCC1992-0247.

# **BRITISH COLUMBIA**

# Queen Charlotte Ids., ELB Stns., 1957:

H2, Parry Passage, E. of Kiusta (54°10'N, 133°01'W), *Phyllospadix*, kelp, over coarse sand, LW, Aug. 24. - 1 Q, NMCC-1992-0203.

# Northcentral coast, ELB Stns., 1964:

H5, Hinks I., N. end Aristazabel I. (52°38'N, 129°05'W), *Phyllospadix*, kelp, LW, July 9. - 1 Q, NMCC-1992-0220. H20, McCauley I., N. end (53°43'N, 130°15'W), fine sand, LW, July 17. - 2 QQ, NMCC1992-0221. H47, Codfish Passage, Miles I. (52°05'N, 128°19'W), *Zostera*, kelp, algal mats, coarse shelly sand, LW, Aug. 5- 1 °C, 5 QQ, NMCC-1992-0221. H50, Goose I. South beach (51°57'N, 128°26'W), *Zostera*, algae, fine shell, sand, Aug. 6. - 1 Q, NMCC1992-0229. H57, cove off Nolan Pass, S. end Hunter I. (51°43'N, 128°05'W), shells, gravel, mud, LW, Aug. 8. - 2 QQ,

NMCC1992-0231. H65, Christie Pass, cove on S. side Hurst I. (50°50'N 127°36'W), kelp, shelly gravel, LW, Aug 11. - 1 Q, NMCC1992-0232.

# Northern Vancouver I., ELB Stns., 1959:

O3, Grant Bay, Quatsino Sound (50°28'N, 128°05'W), coarse shelly sand, LW, July 18. - 3QQ, NMCC1992-0209. O11, Hesquiat, at Matlakaw Pt. (49°23'N, 126°28'W), *Phyllospadix*, kelp, over gravel -1 Q,NMCC1992-0208. N11,Port Progress (50° 55'N, 127°16'W), *Zostera* over sandy mud, stones, LW, Aug. 4. - 1Q, NMCC1992-0205. V5, Lemon Pt., Nigei I. (50°51'N, 127°46'W), *Phyllospadix*, fucoids, *Corallina*, over stones, LW. - 6QQ, NMCC-1992-0210. V4b,RollerBay,HopeI. (50°56'N,127°56'W), *Phyllospadix*, kelp, coarse sand, LW, July 22. - 3QQ. NMCC1992-0209.

## Southern Vancouver I., ELB Stns.

**1955:** F1 Wiffen Spit, Sooke (48°21'N, 123°45'W), algae on gravel, stones, LW - 4 QQ, NMCC1992-0201. **1970:** P718, Becher Bay at Head (48°21'N, 123°35'W), algae on stones, gravel, LW, July 31 - 1Q, NMCC1992-0234. **1977:** B6a, Trial Island Pt., Victoria (48°24'N, 123°19'W) - 1 Q, NMCC 1977-181.

**1980:** Deer I., Victoria region (50.6°N, 127.9°W?) - 2 ♀♀, NMCC1992-0244.

1981: Victoria region (48°N, 123°W), KEC Stn.?- 4 QQ, NMCC1992-0234?; Ibid. - 1 &, 3QQ, NMCC1992-0248; Ibid. - 1 &, 1Q, NMCC1992-0249; Ibid.- 4 &, 1Q, NMCC1992-0251.

# Vancouver I., outer coast, ELB Stns. 1976:

B4, off Brady's Beach, Bamfield (48°50.03'N,125°08'W), sand, algae, 60-70 m dredge, June 25 - 2 QQ, NMCC1992-0235. B5, Brady's Beach, S. side (48°49.08' N, 125°08' W), *Phyllospadix*, kelp, fucoids, on sand and rock, LW. - 3 QQ, NMCC1992-0236. B7, Broken Islands, W. side of Wouwer I. (48°51.6'N, 125°21'W)Phyllospadix, kelp, on bedrock, LW. - 1 Q, NMCC1992-0237.

# 1977:

B8, off Brady's Beach, Bamfield (48°49.6'N, 125°09.2'W), sand and algae, 5-10 m dredge, May 21. - 3 QQ, 2 imm, NMCC1992-0239. B13, Trevor Channel, off Brady's Beach (48°52'N 125°08'W), hard sand algae, 6-14 m dredge, May 25. - 1Q, NMCC1992-0290. B14, Trevor Channel off Execution Rock (48°48'N, 125°11.2'W), sandy mud, algae, 44-54 m dredge, May 25. - 1 Q, NMCC1992-0241. B21b, off Brady's Beach, Bamfield (48°49.6'N, 125°09.2'W). sand, algae, 10-20 m dredge, June 1. - Q (2.8 mm) (fig'd specimen);10 QQ, NMCC1992-0242.

## **US MAINLAND**

# Washington-Oregon, ELB Stns., 1966:

W36, Clallam Bay, WA, atriver mouth (48°15'N, 124°16'W), fine organic sand, *Phyllospadix, Chorda*, LW - 1 Q, NMCC-1992-0233.

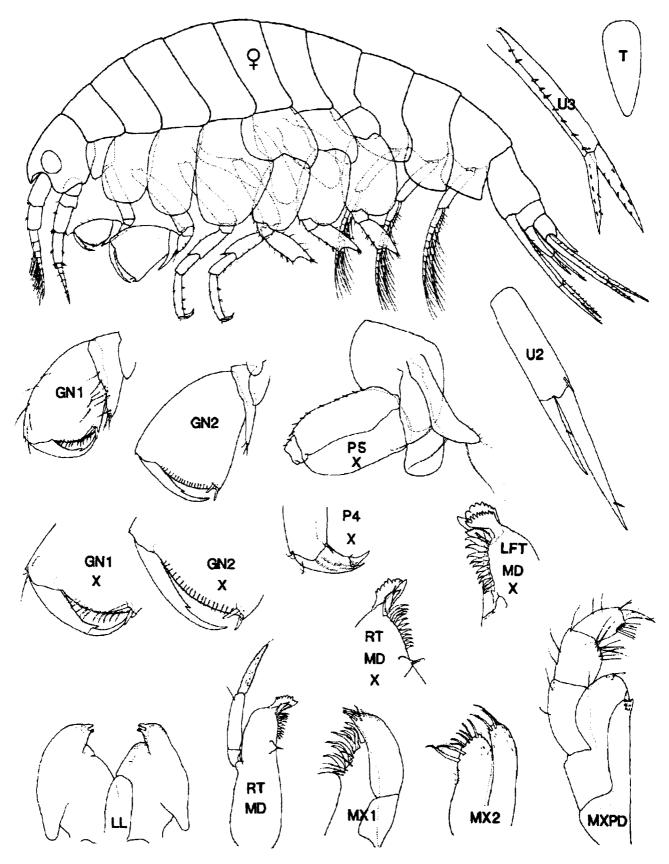


Fig. 5. Apolochus litoralis (Stout). Female ov. (2.8 mm). Off Brady's Beach, Vancouver I., B. C.

Diagnosis: Female ov. (4.0 mm) (fig'd specimen).

Rostrum strong, apex little deflexed. Eye medium, nearly round. Antennae short, subequal, flagella 7-8 segmented; accessory flagellum 1-segmented.

Mandible: molar a small triangular knob, apex with two setae; left mandible, lacinia 9-10 cuspate; incisor 9-dentate; spine row with 10-12 slender blades, stoutest distally; palp segment 3 little longer than 2, inner margin finely pectinate, apex blunt, with single short seta. Maxilla 1, inner plate, apex oblique, with 7 curved spine-teeth and 4-5 setae at inner angle; palp stout, segment 1 large. Maxilla 2, plates medium, inner plate with 8 apical setae. Maxilliped, inner plate narrow, apex subtruncate; outer plate broad inner margin smooth; palp segment 1 large, segment 2 extending considerably beyond outer plate.

Coxa 1 short, little concealed by coxa 2; coxae 2-4 large, deep, smoothly rounded below. Gnathopods 1 & 2 strongly subchelate. Gnathopod 1 much smaller; propod, palmar margin convex; oblique; dactyl stout, smooth behind, unguis medium; carpus short, posterior lobe short, anteriorly spinose-setose. Gnathopod 2, propod large, expanding distally, palm shallowly convex, nearly vertical, sharply demarcated at posterior angle by paired spines; dactyl stout, smooth behind, unguis medium; carpus short, posterior lobe short, nearly base, produced 1/3 length of posterior margin of propod.

Peraeopods 3 & 4 ordinary, posterior margin of segment 6 with 3 spines; dactyls short. Coxae 5-7 normally posterolobate, margins unarmed. Peraeopods 5-7 regularly and subequally homopodous; bases regularly expanded, posteriorly slightly increasing in size; segment 4 not elongate; dactyls short.

Pleon side plate 2 convex below, 3 nearly straight, corners not produced. Pleopod rami long, 9-10 segmented. Uropod 1, rami subequal, margins weakly spinose. Uropod 2, rami slender, nearly bare, outer ramus > 1/2 inner. Uropod 3 elongate, rami unequal, marginally spinose, greatly exceeding telson. Telson smooth, length about twice width, apex narrowly rounded.

Brood plates medium broad; 5 with 2-3 distal marginal setae.

**Distribution:** Intertidal and LW habitats, from southern California, north through Oregon, Washington, and B. C. to southern S.E. Alaska,

Taxonomic Commentary: As indicated in the key, Amphilochus litoralis and other American Pacific coast

species are distinct from North Atlantic and Gulf species.

# Apolochus barnardi new species (Fig. 6)

Amphilochus ?neopolitanus cf. Della Valle fide Barnard, 1962: 126;—Barnard 1964: 105(?)—Barnard 1969b: 82.

# Material Examined: None.

Diagnosis (partly after Barnard 1962): Female ov. (2.5 mm): Rostrum medium. Eye medium, narrowly subovate. Antennae medium short, subequal. Antenna 1, peduncular segments 1 & 2 short and deep, 2 with posterodistal tuft of setae; 3 small, narrow; flagellum 8-9 segmented; accessory flagellum minute. Antenna 2, flagellum 9-10 segmented.

Mandibular molar small, broadly triangular. Left mandible, lacinia 8-9 cuspate; spine row with 15-17 slender blades, distinctly largest distally; incisor multidentate; palp segment slightly longer than 2, inner margin finely pectinate, apex with single short seta. Maxilla 1, apical margin of inner plate nearly vertical, with 7 spine-teeth and 6-8 setae at inner angle; palp segments stout, segment 1 large. Maxilla 2, plates medium, inner plate with 6 marginal setae, proximally plumulose. Maxilliped, inner plates tall, narrow, apex subtruncate; outer plate short, broad, distal margin with several setae and stout spine, inner margin smooth; palp segment 2 distinctly exceeding outer plate; segment 3, inner distal margin with narrow denticles.

Coxa 1 short, little occluded by 2; coxae 2-4 successively deepening, rounded below. Gnathopods 1 & 2 distinctly subchelate. Gnathopod 1, propod slightly expanding distally, palm convex, oblique; dactyl slender body denticulate behind, unguis elongate, slightly exceeding palmar angle; carpus narrow, lobe medium, extending about 1/2 posterior margin of propod. Gnathopod 2, propod large, broadening distally, palm convex, finely crenulate, nearly vertical, sharply demarcated at posterior angle by paired spines; dactyl slender, body finely pectinate behind, unguis elongate slightly exceeding palm; carpus short, posterior lobe elongate extending length of posterior margin of propod.

Peraeopods 3 & 4 medium, segment 6 with 4 posterior marginal spines; dactyls short, unguis short. Coxae 5-7 normally posterolobate, hind lobes rounded below, posteroventral margin of 7 weakly spinose. Peraeo-

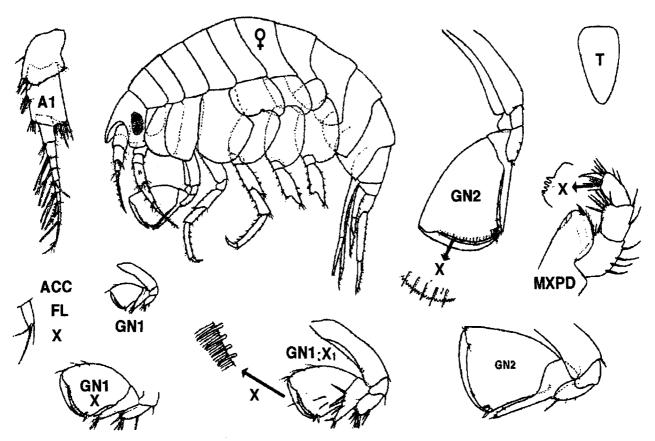


Fig. 6. Apolochus barnardi, new species (=A. neopolitanus cf. Della Valle fide J. L. Barnard, 1962) (modified from Barnard, 1962).

pods 5-7 regularly homopodous; bases regularly expanded, posteriorly slightly increasing in size; segment 4 not elongate; distal segments marginally spinose, esp. anteriorly; dactyls short.

Pleon side plates 2 & 3 convex below, hind corners not acuminate. Pleopod rami distinctly longer than peduncle, 9-10 segmented. Uropod 1 slender, rami unequal, margins spinose. Uropod 2, rami marginally short-spinose; outer ramus <1/2 inner. Uropod 3 elongate, greatly exceeding telson; rami medium, unequal, marginally spinose. Telson subtriangular, length slightly less than twice width, apex narrowly rounded. Brood plates medium broad, 5 narrow.

**Distributional Ecology:** Apolochus barnardi occurs in the *Phyllospadix* and *Egregia* sublittoral zone to depths of ~20 m, mainly on bottoms of coralline algae, stones, and sessile invertebrates, from Central to Southern California.

Etymology: The name is a tribute to the early recognition of this distinctive form by the late J. L. Barnard, and to his major contributions to knowledge of the North American Pacific amphipod fauna.

Remarks: Apolochus barnardi is distinct from A. neopolitanus DellaValle 1893, as figured by Krapp-Schickel (1982) in characters of the key (p. 13), It is also distinguished from A. staudei by characters of the key and as noted elsewhere (below).

# Apolochus staudei new species (Fig. 7)

Amphilochus neopolitanus Della Valle, fide Staude, 1987: 379, fig. 18.40?;—Austin 1985: 593. non: Amphilochus neopolitanus cf. Delle Valle fide Barnard 1962 (California).

Material Examined: 15 specimens at 7 stations:

#### **BRITISH COLUMBIA**

## North central coast, ELB Stns., 1964:

H12, Stephens I., NW end (54°11'N, 130°48'W), *Phyllospadix*, kelp, LW, July 13. - 1 Q; NMCC1992-0222. H20, McCauley I., NH end (53°43'N, 130°22'W), fine sand, LW, July 17 - 2 QQ, NMCC1992-0221. H21, N. end Banks I. (53°25'N, 130°10'W), 40-60 m. - 1  $\sigma$ ; 2 QQ; NMCC1992-0223. H22, 1/2 mile off Larsen Hd., Banks I. (53°34'N, 130°34'W), kelp on sand and shell, 20 m dredge. July 17. -

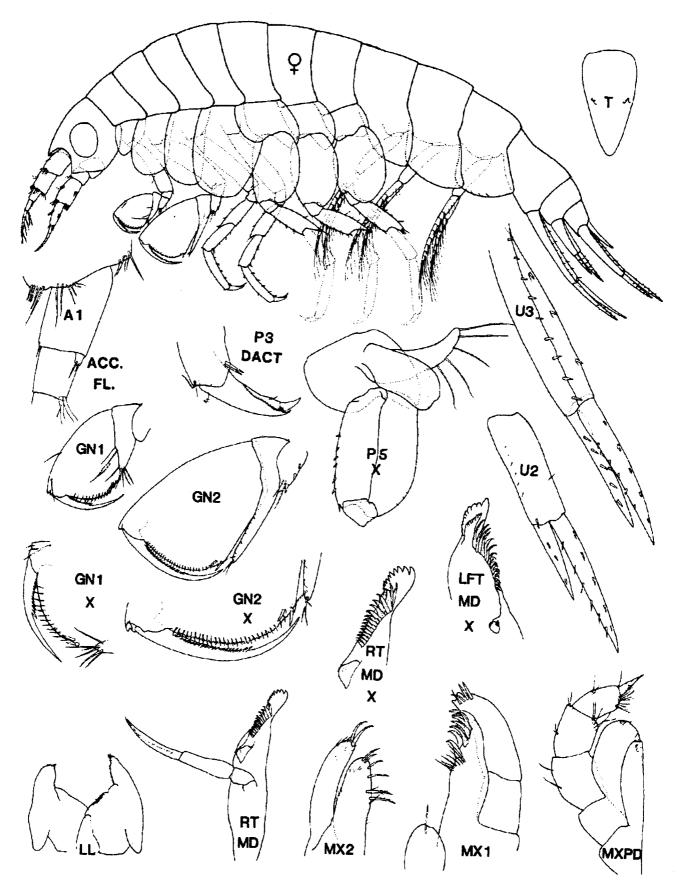


Fig. 7. Apolochus staudei, n. sp. Female ov. (2.4 mm) Holotype. N end of Rennison I., B. C.

1 Q, 2 imm, NMCC-0224. H30, N. end of Rennison I. (52°51'N, 129°21'W), kelp and sand, 8-25 m dredge, July 20. - Q Holotype (slide mount); 34 QQ Paratypes, 3 & Allotypes, 9 im, Paratypes, NMCC1992-0226. H53, Townsend Pt., St. John Harbour (52°12'N, 128°28'W), Phyllospadix, kelp, Corallina, bedrock, LW, Aug. 7. - 1 Q, NMCC1992-0230.

San Juan's Brown I., E. side, Queen Charlotte Str. (51°19'N, 127°46'W), 50-60 m dredge, FRB?, 1983. - 1 Q, NMCC-1992-0253.

Diagnosis: Female ov. (2.4 mm) (holotype).

Rostrum medium. Eye large, subovate. Antennae short, subequal. Antenna 1, peduncular segment 1 & 2 short and deep, 3 small; flagellum 6-7 segmented; accessory flagellum minute. Antenna 2, flagellum 6-7 segmented.

Mandibular molar small, broadly triangular, with apical setules. Left mandible, lacinia 8-9 cuspate; spine row with 15-17 slender blades, distinctly largest distally; incisor multidentate; palp segment slightly longer than 2, inner margin finely pectinate, apex with single short seta. Maxilla 1, apical margin of inner plate nearly vertical, with 7 spine-teeth and 6-8 setae at inner angle; palp segments stout, segment 1 large. Maxilla 2, plates medium, inner plate with 6 marginal setae, proximally plumulose. Maxilliped, inner plate tall, narrow, apex subtruncate; outer plate medium broad, tall, inner margin smooth; palp segment 2 only slightly exceeding outer plate.

Coxa 1 short, little occluded by 2; coxae 2-4 successively deepening, rounded below. Gnathopods 1 & 2 distinctly subchelate. Gnathopod 1, propod slightly expanding distally, palm convex, oblique; dactyl slender body denticulate behind, unguis elongate, slightly exceeding palmar angle; carpus narrow, lobe medium, extending about 1/2 posterior margin of propod. Gnathopod 2, propod large, broadening distally, palm convex, finely crenulate, nearly vertical, sharply demarcated at posterior angle by paired spines; dactyl slender, body finely pectinate behind, unguis elongate slightly exceeding palm; carpus short, posterior lobe elongate extending length of posterior margin of propod.

Peraeopods 3 & 4 medium, segment 6 with 4 posterior marginal spines; dactyls short, unguis short. Coxae 5-7 normally posterolobate, hind lobes acute below, margins unarmed. Peraeopods 5-7 regularly homopodous; bases regularly expanded, posteriorly slightly increasing in size; segment 4 not elongate; dactyls short.

Pleon side plates 2 &3, gently convex below, hind corners not acuminate. Pleopod rami distinctly longer

than peduncle, 9-10 segmented. Uropod 1 slender, rami slightly unequal, margins weakly spinose. Uropod 2, rami marginally short-spinose; outer ramus >1/2 inner. Uropod 3 elongate, greatly exceeding telson; rami medium, unequal, marginally spinose. Telson narrowly triangular, length about twice width, apex sharply rounded.

Brood plates medium broad; plate 5 narrow, with 5-6 longish distal marginal setae.

Etymology: The species name recognizes Dr. Craig P. Staude, Friday Harbor Laboratories, for his outstanding contribution to knowledge of the systematics and ecology of amphipods of the northeastern Pacific marine region.

**Distributional Ecology:** Known only from the Queen Charlotte Sound coast of north central British Columbia south to northern Queen Charlotte Strait, LW and shallow sublittoral to 60 m in depth.

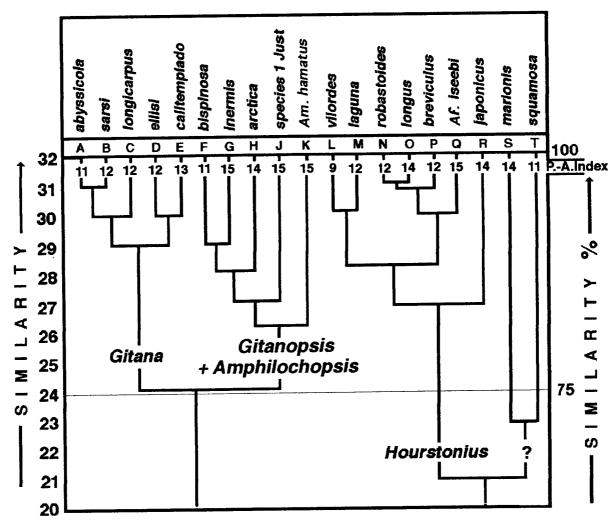
**Remarks:** Although most closely related to A. barnardi, Amphilochus staudei differs mainly in the form of the gnathopods, especially gnathopod 1, the distinctly posteriorly pectinate dactyls, the form of the maxilliped plates and palp, and the slightly longer and more acutely pointed telson.

# **DISCUSSION**

#### Phyletic Reclassification

In phyletic revisions of the Gammaridea, family Amphilochidae has been placed within superfamily Leucothoidea (Bousfield 1979, 1982, 1983, 2000, 2001; Bousfield & Shih 1994). Lowry & Myers (2000) have recently proposed superfamily Iphimedioidea which combines former leucothoidean families Iphimedidae, Lafystiidae, and Laphystiopsidae witheusiroidean families Epimeridae and Amphithopsidae.

Remaining within Leucothoidea are families Leucothoidae, Anamixidae, Amphilochidae, Pleustidae, Stenothoidae, Thaumatelsonidae, and Cressidae. However, the Stenothoidae, Thaumatelsonidae, and Cressidae differ markedly in lacking a conspicuous rostrum, but exhibit sexually dimorphic gnathopods, strongly reduced maxilliped plates, frequent fusion of urosome segments and/or telson, and 2-segmented outer ramus of uropod 3. Furthermore, the gnathopods are frequently sexually dimorphic. Bousfield (2001b) formally utilizes the superfamily name Stenothoidea to encompass these three families. Based on the principal



Fig, 8. Phenogram of morphological similarities abnd possible phyletic relationships within *Gitana*, *Gitanopsis*, and *Hourstonius*.

character state differences noted above, and pending further detailed analysis, the superfamily name Stenothoidea is herewith formally recognized. Family Amphilochidae therefore remains within superfamily Leucothoidea.

# Reorganization of genera

Taxonomic placement of species within northern hemispheric genera of amphilochid amphipods has long been unsatisfactory. Difficulties encountered, and partial generic revisions attempted by Lincoln (1979), Karaman (1980), and to some extent Krapp-Schickel (1982) and Hirayama (1983), are reflected in the number of character state "variables" specified by Barnard & Karaman (1991), especially within the genera Gitana, Gitanopsis, Amphilochus, and Amphilochopsis. Likewise, the present study encountered a persistence of unsatisfactory taxonomic categorizations within North Pacific species, and absence of previous numerical analysis. The authors have here attempted a

realignment of species on more comprehensive and more natural generic conceptualizations.

The present treatment of species and genera utilizes a semi-phyletic modification of the UPGMA system of Sneath & Sokal (1973), as in previous analysis of other NorthPacificamphipodgroups (e.g., Jarrett & Bousfield 1994; Bousfield & Chevrier 1996). Character states are ordered plesio-apomorphically and relative phyletic placement of a taxon is represented by a numerical sum of plesiomorphic, intermediate, and apomorphic character states values (0, 1, and 2, resp.) in a Plesio-Apomorphic (P.-A.) Index. Tabular data on which the resulting phenograms are based are considered overly bulky and repetitive for publication here, but may be supplied on request.

Fig. 8 graphically portrays morphological similarities within species of *Gitana*, *Gitanopsis* sens. str. (effectively encompassing the arctic monotypic genus *Amphilochopsis*), and boreal-warm temperate, North Pacific and North Atlantic species of *Gitanopsis* (=

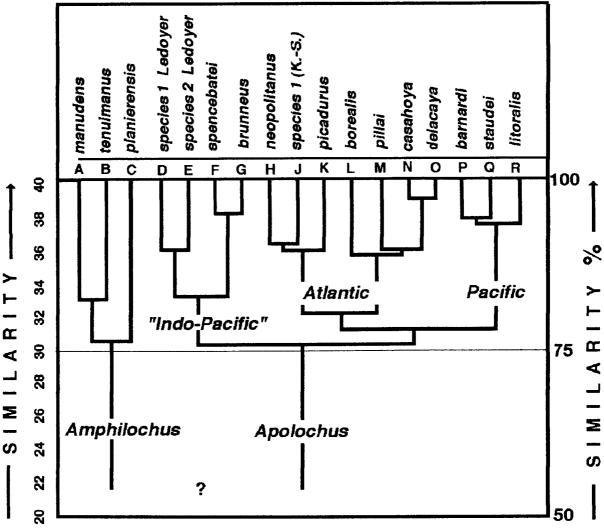


Fig. 9. Phenogram of morphological similarities and possible phyletic relationships within the genera *Amphilochus* and *Apolochus*.

Hourstonius). Species groupings are distinct above the 75% similarity level within Gitana, Gitanopsis sens. str., and Hourstonius. The former two genera cluster at about the 75% similarity level, with the genus Amphilochopsis somewhat intermediate between the two. However, the genus Hourstonius remains distinct below the 60% similarity level. The eastern Pacific species, H. vilordes (J.L. Barnard) is similar to species of both the western Pacific and Caribbean (Gulf of Mexico) regions, described mainly by Hirayama and McKinney, respectively. Not unexpectedly it is relatively remote from species of the South Atlantic (e.g., H. magdai, H. squamosa) described elsewhere.

This limited analysis tends to validate generic realignment of species within *Gitanopsis* Sars, 1895, and formal recognition of the generic concept *Hourstonius*. However, further study of relationships of species of the southern hemisphere, and of groups commensal with crustaceans, is clearly needed.

Fig. 9 portrays character state similarities within the North Atlantic genus Amphilochus Bate (sens. str.), based on the type species A. manudens, and species of the boreal-warm-temperate North Pacific, North Atlantic and Mediterranean-Indo-Pacific regions (= Apolochus, n. g.). Species groupings are distinct above the 75% similarity level within both groups, but the two genera remain distinct below the 50% similarity level. Apolochus here encompasses three subgroups: (1) an eastern Pacific complex of A. litoralis (Stout, 1912) and two closely similar species newly described herein; (2) a more speciose, essentially Atlantic (Caribbean-Mediterranean) subgroup encompassing A. neopolitanus Della Valle, A. picadurus (J. L. Barnard) and several superficially similar species [e.g., figured but unnamed by Lincoln (1979), Krapp-Schickel (1982)]; and (3) a Mediterranean Indo-Pacific subgroup encompassing A. brunneus, A. spencebatei and species attributed to "A. neopolitanus" by Ledoyer (1977).

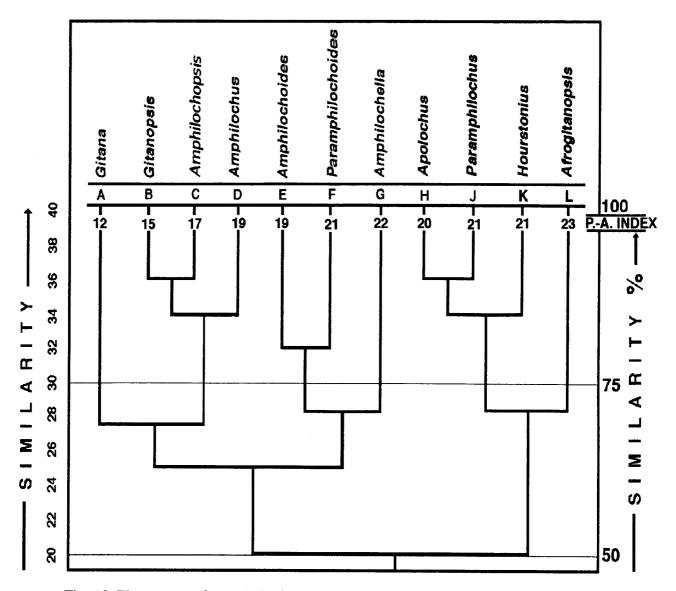


Fig. 10. Phenogram of morphological similarities and possible phyletic relationships within genera of Amphilochidae.

Species realignment within Amphilochus Sars, 1895, and formal recognition of the generic concept Apolochus seem clearly in order. Species attributable to genus Apolochus exhibit significantly higher A.-P. indices than the three more primitive species here attributed to Amphilochus Bate sens. str. However, further study, especially of Indo-Pacific regional taxa, is much needed.

Fig. 10 is a phenogram of morphological similarities within genera of family Amphilochidae, mainly of the northern hemisphere. The genera form three main subgroups at, or slightly below, the 75% similarity level: (1) an Arctic-North Atlantic complex of the primitive genus *Gitana* and the closely related *Gitanopsis*, *Amphilochopsis* and *Amphilochus*, having low P.-A. values ranging from 12 to 19; (2) a Mediterranean-Indian oceanic complex of advanced genera

Amphilochoides, Paramphilochoides and Amphillochella, with intermediate P.-A. values of 19-21; and (3) a moderately advanced group of the closely related genera Hourstonius and Apolochus "satellite genera" Paramphilochus and Afrogitanopsis respectively, all with intermediate to high P.-A. values of 20-23. The two principal genera encompass about half the known species within the entire family.

The analysis further tends to confirm generic realignment of species within the new generic concepts of *Hourstonius* and *Apolochus*. The overall morphological closeness of these two genera underscores a need for use of multiple-character analysis, and avoidance of single- or few-character diagnoses, in defining taxonomic concepts at generic level and higher.

# Phyletic and Biogeographic Conclusions

Members of family Amphilochidae are ectocommensals on gorgonians, hydroids and other sessile marine invertebrates. Their overall body and limb morphology is relatively primitive, in many ways similar to that of leucothoidean family Pleustidae. Such is expressed in the distinct rostrum, deep coxal plates, homopodous peraeopods, posterolobate coxae, and lanceolate uropod rami. However, morphological specializations including near-total loss of an accessory flagellum, modification of mouthparts for carnivory, and development of strongly subchelate gnathopods, are considered apomorphic.

Members of the primitive genus Gitana are mainly arctic-boreal and deep water, those of the more advanced genera Gitanopsis (sens. str.), Amphilochopsis, and Amphilochus (sens, str.) are actic-boreal and temperate, whereas those of the most advanced genera Hourstonius, Apolochus and Paramphilochus exhibit temperate, warm-temperate distributions in the northern hemisphere. These trends somewhat reflect the significance of higher phyletic classification in biogeographical relationships of North American marine amphipod taxa (Bousfield 2001). In this scenario, the most primitive higher taxa tend to occur mainly in Arctic waters, secondarily along the Pacific coast, and the most advanced taxa in the North Atlantic and Gulf This phenomenon may reflect two major long-term evolutionary factors. Firstly, morphological evolution proceeds at a higher rate at higher ambient temperatures, and conversely at a lower rate at lower temperatures. Secondly, it may also reflect the longterm stability of a given marine region over geological time, wherein faunas of the ancient Pacific coast prove to be more primitive than those of the relatively recently developed North Atlantic Basin. As a corollary, the presence of ancient and relict coastal marine faunas within a higher taxon are more likely to be found in cold-temperate and Arctic regions, especially of long-Conversely most highly adterm geological age. vanced faunas are likely to be found in warm temperate and tropical regions, especially those of relatively recent geological origin.

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# **Legend for Figures**

<b>A</b> 1	_	antenna 1	MD	-	mandible
A2	_	antenna 2	MX1	-	maxilla 1
ACC FL	_	accessory flagellum	MX2	-	maxilla 2
ABD		abdomen	MXPD	-	maxilliped
Br PL	_	brood lamella	P5-7	-	peraeopods 5, 6, 7
CX	-	coxal plate	PLP	_	pleopod
	-	<u>-</u>	RT	_	right
EP	-	abd. side plate	SP	_	spine
GN1	-	gnathopod 1	T	_	telson
GN2	-	gnathopod 2	Û	-	uropod
HD	-	head	o o		male
LFT	-	left	<del>-</del>	-	
LL	-	lower lip (labium)	φ	-	female

# The Amphipod genus *Anisogammarus* (Gammaroidea: Anisogammaridae) on the Pacific coast of North America.

# E. L. Bousfield, Research Associate Royal Ontario Museum, Toronto, ON, Canada M5S 2C6.

#### **ABSTRACT**

The genus Anisogammarus Derzhavin (sens. lat.) (Amphipoda: Gammaroidea: Anisogammaridae) is represented in the eastern North Pacific coastal marine region by A. pugettensis pugettensis (Dana), A. slatteryi, n. sp., A. epistomus, n. sp., and A. amchitkana, n. sp. Anisogammarus tvetkovae, new species, occurs in the northwestern Sea of Japan and Okhotsk Sea, along with the western Pacific subspecies A. pugettensis dybovskyi Derzhavin. Anisogammarids are free-living omnivores, occurring in the shallow sublittoral of cold-water, high salinity coastlines. The large coxal gills, each bearing accessory gills, are presumably advantageous for survival in partly anoxic habitats where they commonly occur.

# Introduction

The first anisogammarid species was described under the name Gammarus pugettensis by J. D. Dana (1853) from material collected in Puget Sound by the U. S. Exploring Expedition. Common regional amphipods described by Stimpson (1857) contained the sole anisogammarid, Gammarus confervicolus. Stebbing (1906) summarized records of four Pacific anisogammarid species under various names within Gammarus (sens. lat.), mostlywithin family Gammaridae (sens. lat.). However, Stebbing (loc. cit.) assigned Dana's "Gammarus pugettensis", also listed by Holmes (1904), to genus Liljeborgia.

During the first half of the 20th century, few anisogammarids were recorded from the North American Pacific coast. Barnard (1954) more fully illustrated Dana's Anisogammarus pugettensis based on extensive collections from Oregon, and Shoemaker (1955) described A. macginitiei from Pt. Barrow, Alaska. Extensive amphipod material from British Columbia and adjacent regions was collected by National Museum of Canada marine biological expeditions during 1955-1980 (see below). Mainly from this material, the author (1979, 1981) described and illustrated a number of new anisogammarid genera and species. Anisogammarus macginitiei was also transferred to the new genus Barrowgammarus where is used as an outgroup in later analysis (p. 45). Some of these, and earlier records, are embodied in the general faunistic guides and catalogues of Ricketts & Calvin (1968), Barnard (1975), Austin (1985), and Staude (1987).

Gurjanova (1951) summarized early work on western Pacific anisogammarids, updated by the comprehensive study of Tzvetkova (1975) and the world-wide compilation of Barnard & Barnard (1983). Ishimaru (1994) summarized earlier records from Japan. The present study attempts to provide a more complete analysis of the systematics and distributional ecology of North American Pacific species of *Anisogammarus*.

# Acknowledgments

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The original taxonomic work was performed as a staff member of the National Museum of Natural Sciences at the Holly Lane Laboratory, Ottawa, ON, 1979-1983. Original line illustrations were prepared with the capable assistance of artist Floy E. Zittin, Cupertino, CA.

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# **SYSTEMATICS**

# Anisogammaridae Bousfield

Anisogammaridae Bousfield 1977: 295;—Bousfield 1979: 307 (+key to genera);—1981: 72-76, figs. 1-4;—:259;—1983: 267;—Barnard & Karaman 1991: 114;—Ishimaru 1994: 46;—Bousfield & Shih 1994: 129. Anisogammarids: Barnard & Barnard 1983: 582 (+key to genera).

Gammaridae (part): Stebbing 1906: 364; — Gurjanova 1951: 760; — Barnard, 1969 (part): 242; — Tzvetkova 1975 (part): 30.

Type Genus: Anisogammarus Derzhavin, 1927: 8.

Genera: Barrowgammarus Bousfield, 1979: 321; Eogammarus Birstein, 1933: 149; Spinulogammarus Tzvetkova, 1972: 954; Spasskogammarus Bousfield, 1979: 332; Locustogammarus Bousfield, 1979: 322; Jesogammarus Bousfield, 1979: 335; Ramellogammarus Bousfield, 1979: 337; Carineogammarus Bousfield, 1979: 343.

Diagnosis: Head, rostrum very short; inferior antennal sinus large, occasionally with narrow posterior notch. Antennae medium, subequal, accessory flagellum prominent, Antenna 2, peduncle large, flagellum occasionally calceolate.

Mouthparts regular, little modified. Lower lip, inner lobes variously developed. Mandible: left lacinia 5-dentate; spine-row strong.

Peraeon dorsally smooth. Coxal plates 1-4 medium deep, regular; plates 5 & 6 shallowly anterolobate. Gnathopods powerfully subchelate (male); gnathopod 1 larger than 2; palmar margins bearing peg spines (male), simple or pectinate (female); carpus short, lobe small. Peraeopods 5-7, bases weakly heterpodous; dactyls short. Peraeopods 2-7 with large coxal gills, 2-5 with 2, P6 with 3, and P7 with 1-2 accessory gills.

Pleosome and urosome variously dorsally carinate, toothed, spinose, or smooth. Uropods 1 & 2, rami usually short, linear, spinose. Uropod 3 large, subaequiramous, terminal segment small. Telson bilobate, with marginal and apical spines. Female brood plates large, unequal, with numerous long marginal setae.

Remarks: During amplexus, males position themselves dorsally and grasp the anterior margin of coxal plate 4, typically by means of the dactyl and propod of gnathopod 1 (Bousfield & Shih 1994).

Allometric growth changes are often noticeable. Compared with the adult stage, juveniles tend to be armed with fewer but relatively large spines and dorsal tooth of urosome 2, and the inner ramus of uropod 3 is relatively short.

# Anisogammarus Derzhavin

Anisogammarus Derzhavin, 1927:8; — Gurjanova 1951: 776; — Tzvetkova 1975: 94 (part, + key to species); — Barnard & Barnard 1983: 584; — Ishimaru 1994: 46.

Type species: Gammarus pugettensis Dana, 1853

Species: Anisogammarus pugettensis dybovskyi Derzhavin, 1927; A. slatteryi n. sp. (p. 34); A. epistomus n. sp. (p. 36); A. amchitkana, n. sp. (p. 39); A. tzvetkovae, n. sp. (p. 41).

Diagnosis: Anterior head lobe acute above, rounded below, with shallow lateral notch. Eye medium, reniform. Antenna 1 shorter than 2; accessory flagellum well developed. Antenna 2, peduncle stout, segment 5 shorter than 4, often with clusters of fine spines with extended tips (male); flagellum lacking calceoli (male).

Mouthparts basic, with few modifications. Lower lip, inner lobes incompletely developed. Mandible: left lacinia 5-dentate; palp slender, terminal segment with well developed "D" spines and "E" setae, but only one cluster of "A" setae (of Cole 1980). Maxilla 1, palp 2-segmented. Maxilla 2, inner plate with full row of oblique facial setae. Maxilliped, inner plate with 3 apical spine teeth; palp setose, not raptorial.

Coxae 1-4 medium deep, smooth, rounded below; coxae 5 & 6 weakly anterolobate. Gnathopod 1 (male) larger than 2 but usually similar in form; in the female it is much larger and of different form than gnathopod 2; carpus short; propodal palm (male) with peg-spines variously developed. Peraeopods 3 and 4, segment 5 short, dactyls short. Peraeopods 5-7, bases broadened proximally, weakly heteropodous; segment 5 longer than 4; peraeopod 7 not longer than 6. Coxal gills on peraeopods 2-5 and 7 each with 2 and on peraeopod 6 with 3, linear accessory gills. Female brood lamellae broad, with numerous long simple marginal setae.

Pleosome smooth above, lacking spines or setae; Epimeral plate 3, hind corner quadrate or slightly produced. Pleopods regular, outer ramus basally with split-tipped "clothespin" spines. Urosome 1 with middorsal hump and 3 groups of spines; uropod 2 with

# KEY TO SPECIES OF ANISOGAMMARUS AND BARROWGAMMARUS

1. Antenna 1 and 2 subequal in length; peraeopods 5-7, bases sublinear, not broadened posteriorly; urosome segments 1 & 2 lacking dorso-lateral spines or teeth; uropods 1 & 2, rami lanceolate, unarmed
2. Gnathopod 2 (\$\sigma\$) small, weakly subchelate, as in \$\mathbb{Q}\$; uropod 3 (\$\sigma\$, \$\mathbb{Q}\$), rami with marginal spines, lacking setae; telson short, length not greater than width
3. Gnathopods 1 & 2 (\$\sigma\$), propodal palmar margins with heavy blunt peg spines; mandibular palp elongate; peraeopod 4, segment 4 elongate ~2X segment 5
<ol> <li>Antenna 1, peduncular segment 2 short, length &lt;1/2 segment 1; epimeral plate 3, hind corner squared or slightly acuminate; urosome 1 with 1-2 weak dorsolateral spines; mandibular palp segment 3 short, "D" spines enlarging distally</li></ol>
5. Coxae 1-3, lower margin richly armed with longish setae; uropod 3 inner ramus markedly shorter than (2/3 length of) outer ramus; telson. distal marginal cluster with one very large, elongate spine (>2X length of other spine)
6. Antenna 1 (3), peduncular segment 5 with scattered clusters of slender, tip-extended spines; uropod 3, outer ramus broad nearly straight

acute mid-dorsal tooth, and weak postero-lateral cusp on each side. Uropods 1 & 2 short, stout. Uropod 3 subequally biramous, margins spinose and/or plumose-setose; outer ramus with short terminal segment. Lobes of telson each with two groups of lateral spines.

**Distribution:** Panboreal North Pacific, in algae, mainly on sedimentary bottoms, low intertidal to ~30 m.

Anisogammarus pugettensis pugettensis (Dana) (Fig. 1)

Gammarus pugettensis Dana, 1853: 957, fig. 1;—Holmes 1904; 239.

AnisogammaruspugettensisGurjanova1951(part):777, fig. 541;—Barnard 1954: 13, pls. 12-14;—Tzvetkova 1975(part):98, fig. 35;—Bousfield 1979:310 (key);—Bousfield 1982: 72, fig. 1;—Barnard & Barnard 1983 (part): 584, fig. 38;—Austin 1985: 607;—Staude 1987: 383.

Material Examined: More than 600 specimens in 99 100 lots.

ALASKA.

SE Alaska, ELB Stns., 1961 (see Bousfield & McAllister, 1962):

A5, Tongass Narrows, near Ketchikan - O (17 mm); lot #2 - Q ov (11.5 mm), **fig'd specimens**, CMNC 1980-0053; A7,

Bostwick Bay, June 2/61 - Q (br. II) (14.5 mm), slide mounts, CMNC 1980-0084; Lot #2 - 2  $\Omega$ ; Lot #3 (18  $\Omega$  ); lot #4-5QQov, CMNC 1980-0087; CMNC 1980-0092; CMNC 1980-0094; A11 (100 of of & QQ ov, small im); Lot #2 (Q, 1 im); Lot #3 ( $\sigma$ , im); A12 (22  $\sigma\sigma$ , 33 QQ ov, 5 im), Lot #2 -1Qov); A18(1 im); A16(1 im); A20 (1 $\sigma$ , 1 $\varphi$ ov, 2 im); A25(Q, 2 im); A27 (100 large of of (to 15.5 mm); A27 (Lot #2-12 QQ ov); A30 (4 QQ ov, 4 im); A33 (5 QQ ov, 3 juv); A34 (5 $\sigma\sigma$ , 4QQ ov, 5 im); A37 (1 $\sigma$ ); A43 (1Q ov), Lot #2 - 12 &&, 15 QQ, 20 im; #3 - 14 &&, 33 Q Q ov, 15 im); A48 (1 QQ ov); A54 (1 juv); A55 (1 of, 1Q, Lot #2 - 12 im); A65 (1 o); A67 (1 Q, 14 juv); A71 (12 oo, 20 QQ, 14 im; lot #2 -30 im); A73 (12 or , 9 QQ ov, 5 im); Lot #2 (8 or , 14 QQ, 2 im); A 81 (10 ord, 7 99 ov, 30 im); A83 (3 ord, 10 99 ov, 17 juv); A84 (60 ord, QQ ov large); A86 (10); A88 (300, 12 QQ, 2 im); A93 (24 im); A136 (1 of, 13 im); A139 (3 of of 5 QQ, 5 im); A140 (9 or or, 15 QQ, 30 im & juv); lot #2 (1 Q. 3 im); A141 (10°); A153 (1 im); A 171 (2 juv); A174 (1 o, small); Lot # 2 (25 adult, 17 juv).

**ELB Stns., 1980** (see Bousfield & Jarrett 1981): S14L1 (3 imm).

## **BRITISH COLUMBIA:**

Queen Charlotte Islands, ELB Stns., 1957 (see Bousfield 1963):

H5 (6 σσ, 8 QQ, 12 im); N4 (2 juv).

North Central Coast, ELB Stns., 1964 (see Bousfield 1968):

H5 (1 juv); H13 (1 Q ov, 35 im); H16 (200, 3 QQ, 12 im); H17 (1 Q, 12 im); H18 (1 juv); H39 (1 juv); H50 (2 im); H56 (4 OO, 10 QQ, 13 juv); Lot #2 (8 im).

Pearl Harbour, nr. Prince Rupert, silty sand, eel grass, LW, D. E. McAllister, June 23/65 - 10.

Northern Vancouver Island, ELB Stns., 1959 (see Bousfield 1963):

V17 (7 $\sigma\sigma$ , 10 QQ ov, 11 im); V18 (1 $\sigma$ , 3 im); V22 (75 spms., mostly large QQ ov); lot #2 (1 $\sigma$ , gnathopods dissected); N18 (1 $\sigma$ , 4QQ, 17 juv).

## Southern Vancouver island, ELB Stns.

1955 (see Bousfield 1958):

F3 (1 im); F4 (Q ov, 13 im); F6 (1 or, 43 QQ, 5 im, dried); M2 (1 im); M2 (1 or, 2 QQ); M5 (29 im & juv); G4 (3 juv); G10 (5 im & juv); G11 (8 im & juv); G15 (1 or, 3 QQ, 2 im).

**1970** (for Stns. of 1970-80, see Bousfield & Jarrett 1981): P717 (sev. im).

1975:

Friiday Harbor, May /75 - 2 of (20 mm).

1976:

Pacific Environmental Institute, West Vancouver, in halibut tank, June 8 - 1 & (18 mm).

#### 1977:

B2 (300, 700, 5im); B7a, Willis Beach, Oak Pt., Victoria, May 19 - 18 00, 30 00 subad (16 mm), slide mount, CMNC 1980-0029; CMNC 1980-0038; CMNC 1980-0039; E2 (2 00 ov).

## Misc. CMN collections:

Ladysmith Hbr., Vancouver I., B. C., D.B.Quayle coll., June 8/38-27 & Q ov (broken specimens); Saturna I., Bruce Bight, B. C., J.F.L. Carl coll., Aug. 26/55-2 Q Q ov; <u>Ibid.</u>, night light over kelp, Aug 24/55-1 &, 1 Q, 2 juv;

Porpoise Hbr, B. C., 20 m, M. Waldichuk coll., Sept. 24/64 - 3 QQ; <u>Ibid.</u>, Sept. 18/62 - 3 &&, 7 QQ ov, 1 im, NMNS Cat. No. 6-90; Nass Hbr., Iceberg Bay, on dead fish in trap, S. Gorham coll., June 20/65 - 7 &&, 4 QQ ov., 2 im

Off Cordova, Orca Inlet, Prince William Sound, SE Alaska, 13 m dredge, K. E. Conlan, Feb. 18/89 - ♂, ♀ mating pair.

# WASH.-ORE, USA.

ELB Stns., 1955 (see Bousfield, 1958):
F8, Garrison Bay, San Juan I., 9 σσ, 6 QQ, 4 im.
ELB Stns., 1966 (see Bousfield & Jarrett, 1981):
W3 (1 σ, 1 Q, 10 im); W4 (1 im); W5 (1 juv); W7, Meadow
Point, Puget Sound, July 17. - σ (14.0 mm); Q ov. (11 mm),
slide mounts, CMNC 1980-0065; Ibid., Lot # 2 - 20 spms;
W10 (4σσ, 7 QQ ov, 5 im); W11 (1 juv); W18 (1 juv); W22
(1 im); W33 (σ, 10 im); W39 (6 juv); Ibid. (Lot #2 - 3 σσ,
7 QQ, 35 im); W44 (3 im); W69 (Q ov).

**Diagnosis** Male (16 mm): Anterior head lobe slightly incised. Eye medium, sub-reniform. Antenna 1, peduncular segment 2 medium, length 1/2 peduncle 1; flagellum ~20-segmented, little exceeding peduncle of antenna 2. Antenna 2, peduncular segment 5=4, with few clusters of tip-extended slender spines; flagellum 17-segmented, shorter than peduncle.

Mandibular spine row with 8-9 blades; palp relatively short; segment 3 > 2/3 segment 2, "D" spines uniform, extending 2/3 of inner margin; segment 2, beta and gamma setae very short. Maxilla 1, palp little broadening distally. Maxilliped, inner plate apically truncate, outer plate little broadened; palp segment 3 regular, length > 1/2 segment 2.

Gnathopods 1 & 2 stout, dactyls with short unguis; Gnathopod 1, palmar angle with 8-10 inner and outer rows of simple spines. Gnathopod 2, propodal posterodistal angle with inner submarginal row of 6 short simple spines. Peraeopods 3 & 4, segment 6 relatively

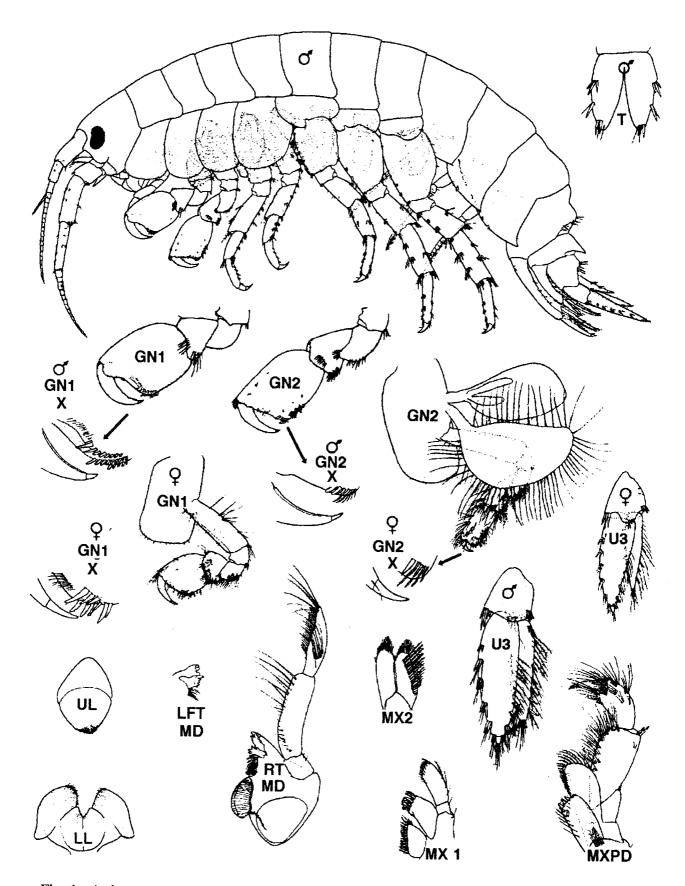


Fig. 1. Anisogammarus pugettensis pugettensis (Dana). O (17 mm); Q ov. (11.5 mm). Tongass Narrows, SE alaska.

short, arched, little longer than segment 5. Peraeopod 7, basis with slight postero-distal marginal excavation. Coxal gill on peraeopod 7 relatively large, broad.

Epimeral plates 2 and 3, hind corner acute, distinctly produced. Urosome 1, mid-dorsal hump medium, with cluster of 8-10 medium spines; lateral clusters with 3-4 spines. Urosome 2 with strong median tooth and single postero-dorsal cusp on each side. Urosome 3 with mid-dorsal and dorsolateral clusters of 2-3 medium spines. Uropods 1 & 2, rami shorter than peduncles, margins moderately spinose. Uropod 3, outer ramus medium broad, inner margin plumose-setose, slightly but distinctly longer than slender inner ramus; terminal segment short.

Telson lobes medium, each side with proximolateral group of three spines, and distolateral longish marginal spine.

Female ov. (14 mm). Gnathopod 1, propod relatively large, subquadrate, posterodistal angle with groups of 3 inner, and 5-6 outer submarginal simple spines. Gnathopod 2, propod subrectangular, postero-distal angle with submarginal row of 1 simple and 4 pectinate spines; brood plate large, broad, with numerous marginal setae. Uropod 3, rami shorter than in male, inner margin plumose-setose.

**Distributional Ecology:** Aleutian Islands and S. E. Alaska, through B. C. and Washington state south to Coos Bay, Oregon, and Northern California, low intertidal to subtidal, in *Ulva* and *Enteromorpha*, and in partially anoxic bottom deposits of wood chips (Waldichuk & Bousfield 1962).

**Remarks:** A very similar form has been recorded under this name from the northern Sea of Japan and Sea of Okhotsk by Gurjanova (1951) and Tzvetkova (1975).

### Anisogammarus pugettensis (Dana), subsp. dybovskyi Derzhavin (Fig. 2)

Anisogammarus dybovsky Derzhavin, 1927: 8;— Stephensen 1944: 47, figs. 10. 11;—Ishimuru 1994 (part): 46.

Gammarus pribiloffensis Pearse, 1913: 571, fig. 1. Anisogammarus pugettensis Gurjanova 1951 (part): 777, fig. 541;—Tzvetkova 1975 (part): 99, fig. 35;—Ishimaru 1994 (part): 46.

### **Material Examined:**

3 lots from East Kamchatka, USSR, K. Vinogradov coll.,

1933 - & (13 mm), slide mount; 2 & & (13 mm); Q ov. (11 mm), slide mount (identified as A. pribilofensis by E.F. Gurjanova, 1933), Zoological Museum collns., St. Petersburg, Russia.

### Alaska-Bering Sea P. Slattery coll:

Mukmuk Bay, St. Lawrence I., 40 ft. scoop, July 1/83 - 3 QQ ov, 3 juv, IZ 1989-002.

NE St. Lawrence I., July/83 - 1 of (18.5 mm). Unimak I, P. Slattery, June-Oct/82 - 2 of of, 5 QQ.

**Diagnosis:** Male (16 mm). Very similar to *Anisogammarus p. pugettensis* (Dana, 1853) but differing in the following features:

Eye large, reniform. Antenna 2 (male), peduncle 5 subequal to 4, with numerous groups of tip-extended slender spines. Mandibular palp, segment 3 with fewer "A" and "E" setae. Coxa 1 more strongly setose below. Gnathop;od 1, propodal palmar spines shorter and thicker, apex more blunt; carpus, posterior lobe narrow, subacute. Peraeopod 7, posterodistal marginal excavation lined with fine setae; segment 6 with a few clusters of longish setae, rather than clusters of short spines. Epimeral plates 2 & 3, hind corner less strongly produced. Coxal gill 7 small and short relative to coxal gill of peraeopod 6. Uropod 3, outer ramus relatively narrow, length 4X width, curved distomedially. Telson lobes each with pair of distolateral short spines.

Distributional Ecology: Western Pacific coastal marine waters, northern Japan Sea and Sea of Okhotsk to werstern Bering Sea, mostly along open coasts, on sandy and silty substrata, from lower intertidal to depths of 280 m (Tzvetova, 1975); waters around Japan (Ishimaru, 1994); animals scavenge drowned dead human bodies (Kosek et al 1962).

Remarks: This species has been synonymized with A. pugettensis, originally described from the eastern Pacific by Dana, 1853. However, sufficient differences exist (above, and key) as to distinguish the two forms at subspecies level.

# Anisogammarus slatteryi, n. sp. (Fig. 3)

Anisogammarus sp. 1, Austin, 1985: 607.

### **Material Examined:**

#### ALASKA:

St. Lawrence I., Bering Sea, 6 m sand, P. Slattery coll., June 6/87-7 juv (2-4 mm); <u>Ibid.</u>, lot #2-7 juv (2-4 mm). <u>Ibid.</u>, Lot #3. - 40 juveniles, CMN collections.

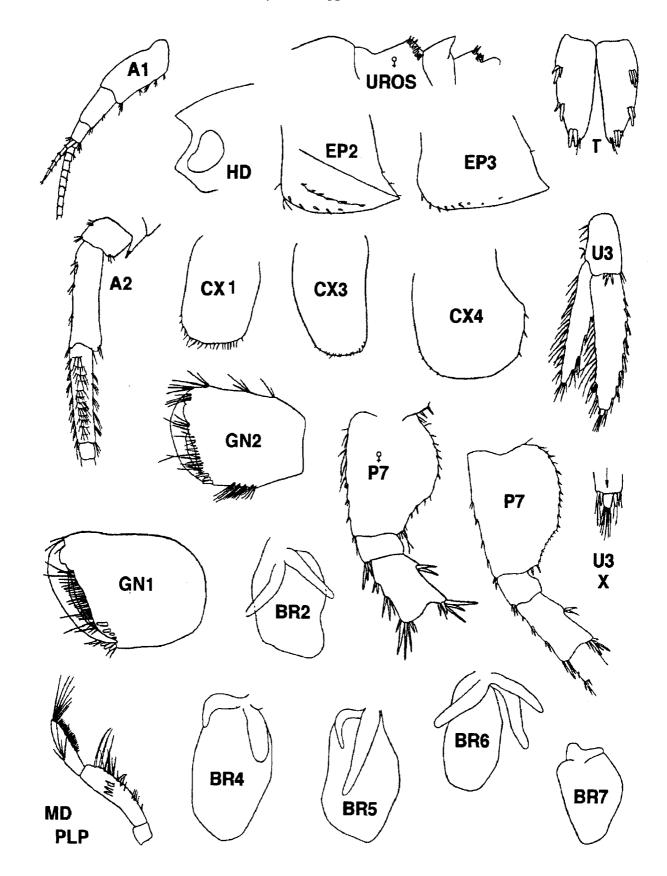


Fig. 2. Anisogammarus pugettensis dybovskyi Derzhavin. O (16 mm), Japan Sea; Q ov (14 mm). Kurile Islands, Okhotsk Sea. [Modified from Tzvetkova (1975)].

#### **BRITISH COLUMBIA:**

ELB Stn. H13, Lulu I., NW end, July 14/64 - Q subadult, br. I (3.5 mm), CMN coll'ns.

Pachena Bay, Vancouver I., whale pit No. 1, 13 m sand, P. Slattery coll., April 13, 1983 - & (8.0 mm), Holotype, (slide mount), CMNC2001-0012; Q ov. (6.5 mm), Allotype, (slide mount), CMNC 2001-0013; & (8.0 mm), Paratype, CMNC 2001-00144; Ibid, J. Kendall & P. Slattery coll., Apr. 15/82 - 1 Q (5 mm), NMNS Cat. No. 121555.

### WASH.-ORE., ELB Stns., 1966:

W46, Leadbetter Point, open sandy beach, LW, Aug. 4, 1966 - 1 & subadult (4.5 mm), CMN coll'ns.

Diagnosis. Male (8.0 mm): Anterior head lobe, frontal margin straight. Eye medium large, subreniform. Antenna 1, peduncular segment 2 very short, length ~1/3 peduncle 1; flagellum ~14-segmented, little exceeding peduncle of antenna 2. Antenna 2, peduncular segment 5 shorter than 4, with scattered clusters of tip-extended slender spines; flagellum 10-12-segmented, shorter than peduncle.

Mandibular spine row with 5 blades; palp relatively short, segment 3 > 2/3 segment 2; segment 3, "D" spines in short row, increasing in length distally. Maxilla 1, palp slightly narrowing distally. Maxilliped, inner plate apically oblique, outer plate little broadened, with long apical pectinate setae; palp segment 3 short, length  $\sim 1/2$  segment 2.

Coxae 2-4, lower margins with 8-10 mainly longish setae. Gnathopod 1 very stout, distinctly larger than gnathopod 2; dactyls with short unguis. Gnathopod 1, palmar angle with inner and outer submarginal rows of 6-7 and 3-4 simple spines respectively. Gnathopod 2, palmar angle with inner submarginal rows of 4 and 2 short simple spines respectively. Peraeopods 3 & 4, segment 6 straight, longer than segment 5. Coxae 3-4 distinctly anterolobate. Peraeopods 5-7, bases distinctly heteropodous; peraeopod 6 slightly the longest. Peraeopods 6 & 7, basis with slight postero-distal marginal excavation. Coxal gill on peraeopod 7 large, about equal in size to that of peraeopod 6.

Epimeral plate 3, hind corner squared. Urosome 1, mid-dorsal hump very low, with 1-2 small spines and weak lateral clusters of 2 spines. Urosome 2 with small median tooth, posterodorsal cusps lacking. Urosome 3 with single mid-dorsal and dorsolateral medium spines. Uropods 1 & 2, rami shorter than peduncles, outer ramus of uropod 2 lacking marginal spines. Uropod 3, outer ramus short, medium broad, margins spinose; terminal segment distinct; inner ramus short, ~1/2 outer ramus, inner margin with few plumose setae.

Telson lobes short, each side with proximolateral group of three spines, and distolateral pair of unequal spines.

Female ov. (6.5 mm). Antenna 2, flagellum 10-segmented. Gnathopod 1 medium large, subquadrate, spination of posterodistal angle similar to that of male. Gnathopod 2, propod short, subrectangular, posterodistal angle with inner submarginal row of 3 simple, outer row of 4-5 pectinate spines. Brood plate large, broad, but with relatively few (<30) marginal setae. Uropod 3, rami shorter than in male, margins spinose, with a few simple setae.

Etymology: The name recognizes marine biologist Dr. Peter F. Slattery, who has contributed broadly to knowledge of marine benthic communities on the Pacific coast of North America.

**Distribution:** Bering Sea south through Vancouver I. to Washington State, LW and subtidally, to depths of ~13 m, on sand and in feeding pits of the gray whale, *Eschrichtius robustus*.

**Remarks:** The species is very similar to *A. epistomus* but differs mainly in its smaller size, normally unproduced epistome, and other character states of the key (p. 31).

The small subadult female from Lulu I., has markedly unequal rami of uropod 3, and long coxal setae.

Although the small specimen from Leadbetter Pt. was not dissected, it exhibits some characteristics of A. slatteryi, including a small mid-dorsal tooth on urosome 2, and relatively large and powerful gnathopods. The inner ramus of uropod 3 is relatively short and thin.

Anisogammarus epistomus, n. sp. (Figs. 4, 4A)

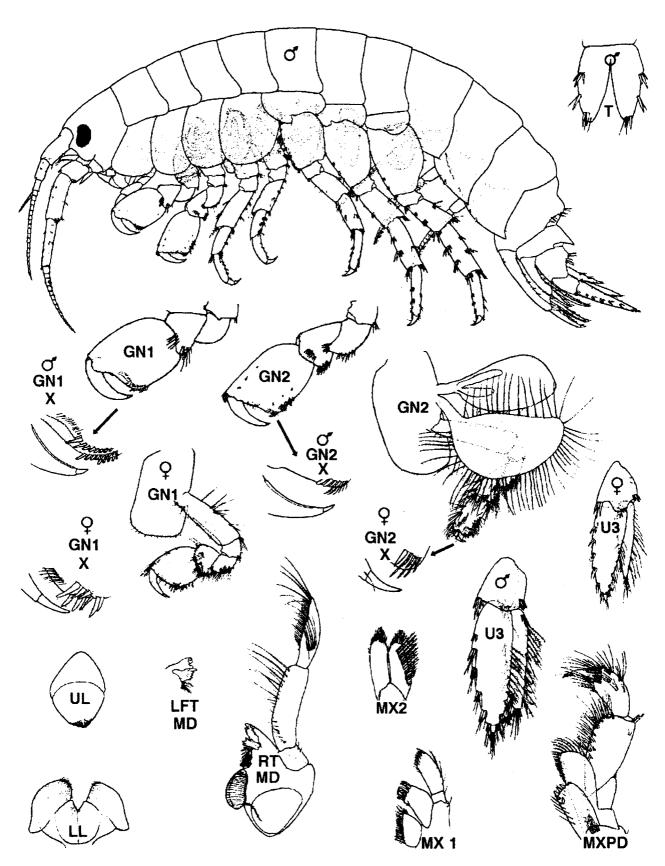
Anisogammarus sp. 2, Austin, 1985: 607.

# Material Examined. BRITISH COLUMBIA: Southern Vancouver I., ELB Stns. 1955:

P6a, Long Beach, SE end Wickaninnish Bay, under algal debris on sand, LW, Aug. 2 -  $\mathcal{O}$  (13.0 mm), **Allotype**, (slide mount), CMNC 2001-0010; 1  $\mathcal{O}$  subadult (10.0 mm), **Paratype**, CMNC 2001-0011.

1970:

P710b, Cape Beale (48° 47.2'N, 125° 13'W), sand, algae, and bedrock, LW level, July 19 - Q ov. (13.0 mm), **Holotype**, (slide mount). Fig'd type specimen, and slide mount, could not be located in CMN collections at time of writing).



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Fig. 3. Anisogammarus slatteryi, n. sp. Male (8.0 mm), Holotype; Q ov (6.5 mm), Allotype. Pachena Bay, Vancouver I, B.C.

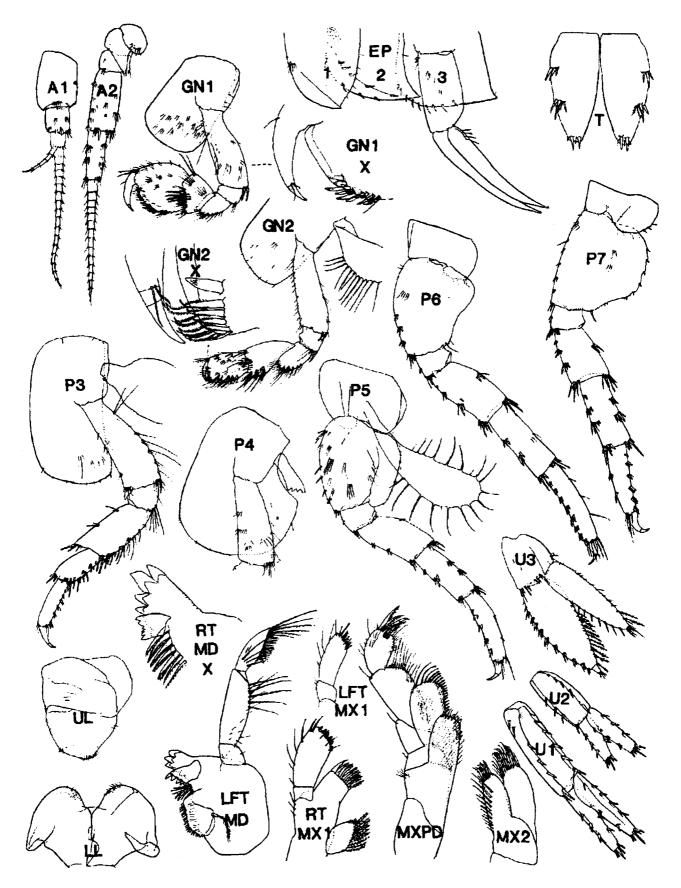


Fig. 4. Anisogammarus epistomus n. sp. Q ov (13 mm), Holotype. Cape Beale, Vancouver I., B.C.

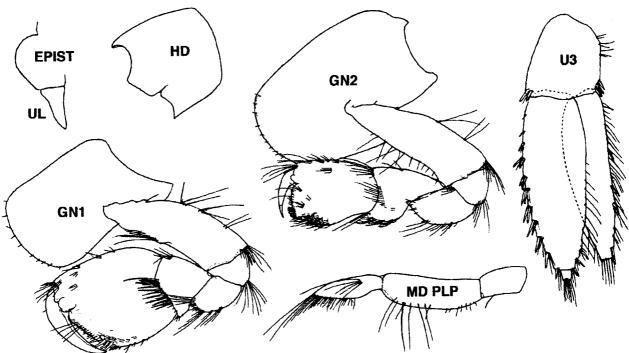


Fig. 4A. Anisogammarus epistomus n. sp. & (13.0 mm), Allotype. Long Beach, V. I., B. C.

**Diagnosis.** Female ov (13.0 mm), Holotype: Anterior head lobe not incised; inferior antennal sinus shallow, posterior "notch" at right angles to it. Eye medium subreniform. Antenna 1, peduncular segment 2 short, ~ 1/3 peduncle 1; flagellum ~16-segmented, distinctly exceeding peduncleof antenna 2. Antenna 2, peduncular segment 5 shorter than 4, surfaces with a few clusters of short spines; flagellum 15-segmented, shorter than peduncle.

Mandibuar spine row with 7 blades; palp relatively short, segment 3 < 1/2 segment 2, "D" spines extending 2/3 of inner margin. Maxilla 1, right palp slightly broadening distally. Maxilliped, inner plate apically subtruncate, outer plate slightly broadened; palp segment 3 medium, length > 1/2 segment 2.

Gnathopods 1 & 2 large, strong; dactyls with short unguis. Gnathopod 1, palmar angle with 8-10 inner and outer rows of simple spines. Gnathopod 2, propodal postero-distal angle with inner submarginal row of 6 short simple spines. Peraeopods 3 & 4, segment 6 relatively short, arched, little longer than segment 5. Peraeopod 7, basis with slight post-erodistal marginal excavation. Coxal gill on peraeo-pod 7 relatively large, broad.

Epimeral plates 2 and 3, hind corner acute, slightly produced. Urosome 1, mid-dorsal hump medium, with cluster of 8-10 medium spines; lateral clusters with 3-4 spines. Urosome 2, with strong median tooth and single postero-dorsal cusps on each side. Urosome 3, with mid-dorsal and dorsolateral clusters of 2-3 me-

dium spines. Uropods 1 & 2, rami shorter than peduncles, margins moderately spinose. Uropod 3, outer ramus medium broad, inner margin plumose-setose, slightly but distinctly longer than slender inner ramus; terminal segment short.

Telson lobes medium, each side with proximolateral group of three spines, and distolateral longish marginal spine.

Male (13.0 mm), Allotype: Antenna 1 elongate, flagellum of 22 segments; accessory flagellum 6-segmented. Antenna 2, peduncular segment 5 with few surfac-ial clusters of slender spines.

Upper lip, epistome prominently bulging anteriorly. Mandibular palp with 5 "A" setae.

Coxae 2-4, lower margins nearly bare, armed sparsely with short setae. Gnathopod 1, propod and dactyl powerful, propodal palmar spines regular, tips little or not broadened. Gnathopod 2, propod much less powerful, similar in form and armature to that of female but slightly more powerful.

Peraeopod 5, basis very broad, hindmargin rounded. Uropod 3, rami subequal in length; outer ramus with 9-11 groups of spines, inner margin distally plumose-setose; inner ramus, inner margin with spines and setae; terminal segment very short.

Telson, lobes normal, longer than basal width.

Etymology: From "epi" + "stomum", alluding to the large epistome protruding over the upper lip.

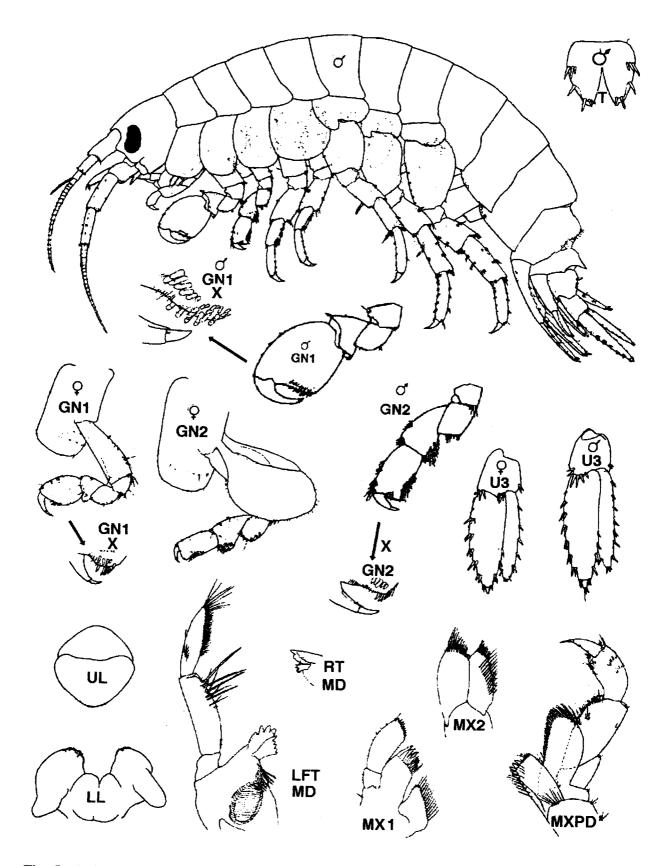


Fig. 5. Anisogammarus amchitkana n. sp. o (15 mm), Holotype; Q ov (14.0 mm), Allotype. Cyril Cove, Amchitka, Alaska.

Distributional Ecology: Known only from the outer coast of Vancouver Island, from Pachena Bay to Wickaninnish Beach; under algal debris, on open surf-exposed sand, LW level, probably shallow subtidal.

Remarks: Character states of Anisogammarus epistomus, especially of the male, suggest that the species is a member of the pugettensis group, with weakly developed palmar peg spines, but closer to A. amchitkana, having weakly developed gnathopod 2 and large aequiramus uropod 3.

# Anisogammarus amchitkana, n. sp. (Fig. 5)

### Material Examined.

# Bering Sea-Alaska region:

Lot#1, Square Bay, Cyril Cove, Amchitka, Aleutian Islands, C. E. O' Clair coll., Mar. 24, 1969 - O' (15 mm), Holotype, slide mount, CMNC2001-0015; 1 Q ov, Allotype (14 mm), slide mount, CMNC2001-0016; 5 QQ ov, Paratypes (1 Q ov, dissected), CMN collns.

Constantine Harbor, Amchitka I., among algae on dock pilings, P. Slattery coll., Sept. 7. 1969 - 1 & (12 mm), CMN Acc. No. 1982-79.

St. Lawrence I., SE Cape, in kelp & mysid swarms, P. Slattery coll., June 6/86 - 54 subadult specimens (3-5 mm), CMN collns.

Kialegak camp, SW St. Lawrence Bay, Aug. 25, 1985 - 1 Q br. II (11 mm) + 4 QQ im (8-10 mm), CMN collns.

**Diagnosis.** Male (15 mm): Anterior head lobe distinctly incised. Eye medium large, subreniform. Antenna 1, peduncular segment 2 medium, length >1/2 peduncle 1; flagellum  $\sim$ 20-24-segmented, little exceeding peduncle of antenna 2. Antenna 2, peduncular segment 5=4, with few clusters of tip-extended slender spines; flagellum  $\sim$ 20-segmented, nearly as long as peduncle.

Mandibuar spine row with 7 blades; palp short, segment 3 > 2/3 segment 2. Maxilla 1, palp slightly broadening distally. Maxilliped, inner plate apically truncate, outer plate slightly broadened; palp segment 3 regular, length > 1/2 segment 2.

Coxae 1-4 medium deep, lower margins rounded, weakly setulose. Gnathopods 1 & 2 very unequal in size; gnathopod 1 large, powerfully subchelate, gnathopod 2 weakly subchelate, as in female; dactyls with short unguis. Gnathopod 1, palmar angle with inner and outer rows of 8-12 mostly peg spines, inner row extending well up palm. Gnathopod 2, propodal subrectangular, posterodistal angle with inner and outer submarginal rows of 5 and 6 short simple spines,

respectively. Peraeopods 3 & 4, segment 6 relatively short, arched, litle longer than segment 5. Coxae 5 & 6 shallowly anterolobate. Peraeopods 5-7, bases weakly heteropodous. Peraeopod 7, basis relatively narrow, posterodistal margin straight. Coxal gill on peraeopod 7 small, narrow relative to gill on peraeopod 6.

Epimeral plates 2 and 3, hind corners weakly acute. Urosome 1, mid-dorsal hump low, with cluster of 8-10 medium spines; lateral clusters each with 3-4 spines. Urosome 2 with ordinary median tooth and single posterodorsal cusps on each side. Urosome 3 with middorsal and dorsolateral clusters of 2-3 medium spines. Uropods 1 & 2, rami subequal in length to peduncles, margins moderately spinose. Uropod 3, outer ramus medium broad, margins with 6-7 clusters of short spines, distinctly longer than slender spinose inner ramus; terminal segment short.

Telson lobes short, basally broad, each side with proximolateral group of three spines, and distolateral single short marginal spine.

Female ov (14 mm). Gnathopod 1, propod relatively small, subovate, posterodistal angle with groups of 5 inner, and 4 outer submarginal simple spines. Gnathopod 2, propod subrectangular, posterodistal angle with submarginal row of 1 simple and 4 pectinate spines; brood plate large, broad, with numerous marginal setae. Uropod 3, rami shorter and broader than in male, margins spinose.

Etymology: The species name acknowledges the type locality on the Aleutian Island of Amchitka.

**Distributional Ecology:** Amchitka and Aleutian Islands, from LW intertidal to depths of ~10 m.

Remarks: The small body size, relatively large size of both gnathopods 1 & 2 (male), and presence of more strongly developed propodal palmar peg spines remove amchitkana from the A. pugettenis - slatteryi complex (see Fig. 8).

# Anisogammarus tzvetkovae, n. sp. (Fig. 6)

Anisogammarus possjeticus Tzvetkova, 1975 (part?).

Material Examined: Peter-the-Great Bay, Russia, LW intertidal, Nina L. Tzvetkova coll. - O (24.5 mm), Holotype; Q ov. (18.0 mm), Allotype; slide mounts, loan material, Zoological Institute, St. Petersburg, Russia.

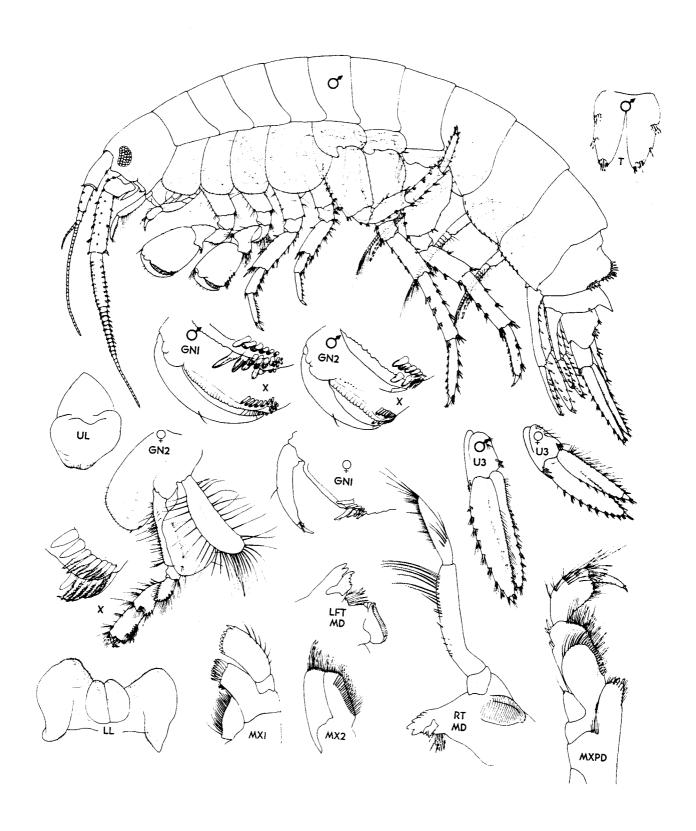


Fig. 6. Anisogammarus tzvetkovae, n. sp. & (24.5 mm), Holotype; Q ov (18 mm) Allotype. Peter-the-Great Bay, Sea of Japan.

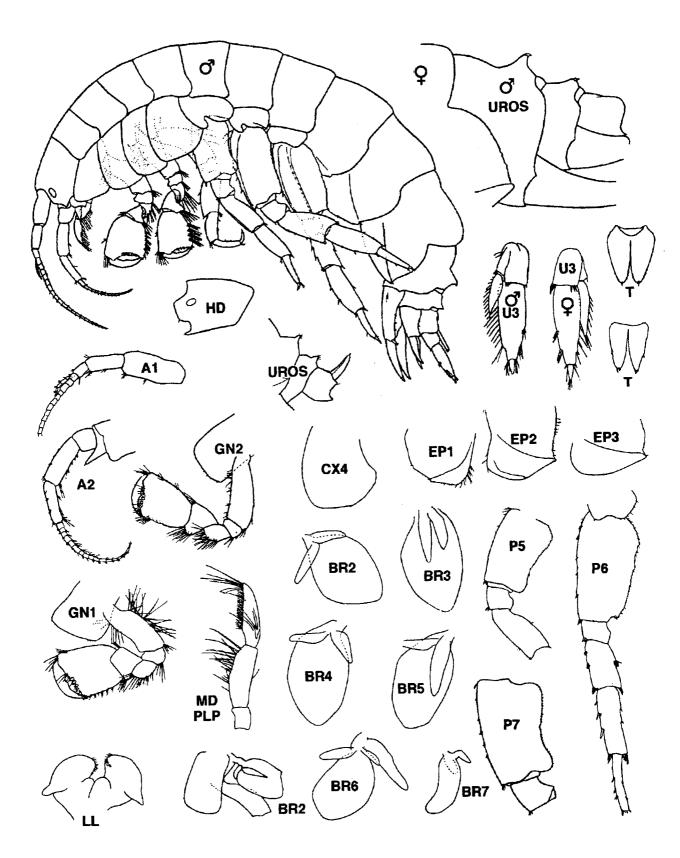


Fig. 7. Barrowgammarus macginitiei (Shoemaker, 1955). O (37 mm). Point Barrow, Alaska. [after Shoemaker(1955) and Tzvetkova (1975)].

Diagnosis: Male (24.5 mm). Anterior head lobe slightly incised. Eye smallish, subreniform. Antenna 1, peduncular segment 2 medium long, 2/3 length of peduncle 1; flagellum elongate, ~30-segmented, exceeding peduncle of antenna 2. Antenna 2 large, peduncular segment 5 nearly equal in length to 4, with numerous anterior and posterior marginal clusters of slender spines with extended tips, continuing onto proximal flagellar segments; flagellum of 20+ segments, shorter than peduncle.

Mandibuar spine row with 6 blades; palp slender, elongate; segment 3 > 1/2 segment 2, "D" spines short, extending proximad of facial cluster of "A" setae; segment 2 with 8-10 long alpha setae. Maxilla 1, palp distinctly broadening distally, apex with 7-8 short spines. Maxilliped, inner plate apically truncate, outer plate tall, broadened; palp segment 3 regular, length  $\sim$  2/3 segment 2.

Coxae 1-4 relatively deep, 1-3 narrow, lower margin with a few short setae. Gnathopods 1 & 2 stout; dactyls with short unguis. Gnathopod 1, palmar margin rugose, file-like, posterior angle with 6-8 inner, medial, and outer rows of stout peg-spines; carpus with short narrow posterior lobe. Gnathopod 2, propodal postero-distal angle with inner and outer submarginal row of 4-6 short peg spines. Peraeopods 3 & 4, segment 4 elongate, segments 5 & 6 relatively short, subequal; dactyls very short. Coxae 5 & 6 shallowly anterolobate. Peraeopods 5-7, bases relatively narrow, little broadened; basis of peraeopod 7 with slight postero-distal marginal excavation. Coxal gill on peraeopod 7 large, broad, deep, nearly as large as gill of peraeopod 6.

Epimeral plates 2 and 3, hind corner minutely acute, lower margins spinose. Urosome 1, mid-dorsal hump large, with mid-dorsal "V" of ~20 stout spines; dorso-lateral clusters each with 3-4 spines. Urosome 2 with strong median tooth and single posterodorsal short spines on each side. Urosome 3 with mid-dorsal and dorsolateral clusters of 2-4 medium spines. Uropods 1 & 2, rami shorter than peduncles, margins spinose. Uropod3, rami large, slender, inner slightly the shorter, margins with 8-10 clusters of short spines and setae; terminal segment small.

Telson lobes medium long, narrowing distally, proximolateral and distolateral spines short.

Female ov (18 mm). Gnathopod 1, propod medium large, subrectangular, posterodistal angle with groups of 5 inner, and 4 outer submarginal simple spines. Gnathopod 2, propod slender, elongate-rectangular, posterodistal angle with inner submarginal row of 2 simple and 6-7 pectinate spines, and outer submarginal

row of 1 simple spine and 5-6 pectinate spines. Brood plate on peraeopod 2 relatively small and slender, with ~30 longish marginal setae. Uropod 3, rami shorter than in male, and margins less setose.

Etymology: In recognition of Dr. Nina L. Tzvetkova, Zoological Institute, St. Petersburg, Russia, who has contributed in an outstanding manner to knowledge of gammaroideans and littoral marine amphipoda of the northwestern Pacific Ocean.

Distributional Ecology: Known only from the coasts of North and South Korea, the northwestern coast of Japan, and Peter-the-Great Bay, Russia.

Remarks: Material and illustrations from the east coast of South Korea, kindly supplied by Dr. Chang Bae Kim in 1992 (pers. commun.) is virtually identical with that of Dr. Nina Tzvetkova from Peter-the-Great Bay (above).

### Barrowgammarus Bousfield

Barrowgammarus Bousfield, 1979: 321;—Barnard & Barnard 1983: 586.

**Diagnosis:** Body very large. Eyes small, oval. Antennae subequal in length, sparesly setose, not calceolate.

Mouthparts poorly described. Mandibular palp, segment 3 slender, "D" setae uniformly short, extending proximally to distal group of "A" setae.

Gnathopods powerfully subchelate, propodal palmar margins with peg spines (male). Peraeopods 5-7, bases little expanded, each with distinct posterodistal lobes; dactyls short. Coxal gills 2-5 with paired accessory gills; coxal gills 6 & 7 with single accessory gills.

Pleon smooth above. Urosome segments 1 and 2 each with prominent mid-dorsal tooth. Uropods 1 & 2, rami lanceolate, lacking marginal spines. Uropod 3, inner ramus short, < 1/2 outer ramus, inner margins of both are plumose-setose; terminal segment distinct.

Telson lobes narrowing distally, fused basally.

# Barrowgammarus macginitiei (Shoemaker) (Fig. 7)

Anisogammarus macginitiei Shoemaker, 1955: 54, fig. 16;—Tzvetkova 1975: 103, fig. 37. Barrowgammarus macginitiei Bousfield 1979: 321; Barnard & Barnard 1983: 586.

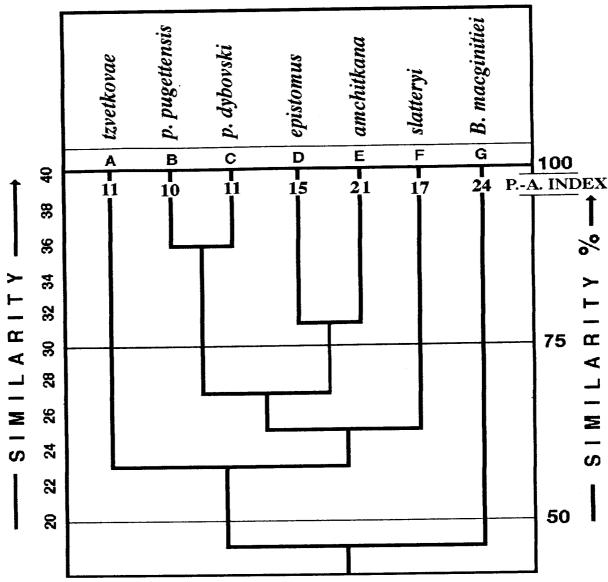


Fig. 8. Morphological smilarities and possible phyletic relationships among species of *Anisogammarus* and *Barrowgammarus*.

Diagnosis: With the characters of the genus.

Distribution: Beaufort Sea, Okhotsk Sea, sublittoral.

Remarks: This monotypic taxon is undoubtedly a member of family Anisogammaridae, most closely related to the genus Anisogammarus, and is included here as an outgroup. The female is about the same size as the male but has not been described in detail. The presence of dorsal protruberances on urosome segments 1 & 2, and of dorsal armature on the pleosome, the form of the gnathopods (male) and the inaequiramous form of uropod 3 suggest a common ancestry with Anisogammarus pugettensis. Calceolation of antenna 2 (male) has not been confirmed.

### Discussion.

The present treatment of anisogammarid species utilizes a semi-phyletic modification of the UPGMA system of Sneath and Sokal (1973), as in previous analyses of other North Pacific amphipd taxa. Character states are ordered plesio-apomorphically and the relative phyletic placement of a given taxon is represented by a numerical sum of plesiomorphic, intermediate, and apomorphic character state values (0, 1, and 2, respectively) in a Plesio-Apomorphic (P.-A.) Index. Tabular data on which the resulting phenograms are based are considered overly bulky and repetitive for publication here, but can be supplied on request.

Fig. 8 portrays character state similarities within the North Pacific genus Anisogammarus and the selected

outgroup species Barrowgammarus macginitiei (Shoemaker). The outgroup species, formerly Anisogammarus macginitiei, is now recognized at the generic level, Barrowgammarus, a decision in agreement with the "less than 50% similarity" that it here demonstrates with the six other species and subspecies of Anisogammarus. The two subspecies of A. pugettensis, and the species A. amchitkana and A. epistomus cluster above the 75% similarity level and these two fuse at the 68% level. The specialized sand-dwelling species A. slatteryi (P.-A. Index = 17) and the primitive western Pacific species A. tzvetkovae (P.-A. index = 12) join these at levels of 62% and 58% similarity respectively. Positive consideration of elevating some taxa to subgeneric rank might be justified. However, since other regional species may await formal recognition, elevation of taxa at this time seems premature.

The known species of Anisogammarus are coldtemperate (boreal) North Pacific in biogeographic affinity. They are included in an updated list of N. American amphipod species on which comparative biogeographical studies were also based (Bousfield, 2001). Four species are apparently exclusively North American, ranging from the Bering Sea region southward to northern California. Two species range from the western Bering Sea and Kamchatka peninsula, southward along the Asiatic coast to the northern Sea of Japan, consistent with the penetration of cold-water elements into that region (Derzhavin 1930). The distribution of only one full species, Barrowgammarus macginitiei, apparently overlaps the central Bering Sea divisional region. The biogeographic separation into eastern and western species groups appears to match the east-west distributional separation of species within other anisogammarid genera, notably the speciesrich and more southerly ranging genus Eogammarus (Tzvetkova 1975; Bousfield 1979). However, cognizant of the current lack of a fossil record and other evidence of past distributions, reasons for these biogeographical consistencies "across the anisogammarid taxonomic board" remain speculative.

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### **Legend for Figures**

					<u>1</u>
<b>A</b> 1	-	antenna 1	P5-7	-	peraeopods 5, 6, 7
A2	-	antenna 2	PL	-	pleopod
ACC FL	_	accessory flagellum	PLP	-	palp
ABD	-	abdomen	RT	-	right
BR		brood lamella	SP	-	spine
CX	-	coxal plate	T	-	telson
EP	-	abdominal side plate	U	-	uropod
<b>EPIST</b>	-	epistome	UL	-	upper lip (labrum)
GN1	-	gnathopod 1	UROS	-	urosome
GN2	-	gnathopod 2	X	-	enlarged
HD	_	head	♂"	-	male
LFT	-	left	Q	-	female
LL	_	lower lip (labium)	im	-	immature
MD	-	mandible	juv	-	juvenile
MX1	-	maxilla 1	ov	-	ovigerous
MX2	_	maxilla 2	subad.	-	subadult
		<del></del>			

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## The Canadian Field-Naturalist: 120 years of northern biodiversity publication.

The Canadian Field-Naturalist publishes articles and notes on original research and observations on natural history relevant to Canada (therefore on northern portions of both Nearctic and Palaearctic regions) including distribution, faunal analyses, taxonomy, ecology, and behaviour, and items of news, comment, tributes, review papers, book reviews and new titles. The official publication of The Ottawa Field-Naturalists' Club, it prints minutes of the annual meeting and awards presented by the Club. Since 1984, it has featured edited Status Reports for many individual species designated by the Convention on Species of Endangered Wildlife in Canada (COSEWIC), particularly those on fish and marine mammals. As well, recent special issues have featured the history of botanical investigation of Canada, St. Pierre et Miquelon, and Greenland; a biography of the Canadian ornithologist Percy A. Taverner, a history of the Canadian Wildlife Service, and an analysis of the Orchids of the Ottawa district.

The Ottawa Field-Naturalists' Club was formed in 1879 by scientists from embryonic federal departments, including the Geological Survey and the Dominion Experimental Farm, together with leading amateurs of the time; a similar mix remains as its strength to this day. The Club quickly emphasized publication, and for seven years beginning in 1880, it annually issued the Transactions of the Ottawa Field-Naturalists' Club. With volume 3 in 1887, the Transactions became a subtitle for Volume 1 of The Ottawa Naturalist, a new monthly publication. With Volume 3 of The Ottawa Naturalist in 1889 emphasis shifted from largely local members reports to national ones and in 1919 the journal was renamed The Canadian Field-Naturalist (starting with Volume 33 which was Volume 35 of the Transactions, although this subtitle was soon omitted). The issues per year were gradually reduced from 12 to 9 to 6 and, eventually, to 4; the latter beginning with Volume 67 in 1953, but the individual issue size increased. The annual pages published reached a record of 794 in 1988 (volume 102) and 1994 (volume 112). The largest single issue 254 pages was, however, published in 1996 as 110(1). Since 1967, the Club has separately published a local (Ottawa area) natural history journal, Trail & Landscape, now also issued 4 times a year.

Submissions to The Canadian Field-Naturalist and its predecessors have been peer reviewed since its inception, first through a "Publishing Committee", later "Sub-editors", and then "Assistant Editors" until the present designation "Associate Editors" was adopted in 1885. Currently, most submissions also go to at least one (often more) additional reviewer(s). Associate Editors are listed in every issue and, since 1982, additional reviewers been acknowledged individually in the Editor's Report annually. A formal publication policy was published in The Canadian Field-Naturalist 97(2): 231-234. "Advice to Contributors" is publ-ished in one or more issues annually giving format and charges. The journal is entirely supported through a portion of club membership (40%), subscriptions (100%), annual interest on Club investment funds (80%) and publication charges for pages and reprints. The Ottawa Field-Naturalists' Club at the beginning of 2000 had 957 members and The Canadian Field-Naturalist an additional 253 individual and 497 institutional subscribers in 22 countries, for a distribution of 1707 copies.

The Current annual subscription rate is \$28 for individuals and \$45 for institutions. Membership in The Ottawa Field-Naturalists' Club (which includes receipt of The Canadian Field-Naturalist) is \$28 for individ-uals and \$30 for families. Postage outside Canada is \$5.00 additional. Subscriptions should be sent to The Canadian Field-Naturalist, Box 35069 Westgate P.O., Ottawa, Ontario, Canada K1Z 1A2. Manuscripts for consideration should be addressed to Dr. Francis R. Cook, Editor, Canadian Field-Naturalist, RR 3, North Augusta, Ontario K0G 1R0, Canada.

Francis R. Cook
Editor, Canadian Field-Naturalist
fcook@achilles.net

# An updated commentary on phyletic classification of the amphipod Crustacea and its applicability to the North American fauna.

Edward L. Bousfield, PhD, FRSC, Research Associate Royal Ontario Museum, 100 Queen's Park, Toronto, ON K2B 8E3.

#### **ABSTRACT**

Bousfield & Shih (1994, Amphipacifica 1(3):76-134) provided a phyletic classification of the Amphipoda consistent with superfamily-level standards of classification in use for the Hyperiidea, Caprellidea, Ingolfiellidea, and Gammaridea. For gammaridean amphipods, the basis for phyletic classification is reproductive form and behaviour. Detailed character-state analyses support the view that the ancestral amphipod was a "swimmer-clinger", rather than a benthic "crawler-burrower". This study comments on difficulties posed to morphological classification by near-universal occurrence of homoplasy within major character states. Thepresent phyletic classification is here applied to a list of ~1650 scientific names of amphipod crustaceans from marine, freshwater and terrestrial habitats of North America (north of Mexico), updated to the end of the 20th century. Character state variation of antennal callynophore, brush setae, calceoli, uropods, and telson, and sexual dimorphism of gnathopods are further analysed. Suborders and gammaridean superfamilies are phyletically classified and annotated in tabular form. Although phyletic classification is presently controversial, alternative or more suitable phyletic groupings proposed by cladistic and/or rDNA analyses are yet lacking or unproven. Broad acceptance and/or usage of gammaridean superfamilies (or equivalents) outlined here provide demonstrably greater meaning and functionality to taxonomic interrelationships, and therefore greater research credibility than simple alphabetical listings of families and genera.

### INTRODUCTION

Classification is the naming of essentially discreet groups of living organisms in a manner that reflects their probably correct phylogenetic history. Development of a classification requires input by scientists who are knowledgeable in animal systematics, and experienced in recognition of the significance of morphological characters and the probably correct ordering of the character states within the group concerned. Ideally, classification discriminates true phyletic relationships from homoplasious (artifical, convergent) similarities. Phyletic classification is thus distinct from, and far more useful than, an alphabetical listing of previously described taxa.

If the Darwinian theory of evolution is essentially correct for multi-cellular organisms, it follows that amphipod crustaceans evolved in only one manner, and left only one biohistorical "track record". As a corollary to that thesis, all species were at one time or another linked by so-called "intermediate" forms which, especially if extant, tend to mask the "clean" separation of lineages into pragmatically distinct clades or higher taxonomic groupings. For several reasons, however, phylogenists are unlikely to discover that record precisely. These factors include: (1) lack of a significant (long-term) amphipod fossil record (not earlier than Cenozoic); (2) incomplete description of extant taxa, especially of species from hypogean waters and the deep sea; and (3) a relatively undeveloped state of broadly applicable phyletic analysis. Clues to natural

relationships are provided mainly by analysis of external and internal morphology, behaviour, physiology, and distributional ecology of extant species.

Methods of phyletic analysis, whether intrinsic, phenetic, cladistic, genetic, or in combination, require careful research input. Particlarly in treatment of speciose higher-level taxa, methodologies to date have proven neither "infallible", nor "guaranteed" to provide a realistic, credible result. Thus, in cladistic analysis, prior choice of ingroup/outgroup taxa, selection of numbers and kinds of morphological characters, and ordering of character states, all constitute subjective (and fallible) decisions that directly effect the quality of the results. Thus, sheer numbers of characters and character states, if inappropriately selected and/or wrongly ordered, may produce results that are actually misleading, internally conflicting, or otherwise of low credibility, particularly when compared with results employing other methodologies. Nor can a correct result be assumed because of the "sophistication" of methodology or computerized format.

The main text of this paper was first presented at the 10th International Colloquium on Amphipoda held at Heraklion, Crete, April 16-21, 2000. The purpose of the work is to review the status of phyletic classification of the Amphipoda, and demonstrate its applicability to a recently compiled list of amphipod families, genera, and species recorded to date from the North American continent north of Mexico.

### **ACKNOWLEDGMENTS**

The author is grateful to many colleagues for their stimulating taxonomic and phyletic input, especially Dr. Michael J. Thurston (deep-water taxa), Dr. Jorgen Berge (stegocephalid reclassification), Dr. J. Emmett Duffy (genetic methodologies), Dr. C.-t. Shih (hyperiid classification), and Dr. J. K. Lowry (lysianassoid and podocerid phyogeny).

Compilation of the list of North American amphipods (Appendix I) involved the services of many colleagues, co-ordinated through a Committee on Scientific and Common Names of Invertebrate Animals (CNIA), chaired by Dr. Donna D. Turgeon, NOAA, Washington, DC. A full list of contributors is to be included in a final CNIA report and publication. Especially helpful to the author, who served as amphipod subcommittee chairperson and project co-ordinator, have the been the following amphipod systematists: Dr. Pierre Brunel, Université de Montréal, (Atlantic gammarideans); Dr. Donald B. Cadien, Marine Biology Lab, Carson, CA (SW Pacific gammarideans); Dr. Kathleen E. Conlan and E. A. Hendrycks, Canadian Museum of Nature, Ottawa, ON (Arctic and Pacific gammarideans); Dr. John Foster, Panama City, FL (Hyperiidea, Gulf of Mexico); Stephen Grabe, Environmental Protection Commission, Tampa, FL (Gammaridea, Ingolfiellidea: Gulf of Mexico); Dr. John R. Holsinger, Old Dominion University, Norfolk, VA (freshwater amphipods); Diana R. Laubitz, Canadian Museum of Nature, Ottawa, ON (Caprellidea); Sara E. LeCroy, Gulf Coast Research Laboratory, Ocean Springs, MI (Gammaridea: Gulf of Mexico); Dr. Chiangtai Shih, Fisheries Research Institue, Taiwan (Hyperiidea); and Dr. Craig P. Staude, Friday Harbor Laboratories, WA (Pacific Gammaridea).

### CLASSIFICATORY SYSTEMATICS.

The malacostracan order Amphipoda has long been considered an especially difficult problem of phyletic classification (Riley 1983; Schram 1986). The problem of internal classification of this ordinal crustacean group is complicated by extreme diversity of body form ranging from thick-bodied spiny-legged burrowing haustoriids; big-eyed fast-swimming oceanic hyperiids; slender-bodied skeleton shrimps, to eyeless, vermiform infaunal ingolfiellids. How might we find commonality of relationships among widely diverse external pigmentation, from the pure white of burrowing phoxocephaloideans, through beautifully cryptic maculation of "swash-zone" pontogeneiids and calliopiids, to the vertical striping of odiids and

multivariate pigmentation of "thick nosed" pleustids and minute commensal stenothoids? What natural ordering, if any, might exist between such diverse feeding types as free-swimming predaceous eusiroideans and pardaliscodeans, longicorniculate trypton-feeding podocerids, and vertically tube-building ampeliscids? Phyletic classification seeks to provide answers to these questions and bring a semblance of natural order out of almost chaotic diversity of form and behaviour.

The history of development of amphipod classificatory systems has been outlined by Bousfield and Shih (1994) and is briefly summarized here. In essence, during a period of taxonomic discovery lasting approximately two centuries since the time of Linneus (1758), phyletic (superfamily-level) classifications finally came into standard use for the Hyperiidea through the work of Bowman & Grüner (1973), for Ingolfiellidea by Stock (1977), and for Caprellidea notably by Vassilenko (1974) and D. R. Laubitz (1993).

Within the diverse and taxonomically more difficult suborder Gammaridea, however, the story is more complex. For nearly two centuries (to the mid-1950's) gammaridean classification had been essentially phyletic, stabilized by the semi-phyletic, non-alphabetical arrangements of families proposed by Sars (1895) and Stebbing (1906). This system was broadly accepted and utilized by amphipod systematists at least until the early fifties (e.g., Shoemaker 1930; Gurjanova 1951; Dunbar 1954). However, two major weaknesses in these classifications remained: (1) several large families such as "Gammaridae" and "Lysianassidae" were weakly defined, effectively polyphyletic, or otherwise "unwieldy", and (2) other, mostly smaller families "begged" for inclusion within higher "umbrella" categories that would recognize their close phyletic similarities. In the second instance, Bulycheva (1957) proposed the super-family name Talitroidea to encompassthenaturallyrelatedfamiliesHyalidae,Hyalellidae, and Talitridae. J. L. Barnard (1973) combined a number of domicolous families within superfamily Corophioidea. In the first instance, the formal task if unravelling family-level units within polyphyletic family "Gammaridae" was initiated mainly by Bousfield (1973, 1977). Recombination within superfamily categories, of several older family names and those newly proposed, soon culminated in a fully phyletic classification of suborder Gammaridea (Bousfield 1979, 1982a, 1983). This classification was adopted to various degrees by Riley (1983), Schram (1986), and Ishimaru (1994). Some superfamily concepts were also revised and expanded by others [e.g., Crangonyctoidea by Holsinger 1992a; Lysianassoidea by Lowry and Stoddart 1997). As updated by Bousfield and Shih (1994), the "new" phyletic classification proved basically not unlike the semi-phyletic family "arrangement" of Sars (1895) and Stebbing (1906), since both recent and older systems were presumably based on similar conceptual ordering of character states of reproductive morphology and behaviour.

In the interim, however, J. L. Barnard had become dissatisfied with perceived anomalies of the Sars-Stebbing classification and the apparent intractability of their ready solution. Although he informally diagrammed suggested relationships between known amphipod families, based on a "Gammarus-like" prototype, he commenced listing gammaridean families and genera in alphabetical sequence (1958, 1969). The pragmatics of a simple alphabetical treatment of higher gammarideantaxa, then approaching 100 family names, was soon widely adopted. In further updatings and expansions of these original compendia (Barnard & Barnard 1983; Barnard & Karaman 1991), a number of anglicized concepts of some higher groups were pro-These included the names "gammaridans", "hadzioids", etc., and later (Williams & Barnard 1988) "crangonyctoids", as well as a broadening of some original formal family-level concepts (e.g., Eusiridae, Corophiidae). Notably perhaps, these names corresponded, with about 75% similarity, to superfamily concepts formally proposed earlier in the phyletic literature. However, with Gordan Karaman (1991, p. 7), Barnard steered away from formal phyletic classification and concluded this final major work with an alphabetical listing of all families and component gen-

During the past two decades, some major regional faunistic studies have utilized mainly alphabetical listings and retained older treatments of higher taxa such as "Gammaridae" (e.g., Ruffo et al 1982,1988, 1993, 1998; Camp (1998). However, with increasing sophistication of cladistic analytical methodology (e.g., Lowry& Myers, in prep.), earlier superfamily concepts are now being re-analysed [e.g., Serejo 2000 in press (Talitroidea); Berge and Vader 2000, in press (Stegocephaloidea)], and new superfamily taxa proposed (e.g., Iphimedioidea Lowry & Myers, 2000). In the light of recently proposed phyletic studies utilizing genetic methodology (e.g., Shram, 2000; Macdonald 1999), a resumption of development of phyletic classification of the gammaridean Amphipoda now seems promising.

### **Character State Analyses**

As noted above, the present analysis of phyletic classification within the order Amphipoda is based mainly on reproductive morphology and behaviour, updated from earlier work (Bousfield & Shih, 1994). To some degree, modified repetition of material here compensates for the limited original circulation of that source paper, now out of print. The present analysis, however, utilizes only seven mostly reproductively significant, characters and character states. These include sensory organelles of the antennae (callynophore, brush setae, and calceoli); form of the telson, and degree of sexual dimorphism and use of the gnathopods during amplexus. To these has been newly added the form of the rami of uropods 1 & 2. The character states vary widely and homoplasiously from group to group, as do those of the mouthparts, coxal plates, peraeopods, and uropod 3 of the earlier study. Nonetheless, collectively and judiciously, they provide a consistent and verifiable morphological basis for phyletic grouping of higher amphipod taxa.

In general, the ordering of character states is based on an assumed plesiomorphic condition in more primitive "outgroup" members of the superorder Peracarida, such as the Mysidacea and Cumacea, and more primitive members (shrimp-like groups) within the Decapoda. Thus, in members of phyletically primitive amphipod groups ("swimmers"), the sensory organelles of the antennae are well developed, the telson is typically bilobate, and sexual dimorphism of the gnathopods is rare or lacking. Since the mating process usually takes place in the open water column, precopulatory "holding" of the female by the male gnathopods is apparently not developed. Conversely, in members phyletically more advanced gammaridean superfamilies ("crawlers"), the antennal sensory features are much reduced or lacking and the telson lobes are often fused apically. Since mating usually occurs on (or in) the bottom substrata, often in strongly lotic waters, the male gnathopods are typically strongly modified for pre-amplectic grasping and holding of the female and/or agonistic behaviour with other males.

### The Antennal Callynophore

The callynophore consists of a bundle of close-set aesthetases on the postero-medial margin of the fused (or conjoint) basal segments of the flagellum. This organelle occurs typically within pelagic ordinal groups of the higher Malacostraca and, within the Amphipoda, characterizes superfamily groups of the "Natantia", especially the Hyperiidea (Fig. 1d). Its primary func-

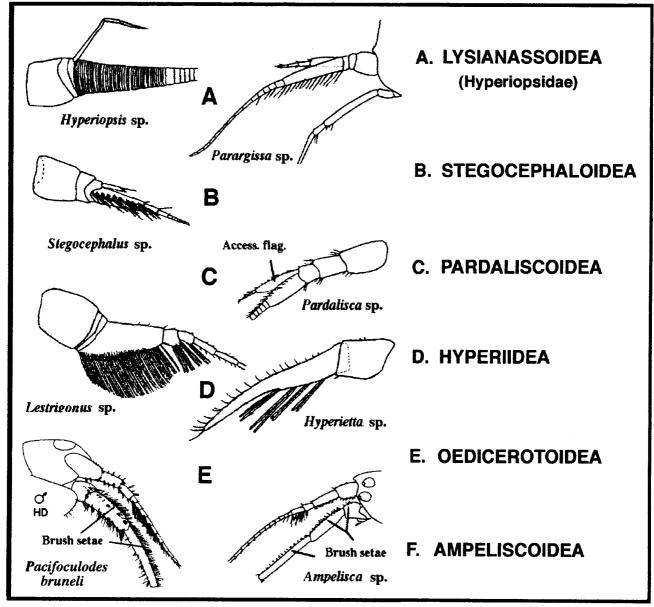


Fig. 1. Types of antennal callynophores [after Barnard (1969), Bowman & Grüner(1973), Bousfield & Chevrier (1996), and unattributed sources].

tion is almost certainly chemosensory. Its presence mainly in the final adult male instar would seem to be of direct reproductive significance in the detection of females within the water column. However, in some lysianassoidean and synopioidean subgroups, callynophore-like structures may also be present in mature females and subadult stages, perhaps indicating a possible secondary role in detection of food resources.

Representative forms of callynophores within the Amphipoda are illustrated in Fig. 1. Lowry (1986) has described a one-field arrangement of the callynophore within families Platyischnopidae, Urothoidae and Phoxocephalidae (Phoxocephaloidea), a condition he considers primitive, and in some hyperiids (e.g.,

Archaeoscinidae), perhaps convergently. In all other taxa the arrangment is two-field.

The possible significance of the callynophore in phyletic classification was first introduced by Lincoln and Lowry (1984) and amplified formally by Lowry (1986). Although strongly developed in pelagic carnivores and necrophages, especially where calceoli are weak or lacking (e.g., Synopioidea, Pardaliscoidea, Stegocephaloidea, and Hyperiidea), the organelle is generally weak or lacking in reproductively pelagic but vegetatively benthic groups such as the nestling Dexaminoidea and tube-building Ampeliscoidea, and in the fossorial Phoxocephaloidea and Pontoporeioidea. It is virtually lacking in several "natant" subgroups

where the entire life cycle is essentially infaunal (e.g., Haustoriidae), or commensal or parasitic (e.g., some Lysianassoidea) and/or where preamplexing reproductive behaviour has secondarily and convergently developed (e.g., Paracalliopiidae and Exoedicerotidae within Oedicerotoidea). Curiously, the callynophore is surprisingly weakly developed in the mainly marine but mainly acalceolate family Oedicerotidae and even within the Eusiroidea (e.g., in the pelagic, primitive family Eusiridae, but not found in Pontogeneiidae, nor Calliopiidae).

The callynophore is essentially lacking in reproductively benthic Reptantia, including the Caprellidea and Ingolfiellidea, and not found in freshwater taxa, even in those that have apparently become secondarily pelagic such as *Macrohectopus* within the Gammaroidea. However, callynophore-like structures have been reported from a few Amphilochidae (e.g. *Austropheonoides*, *Peltocoxa*) and Cressidae (*Cressa cristata*) within primitive subgroups of superfamily Leucothoidea (Lowry 1986).

The presence or absence of a callynophore may therefore offer a useful criterion of reproductive life style. Although its occurrence appears subject to homoplasious tendencies, such aberrancies may be correlated with non-reproductive features of life style and are thus predictable. In broader perspective, the presence of a callynophore is a plesiomorphic, or basic feature of malacostracan reproductive morphology. As concluded previously (Bousfield & Shih 1994), the callynophore provides a primary basis for development of a phyletic classification within the Amphipoda.

### **Antennal Brush setae**

The term "brush setae" applies to dense tufts or clusters of short brush-like setae that variously line the anterior margins of peduncular segments 3, 4, and 5 of antenna 2. Brush setae may occur also on the posterior (lower) margins of peduncular segments 1-3 of antenna 1 (e.g., in Dexaminoidea). Similar types of setae occur in other peracaridan taxa, including the Cumacea and Mysidacea.

Within the Amphipoda these organelles have been found only in the terminal male stage of pelagically reproductive amphipod superfamilies, and not in subadult males, females, and/or immature stages. Their function is yet unknown and conjectural. Although brush setae may not have been studied in ultrastructural detail, their gross morphology is similar to modified setae rather than thin-walled aesthetascs. Their role may be tactile when, during the process of copulation,

the male is briefly in close contact with the female.

The potential usefulness of brush setae in phyletic classification was previously suggested by Bousfield (1979); Bousfield & Shih (1994). These organelles are most strongly developed in non-calceolate primitive superfamilies of Natantia (e.g., Pardaliscoidea, Synopioidea), and moderately developed in some calceolate "natant" taxa (e.g., Lysianassoidea, Phoxocephaloidea, Eusiroidea, Oedicerotoidea), and acalceolate "transitional" super-families (e.g., Dexaminoidea, Ampeliscoidea, and Mel-phidippoidea). They are less well developed or rare within the Stegocephaloidea and Hyperiidea (Fig. 1).

The presence of brush setae in males only indicates that their function is reproductively significant. Their limited distribution within the Natantia and total absence from the Reptantia indicates a potentially primary value in phyletic classification.

### The Antennal Calceolus

The calceolus is a slipper-shaped membranous microstructure attached variously to the anteromedial segmental margins of the flagella and peduncles of both antenna 1 (antennule) and antenna 2 of some gammaridean Amphipoda. Principal features of these micro-structures have been described, across a broad range of higher taxa, by Lincoln and Hurley (1981) and, with special reference to genera within the primitive "reptant" superfamilies Crangonyctoidea and Gammaroidea, by Godfrey et al (1988). The calceolus is not to be confused with the aesthetasc, a sublinear thin-walled microstructure of mainly chemosensory function, found only on flagellar segments of antenna I in most species of Amphipoda. The aesthetasc also occurs widely across malacostracan ordinal subgroups, including the Decapoda. The calceolus is also structurally readily distinguishable from brush setae and other seta-like structures co-occurring on antennal peduncular and flagellar segments.

Representative types of amphipod calceoli are illustrated in figs. 2 & 3. Calceolus-like structures are found on the proximal flagellar segments of antenna 1 (male) of a few other malacostracans, notably within the Syncarida (e.g., Koonunga cursor) and the Mysidacea (e.g., Xenacanthomysis pseudomacropsis). Such structures are not considered calceoli by Lincoln (pers. commun.) since they may be convergent in form and/or of different function. However, these organelles are included here as of possible phyletic significance within the Malacostraca and, in my view, merit further comparative micro-anatomical and behavioural study.

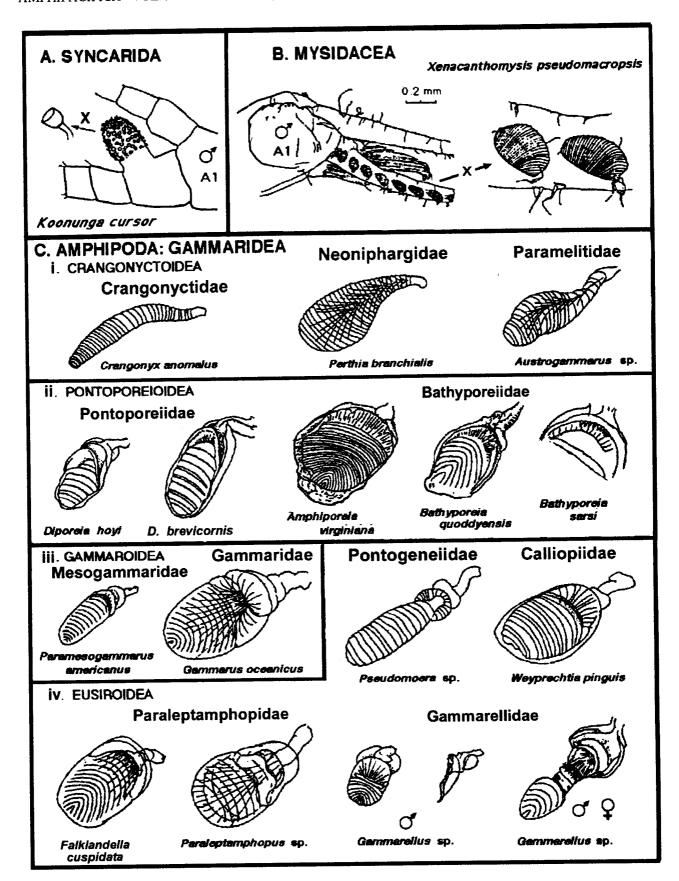


Fig. 2. Types of antennal calceoli in gammaridean Amphipoda, and positionally similar organelles in other malacostracan Crustacea (modified from Bousfield & Shih 1994).

The presumed "advanced" form of the calceolus is grossly similar to that of a parabolic radar "dish" (Fig. 2C,D). Combined with its anterior antennal location, this morphology suggests that the organelle functions primarily as a mechanoreceptor for aquatic acoustical vibrations. However, its innervation and connection to the brain has not yet been ascertained, nor have microacoustical studies yet confirmed its true function (Lincoln & Hurley 1981).

The distribution of calceoli between the sexes suggests that calceoli developed initially in males only, presumably as a device for detection of vibrations from swimming females of its own species. In free-swimming raptors (e.g., Gammarellidae within the Eusiroidea), special types of calceoli have apparently developed in females and immatures, and occur alongside the reproductively functional form of calceolus in terminal stage males. As described by Steele & Steele (1993), these organelles appear to have became more complex structurally, presumably, and possibly secondarily adapted, for detection of escape vibrations of free-swimming prey. However, the primary reproductive function of calceoli apparently diminished or disappeared in concert with changes in life style from pelagic to benthic, neritic to abyssal, lotic to lentic, marine to freshwater, epigean to hypogean, and corresponding development of pre-amplexing gnathopods (see p. 61). As indicated in Fig. 3, reduction and disappearance of calceoli occurred initially in antenna 1 and subsequently in antenna 2. Within the latter, the sequence of loss was initially from the peduncle and distal flagellar segments, and finally from the proximal flagellar segments. However, as noted above, calceoli persisted in both males and females of some epigean freshwater groups (e.g., some Gammaridae. Anisogammaridae) and/or cave pool amphipods where life styles presumably remained free-swimming and raptorial (e.g., Crangonyx packardi and Sternophysinx calceola (Crangonyctoidea); Sensonator valentiensis (Melphidippoidea?), and several eusiroideans of southern continental land masses (Bousfield 1980).

The possible significance of antennal calceoli in phyletic classification of the Amphipoda has been alluded to variously by Bousfield (1979, 1983), Lincoln and Hurley (1981), Lincoln & Lowry (1984), and more recently by Godfrey et al. (1988), Stapleton et al (1988), Holsinger (1992a), and Steele & Steele (1993). These views were analysed and expanded upon by Bousfield & Shih (1994) and are here summarized and updated, with special application to the North American amphipod fauna (Appendix I).

The external morphology of the calceolus within the primitive reptant superfamily Crangonyctoidea (category 9, Lincoln and Hurley 1981) appears to be the most simplified, and thus probably the most plesiomorphic extant form (Figs. 2 A & 3). It consists only of a basal stalk and elongate body that bears numerous (20+) elements of similar simple structure. Holsinger (1992a) has distinguished two subcategories of calceoli within the Crangonyctoidea. In members of holarctic family Crangonyctidae (Crangonyx, Synurella, pp. 101-104) the form is slender and elongate, with a simple branched internal "tree trunk" configuration. Some separation of basal elements in Crangonyx richmondensis, illustrated by Godfrey et al. (1988), are suggestive of "protoreceptacles". By contrast, the calceolus within austral families Sternophysingidae and Paramelitidae is typically broad, paddle-shaped, and its internal tree-trunk configuration has more numerous indistinct branches, a seemingly more plesiomorphic condition. In slightly more advanced types of calceoli (Fig. 3, upper: Phoxocephaloidea), the elements are fewer (10-15 in Platyischnopidae; 4-6 in Phoxocephalidae) and the body may be short and spatulate, or barrel-shaped.

With respect to the sexes, the more plesiomorphic types of calceoli occur (with very few exceptions) in the 'males only' category of presumed most primitive superfamily taxa such as the Crangonyctoidea, Phoxocephaloidea, Pontoporeioidea, and most of the Lysianassoidea (Fig. 2, i, ii; Fig. 3, upper two rows).

In more advanced types of calceoli (Fig. 2, iii), the basal element is broadened and forms a receptacle that is weakly developed in Pontoporeioidea and Gammaroidea but strongly so in Eusiroidea (Fig. 2, iv). The basal stalk is distally expanded into a bulla or resonator, weakly and more strongly in those same groups respectively. In some Pontoporeioidea (Bathyporeiidae), finger-like processes protrude over the proximal elements. In the most advanced types of calceoli (viz., in some Eusiroidea: Gammarellidae, Eusiridae), and in some pelagic Lysianassoidea (e.g., Ichnopus spp., Lowry and Stoddart 1992), the distal elements are few andwidelyseparatedfromoneormorelarge, cup-shaped receptacles, and the bulla may be prominent.

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

A graphical plot of the types of calceoli and their

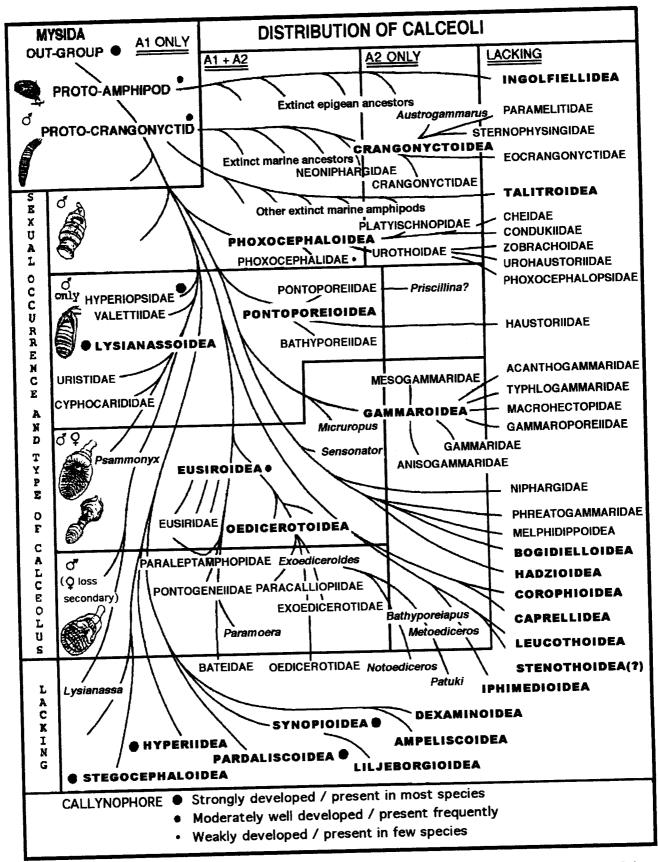


Fig. 3. Suggested phylogenetic relationships within the Amphipoda based on distribution of the calceoli on the antenna and between the sexes (modified from Bousfield & Shih 1994).

distribution by antennal site, sex, and higher taxon, can be linked by means of a branching arrangement with relationships that, in part, are remarkably similar to phyletic arrangements derived elsewhere from analysis of other character states (Fig. 3). In the first two categories, this arrangement goes somewhat beyond the relationships proposed by Lincoln & Lowry (1984) on the basis of the taxonomic (classificatory) distribution of calceoli. In the present chart, the positions of the major taxa in the various "boxes" are correlated primarily with the distribution (or lack) of calceoli on one or other (or both) antennae, along the horizontal axis and withthemorphologicaltypeanditssexualoccurrence,on the vertical axis. The vertical and horizontal axes also simulate, fanwise, an approximate evolutionary time scale for the probable frst appearance of the ancestral type of each major taxonomic group.

The arrangement of calceoli is here rooted in a presumed mysid-like out-group in which calceolus-like structures are known, at least on antenna 1 of the male. Such structures may have occurred in presumed former epigean and pelagic marine ancestors of the now hypogean relict suborder Ingolfiellidea, and of the continental freshwater-endemic Crangonyctoidea. Such epigean and marine ancestral types have not yet been found extant, or in the fossil record, but are predicted from this study and from earlier considerations (e.g., Bousfield 1982b). In this two-dimensional scheme, all members of the seven calceolate superfamilies, and the enigmatic hypogean calceolate Sensonator valentiensis Notenboom, 1986 (Melphidippoidea?), cannot be confined cleanly within any given graphical box. Such variance is attributable to parallel development, diversification, and subsequent loss of calceoli from the antenna of both sexes, presumably in response to changing life styles within the various taxonomic subgroups (above). Notably, the more strongly calceolate superfamily groups (calceoli on both A1 and A2, left column) are those in which members are primarily pelagic and/or reproduce freely in the water column. These include most Phoxocephaloidea, Pontoporeioidea, Lysianassoidea, Eusiroidea, and Oedicerotoidea. The less strongly calceolate superfamilies (with rare exceptions, calceoli on A2 only, right column) are found in the most primitive members of benthic superfamilies of the Reptantia (Crangonyctoidea, Gammaroidea). The position of acalceolate superfamilies is tentative, but is suggested partly by the presence or absence of other presumably plesiomorphic, often vestigial characters such as antennal callynophore and brush setae (above).

The presence or absence and type of antennal calceolus are character states of undoubted phyletic

significance. However, their restricted distribution among extant gammaridean superfamilies limits their use to cases of phyletic classification where other parameters of broader classificatory applicability (e.g., form of uropods, coxal plates, gnathopods) are known.

### Uropods 1 & 2.

The uropods of amphipods are biramous appendages of the three posterior abdominal segments. They function mainly in forward propulsion during swimming or crawling activities. The uropods are well developed and conspicuous in most gammarideans, hyperiideans, and ingolfiellideans, but minute or lacking in caprellideans. The rami are seldon equal in size, the outer usually being noticeably the shorter. Only within the Ingolfiellidea is uropod 2 typically larger than uropod 1.

Morphological variation in the rami of uropod 3 and its utilization in phyletic classification have been analyzed previously (Bousfield and Shih 1994). In this study, the form and armature of the rami of uropods 1 & 2 are similarly investigated. In nektonic forms, the rami are often lamellate or lanceolate, whereas in benthonic crawling or burrowing forms the rami are typically styliform (Schram 1986). The rami may also be modified for specialized functions in domicolous and/or commensal species, and for presumed copulation (in males) widely across the taxonomic spectrum (e. g., in some Lysianassoidea, Crangonyctoidea, Talitroidea, and Gammaroidea). At higher taxonomic levels, armature of the peduncle may also prove phyletically significant, particularly the development of baso-facial spine(s) in gammaroidean superfamilies, and distolateral spines in gammarioideans and some fossorial superfamilies (e.g., Phoxocephaloidea and Pontoporeioidea).

Figure 4 illustrates three main types of rami of uropods 1 & 2 and their occurrence in representative gammaridean superfamilies. Lanceolate rami (A) are generally slender and taper distally to an acute apex that lacks distinct apical spine(s) or spine clusters; marginal spines (when present) are typically arranged in opposing, evenly spaced series. Lanceolate rami typify the most primitive superfamilies of reproductive "swimmers" (Natantia), including the Lysianassoidea, Phoxocephaloidea, Pardaliscoidea and most Eusiroidea. Linear rami (C) are generally thick and robust (styliform), with subparallel margins that tapering only slightly distally; the apex is rounded or blunt, and usually bears a distinct cluster of spines of unequal length. These rami typify mostly benthonic crawling or burrowing superfamilies, with reproductively pre-

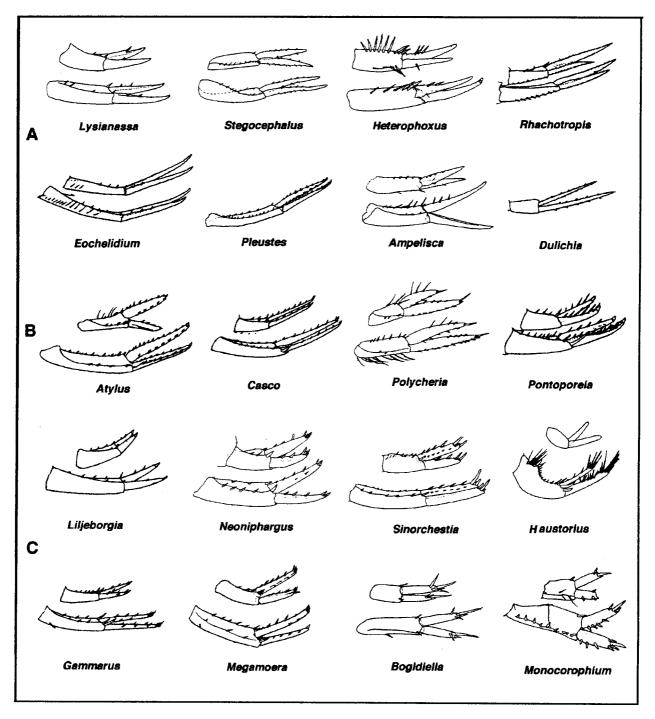


Fig. 4. Form of rami of uropods 1 & 2. A. Lanceolate; B. Transitional; C. Linear. (After Bousfield (1973) and unattributed sources)

amplexing gnathopods (Reptantia), such the Crangonyctoidea, Talitroidea, Gammaroidea, and Corophioidea. Transitional rami (B) taper variously to a subacute apex that may bear a single spine or a few very short spines; marginal spines are usually present and serially arranged (e. g., Dexaminoidea and Melphidippoidea).

The form and armature of the rami of uropods 1 &

2 apparently transcends these categories within a few gammaridean superfamilies (e.g., Pontoporeioidea). Also, within family Podoceridae, the dulichiid subgroup possesses lanceolate uropod rami that are atypical of superfamily Corophioidea, to the other character states of which the dulichiids conform reasonably well. The vestigial uropod rami of cercopid caprellidean amphipods are also lanceolate. Such a character state

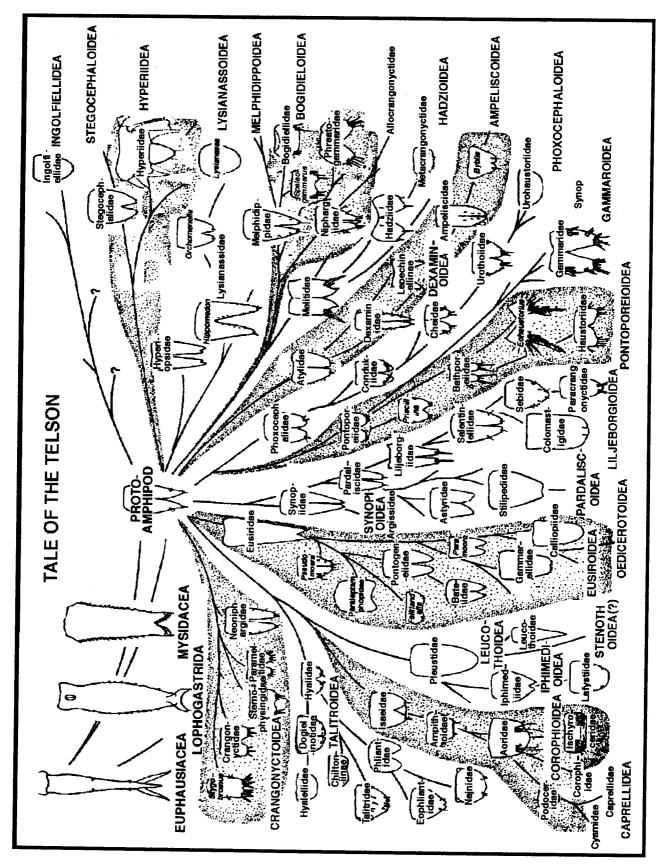


Fig. 5. Suggested evolutionary relationships of the telson within the Amphipoda. (modified from Bousfield & Shih 1994).

"anomaly" apparently supports direct phyletic ancestry of dulichiids to the cercopid line of Caprellidea, as proposed by Laubitz (1993). It may suggest a possible diphyletic origin of the Corophioidea, and consideration of a possible leucothoidean ancestry for the dulichiid podocerids (see fig. 7; Bousfield & Shih 1994).

However, broadly across families of most gammaridean superfamilies, the uropod ramal condition is remarkably stable and correlates well with the phyletic status of other character states in those same taxa. Thus, the lanceolate condition is typical of superfamilies that exhibit plesiomorphic states of antennal sensory organelles and sexually similar gnathopods. Conversely, the linear ramal condition is associated most frequently with apomorphic reduction of antennal sensory organelles, presence of sexually dimorphic gnathopods, and reproductive pre-amplexing behaviour. Not surprisingly, the transitional ramal form occurs mainly in higher taxa with a phyletically "intermediate" status of other character states. Thus, the form and armature of uropods 1 & 2 appear to be character states of high-level classificatory significance.

#### The Telson.

The form of the telson has long been considered a character of prime taxonomic significance (Stebbing 1906; Barnard & Karaman 1991). Its probable function in both free-swimming and benthonic life styles, and its overall significance in superfamily level classification has been reviewed by Bousfield & Shih (1994). The deeply bilobate form is generally deemed the plesiomorphic condition within amphipodan, peracaridan, and indeed, all malacostracan crustaceans (Schram 1986). Conversely, the entire, platelike, or "fleshy" form of the telson, presumably represents a distal fusion of the two primary lobes (e.g., as in superfamilies Leucothoidea and Corophioidea respectively) and thus the typical apomorphic state. A very advanced condition is seen in the Thaumatelsonidae and many Hyperiidea, where the plate-like telson is fused with the urosome. A less frequent but presumably apomorphic condition occurs where the lobes become separated throughout their entire length (as in most Gammaroidea and certain Hadzioidea) and attains an extreme separation dorsally on urosome 3 (abominal segment 6) in the advanced fossorial genus Eohaustorius (Pontoporeioidea).

A panoramic view of telson types across the spectrum of higher amphipod taxa is provided in Figure 5. The prototype amphipod is depicted with a bilobate

telson, the apex of each lobe having a "notch and spine" configuration derived from a presumed pelagic peracaridan (primitive malacostracan) ancestral outgroup. Following evolutionary lines outwards from this base through each superfamily group, we find that member species and genera having the greatest number of plesiomorphic character states (those nearest the base) also tend to have a fully or partially bilobate telson. Conversely, member species and genera with the most apomorphic or derived character states, in balance, usually show the most strongly fused or plate-like form of the telson. The totally bilobate apomorphic form may be noted in advanced members of the Gammaroidea and in some members of the Pontoporeioidea (family Haustoriidae).

However, the overall form of the telson proves not directly significant in development of a phyletic classification. As noted in fig. 5, development of a plate-like telson takes place independently and homoplasiously within nearly every superfamily group. Derivation of a superfamily group based solely on a plate-like telson would encompass members of at least ten different major groups, and thus be totally artificial. However, within component families of the most primitive superfamilies of "Natantia" (e.g., Lysianassoidea, Phoxocephaloidea, Eusiroidea, Pardaliscoidea) the deeply bilobate form of the telson is dominant. Conversely, within the more advanced "natant" superfamilies such as the Oedicerotoidea and Leucothoidea, the Hyperiidea, and among most reptant superfamilies (e.g., Crangonyctoidea, Talitroidea, Bogidielloidea, Corophioidea), the distally notched or plate-like form is dominant.

Despite contrary views of some (e.g., Barnard & Karaman 1981, 1991), the balance of evidence strongly supports the overall conclusion that a deeply bilobate telson is the plesiomorphic or ancestral condition within the Amphipoda. Conversely, a plate-like or apically entire telson is the apomorphic or advanced condition. However, structure of the telson appears to be more dependent upon factors of life-style at lower taxonomic levels rather on the more broadly "stable" features of reproductive biology. Character states of the telson may therefore be phyletically significant only at family, subfamily, or even generic classificatory levels.

### Phyletic Significance of Gnathopod Structure

The external morphological features of the gnathopods (peraeopods 1 & 2 of formal malacostracan terminology) have previously been considered one of the most significant and fundamental indicators of high level phyletic relationships within suborders Gammaridea (Stebbing 1906); Barnard & Karaman 1991) and Caprellidea (Laubitz 1993; Takeuchi 1993). A cross-section of amphipod gnathopod types was also analyzed by Bousfield & Shih 1994.

Early taxonomic studies had long detailed the sexually dimorphic, powerfully subchelate form of the gnathopods of intertidal and freshwater species of *Gammarus* of northwestern Europe. In females and immature stages, these anterior appendages were used mainly as implements of food-gathering but, in sexually mature males, are utilized in precopulatory carrying of the female, thus ensuring close proximity of the sexes at the time of her "mating" moult (ecdysis). Justified or not, *Gammarus* was considered by many workers to be the basic or ancestral amphipod reproductive form (e.g., Barnard 1969).

More recent studies (e.g., Borowksy 1984; Conlan 1991a) have investigated gnathopod morphology and sexual dimorphism across a broad spectrum of amphipod superfamilies. The results have been compared with a pre-amplexing and/or mate-guarding form of reproductive behaviour in species of *Gammarus* of northwestern Europe. As indicated by Schram (1986), this form of reproductive behaviour is now considered by most workers as relatively highly evolved and specialized within the Amphipoda.

The search for a probable ancestral form of the gnathopods first centred on members of superfamilies that were classified as primitive on the basis of other plesiomorphic character states. Over a range of family and generic morphotypes within the primitive superfamily Lysianassoidea (e.g., Barnard and Ingram 1990; Lowry & Stoddart 1997), the distal portions (carpus, propod and dactyl) of both gnathopods in both sexes, are found to be consistently subsimilar. Despite minor modifications within an increasingly sophisticated generic series, the plesiomorphic form of both gnathopods may be described as weakly subchelate, with slender carpus and propod, and clearly not sexually dimorphic. Within the Lysianassoidea, mating takes place freely and rapidly in the water column, there is no pre-amplexus or mate-guarding phase, and by corollary represents the plesiomorphic reproductive (mating) behaviour.

Amphipod superfamilies grouped within the category Natantia (Table I, p.67) are typified by pelagic reproductive (mating) behaviour, and by nonsexually dimorphic gnathopods that are primitively weakly subchelate and subsimilar in form. Exceptions can be explained, at least tentatively, on the basis of (1)

independent or convergent evolution within geographically isolated sub-taxa that have been exposed to similar, mainlyecological, evolutionary stresses (e.g., southern families of Oedicerotoidea); (2) a morphological vestige of presumed ancestral types whose evolutionary "thrust" devolved mainly into other superfamily groups that are, today, essentially "reptant" in reproductive life style (e.g., in Pontoporeiidae); or (3) a probable extant precursor of more widespread and diverse modern taxonomic groups (e.g., in Dexaminoidea, Melphidippoidea).

Within subcategory Reptantia, gnathopod morphology is basically different, and the range of morphotypes is considerably greater than seen in the Natantia (Bousfield & Shih 1994). Thus, in most component superfamilies the gnathopods are characteristically sexually dimorphic and strongly subchelate or cheliform, especially in males. However, many exceptions to these overall trends have been noted. These plausibly include a secondary use of sedimentary benthic substrata as a "fluid" mating medium wherein sexually dimorphic gnathopods and pre-amplexing mating behaviour may not be required (e.g., in Haustoriidae).

In summary, within component superfamilies of Reptantia, sexual dimorphism of the gnathopods, and benthic pre-amplexing reproductive styles are typical. These types are mainly vegetatively free-living and epigean in physically rigorous habitats such as coastal shallows, estuaries, and fresh-waters. Conversely, in members that have become secondarily commensal with other marine animals or plants, penetrated into hypogean brackish- and fresh-water or the deep sea, or have become fully terrestrial, sexual dimorphism of the gnathopods is markedly reduced or lacking. Secondarily and neotenically, the sexually dimorphic form may revert to a morphology suited to the vegetative life style of both sexually mature adults and immature stages.

### Mating Behaviour Within the Amphipoda

The significance of precopulatory mating behaviour and sexual dimorphism in phyletic relationships of amphipod crustaceans has been broadly investigated by Conlan (1991) and summarized by Bousfield & Shih (1994). To ensure proximity of males and females at the time of female ovulating ecdysis, amphipods employ two basic reproductive strategies:

(1) mate-guarding, in which the males are either (a) carriers involving pre-amplexing, with concomitant modification of male gnathopods for the purpose, or (b) attenders, where they remain domiciled with the fe-

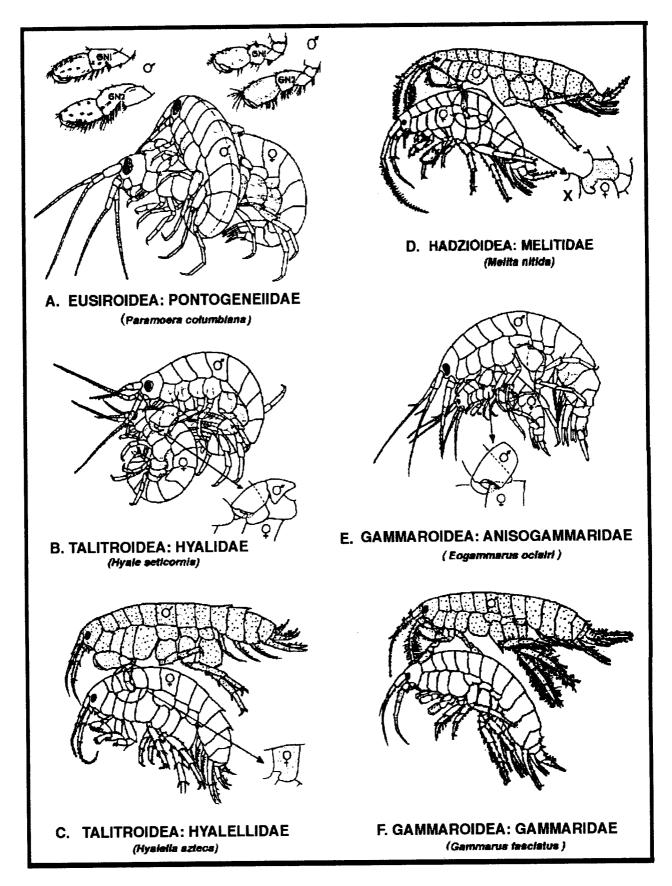


Fig. 6. Precopula in representative superfamilies of gammaridean Amphipoda. (after Bousfield & Shih 1994)

male and employ the gnathopods mainly in agonistic manner to ward off competing males.

(2) non-mate-guarding, in which the mature male simply seeks out females wherever they may be at the time of ovulation. These males are classified as (a) pelagic searchers if the female is in the water column, or (b) benthic searchers if the female is on or in the bottom substrata. In either case the gnathopods are little or not sexually dimorphic, and no pre-amplexus takes place.

Both strategies are determined by the period of ovulation of the female, at which time the male must be present if fertilization of the eggs is to take place. For a short period immediately following moulting, the cuticle of the female is sufficiently flexible to allow for release of the eggs into the brood pouch or marsupium. Sperm is deposited there by the male during copulation, and fertilization of the eggs can then take place.

Conlan (1991) concluded that the searching strategy is a primitive, and mate-guarding an advanced, form of reproductive behaviour in amphipods. This conclusion provides the principal basis for the present updated semi-phyletic classification of amphipod superfamilies (Table I, p. 67).

In these mating strategies, the reproductive morphology of the mature female is seldom significantly different from that of the vegetative or feeding stages, except in some species of *Melita* and some aquatic talitroideans where the coxae are modified to accept the dactyl of the precopulatory gnathopod of the male. However, the breeding frequency and fecundity reflect overall differences in mating strategy. Thus, females of mate guarders tend to be iteroparous, with several broods in a lifetime, whereas non-mate-guarders tend to be semelparous, with only one brood in a lifetime.

In the most primitive superfamily groups within Natantia, contact between the mate-seeking male and the female takes place only during actual copulation, and its duration is brief (Conlan 1991). These positions have been illustrated for a number of representative families and superfamilies of both Natantia and Reptantia. (Bousfield & Shih 1994). The positions vary according to the relative size of males and females, and on environmental conditions. All ensure rapid sperm transfer at the time of the female's ovulation moult.

Some pre-amplexing positions are illustrated in Fig. 6. Preamplexing is rare within superfamilies of Natantia, and where it does occur briefly, differs little from that of amplexus. Within Reptantia, however, preamplexus is nearly the rule. In the primitive Gammaroidea, males of Anisogammaridae (e.g., Eogammarus

oclairi, Fig. 6E) grasp the smaller female by the base of coxa 4, usually by means of gnathopod 1. In family Gammaridae (e.g., Gammarus, Fig. 6F), the male carries the female by means of a "fore-and aft" clutching of the anterior edge of peraeon plate 1 and posterior edge of peraeon 5, facilitiated by the very oblique palm of gnathopod 1. Within the Hadzioidea, the male of Melita nitida (Fig. 6D) employs his small gnathopod 1 to grasp the female by the specially modified anterior lobe of coxa 6. His much enlarged gnathopod 2 may be used in fending off competing males. In many aquatic Talitroidea, especially in Hyalella and Allorchestes (Hyalellidae, Fig. 6C) and in Hyale and Parallorchestes (Hyalidae, Fig. 6B), the dorsally positioned male inserts the dactyl of gnathopod 1 in a precopulatory notch in the lower anterior margin of peraeon 2 of the smaller female. Again, the much enlarged gnathopod 2 apparently functions agonistically towards other males. In some species of Hyale, however, the dactyl of gnathopod 2 may be used in grasping and/or rotating the female.

The widespread phenomenon of convergent evolution of high-level characters states is well illustrated by these superficially similar mating strategies, that differ morphologically and tactically at family and subfamily levels.

### The Phylogenetic Tree.

Possible natural relationships among subordinal and superfamily groups may be represented in the form of a phylogenetic tree (Fig. 7). This dendrogram is modified from Bousfield & Shih (1994) to include superfamilies Iphimedioidea Lowry and Myers, 2000 and Stenothoidea Bousfield, 2000, and reflect the influence of additional characters and character states. The plesiomorphic character states, especially of the antennal sensory organelles, are most strongly evinced in taxa, extant or extinct, that are closest to the trunk and main branches. The apomorphic or advanced and specialized features are best developed in taxa placed near the branching extremities. The phylogenetic "tree" may be viewed, in effect, as a form of cladogram in which the character states are ordered and arranged "parsimoniously", but without numerical basis.

The present version is little changed from the earlier tree (1994). During the past 10 years the number of species in each group has increased, variously, by only about 5-10%, few major new taxa have been discovered, and the ordering of character states has remained basically unchanged. However, as noted above (Fig. 4) the form of the rami of uropods 1 & 2 have here been

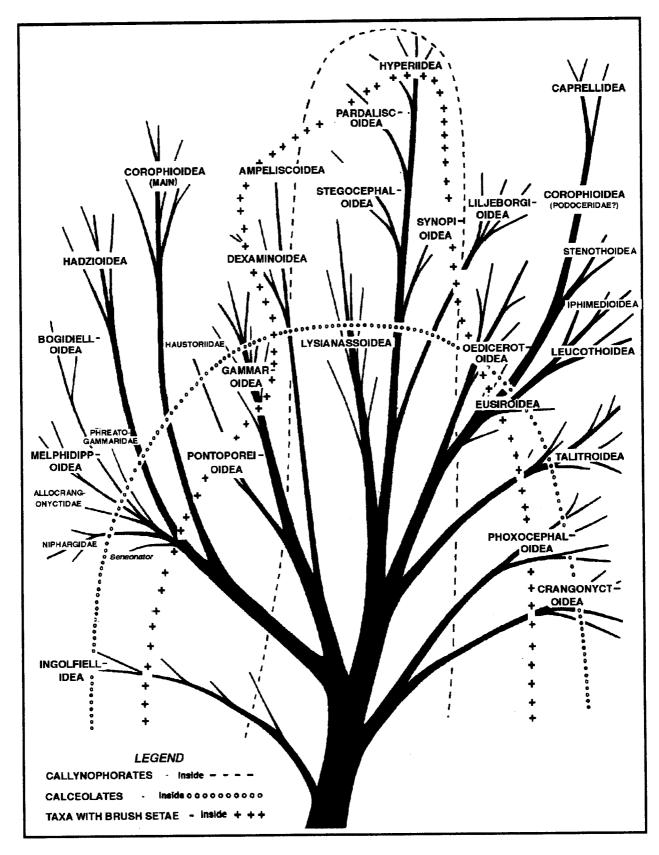


Fig. 7. Phylogenetic tree of suggested natural relationships within suborders and superfamilies of the Amphipoda (modified from Bousfield & Shih 1994).

suggested as significant indicators of phyletic relationships. The degree of anterolobation of coxae 5 & 6, and of heteropody of pereopods 5-7, deserve further study as indicators of phyletic significance. Emphasis on such parameters has here altered the position of the main trunk which now centrally subtends superfamilies of Natantia leading to the Hyperiidea, the most highly modified (advanced) of fully natatory taxa.

The phyletic position of the Liljeborgioidea, a group not yet rigorously defined, remains uncertain. North American family inclusions (p.100) are mainly benthic, commensal, deep-demersal, or hypogean in fresh water. Antennal reproductive sensory organelles are lacking in all subgroups, and most have developed sexually dimorphic gnathopods and pre-amplexing mating behaviour. Paradoxically it seems, component families retain lanceolate or transitional type uropod rami, posterolobate or weakly anterolobate coxae 5 & 6, and peropods 5-7 are basically homopodous. Other enigmatic family- or perhaps superfamily-level groups elsewhere include the Niphargidae, Phreatogammaridae, and the monotypic Sensonator valentiensis Notenboom, 1986.

In phylogentic analysis of the 10 suborders of the Isopoda, Brusca & Wilson (1991) have employed cladistic methodology leading to major classificatory recommendations. However, the universal applicability and adequacy of cladistic analyses for this purpose has been questioned by some (e.g., Gosliner & Ghiseln 1984). Relative to the taxonomically "difficult" order Amphipoda, the superficially similar peracaridan order Isopoda is more uniformly benthic in life style, with much greater development of both external and internal parasitic forms. It is palaeohistorically more ancient (Bousfield & Conlan 1990), and thus with perhaps fewer "intermediate" stages that frustrate creation of neatly defined phyletic units based on one or two character states only.

A full cladistic analysis of the Amphipoda is beyond the scope of this paper. Serious problems concerning character state homoplasy, and the status of so-called "intermediate" taxa have yet to be resolved (e.g., in Berge et al 2001). However, a phyletic tree based on "first principles" here provides a useful visual basis for eventual numerical establishment of a true phyletic classification of the Amphipoda.

### PHYLETIC ARRANGEMENT OF HIGHER TAXA

The present phyletic classification of higher amphipod taxa (Table I) is based on relatively few characters and character states, most of which exhibit high classificatory value. The North American species list (Appendix I, p. 75) follows this arrangement of higher taxonomic names.

The present analysis recognizes the Ingolfiellidea and Gammaridea as distinct and valid subordinal divisions of Order Amphipoda. However, the Hyperiidea and Caprellidea are of lesser significance, here submerged within subcategories of Natantia and Reptantia, respectively. This conclusion agrees in part with the results of a limited cladistic anlysis of the Amphipoda by Berge et al (2001). That study likewise combines hyperiids and caprellids variously within the Gammaridea, but is less demonstrative of the subordinal distinctness of the Ingolfiellidea.

Within suborder Gammaridea, the pragmatic terms "Natantia" and Reptantia" continue to encompass almost the same superfamily groups as earlier proposed (Bousfield & Shih 1994). Introduction of the form of the rami of uropods 1 & 2 as primary phyletic indicators reinforces the applicability of those subcategories, at least on a semi-phyletic basis. Thus, the newly proposed uropod-descriptive terms "Lanceolata" and "Lineata", are essentially interchangeable with the original terms "Natantia" and "Reptantia", since they encompass virtually the same respective superfamily goups.

Two major subgroups may be recognized within the Natantia: the primary Lanceolata, and the transitional Lanceolata. Member of the former are typically fully marine, have a mainly free-swimming life style, their antennal sensory organelles are well-developed, but the gnathopods are not sexually dimorphic. The "Transitionals" are not strictly marine, exhibit a wider variety of benthonic (commensal) life styles, and exhibit varying loss of antennal organelles, but corresponding development of sexually dimorphic, preamplexing gnathopods.

The Reptantia may be subdivided into: (1) primitive superfamilies having posterolobate coxae 5 & 6, and (2) advanced superfamilies in which these coxae are mainly anterolobate. The more primitive "anterolobates" encompass the pontoporeioidean and gammaroidean superfamilies ("gammarida" of Barnard & Barnard 1983). The advanced "anterolobates" contain the most highly evolved groups of gammaridean amphipods, marked by very specialized morphologies and life styles.

As noted above, the position of the Liljeborgioidea remains enigmatic. In conspicuous morphological character states and life style, component members seem clearly assignable to the "Reptantia". However, the condition of the posterior peraeopods and uropod

rami is plesiomorphic and characteristic of most "Natantia". A tentative, but not entirely satisfactory solution is to place the Liljeborgioidea among the "Advanced Transitionals" within Natantia (Table I).

In early phyletic studies (e.g., Bousfield 1979, 1983), the author utilized several other external morphological features, some of which tend to support the present categories. Thus, members of the Natantia usually possess a distinct rostrum, coxal gill on per-aeopod 7, well-developed natatory uropod 3, but relatively short antenna 1; in the Reptantia, however, the rostrum, and coxal gill of peraeopod 7 are usually lacking, uropod 3 is often reduced and non-natatory, and antenna 1 is usually elongate.

Sternal gills, of various form and presumed osmoregulatory function, occur only in freshwater taxa, but may have phyletic significance nonetheless. Thus, within Natantia, all superfamilies that encompass freshwater families and genera contain some species bearing sternal gills (e. g., in Gammaracanthus, Pseudamoera, and Falklandella within Eusiroidea; Paracalliope within Oedicerotoidea; Phreatogammarus within Melphidippoidea; and Paracrangonyx within Liljeborgioidea). In the Reptantia, however, sternal gills are characteristic of the more primitive superfamilies Crangonyctoidea (all families), Talitroidea (Hyalellidae), and Pontoporeioidea (Monoporeia, Diporeia). Sternal gills are lacking in all freshwater gammaroideans and hadzioideans (e.g., weckeliids, pseudoniphargids), to which may be added the European-Mediterranean regional species of Niphargidae, Sensonator, and all members of superfamily Bogidielloidea.

Attempts at utilizing other seemingly phyletically promising characters and states have proven frustrating and ineffective, largely because of homoplasious character state similarities at superfamily level. Mouthpart morphology tends to reflect feeding style and is thus useful mainly in family level classification [e. g., in Stegocephalidae (Berge 2000)]. Seemingly "in defiance of" other phyletic trends across both Natantia and Reptantia, the morphology of female brood lamellae varies between the broad, marginally setose, presumed plesiomorphic condition, and the narrow, strap-like, apomorphic form.

A very few characters have been little utilized to date, and may merit further investigation. Pleopod morphology is seldom figured or described in detail, especially in the early literature. What little is known of their character states (e.g., type of retinacula, "clothespin spines") tends to be conservative "across the taxo-

nomic board". Small morphological differences may therefore be significant at high classificatory level. Presence or absence and size of the accessory flagellum seems not phyletically accountable; its length appears secondarily increased in some deepwater gammarids of Lake Baikal. However, its position of origin (anterior in some Phoxocephalidae and Liljeborgiidae, mediolateral in nearly all other taxa) merits further study. Character states of surface ultrastructure are little known but may be especially promising as phyletic indicators when the difficulties of terminology and function have been resolved (Halcrow & Bousfield 1987).

### **CONCLUSIONS**

Analysis of plesio-apomorphic conditions of selected external morphological characters and reproductive behaviour has resulted in a revised classification of the amphipod Crustacea. Introduction of new characters has lent support to recognition of only two suborders, the primitive Ingolfiellidea, and the more advanced and much more diverse Gammaridea. The analysis also lends further support to the phyletic significance of previous gammaridean subcategories "Natantia and "Reptantia", interchangeable with newly proposed terms "Lanceolata" and "Lineata" respectively. These basic gammaridean morphotypes are represented in Fig. 8 as an assist to vizualizing or conceptualizing morphological relationships among the species of North American amphipods (Appendix I).

Because of homoplasious occurrence of some character states "across the taxonomic board", these subcategory names combine elements of phyletic significance with pragmatic usefulness. Cognizance of such variation within all component species requires that superfamilies be realistically diagnosed by a "best-fit" consensus of character states, rather than by rigorous conformity to one or two morphological criteria.

The classification outlined in Table I may be used as a form of "key" to subordinal and superfamily groups listed in Appendix 1. This extensive list of marine, brackish, freshwater and terrestrial species contains all known suborders and superfamilies, and many of the families allocated to each superfamily (see Martin & Davis 2001).

Phyletic classification has many advantages, not the least of which is conformity with phyletic classifications elsewhere within Class Crustacea, and major ordinal groups within the Animal Kingdom. Superfamily grouping of the North American fauna (Appendix I) has also facilitated comparative biogeogeographical

# TABLE I. Phyletic Classification of the Amphipoda suggested by character states of the uropods superimposed on those of reproductive morphology and belaviour, and other characters.

- I. AMPHIPODA INGOLFIELLIDEA (uropod 2>1; eyes stalked; maxillipeds partly separated basally; peduncle 3 of antenna 2 elongate, body vermiform; 2 families hypogean, marine and freshwater).
- II. AMPHIPODA GAMMARIDEA (uropod 1 > 2; eyes sessile; maxillipeds fused basally; peduncle 3 of antenna 2 not elongate; ~150 families epigean and hypogean, marine, freshwater, and terrestrial).
  - A. LANCEOLATA (=NATANTIA) (rami of both uropods 1 & 2 lanceolate, often with serially arranged marginal spines and lacking apical spines; antennae strongly sexually dimorphic, male with sensory antennalorganelles; gnathopods not (or weakly) sexually dimorphic; uropod 3 usually large, biramous).
    - I. Basic Lanceolates (uropods 1 & 2 rami lanceolate; gnathopods not sexually dimorphic).
      - Callynophorates (with antennal callynophore and brush setae in male)
         Lysianassoidea (antennae calceolate, head not rostrate)
         Pardaliscoidea; Stegocephaloidea: Hyperiidea (non-calceolate; head rostrate)

Hyperiidea (maxilliped lacking palp; coxae 1-4 small; A2 short in female)

Synopioidea (callynophore weak or non-existant, but brush setae present);

- 2. Phoxocephaloideans (callynophore seldom and brush setae infrequent; calceoli plesiomorphic, receptacle and bulla lacking, body with few distal elements; head strongly rostrate; peraeopod 5 dactylate); 5 families ,fossorial, marine, mainly antiboreal).
- II. **Transitionals** (uropods 1 & 2 transitional in form; callynophore & brush setae reduced or lacking,; gnathopods weakly sexually dimorphic, or not).
  - 3. Primitive Transitionals (antennae often calceolate, coxae 5 & 6 posterolobate) Eusiroidea (mostly pelagic; pereopods 5-7 homopodous, segment 4 produced behind) Oedicerotoidea (fossorial; peraeopods 5 & 6 homopodous, P7 elongate; gnathopods sexually dimorphic in 2 families).
    Leucothoidea (benthonic) (uropod 3, outer ramus 1-segmented; gnathopod rarely sex. dimorph.) Iphimedioidea (benthonic): uropod 3, outer ramus 1-segmented, gnathopods weak not dimorph).
  - Stenothoidea (benthonic), uropod 3, outer ramus 2-segmented; gnathopod often sex. dimorphic) 4 Advanced Transitionals (male antennae non-calceolate, with brush setae, callynophore rare; coxae 5 & 6 anterolobate, uroppod 3 biramous, often natatory)

    Dexaminoidea and Ampeliscoidea (urosome 2 & 3 fused; U3 rami large, natatory)

    Melphidippoidea: (urosome 2 & 3 separate; U3 lanceolate, weakly sexually dimorphic)

    Liljeborgioidea (gnathopods sexually dimorphic; life style commensal or freshwater hypogean.
- B. LINEATA (=REPTANTIA) (uropod rami linear, with apical spines, lateral marginal spines irregular; gnathopods sexually dimorphic, usually strongly; usally benthic reproductive behaviour)
  - I. Posterolobate reptants (Coxae 5 & 6 posterolobate; uropod 3 short, rami reduced)

    Crangonyctoidea (Antenna 1 elongate, wth accessory flagellum; A2 calceolate in male);

    Talitroidea (Antenna 1 the shorter, lacking accessory flagellum; A2 non-calceolate)
  - II. Anterolobate Reptants (Coxae 5 & 6 anterolobate; uropod 3, one or both rami large)
    - 1. Primitive Anterolobates (telson bilobate; free-swimming. free-burrowing, or commensal)
      Pontoporeioideans (appendages fossorial, P5 adactylate; gnathopods weakly or not sexually dimorphic; may retain pelagic reproduction, with primitively calceolate antenna 2 (male)
      Gammaroideans (appendages seldom fossorial; gnathopods subsimilar in size and sexually dimorphic; antennae weakly or not calceolate, coxal gill on peraeopod 7; mainly freshwater)
      Hadzioideans (appendages rarely fossorial; antennae not calceolate; gnathopods unlike and strongly sexually dimorphic; antennae not calceolate; P7 lacking coxal gill; marine and brackish)
    - 2. Advanced Anterolobates (telson plate-like or entire; domicolous or excl. hypogean life style) Bogidielloideans (vermiform; uropod 3 subequally biramous; telson plate-like; f.w. hypogean). Corophioideans (body depressed; peraeopods 3 & 4 glandular; uropod 3 reduced, telson fleshy. animals marine, domicolous (tube-buidling); male gnathopods mate guarding). Caprellideans (body slender, cylindrical; coxae lacking; abdomen vestigial; marine, epigean,

semi-sessile; 2 infrorders: Caprellida (skeleton shrimps) and Cyamida (whale lice).

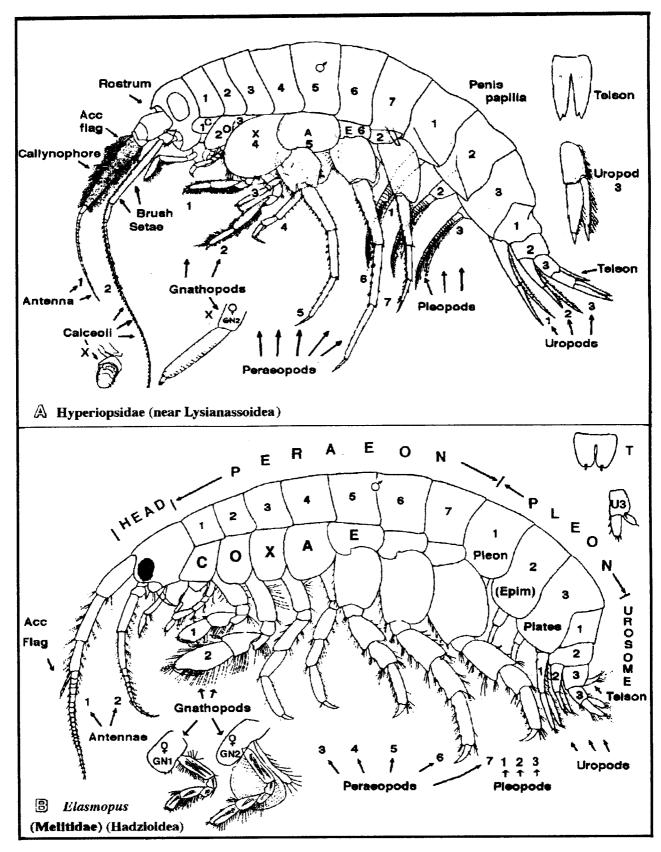


Fig. 8. Representative morphotypes of basic categories of phyletic classification of the Amphipoda A. Lanceolata (=Natantia). B. Lineata (=Reptantia) (after Bousfield & Shih 1994).

analysis of subregional faunas (Bousfield 2001). In summary, Arctic and Pacific coastal marine amphipod faunas are relatively primitive, possibly reflecting the long-term (biohistorical) stability of those regions. The east coast faunas are more advanced, compare phyletically with those of the Mederranean region, and presumably reflect the relatively recent origin of the North Atlantic Ocean (since late Jurassic). Gulf coast amphipods encompass the highest percentage of advanced, and lowest percentage of primitive superfamilies, consistent with its relatively high year-round temperature regime. Thus, within the Amphipoda, evolution of apomorphic features (e.g., sexually dimorphic gnathopods) "classically" proceeds most rapidly in tropical regions; conversely, plesiomorphic features (e.g., antennal sensory organelles) are most frequently retained in cold-water regions and in the deep sea where evolutionary rates are presumably much slower. This biogeographic-phyletic analytical methodology has been extrapolated from North American superfamily groups to other well-studied regional faunas to conclude that the world's most primitive marine assemblages presently occur in the Antarctic.

The North American freshwater amphipod fauna is much more diverse than was believed during the mid 1900's, thanks mainly to the extensive recent work of Dr. John R. Holsinger and colleagues, with much new material yet to be published (per. commun.). It contains a high percentage of ancient relict types with sternal gills, dominated in hypogean habitats by members of the Crangonyctoidea, and in epigean habitats by the exclusively neotropical Hyalellidae (Bousfield 1996) and the arctic-boreal pontoporeioidean genus Diporeia (Bousfield 1987). The more modern gammaroideans and hadzioideans, lacking sternal gills, are widely diverse throughout Eurasia. In North America, however, these advanced groups are represented only peripherally, and by small numbers of species and few families, of which some are recently introduced (e.g., Witt et al, 1997). A few relict species within Gammaracanthidae, Sebidae, and Bogidiellidae complete the North American freshwater complex.

The need for full return to phyletic classication of the Amphipoda, inevitable though it may be, remains urgent. Present analysis indicates that a fully satisfactory phyletic classification still eludes us. Cladistic methodology (e.g., Berge et al, 2001) has not yet solved the problem of suitable outgroups and/or homoplasious occurrence of character states widely accross the taxonomic board. The problem may yet be solved through pooling of results from all analytical methodology, and

employment of some of the characters and character states here developed. Especially promising is genetic methodology, both DNA hybridization and rDNA sequencing (Schram, Duffy, pers. commun.). Although these methodologies have special limitations of their own, they seem minimally affected by homoplasy of external character states, thereby providing a more reliable basis for phyletic classification. The present arrangement of superfamilies is not fully phyletic and is far from a final answer. It is proposed as a potentially useful platform upon which may be reconstructed a probable pathway of morphological evolution within the amphipod crustaceans.

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# APPENDIX I. PHYLETIC LIST OF AMPHIPOD CRUSTACEA OF NORTH AMERICA, NORTH OF MEXICO.

The study of phyletic classification presented in the main text was developed mainly through analysis of North American species listed here. The North American amphipod fauna contains about 1650 species, representative of all known suborders and superfamilies, about 2/3 of families, and perhaps 1/4 of the total number of species world-wide. As noted in the acknowledgements (p. 50), the list was developed, over a 15-year period, by a subcommittee of the Committee on Scientific and Common Names of Aquatic Invertebrates, chaired by Dr. Donna D. Turgeon, NOAA, Washington, D. C. The list encompasses marine, brackish, freshwater and terrestrial faunal components. An additional ~200 species have been recognized from continental North America north of Mexico, including Canada and Alaska, but not Greenland, Bermuda, or the Bahamas. Others are known from the U.S. mid-Pacific state of Hawaii. These undescribed taxa are in the process of being treated by systematic specialists. Their work will be added to an updated final list, including common names where possible, to be published in a special volume on the Crustacea of North America jointly sponsored by NOAA and the American Fisheries Society.

The system of higher classification of amphipods of this list is essentially phyletic, including superfamily level taxa, following standards proposed for Ingolfiellidea by Stock (1977), Hyperiidea by Bowman & Grüner (1973); Caprellidea by Laubitz (1993) and Gammaridea by Schram (1986), updated by Bousfield and Shih (1994) and Bousfield (2000).

Although the arrangement of superfamilies follows that of Table I of the main text (p. 67), the component families and genera are listed alphabetically. Newly proposed subordinal categories of classification are omitted for the present, but if reasonably widely accepted by colleagues, may be introduced in the final CNAI crustacean volume. The former subordinal-level names Hyperiidea and Caprellidea are retained in situ within the list, mainly for pragmatic reasons, even though they have been merged within suborder Gammaridea. The merged older names have yet to be reassessed at suitable classificatory levels.

As noted above, the phyletically arranged list of Northamerican amphipods provides a basis for biogeographical analysis of it subregional marine and freshwater faunas. This study, currently in press (Bousfield 2001b), also contains a detailed numerical analysis of numbers of species by subregion, superfamily, and family level categories.

<b>Ocurrence</b>	Legend		LA	-	Louisiana
A	•,	Arctic	LABR	-	Labrador
AC	-	Acadian	MI	-	Mississippi
At	-	Atlantic	N	-	Northern
AL	-	Alaska	NC	_	North Carolina
ALEUT	-	Aleutians	NFLD	-	Newfoundland
BAR	-	Pt. Barrow	P	-	Pacific
BC	•	British Columbia	ORE	-	Oregon
BER	-	Bering Sea	SE	•	Southeastern
C	-	Carolinian	ST L	-	St. Lawrence Gulf
CAL	-	California	${f v}$	-	Virginian
CHES	-	Chesapeake Bay	WA	-	Washington State
CUBA	-	Cuba	FW	-	Freshwater
E	-	Eastern	ST	-	Semiterrestrial
FL	-	Florida	T	-	Terrestrial
G	-	Gulf of Mexico	TEX	_	Texas
HAT	-	Cape Hatteras	$\mathbf{w}$	-	Western
HAW	-	Hawaii	YUC	-	Yucatan

## SCIENTIFIC NAME

#### **OCCURRENCE**

# SUBORDER INGOLFIELLIDEA HANSEN, 1903

# Family Ingolfiellidae Hansen, 1903

Ingolfiella fuscina Dojiri & Sieg, 1987

At-G (SC-W FL)

# SUBORDER GAMMARIDEA LATREILLE, 1803

# Superfamily Lysianassoidea (Bousfield, 1979; Lowry & Stoddart, 1997)

# Family Lysianassidae Dana, 1849

# Subfamily Lysianassinae Dana, 1849

Acidostoma laticorne G. O. Sars, 1879	At (N, slope)
Aruga oculata Holmes, 1908	P (CAL
A. holmesi (Barnard, 1955)	P (WA-CAL), G (W FL)
Bonassa bonairensis (Stephensen, 1933)	G (FL)
Concarnes concavus (Shoemaker, 1933)	G (FL)
Dissiminassa homosassa Lowry & Stoddart, 1997	G (FL)
D. dissimilis (Stout, 1913)	P(SCAL)
Eclecticus eclecticus Lowry & Stoddart, 1997	G(FL)
Lysianopsis alba Holmes, 1903	At (V-C), G (FL)
L. cubensis Shoemaker, 1933	G (FL.)
L. hummelincki (Stephensen, 1933)	G (FL)
L. ozona Lowry & Stoddart, 1997	G(WFL)
L. subantarctica (Schellenberg, 1931)	G (Fl-tropic?)
Macronassa macromera (Shoemaker, 1916)	P(SCAL)
M. pariter (J. L. Barnard, 1969)	P(CAL)
Menigrates obtusifrons (Boeck, 1861)	At (G, N, slope)
Shoemakerella cubensis (Stebbing, 1897)	G (W FL)
S. nasuta (Dana, 1853)	G (FL) (see Shoemaker, 1948)
Di	

# Subfamily Tryphosinae Lowry & Stoddart, 1997

Allogaussia recondita Stasek, 1958	P (BC-CAL)
Hippomedon coecus (Holmes, 1908)	P(S CAL)
H. columbianus Jarrett & Bousfield, 1982	P (BC-ORE)
H. denticulatus (Bate 1857)	At (N, slope)
H. granulosus Bulycheva, 1955	P (BER-BC)
H. holbolli (Kroyer, 1946)	At (ST L)
H. pensacola Lowry & Stoddart, 1997	G (W FL)
H. propinguus Sars, 1890	At (ST. L-HAT)
H. serratus Holmes, 1905	At (AC-CHES)
H. subrobustus Hurley, 1963	P (CAL?)
H. tenax Barnard, 1966	P (S CAL?)
H. tricatrix Barnard, 1971	P (ORE, deep)
H. zetismus Hurley, 1963	P (CAL, deep)
Koroga megalops Holmes, 1908	P (BC-WA, offshore)

Lanidanaoralla	ahama Damand 1066	D/CAT 1 O
	charno Barnard, 1966	P(CAL-deep?)
	des nubifer Barnard, 1971 neoum Gurjanova, 1951	P (ORE-deep)
L.	•	P (BER-CAL)
L.	nubifer Barnard, 1971	P (ORE, deep)
L.	garthi Hurley, 1963	P (BC-CAL)
L. L.	gurjanovae Hurley, 1963	P (BC-CAL)
L. L.	serraculum Dalkey, 1998	P((CAL)
	serratum Stephensen, 1925	At (G, N, slope)
	decipiens Hurley, 1963	P(CAL)
	holmesi (Hurley, 1963)	P (BC-CAL)
_	minuta (Kroyer, 1846)	P (AL-ORE)-A-At (ST L)
4	pacifica (Gurjanova, 1951)	P (BER-CAL)
	perdido Lowry & Stoddart, 1997	G (W F)
	homasi Lowry & Stoddart, 1997	G (W FL)
O.	pressa Shoemaker, 1930	At (AC, shelf)
O.	holmesi (Hurley, 1963)	P (CAL)
O.	limodes Meador & Present, 1985	P (CAL)
O. O.	macroserrata Shoemaker, 1930	At (AC, shelf)
0. 0.	magdalensis (Shoemaker, 1942)	P(S CAL?)
0. 0.	nugax (Holmes, 1904)	P (BER-WA)
0. 0.	obtusa (Sars, 1891)	P (SE AL-CAL), At (ST L)
0. 0.	pectinata Sars, 1882	At (ST L)
	serrata (Boeck, 1861)	At (AC-V)
	tosus Stephensen, 1923 s abyssi (Goes, 1866)	At (ST L, slope)
		A-At (G-BCN)
	ngimerus Jarrett & Bousfield, 1982	P (BC-ORE)
P. 100	bilis (Stimpson, 1853)	At (AC-DEL)
	terranovae Steele, 1979	At (AC-NFLD)
R.	ridiana Lowry & Stoddard, 1997	G (W FL)
	rima (J. L. Barnard, 1964) Ichra (Hansen, 1887)	P(S CAL)
	a (Fabricius, 1780)	At ST L slope)
T.	gulosus (Kroyer, 1845)	At (ST L -AC)
	ulachicola Lowry & Stoddart, 1997	At (ST L)
T.		G (W FL)
<i>T</i> .	compressa (Sars, 1891) groenlandica (Hansen, 1887)	At (ST Lslope)
<i>T</i> .	gulosus (Kroyer, 1845)	At (ST L slope)
<i>T.</i>	index (Barnard, 1966)	At (N, slope)
T.	metacaecula Barnard, 1967	P(CAL)
<i>T</i> .	nanoides (G. O. Sars, 1895)	P(CAL)
<i>T</i> .	orchomenoides Stephensen, 1925	At (St.L)
<i>T</i> .	rotundata (Stephensen, 1923)	A-At
<i>T</i> .		At (ST L, slope
T.	spitzbergensis (Chevreux, 1926) triangula (Stephensen, 1925)	A-At (ST L, slope)
	comus (Barnard, 1971)	At (ST L)
W.	similis Jarrett & Bousfield, 1982	P (SE AL-ORE)
<i>W</i> .	wirketis (Gurjanova, 1962)	P (BER-SE AL)
***	wa keus (Guijanova, 1902)	P (BER-AL)

# Family Uristidae Hurley, 1963

<i>A</i> .	barrowensis Steele,1882	P-A (BAR)
<b>A</b> .	beringi Steele, 1982	P (BER)
<i>A</i> .	comecrudus J. L. Barnard, 1971	P (ORE)
A.	compactus Gurjanova, 1962	P (BER?), At (ST L)
A.	dalli Steele, 1983	P (BER?)
A.	debruyni Hoek, 1882	At (ST L)
A.	epistomaticus Kudrjaschov, 1965	P (BER?)
A.	filiger Stimpson, 1864	P (WA?)
A.	hurleyi Steele, 1986	P(AL?)
A.	laticoxae Gurjanova, 1962	P (BER?)
A.	lilljeborgi Boeck, 1871	P (AL-CAL)-A-At (AC)
A.	makarovi Gurjanova,1962	P (BER)A-At (ST L)
A.	m. nugax (HYBRID, Brunel MS))	At (ST L)
A.	nugax (Phipps, 1774)	P (BER-CAL?)-A-At
<i>A</i> .	ochoticus Gurjanova, 1962	P (BER?)-A-At
A.	pacificus Gurjanova, 1962	P(AL-WA)
A.	petersoni Steele, 1986	P (BER?)
A.	schefferi Steele, 1986	P(AL?)
A. A.	sculptifer Gurjanova, 1982	P (BER?)
A. A.	shoemakeri Steele, 1983	P (BER?)
	on pavor Barnard, 1966	P (ORE-CAL)
C.	pumilus (Liljeborg, 1865)	At (ST L)
	uaeus Barnard, 1967	P (deep)
	coenlandica (Hansen, 1887)	At (ST L)
_	a fidenter Barnard, 1966	P (CAL)?
	Shoemaker, 1964	P (ALEUT)
•	Onisimus) litoralis (Kroyer, 1845)	A-At (N)
	Boekosimus) edwardsi (Kroyer, 1846)	At (G, N)
	lacialis (G. O. Sars, 1900)	At (G, N) At (G)
	ormani (Sars, 1891)	At (ST L slope)
		At (ST L slope)
	lautus (Kroyer, 1845) us barentsi (Stebbing, 1894)	A-At (N, slope)
	sites abyssi (Goes, 1866)	At (deep)
	a cedrosiana Barnard, 1967	P (CAL)
	cocula Barnard, 1966	P (BC)
S	dorotheae (Hurley, 1963)	P (CAL)
S.	· · · · · · · · · · · · · · · · · · ·	P (deep)
S.	grabenis Barnard, 1967 totorami Barnard, 1967	P (CAL)
S.		P(S CAL)
S. S.	tracalero (Barnard, 1966)	P(S CAL)
	zopa Barnard, 1966	P (CAL)
	robertsoni Stebbing & Robertson, 1891	
-	biscayensis (Chevreux, 1908)	G (FL)
	lifornicus Hurley, 1963	P(CAL)
	ewsoni Hurley, 1963	P(CAL2)
	talladurus Barnard, 1963	P (CAL?)
-	rspinus Barnard, 1967	P (ORE, deep)
U. un	nbonatus (Sars, 1882)	At ST L slope)

## Family Scopelocheiridae Lowry & Stoddart, 1997

Paracallisoma coecum (Holmes, 1908) P (AL-BC, offshore)

# Family Trischizostomatidae Lilljeborg 1865

Trischizostoma sp. (Bousfield, 1987 proposed) P-At (AL-CAL, deep)

#### Family Opisidae Lowry & Stoddart, 1995

Opis	sa eschrichti Kroyer 1842	P (BC-CAL), At (AC)
Ο.	tridentata Hurley, 1963	P (BC- CAL)
0.	odontochela Bousfield, 1987	P (SE AL-BC)

# Subfamily concept Conicostomatinae Lowry & Stoddart proposal; Barnard & Karaman 1991?

Acidostoma hancocki Hurley, 1963	P (BC-CAL)
A. obesum subsp. ortum J. L. Barnard, 1967	P (CAL, deep)
Ocosingo borlus Barnard, 1964 (= Fresnillo Barnard)	P (BC-CAL)
Pachynus barnardi Hurley, 1963	P (WA-CAL)
Prachynella lodo Barnard,1964	P (WA-CAL)
Socarnes hartmanae Hurley, 1963	P(CAL)
S. vahli (Kroyer, 1838)	At (ST L, slope)
Socarnoides illudens Hurley, 1963	P (ORE-CAL)

## Family Cyphocarididae Lowry & Stoddart, 1997

Cyclocaris guilelmi Chevreux, 1899		P(SCAL?)
Cyphocaris challengeri Stebbing, 1880		P(AL-CAL)
<i>C</i> .	faurei K. H. Barnard, 1918	P(S CAL?)
<i>C</i> .	guilelmi Chevreux, 1899	P(AL-CAL)
<i>C</i> .	richardi Chevreux, 1905	P (BC-CAL)
<i>C</i> .	anonyx Boeck, 1871	P (BC, offshore)
<i>C</i> .	tunicola Lowry & Stoddart, 1997	G (W FL)
Metacyphocaris helgae Tattersall, 1906		P(AL-CAL)

# Family Aristiidae Lowry & Stoddart, 1997

Aristias captiva Lowi	y & Stoddart, 1997	G (W FL)
A. expers Ba	rnard, 1967	P(CAL?)
A. pacificus	Schellenberg, 1936	P (BC-WA)
A. topsenti (	Chevreux, 1900	At ST L, slope)
A. tumidus (1	Kroyer, 1846)	P(WA), At (ST L, slope)
A. veleronis	Hurley, 1963	P (BC-CAL)
Boca campi Lowry &	Stoddart, 1997	G (W FL)
B. elvae Lowry & Sto	oddart, 1997	G(E&WFL)
B. megachela Lowry	& Stoddart, 1997	G (W FL)

## Family Endevouridae Lowry & Stoddart, 1997

Ensayara	a entrichoma Gable & Lazo-Wasem, 1990	G (W FL)
<i>E</i> .	ramonella Barnard, 1964	P (S CAL?)

# Family Hyperiopsidae Bovallius, 1886

(near Cyphocarididae Lowry & Stoddart?)

Parargissa americana Barnard, 1961 P (CAL, BC, deep)
P. galatheae Barnard, 1961 P (CAL?)

#### Family Valettiidae Stebbing, 1888

Valettiopsis dentata Holmes, 1908 P (BC-CAL, deep)
Cedrosella fomes (Barnard, 1967) P (CAL)?

#### 1. Incerta sedis

Eurystheus grillus Lichtenstein, 1882 P (abyssal)

#### Superfamily Stegocephaloidea Bousfield, 1979

#### Family Stegocephalidae Dana, 1855

## Subfamily Adanieniexinae Berge, 2000

Andaniexis abyssi Boeck, 1871	P (deep), A-At (AC)
A. elinae Berge & Vader, 1997	Α
A. gracilis Berge & Vader, 1997	Α
A. lupus Berge & Vader, 1997	Α
Parandania boecki (Stebbing, 1888)	P (BC)
Parandaniexis mirabilis Schellenberg, 1929	P (BC?)

#### Subfamily Andaniopsinae Berge, 2000

Andaniopsis nordlandica (Boeck, 1871)

Andanieopsis pectinata (Sars, 1882)

At (BF)

A-At (NFLD)

#### Subfamily Stegocephalinae Berge, 2000

Bousfieldia mammilidacta (Moore, 1992)	P(BC)
Gordania camoti (Barnard, 1967)	P (CAL)
Phippsia romeri Schellenberg, 1925	Α
Pseudo viscaina (Barnard, 1967)	P (CAL)
Stegocephalexia penelope Moore, 1992	P (BC)
S, hancocki (Hurley, 1956)	P (S CAL, deep)
S. minima (Stephensen, 1925)	A-At (NFLD)
S. pajarella (Barnard, 1967)	P(CAL)
Stegocephalus ampulla (Phipps, 1774)	Α
S. abyssicola (Oldevig, 1959)	Α
S. inflatus Kroyer, 1842	PA (BER)-A-At (ST L)
S. cascadiensis (Moore, 1992)	P (ORE, deep)
S. similis (Sars, 1895)	A

#### Superfamily Pardaliscoidea Bousfield, 1979

#### Family Pardaliscidae Boeck, 1871

Caleidoscopsis tikal (J. L. Barnard, 1967)	P (CAL)
Halice abyssi Boeck, 1871	At (ST L)
H. malygini (Gurjanova, 1936)	Α
H. ulcisor Barnard, 1971	P (ORE)
Halicoides lolo (Barnard, 1971)	P (ORE)
H. synopiae (Barnard, 1962)	P (ORE)
H. tambella (Barnard, 1961)	P (CAL)
Pardaliscella symmetrica Barnard, 1959	P(CAL)
P. yaquina Barnard, 1971	P (ORE)
Pardaliscoides fictotelson J. L. Barnard, 1966	P (CAL, deep)
Parahalice mirabilis Birstein & Vinogradov, 1962	P (abyssal)
Rhynohalicella halona (Barnard, 1971)	P (BC-CAL)
Tosilus arroyo Barnard, 1966	P (S CAL, deep)

#### Family Stilipedidae Holmes, 1908

#### Subfamily Stilipedinae Holmes, 1908 (revised Holman & Watling, 1983)

Stilipes distincta Holmes, 1908

P (AL-CAL)

#### Subfamily Astyrinae Pirlot, 1934 (revised Holman & Watling, 1983)

Astyra abyssi Boeck,1871

At (ST L)

#### Family Vitjazianidae Birstein & Vinogradov, 1955

Vitjaziana gurjanovae Birstein & Vinogradov, 1955

P (BER, deep)

#### Family Vemanidae Bousfield 1979 (see Thurston, 1989)

Vemana lemuresa Barnard, 1967

P (B CAL, deep)

#### Superfamily Synopioidea Bousfield, 1979

## Family Synopiidae Dana, 1855

Bruzelia tuberculata Sars, 1866	P (AL-CAL), A-At (ST L)
B. inlex Barnard, 1967	P (CAL)
B. guayacura Barnard, 1972	P (CAL?)
B. ascua Barnard 1966	P (CL, deep)
Bruzeliopsis cuspidata Barnard, 1962	P (CAL)
B. turba Barnard, 1964	P(CAL)
Priscosyrrhoe priscis (Barnard, 1967)	P (S CAL)
Garosyrrhoe bigarra (Barnard, 1962)	P (S CAL)
G. cf. bigarra (Barnard, 1962)	G (FL)
G. laquei Ortiz, 1985	G (FL - CUBA)
Pseudotiron pervicax Barnard, 1967	P (CAL)
P. golens Barnard, 1962	P (CAL)

P. coas Barnard, 1967	P (CAL)
Synopia ultramarina Dana, 1853	G (FL)
S. scheeleana Bovallius, 1886	G (SEFL)
Syrrhoe crenulata Goes, 1866	P(AL-CAL), A-At(ST L - AC)
S. longifrons Shoemaker, 1964	P (BC-CAL)
S. oluta Barnard, 1972	P(CAL)
Syrrhoites columbiae Barnard, 1972	P (ORE, deep)
S. cohasseta Barnard, 1967	P (CAL)
S. dulcis Barnard, 1967	P(CAL)
S. lorida Barnard, 1962	P(CAL)
S. silex Barnard, 1967	P (CAL)
S. terceris Barnard, 1964	P(CAL)
S. trux Barnard, 1967	P (CAL, deep?)
Tiron biocellata Barnard, 1962	P (BC-CAL)
T. spiniferus (Stimpson, 1854)	A-At (AC)
Metatiron cf. bellairsi (Just, 1981)	G (FL)
M. triocellatus (Goeke, 1985)	G (FL)
M. tropakis (Barnard, 1972)	P (CAL?), At (V-C) G (FL?)

## Family Argissidae Walker, 1904

Argissa hamatipes (Norman, 1869)

P (BER-CAL), A-At (ST) G (NW FL)

# SUBORDER HYPERIIDEA MILNE EDWARDS, 1830

# Infraorder Physosomata Pirlot, 1929

## Superfamily Scinoidea Bowman & Gruner, 1973

# Family Scinidae Stebbing, 1888

Scina borealis (G. O. Sars, 1882)	P (BER-CAL)-At
S. crassicornis (Fabricius, 1775)	P (ORE-CAL)
S. nana Wagler, 1926	P (CAL)
S. rattrayi Stebbing, 1895	P (BC-WA, slope)-At
S. tullbergi (Bovallius, 1885)	P (CAL)-At (G)
Proscina vinogradovi Shih & Hendrycks, 1996	P(AL) (54 40'N 155 10'W)
Cheloscina antennula Shih & Hendrycks, 1996	P(AL) (53 20'N 155 16'W)

## Family Mimonectidae Bovallius, 1885

Mimonectes sphaericus Bovallius, 1885 P (BER)-A-At M. gaussi Woltereck,1904? P (BC-WA)

# Superfamily Lanceoloidea Bowman & Gruner, 1973

## Family Lanceolidae Bovallius, 1887

Scypholaneola aestiva Stebbing, 1888	P (WA-CAL, deep)-At
S. vanhoeffeni Woltereck, 1909	P (BC-WA)

Lance	ola loveni Bovallius, 1885	P (ORE, deep)-At
L.	serrata Bovallius, 1885	P (CAL, deep)
L.	pacifica Bowman 1973	P (BC-WA)
L.	sayana Bovallius, 1885	P (BER)

# Family Chuneolidae Woltereck, 1909

Chuneola parasitica Vinogradov, 1956

P (BER-W ALEUT)

# Infraorder Physocephalata Bowman & Gruner, 1973

# Superfamily Vibilioidea Bowman & Gruner, 1973

#### Family Vibiliidae Dana, 1852

Vibilia armata Bovalli	ius, 1887	P (ORE-CAL)
V. australis Stebl	bing, 1888	P (BC-WA)-At - G
V. viatrix Bovalli	ius, 1887	P(CAL)
V. gibbosa? Bova	llius 1887	P (CAL)

# Family Cystosomatidae Willemoes-Suhm, 1875

Cyctosoma fabricii Stebbing, 1888	P (BC-CAL)-At, deep
C. pellucidus (Willemoes-Suhm, 1873)	P (SE AL-CAL)-At

# Family Paraphronimidae Bovallius, 1887

Paraphronima crassipes Claus, 1879	P (BER-CAL, slope)-At (G)
P. gracilis Claus, 1879	P (BC-WA, deep)-At (Gulf)

# Superfamily Phronimoidea Bowman & Gruner, 1973

#### Family Phronimidae Dana, 1853

Phronima atlantica Guerin, 1836	P (BER-CAL)-At-G
P. bowmani Shih, 1991	P (CAL)
P. dunbari Shih, 1991	P(CAL)
P. pacifica Streets, 1877	At-G
P. sedentaria (Forskal, 1775)	P (BC-CAL)-At
P. solitaria Guerin, 1836	At-G
P. stebbingi Vosseler, 1900	At-G
Phronimella elongata (Claus, 1862)	P (ORE)-At-G

# Family Dairellidae Bovallius, 1887

Dairella californica (Bovallius, 1885) P (ORE-CAL, oceanic)

# Family Phrosinidae Dana, 1853 (=Anchylomeridae)

Anchylomera blossevillei Milne-Edwards, 1830

P (WA-CAL)-At-G

Phrosina semilunata Risso, 1822
Primno abyssalis (Bowman, 1968)
P. brevidens Bowman, 1978
P. johnsoni Bowman, 1978
P. lateillei Stebbing, 1888
P (CAL)-At-G
P (BC-CAL)
G
At-G
P (CAL)

## Family Hyperiidae Dana, 1852

P (AL-CAL) Hyperia antarctica Spandl, 1927 P(CAL) H. bengalensis (Giles, 1887?) P (BER)-A-At H. galba (Montagu, 1813) P(CAL) H. leptura Bowman, 1973 P (BER-CAL)-A-At H. medusarum (O.F.Mueller, 1776) P (BC-CAL)-At H. spinigera Bovallius, 1889 P (BC-CAL)-At(G) Hyperietta stephenseni Bowman 1973 P(CAL)-At(G) H. vosseleri (Stebbing, 1904) P (CAL)-At-G H. luzoni (Stebbing, 1888) P(CAL)-At-G) H. stebbingi Bowman, 1973 P-A-At Hyperoche medusarum (Kroyer, 1842) P (CAL)-At-G Hyperioides longipes Chevreux, 1900 At-G Hyperionyx macrodactylus (Stephensen, 1924) At Iulopsis loveni Bovallius, 1887 At -G Lestrigonus bengalensis Giles, 1887 P(CAL)-At-G L. schizogeneios (Stebbing, 1888) At-G L. crucipes (Bovallius, 1889) At-G L. macrophthalmus (Vosseler, 1901) At-G L. latissimus (Bovallius, 1889) P(SCAL) L. shoemakeri Bowman, 1973 P (BER)-A-At, deep Parathemisto abyssorum Boeck, 1870 At-G Phronimopsis spinifera Claus, 1879 At-G Themistella fusca (Dana, 1853) P (BER-CAL) Themisto pacifica (Stebbing, 1888) P(BER)-A-At libellula Lichtenstein, 1822 Т. A-At guadichaudii Guerin 1842 *T*.

# Superfamily Lycaeopsoidea Bowman & Gruner, 1973

#### Family Lycaeopsidae Chevreux, 1913

Lycaeopsis themistoides Claus, 1879

L. zamboangae (Stebbing, 1888)

At-G
P (CAL)-At

# Superfamily Platysceloidea Bowman & Gruner, 1973

## Family Pronoidae Claus, 1879

Eupronoe armata Claus, 1879

E. minuta Claus, 1879

Paralycaea gracilis Claus, 1879

Sympronoe parva (Claus, 1879)

At-G

P (CAL)-At-GULF

P (CAL)-At-G

P (S CAL)-At-G

# Family Anapronoidae Bowman & Grüner, 1973

in the provide restriction of the Diephensen, 1925	Anapronoe	reinhardti	Stephensen,	1925
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P(CAL)

# Family Lycaeidae Claus, 1879

Lycaea pulex Marion, 1874		P(CAL)
L.	vincenti Stebbing, 1888	At-G
L.	bovallioides Stephensen, 1925	G
L.	bovallii Chevreux, 1900	G
Brac	chyscelus crusculum Bate, 1961	P (BC-CAL)-At?
В.	globiceps (Claus, 1871)	At (CUBA)?
В.	rapax Claus, 1871	G `

# Family Oxycephalidae Bate, 1861

Oxycephalus clausi Bovallius, 1887	P (BC-CAL, deep)-At-G
O. piscator Milne Edwards, 1830	At-G
Cranoecephalus scleroticus (Streets, 1878)	At-G
Leptocotis tenuirostris (Claus, 1871)	At-G
Rhabdosoma whitei Bate, 1862	At-G
Simorhynchotis antennarius Claus, 1871	G
Streetsia challengeri Stebbing, 1888	P (BC-CAL, slope)-At-G
S. mindanaonis (Stebbing, 1888)	G
S. pronoides (Bovallius, 1887)	P(CAL)

# Family Platyscelidae Bate, 1862

Amphithyrus bispinosus Claus, 1879	G
A. sculpturatus Claus, 1879	At-G
Hemityphus rapax (Milne-Edwards, 1830)	At-G
Paratyphis maculatus Claus, 1879	At-G
Platyscelus serratulus Stebbing 1888?	P(S CAL)
P. ovoides (Claus, 1879)	At-G
Tetrathyrus forcipatus Claus, 1879	At-G

# Family Parascelidae Bovallius, 1887

Thyropus edwardsi (Claus, 1879)	At-G
T. sphaeroma (Claus, 1879)	At-G
T. typhoides (Claus, 1979)	P (CAL)-G
Schizoscelus ornatus Claus, 1879	At-G

# Superfamily Phoxocephaloidea Bousfield, 1979 [=Haustorioidea Barnard & Drummon, 1982 (part)]

# Family Platyischnopidae Thomas & Barnard, 1983

Eudevenopus honduranus Thomas & Barnard, 1983	At (FL-SC), G
E. metagracilis (Barnard, 1964)	P (S CAL)
Skaptopus brychius Thomas & Barnard, 1983	At (V-C, slope), G
Tiburonella viscana (Barnard, 1969)	P (S CAL)

# Family Urothoidae Bousfield, 1979

Urot	hoe denticulata Gurjanova, 1951	P (BER?)
U.	rotundifrons Barnard, 1962	P(CAL)
Ū.	varvarini Gurjanova, 1953	P (BC-CAL)

# Family Phoxocephalidae G. O. Sars, 1895

# Subfamily Metharpiniinae Jarrett & Bousfield, 1994a

Grandifoxus	s aciculatus Coyle, 1982	P (AL-BC)
G.	acanthinus Coyle, 1982	P(AL)
G.	constantinus Jarrett & Bousfield, 1994a	P (BER)
G.	dixonensis Jarrett & Bousfield, 1994a	P(BC)
G.	grandis (Stimpson, 1856)	P (BC-CAL)
G.	lindbergi (Gurjanova, 1953)	P (BER-BC)
G.	longirostris (Gurjanova, 1938)	P (BER-BC)
G.	nasutus (Gurjanova, 1936)	P(AL)
G.	pseudonasutus Jarrett & Bousfield, 1994a	P (ALEUT)
G	vulpinus Coyle, 1982	P (AL-BC)
Beringiapho	oxus beringianus Jarrett & Bousfield, 1994a	P (BER)
	us major (Barnard, 1960)	P (SE AL-CAL)
М.	maximus Jarrett & Bousfield, 1994a	P (AL-BC)
Foxiphalus	aleuti (Barnard & Barnard, 1982)	P(AL)
F.	apache Barnard & Barnard, 1982	P (S CAL)
F.	cognatus (Barnard, 1960)	P (S CAL)
F.	falciformis Jarrett & Bousfield, 1994a	P (BC-ORE)
F.	fucaximeus Jarrett & Bousfield, 1994a	P(WA)
F.	golfensis Barnard & Barnard, 1982	P (S CAL)
F.	obtusidens (Alderman 1936)	P (ORE-CAL)
F.	secasius Barnard & Barnard, 1982	P(S CAL)
F.	similis (Barnard, 1960)	P (BC-CAL)
F.	slatteryi Jarrett & Bousfield, 1994a	P (BER)
F.	xiximeus Barnard & Barnard, 1982	P (BC-CAL)
Metharpini	a coronadoi Barnard 1980	P (S CAL)
М.	floridana (Shoemaker, 1933)	P (CAL?), G (FL)
<i>M</i> .	jonesi (Barnard, 1963)	P(S CAL)
Rhepoxynii	us abronius (J. L. Barnard, 1960)	P (BC-CAL)
R.	barnardi Jarrett & Bousfield, 1994a	P (BC-CAL)
R.	bicuspidatus (Barnard, 1960)	P (BC-CAL)
R.	boreovariatus Jarrett & Bousfield, 1994a	P (BC)
R.	daboius (Barnard, 1960)	P (BC-CAL)

R.	fatigans (Barnard, 1960)	P (BC-CAL)
R.	gemmatus (Barnard, 1969)	P(SCAL)
R.	heterocuspidatus (Barnard, 1960)	P(SCAL)
R.	homocuspidatus (Barnard & Barnard, 1982)	P(SCAL)
R.	lucubrans (Barnard, 1960)	P(S CAL)
R.	menziesi (Barnard & Barnard, 1982)	P(SCAL)
R.	pallidus (Barnard, 1960)	P (BC-CAL)
R.	stenodes (Barnard, 1960)	P(SCAL)
R.	tridentatus (Barnard, 1954)	P (ORE-CAL)
R.	variatus (Barnard, 1960)	P (BC-CAL)
R.	vigitegus (Barnard, 1971)	P (BC-ORE)
R.	epistomus (Shoemaker, 1938)	At (V-C?) G (FL?)
R.	hudsoni Barnard & Barnard, 1982	At (V-C) G (FL?)

# Subfamily Pontharpiniinae Barnard & Drummond, 1978

Mandibulophoxi	us alaskensis Jarrett & Bousfield, 1994b	P (AL-BC)
<i>M</i> .	gilesi J. L. Barnard, 1957	P (BC-CAL)
<i>M</i> .	mayi Jarrett & Bousfield, 1994b	P (SE AL-BC)

# Subfamily Parharpiniinae Barnard & Drummond, 1978

Eyakia robusta (Holmes, 1908)	P (SE AL-CAL)	
Eyakia sp. 1 (= E. robusta Barnard & Barnard, 1981)	P(CAL)	
Eyakia calcarata (Gurjanova, 1938]	P(CAL)	

# Subfamily Brolginae Barnard & Drummond, 1978

Lobrol	gus chumashi Barnard & Barnard, 1981	P (AL-CAL)
<i>E</i> .	pontarpioides Gurjanova, 1953	P (BER)
E.	spinosus (Holmes,1905)	P?-At(V), G (E FL?)
Paraph	oxus beringiensis Jarrett & Bousfield, 1994b	P (BER)
<i>P</i> .	communis Jarrett & Bousfield, 1994b	P (BC)
<i>P</i> .	gracilis Jarrett & Bousfield, 1994b	P (BC-CAL)
<i>P</i> .	oculatus Sars, 1879	At (ST L)
<i>P</i> .	pacificus Jarrett & Bousfield, 1994b	P (BER-BC)
<i>P</i> .	rugosus Jarrett & Bousfield, 1994b	P (BER)
P.	similis Jarrett & Bousfield, 1994b	P (BC)
<i>P</i> .	simplex Jarrett & Bousfield, 1994b	P (BER?)

## Subfamily Phoxocephalinae Barnard & Drummond, 1978

Cephalophoxoides homilis (Barnard, 1960)	P (BC-CAL)
Leptophoxus icelus Barnard, 1960	P(CAL)
Metaphoxus frequens Barnard, 1960	P (SE AL-CAL)
Parametaphoxus fultoni (in Barnard, 1960 in part)	P (AL-CAL)
Parametophoxus quaylei Jarrett & Bousfield, 1994b	P (BC-ORE)
Phoxocephalus holbolli (Kroyer, 1842)	A-At (AC-CHES)

# Subfamily Harpiniinae Barnard & Drummond, 1978

Coxophoxus hidalgo J. L. Ba	arnard, 1966	P(CAL)
Harpinia antennaria Meiner		AP, At (V, deep slope)
H. clivicola Watling,		At (off DEL)
H. cabotensis Shoema	iker, 1930	At (AC)
H. pectinata G.O. San	rs,1891	AP, At (S to Hatteras) (see Watling)
H. plumosa (Kroyer, 1		At (St.L)
H. propinqua Sars, 18	891	At (AC) C Hat. Watling, 1981
H. serrata Sars, 1879		At, G deep?
H. truncata Sars, 189	94	At (to Mid At) (see Watling)
Harpiniopsis fulgens J. L. B.	arnard, 1960	P (BC-CAL)
H. emeryi Barnar	rd, 1960	P (CAL?)
H. epistomata Ba	rnard, 1960	P(SCAL)
H. fulgens Barnar	rd, 1960	P(CAL)
H. galera Barnaro	d, 1960	P(CAL)
H. gurjanovae B	ulycheva, 1936	P (BER)
H. naiadis Barna	rd, 1960	P(S CAL)
H. percellaris Ba	rnard, 1971	P (ORE, deep)
H. petulans Barns	ard, 1966	P (CAL)
H. profundis Barr	nard 1960	P (CAL?)
H. triplex Barnar	d, 19 <b>7</b> 1	P (ORE, deep)
Heterophoxus affinis (Holme	es, 1908)	P (SE AL-CAL)
H. oculatus (Ho	lmes. 1908)	P (S CAL)
H. conlanae Jar	rett & Bousfield, 1994b	P (SE AL-ORE)
H. ellisi Jarrett d	& Bousfield, 1994b	P (BC-ORE)
H. ellisi variant	Jarrett & Bousfield ,1994b	P(BC)
H. nitellus Barn	ard, 1990	P(S. CAL)
Pseudharpinia excavata Che	evreux, 1887	P (CAL)
	arrett & Bousfield, 1994b	P(BC)
P. sanpedroens	is (Barnard, 1960)	P (S CAL)

# Superfamily Eusiroidea Bousfield, 1979

# Family Amathillopsidae Pirlot, 1934 (transferred to Iphimedioidea by Lowry & Myers, 2000)

Amathillopsis spinigera Heller, 1875 P-At (pelagic)

#### Family Bateidae Stebbing, 1906

Bate	ea catharinensis Müller, 1865	G (FL)
В.	bousfieldi Ortiz, 1991	G (W FL)
В.	lobata Shoemaker, 1926	P(S CAL)
В.	transversa Shoemaker, 1926	P(S CAL)
Car	inobatea cuspidata Shoemaker, 1926	G (W FL)
С.	carinata Shoemaker, 1926	G (FL)

## Family Eusiridae Stebbing, 1888

Cleonardo moirae Bousfield & Hendrycks, 1995a	P (BC, pelagic)
Eusirella elegans Chevreux, 1908	At (ST L)

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E.	multicalceola (Thorsteinson, 1941)	P (BC-WA, pelagic)
Eusiroge	nes deflexifrons Shoemaker, 1930	At (ST L)
Eusiroides monoculoides (Haswell, 1879)		P (CAL)
Eusirus columbianus Bousfield & Hendrycks, 1995a		P (BC)
Eusirus cuspidatus Kroyer, 1845		P, At (ST L)
Eusirus longipes Boeck, 1871		At (ST L, slope)
Eusirus propinquus G. O. Sars, 1893		At (ST L, slope)
Rhachotr	opis aculeata (Lepechin, 1780)	A-P
R.	americana Bousfield & Hendrycks, 1995a	P(BC)
R.	barnardi Bousfield & Hendrycks, 1995a	P (CAL)
R.	boreopacifica Bousfield & Hendrycks, 1995a	P (SE AL-BC)
R.	cervus Barnard, 1957	P(SCAL)
R.	clemens Barnard, 1967	P (CAL)
R.	conlanae Bousfield & Hendrycks, 1995a	P(BC)
<i>R</i> .	distincta (Holmes, 1908)	P (pelagic), At (ST L)
<i>R</i> .	inflata (Sars, 1883)	P(AL-CAL)At(ST L, slope)
R.	ludificor Barnard, 1967	P(CAL)
R.	luculenta Barnard, 1969	P(S CAL?)
R.	oculata (Hansen, 1888)	At-A-P
R.	minuta Bousfield & Hendrycks, 1995a	P(BC)
R.	natator (Holmes, 1908)	P (pelagic)
Rozinante	e fragilis (Goes, 1866)	A-At (ST L)

# Family Gammaracanthidae Bousfield, 1977

Gammaracanthus loricatus Sabine, 1824 A-At (AC)

Pseudacanthus aestuariorum (Lomakinia, 1952) P(AL)-A-At (AC)(Dadswell, 1974)

## Family Gammarellidae Bousfield, 1977

Gammarellus homari (L., 1768) A-At (AC) angulosus (Rathke, 1843) G. At (AC)

## Family Pontogeneiidae Stebbing, 1906

Accedomoera vagor J. L. Barnard, 1969	P (SE AL-CAL)
A. melanopthalma (Gurjanova, 1938)	P (SE AL-CAL)
Nasageneia quinsana (Barnard, 1964)	P(S CAL)
N. yucatenensis Ledoyer, 1986	G (FL)
Paramoera (Paramoera) columbiana Bousfield, 1958	P (SE AL-ORE)
P. (Paramoera) mohri Barnard, 1958	P (CAL-WA)
P. (Paramoera) bousfieldi Staude, 1995	P (SE AL-ORE)
P. (Paramoera) serrata Staude, 1995	P (WA-CAL)
P. (Paramoera) suchaneki Staude, 1995	P (SE AL-S CAL
P. (Rhithromoera) bucki Staude, 1995	P (SE AL-WA)
P. (Rhithromoera) carlottensis Bousfield, 1958	P (SE AL-BC)
P. (Humilomoera) leucophthalma Staude, 1995	P (SE AL-WA)
P. (Humilomoera) crassicauda Staude, 1995	P(AL)
Pontogeneia inermis (Kroyer, 1838)	P (BER-CAL)-A-At
P ivanovi Gurjanova 1951	P (BER-WA)-A
P. rostrata Gurjanova, 1938	P (BER-CAL)-A

Р.	intermedia Gurjanova, 1938	P (BER-CAL)-
Р.	(Tethygeneia) opata Barnard, 1979	P(CAL)
<b>P</b> .	(T.) longleyi Shoemaker, 1933	G (FI)
Р.	(T.) bartschi Shoemaker, 1948	G (FL-CUBA)

# Family Calliopiidae G. O. Sars, 1895

(D) 40 FT	A. (CCTI)
Apherusa bispinosa (Bate, 1857)	At (GST L)
A. cirrhus (Bate, 1862)	A A+(STI)
A. fragilis (Goes, 1966)	A-At (ST L)
A. glacialis Hansen, 1888	A-P
A. megalops (Buchholz, 1874)	A-P (BER)
A. retovskii Gurjanova, 1934	A
A. sarsi Shoemaker, 1930	A
A. tridentata (Bruzelius, 1859)	A
Bouvierella carcinophila Chevreux, 1889	P (BC), At (ST L)
Calliopius behringi Gurjanova, 1951	P (BER)
C. columbianus Bousfield & Hendrycks, 1997	P (SE AL-ORE)
C. carinatus Bousfield & Hendrycks, 1997	P (BC-CAL)
C. laeviusculus (Kroyer, 1838)	A-At-AC)
C. pacificus Bousfield & Hendrycks, 1997	P B(BC-CAL)
C. sablensis Bousfield & Hendrycks, 1997	At (AC)
Cleippides bicuspis Stephenson, 1931	A
C. quadricuspis Heller, 1875	A
Dolobrotus mardeni Bowman 1974	At (AC, deep)
Halirages bispinosus Stephensen 1916	At (ST L, deep)
H. fulvocincta (M. Sars, 1858)	A (Barrow), At (ST L)
H. elegans Norman, 1882	A
H. mixta Stephenson, 1931	A
H. nilssoni Ohlin, 1895	At-A (G, N, deep)
H. quadridentata Sars, 1876	A
Haliragoides inermis (Sars, 1882)	At-A (ST L)
Laothoes meinerti Boeck, 1871	A
L. pacificus Gurjanova, 1938	PA (BER)
L. polylovi Gurjanova, 1946	At (ST L - LABR, deep)
Leptamphopus paripes Stephensen, 1931	P (BC, deep), At (ST L, slope)
Oligochinus lighti J. L. Barnard, 1969	P(AL-CAL)
Oradarea longimana (Boeck, 1871)	P (BC-CAL), At (ST L, deep)
Paracalliopiella pratti Barnard, 1954	P (BER-CAL)
P. beringiensis Bousfield & Hendrycks, 1997	P-A (BER)
P haliragoides Bousfield & Hendrycks, 1997	P-A (BER)
P. kudrjaschovi Bousfield & Hendrycks, 1997	P-A (BER)
P. slatteryi Bousfield & Hendrycks, 1997	P (BER)
	A-P-At (ST L-LABR)
Weyprechtia pinguis (Kroyer, 1838)	A-P-At (ST L)
W. heuglini (Buchholz, 1874)	TET-TH (OT L)

# Superfamily Oedicerotoidea Bousfield, 1979

# Family Oedicerotidae Lilljeborg, 1865.

Acanthostepheia behringiensis (Lockington, 1877)	A (BER)
A malmoreni (Goes. 1866)	P (BER), A-At (ST L, deep)

A. edax J. L. Barmard, 1967 A. goesi Just, 1980 A. latipes (Sars, 1882) A. sedovi Gurjanova, 1946 A. mercichelidium americanum (Bousfield, 1973) A. milisi Bousfield & Chevrier 1996 A. micropleon (Barnard, 1977) A. setosum Bousfield & Chevrier, 1996 A. micropleon (Barnard, 1977) A. setosum Bousfield & Chevrier, 1996 A. micropleon (Barnard, 1977) A. setosum Bousfield & Chevrier, 1996 A. shoemakeri (Mills, 1962) A. rectipalmum (Mills, 1962) A. polymous Bousfield & Chevrier, 1996 A. polymous (M. Sars, 1858) A. polymous (M. Sars, 1858) Bathymedon antennarius Just, 1980 B. covilant J. L. Barnard, 1961 B. flebilis Barnard, 1962 B. obtusifrons (Hansen, 1887) B. roquedo Barnard, 1962 B. obtusifrons (Hansen, 1887) D. intermedius Shoemaker 1930 D. norvegicus (Boeck 1871) D. similis Bousfield & Chevrier, 1996 D. simplex Hansen, 1887 D. tesselatus Schneider, 1884 D. tuberculatus Boeck, 1871 Finoculodes omnifera Barnard, 1961 Hartmanodes hartmanae (Barnard, 1962) M. castalskii Gurjanova, 1936 M. demissus Stimpson, 1833 Kroyera carinata Bate, 1857 M. datimamus (Goeck, 1861) M. datissimanus (Stephensen, 1931) M. latissimanus (Goecs, 1866) M. murrius Barnard, 1962 M. longirostris (Goes, 1866) M. murrius Barnard, 1962	Aceroides distinguendus (Hansen, 1888)	A (DAD)
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Bathymedon antennarius Just, 1980 B. covilhani J. L. Barnard, 1961 P (ORE, deep) B. flebilis Barnard, 1966 P (CAL-deep) B. kassites Barnard, 1966 P (CAL-deep) B. longimanus (Boeck, 1871) D. nanseni Gurjanova, 1946 B. obtusifrons (Hansen, 1887) D. intermedius Shoemaker 1930 D. norvegicus (Boeck, 1871) D. similis Bousfield & Chevrier, 1996 D. simplex Hansen, 1887 D. tesselatus Schneider, 1884 D. tuberculatus Boeck, 1871 Hartmanodes hartmanae (Barnard, 1962) H. nyei (Shoemaker, 1933) Kroyera carinata Bate, 1857 Machaironyx muelleri Coyle, 1980 Monoculodes brevirostris Bousfield & Chevrier, 1996 M. castalskii Gurjanova, 1936 M. demissus Stimpson, 1853 M. demissus Stimpson, 1853 M. demissus Barnard, 1962 M. latissimanus (Stephensen, 1931) M. latimanus (Goes, 1861 M. latissimanus (Stephensen, 1931) M. latimanus (Goes, 1866) M. longirostris (Goes, 1866	· · · · · · · · · · · · · · · · · · ·	P (AL?)
B.         covilhani J. L. Barnard, 1961         P (ORE, deep)           B.         flebilis Barnard, 1966         P (ORE-CAL, deep)           B.         kassites Barnard, 1966         P (CAL-deep)           B.         longimanus (Boeck, 1871)         At (G, N, slope)           B.         nanseni Gurjanova, 1946         P (BER-BC)A-At (ST L)           B.         pumilis Barnard, 1962         P (ORE-S CAL)           B.         obtusifrons (Hansen, 1887)         A-At (ST L)           B.         roquedo Barnard, 1962         P (CAL)           B.         saussurei (Boeck, 1871)         At (ST L)           B.         vulpeculus Barnard, 1971         P (ORE-S CAL, deep)           Deflexilodes enigmaticus Bousfield & Chevrier, 1996.         P (SE AL-BC)           D.         intermedius Shoemaker 1930         A-At (AC) (not FL!)           D.         similis Bousfield & Chevrier, 1996         P (SE AL-BC)           D.         similis Bousfield & Chevrier, 1996         P (AL-BC)           D.         similis Bousfield & Chevrier, 1996         P (AL-BC)           D.         simplex Hansen, 1887         A-At (ST L, slope)           D.         tesselatus Schneider, 1884         At (ST L)           D.         tesselatus Schneider, 1933         G (FL) (see Ortiz		A-At (ST L, slope)
B. flebilis Barnard, 1967 B. kassites Barnard, 1966 B. longimanus (Boeck, 1871) B. nanseni Gurjanova, 1946 B. pumilis Barnard, 1962 B. obtusifrons (Hansen, 1887) B. roquedo Barnard, 1962 B. saussurei (Boeck, 1871) B. vulpeculus Barnard, 1971 Deflexilodes enigmaticus Bousfield & Chevrier, 1996. D. intermedius Shoemaker 1930 D. norvegicus (Boeck 1871) D. similis Bousfield & Chevrier, 1996 D. simplex Hansen, 1887 D. tesselatus Schneider, 1884 D. tuberculatus Boeck, 1871 Finoculodes omnifera Barnard, 1971 Hartmanodes hartmanae (Barnard, 1962) H. nyei (Shoemaker, 1933) Kroyera carinata Bate, 1857 Machaironyx muelleri Coyle, 1980 Monoculodes brevirostris Bousfield & Chevrier, 1996 M. castalskii Gurjanova, 1951 M. diamesus Gurjanova, 1956 M. demissus Stimpson, 1853 M. emarginatus J. L. Barnard, 1967 M. latissimanus (Stephensen, 1931) M. latimanus (Goes, 1861 M. longirostris (Goes, 1866) M. longirostris (Goes,		Α
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B. longimanus (Boeck, 1871) B. nanseni Gurjanova, 1946 B. pumilis Barnard, 1962 B. obtusifrons (Hansen, 1887) B. roquedo Barnard, 1962 B. saussurei (Boeck, 1871) B. vulpeculus Barnard, 1971 Deflexilodes enigmaticus Bousfield & Chevrier, 1996. D. intermedius Shoemaker 1930 D. norvegicus (Boeck 1871) D. similis Bousfield & Chevrier, 1996 D. simplex Hansen, 1887 D. tesselatus Schneider, 1884 D. tuberculatus Boeck, 1871 Finoculodes omnifera Barnard, 1971 Hartmanodes hartmanae (Barnard, 1962) H. nyei (Shoemaker, 1930) Kroyera carinata Bate, 1857 Machaironyx muelleri Coyle, 1980 Monoculodes brevirostris Bousfield & Chevrier, 1996 M. damesus Gurjanova, 1951 M. diamesus Gurjanova, 1956 M. demissus Stimpson, 1853 M. emarginatus J. L. Barnard, 1962 M. latissimanus (Stephensen, 1931) M. latimanus (Goes, 1861 M. longirostris (Goes, 1866)	B. flebilis Barnard, 1967	<u>-</u> '
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B. nanseni Gurjanova, 1946 B. pumilis Barnard, 1962 B. obtusifrons (Hansen, 1887) B. roquedo Barnard, 1962 B. saussurei (Boeck, 1871) B. vulpeculus Barnard, 1971 Deflexilodes enigmaticus Bousfield & Chevrier, 1996. D. intermedius Shoemaker 1930 D. norvegicus (Boeck 1871) D. similis Bousfield & Chevrier, 1996 D. simplex Hansen, 1887 D. tesselatus Schneider, 1884 D. tuberculatus Boeck, 1871 Finoculodes omnifera Barnard, 1971 Hartmanodes hartmanae (Barnard, 1962) H. nyei (Shoemaker, 1933) Kroyera carinata Bate, 1857 Machaironyx muelleri Coyle, 1980 Monoculodes brevirostris Bousfield & Chevrier, 1996 M. damesus Gurjanova, 1936 M. demissus Stimpson, 1853 M. emarginatus J. L.Barnard, 1962 M. glyconicus Barnard, 1967 M. latissimanus (Goes, 1861 M. longirostris (Goes, 1866)	B. longimanus (Boeck, 1871)	At (G, N, slope)
B. pumilis Barnard, 1962 B. obtusifrons (Hansen, 1887) B. roquedo Barnard, 1962 B. saussurei (Boeck, 1871) B. vulpeculus Barnard, 1971 Deflexilodes enigmaticus Bousfield & Chevrier, 1996. D. intermedius Shoemaker 1930 D. norvegicus (Boeck 1871) D. similis Bousfield & Chevrier, 1996 D. simplex Hansen, 1887 D. tesselatus Schneider, 1884 D. tuberculatus Boeck, 1871 P (ORE-S CAL, deep) P (SE AL-BC) A-At (AC) (not FL!) P (S CAL), At -(ST L) A-At (ST L, slope) A-At (ST L, slope) P (AL-BC) A-At (ST L, slope) P (ORE, deep) P (ORE, deep) P (ORE, deep) P (S CAL) H. nyei (Shoemaker, 1933) Kroyera carinata Bate, 1857 Machaironyx muelleri Coyle, 1980 Monoculodes brevirostris Bousfield & Chevrier, 1996 M. castalskii Gurjanova, 1951 M. diamesus Gurjanova, 1956 M. demissus Stimpson, 1853 M. emarginatus J. L. Barnard, 1962 M. glyconicus Barnard, 1967 M. latissimanus (Stephensen, 1931) M. latissimanus (Goes, 1861 M. longirostris (Goes, 1866)	B. nanseni Gurjanova, 1946	
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B. vulpeculus Barnard, 1971  Deflexilodes enigmaticus Bousfield & Chevrier, 1996.  D. intermedius Shoemaker 1930  D. norvegicus (Boeck 1871)  D. similis Bousfield & Chevrier, 1996  D. simplex Hansen, 1887  D. tesselatus Schneider, 1884  D. tuberculatus Boeck, 1871  Hartmanodes manifera Barnard, 1971  Hartmanodes hartmanae (Barnard, 1962)  H. nyei (Shoemaker, 1933)  Kroyera carinata Bate, 1857  Machaironyx muelleri Coyle, 1980  Monoculodes brevirostris Bousfield & Chevrier, 1996  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. demissus Stimpson, 1853  M. demissus Stimpson, 1853  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861)  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)	B. saussurei (Boeck, 1871)	
Deflexilodes enigmaticus Bousfield & Chevrier, 1996.  D. intermedius Shoemaker 1930  D. norvegicus (Boeck 1871)  D. similis Bousfield & Chevrier, 1996  D. simplex Hansen, 1887  D. tesselatus Schneider, 1884  D. tuberculatus Boeck, 1871  Hartmanodes hartmanae (Barnard, 1971  H. nyei (Shoemaker, 1933)  Kroyera carinata Bate, 1857  Machaironyx muelleri Coyle, 1980  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. demissus Stimpson, 1853  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  P (SE AL-BC)  AAt (AC) (not FL!)  P (S CAL), At -(ST L)  P (AL-BC)  A-At (ST L, slope)  P (ORE, deep)  P (ORE, deep)  P (BC?)  P (BC?)  P (BCR)  P (BER)  P (BER)  P (BER)  P (BER)  P (BER)  P (BER)  P (DRE-CAL)  P (ORE-CAL)  P (CAL, deep)  P (CAL, deep)  P (ORE-BC?), At (ST L)  P (SE AL-WA)-A-At (ST L, slope)  A-At (N, slope)	B. vulpeculus Barnard, 1971	
D. intermedius Shoemaker 1930 D. norvegicus (Boeck 1871) D. similis Bousfield & Chevrier, 1996 D. simplex Hansen, 1887 D. tesselatus Schneider, 1884 D. tuberculatus Boeck, 1871 Hartmanodes omnifera Barnard, 1971 Hartmanodes hartmanae (Barnard, 1962) H. nyei (Shoemaker, 1933) Kroyera carinata Bate, 1857 Machaironyx muelleri Coyle, 1980 Monoculodes brevirostris Bousfield & Chevrier, 1996 M. castalskii Gurjanova, 1951 M. diamesus Gurjanova, 1936 M. demissus Stimpson, 1853 M. demissus Stimpson, 1853 M. emarginatus J. L.Barnard, 1962 M. latissimanus (Goes, 1861 M. longirostris (Goes, 1866) M. longirostris (Goes, 1866) M. longirostris (Goes, 1866) M. longirostris (Goes, 1866) M. A-At (AC) (not FL!) P (S CAL), At -(ST L) P (AL-BC) A-At (ST L, slope) P (ORE, deep) P (ORE, deep) P (BC) P (BC) P (BC) P (BC) P (BER) P (BER) P (BER) P (BER) P (BER) P (DRE-CAL) P (ORE-CAL) P (CAL, deep) P (CAL, deep) M. latimanus (Goes, 1866) M. longirostris (Goes, 1866) M. longirostris (Goes, 1866) M. longirostris (Goes, 1866)		_ ·
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D. similis Bousfield & Chevrier, 1996 D. simplex Hansen, 1887 D. tesselatus Schneider, 1884 A.At (ST L, slope) A.At (ST L) D. tuberculatus Boeck, 1871 A.At (ST L, slope) Finoculodes omnifera Barnard, 1971 Hartmanodes hartmanae (Barnard, 1962) H. nyei (Shoemaker, 1933) Kroyera carinata Bate, 1857 Machaironyx muelleri Coyle, 1980 Monoculodes brevirostris Bousfield & Chevrier, 1996 M. castalskii Gurjanova, 1951 M. diamesus Gurjanova, 1936 M. demissus Stimpson, 1853 M. demissus Stimpson, 1853 M. demarginatus J. L.Barnard, 1962 M. glyconicus Barnard, 1967 M. latissimanus (Stephensen, 1931) M. latimanus (Goes, 1861 M. longirostris (Goes, 1866) M. demissus Goes, 1866) M. longirostris (Goes, 1866) M. longirostris (Goes, 1866) M. longirostris (Goes, 1866) A-At (N, slope)	D. norvegicus (Boeck 1871)	
D. simplex Hansen, 1887  D. tesselatus Schneider, 1884  D. tuberculatus Boeck, 1871  Finoculodes omnifera Barnard, 1971  Hartmanodes hartmanae (Barnard, 1962)  H. nyei (Shoemaker, 1933)  Kroyera carinata Bate, 1857  Machaironyx muelleri Coyle,1980  Monoculodes brevirostris Bousfield & Chevrier, 1996  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. demissus Stimpson, 1853  M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1866)  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)		
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D. tuberculatus Boeck, 1871  Finoculodes omnifera Barnard, 1971  Hartmanodes hartmanae (Barnard, 1962)  H. nyei (Shoemaker, 1933)  Kroyera carinata Bate, 1857  Machaironyx muelleri Coyle, 1980  Monoculodes brevirostris Bousfield & Chevrier, 1996  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  A-At (N, slope)		· · · · · · · · · · · · · · · · · · ·
Finoculodes omnifera Barnard, 1971  Hartmanodes hartmanae (Barnard, 1962)  H. nyei (Shoemaker, 1933)  Kroyera carinata Bate, 1857  Machaironyx muelleri Coyle,1980  Monoculodes brevirostris Bousfield & Chevrier, 1996  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. memodes hartmanae (Barnard, 1962)  P (BC)  P (BC)  P (BER)  P (BER)  P (BER)  P (BER)  P (BER)  P (DRE-CAL)  P (ORE-CAL)  P (ORE-CAL)  P (CAL, deep)  P (CAL, deep)  A-At (ST L)  P (SE AL-WA)-A-At (ST L, slope)	,	· · · · · · · · · · · · · · · · · · ·
Hartmanodes hartmanae (Barnard, 1962)  H. nyei (Shoemaker, 1933)  Kroyera carinata Bate, 1857  Machaironyx muelleri Coyle, 1980  Monoculodes brevirostris Bousfield & Chevrier, 1996  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. demissus Stimpson, 1853  M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. nyei (Shoemaker, 1933)  P (BC)  P (BC)  P (BC)  P (BC)  P (BER)  P (BER)  P (BER?-BC)  AT (AC)  P (ORE-CAL)  P (ORE-CAL)  P (CAL, deep)  P (ORE-BC?), At (ST L)  P (SE AL-WA)-A-At (ST L, slope)  A-At (N, slope)		•
H. nyei (Shoemaker, 1933)  Kroyera carinata Bate, 1857  Machaironyx muelleri Coyle,1980  Monoculodes brevirostris Bousfield & Chevrier, 1996  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. myei (Shoemaker, 1933)  G (FL) (see Ortiz, 1979)  P (BER)  P (ORE-BC)  AT (AC)  P (CAL, deep)  P (ORE-BC?), At (ST L)  P (SE AL-WA)-A-At (ST L, slope)  M. longirostris (Goes, 1866)  A-At (N, slope)		•
Kroyera carinata Bate, 1857  Machaironyx muelleri Coyle,1980  Monoculodes brevirostris Bousfield & Chevrier, 1996  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. p (BER)  P (BC)  P (BC)  P (BER)  P (ORE-BC)  AT (AC)  P (ORE-CAL)  P (CAL, deep)  P (ORE-BC?), At (ST L)  P (SE AL-WA)-A-At (ST L, slope)  A-At (N, slope)		
Machaironyx muelleri Coyle,1980  Monoculodes brevirostris Bousfield & Chevrier, 1996  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. manus (Goes, 1866)  P (BER)  P (BE		
Monoculodes brevirostris Bousfield & Chevrier, 1996  M. castalskii Gurjanova, 1951  M. diamesus Gurjanova, 1936  M. demissus Stimpson, 1853  M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. p (BC)  P (BER)  P (BER)  P (BER)  P (BER)  P (BER)  P (DRE-CAL)  P (CAL, deep)  P (ORE-BC?), At (ST L)  P (SE AL-WA)-A-At (ST L, slope)  M. longirostris (Goes, 1866)  M. A-At (N, slope)		•
<ul> <li>M. castalskii Gurjanova, 1951</li> <li>M. diamesus Gurjanova, 1936</li> <li>M. demissus Stimpson, 1853</li> <li>M. emarginatus J. L.Barnard, 1962</li> <li>M. glyconicus Barnard, 1967</li> <li>M. latissimanus (Stephensen, 1931)</li> <li>M. latimanus (Goes, 1861</li> <li>M. longirostris (Goes, 1866)</li> <li>M. longirostris (Goes, 1866)</li> <li>M. P (BER)</li> <li>P (BER)</li> <li>P (BER)</li> <li>P (ORE-CAL)</li> <li>P (CAL, deep)</li> <li>P (ORE-BC?), At (ST L)</li> <li>P (SE AL-WA)-A-At (ST L, slope)</li> <li>M. A-At (N, slope)</li> </ul>		•
M. diamesus Gurjanova, 1936 M. demissus Stimpson, 1853 M. emarginatus J. L.Barnard, 1962 M. glyconicus Barnard, 1967 M. latissimanus (Stephensen, 1931) M. latimanus (Goes, 1861 M. longirostris (Goes, 1866) M. longirostris (Goes, 1866) M. A-At (N, slope)		
M. demissus Stimpson, 1853  M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. A-At (N, slope)		
M. emarginatus J. L.Barnard, 1962  M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. A-At (N, slope)	=J	
M. glyconicus Barnard, 1967  M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. A-At (N, slope)	r	• •
M. latissimanus (Stephensen, 1931)  M. latimanus (Goes, 1861  M. longirostris (Goes, 1866)  M. longirostris (Goes, 1866)  M. A-At (N, slope)	3	
M. latimanus (Goes, 1861 P (SE AL-WA)-A-At (ST L, slope) M. longirostris (Goes, 1866) A-At (N, slope)	0,5	
M. longirostris (Goes, 1866)  A-At (N, slope)	(= F	
Maria (1, slope)	(	
P (CAL)	8 (2000)	
	murtus Dankiu, 1902	P(CAL)

<ul><li>M. necopinus Barnard, 1967</li><li>M. packardi Boeck, 1871</li></ul>	P (CAL, deep) A-At (AC) P (BC-S CAL)	
M. perditus J. L. Barnard, 1966	P (ORE, deep)	
M. recandesco Barnard, 1967	P (Cal, deep)	
M. sudor Barnard, 1967	At (N, slope)	
M. tetutiosituus book, 10.1		
Monoculopsis longicornis (Boeck, 1871)	P (ORE-CAL, deep)	
Vealceroutes treputaria (Burnard, 1901)		
Dealer's boreaus Book, 1071		
O. saginatus Kroyer, 1842	P (BC-ORE)	
Pacifoculodes spinipes (Mills, 1962)  P bruneli Bousfield & Chevrier 1996	P (SE AL)	
	P(CAL)	
	P (BC)	
P. levingsi Bousfield & Chevrier, 1996	P(AL)	
P. crassirostris (Hansen, 1887) P. zernovi (Gurjanova, 1936)	P (BER-BC)	
Paroediceros behringiensis Lockington, 1877	P (BER)-A	
	P (ALEUT), A-At (ST L, slope)	
P. lynceus (M. Sars, 1858)	A-At ST L, slope)	
P. propinquus (Goes, 1866) Perioculodes cerasinus Thomas & Barnard, 1985	G (FL-BL)	
	At (ST L)	
P. longimanus (Bate & Westwood, 1868) Rostroculodes borealis (Boeck, 1871)	P-A (BAR), At-A (G, N)	
	A	
R. hanseni Stebbing, 1894 R. kroyeri (Boeck, 1871)	A-At (ST L, slope)	
R. longirostris (Goes, 1866)	P-A (BAR)	
R. schneideri (Sars, 1895)	P-A (BAR), A-At (ST L)	
R. vibei (Just, 1980)	A-At (LABR)	
Synchelidium tenuimanum Norman 1895	At (ST L, shelf)	
Westwoodilla brevicalcar (Goes, 1866)	P (BC-CAL), A-At (ST L)	
W. megalops (Sars, 1882) (syn with caecula?)	A	

# Superfamily Leucothoidea Bousfield, 1979

# Family Leucothoidae Dana, 1852

Anamixis cavitura Thomas, 1997	G (NE)
A. hanseni Stebbing 1899	G (MI)
A. linsleyi Barnard, 1955	P(S CAL)
Leucothoe alata J. L. Barnard, 1959	P(S CAL)
L. spinicarpa (Abildgaard, 1789)	A-At (ST L)
Leucothoides pacifica Barnard, 1955	P(S CAL)
L. pottsi Shoemaker, 1933	G (FL)
(=Anamixis linsleyi J. L. Barnard, 1955	

# Family Pleustidae Buchholz, 1874

# Subfamily Pleustinae Bousfield & Hendrycks, 1994a

Pleustes (Pleustes) panoplus (Kroyer, 1838)	At (A-AC)
Pleustes (Pleustes) panoplus var 4 Bousfield & Hendycks, 1994b	P (BER)-A
Pleustes (P.) panoplus var. 5 Bousf. & Hendrycks, 1994b	P (BER)

Pleustes (P.)	tuberculatus (Bate, 1858)	P(BER)
Pleustes (Cate	apleustes) victoriae Bousfield. & Hendrycks, 1994b	P (BC)
<i>P</i> .	(C.) constantinus Bousfield & Hendrycks, 1994b	P (BER)
<i>P</i> .	(C.) constantinus var., Bousf. & Hendrycks. 1994b	P(BC)
Thorlaksonius	s amchitkanus Bousfield & Hendrycks, 1994b	P (BER)
<i>T</i> .	borealis Bousfield & Hendrycks, 1994b	P (SE AL-ORE)
<i>T</i> .	depressus (Alderman, 1936)	P (ORE-CAL)
T	platypus (Barnard & Given, 1960)	P(CAL)
<i>T</i> .	brevirostris Bousfield & Hendrycks, 1994b	P (SE AL-CAL)
<i>T</i> .	subcarinatus Bousfield & Hendrycks, 1994b	P (SE AL-ORE)
<i>T</i> .	grandirostris Bousfield & Hendrycks, 1994b	P (BC-CAL)
Thorlaksonius	s carinatus Bousfield & Hendrycks, 1994b	P (SE AL-BC)
<i>T</i> .	truncatus Bousfield & Hendrycks, 1994b	P(BC)

#### Subfamily Mesopleustinae Bousfield & Hendrycks, 1994a

Mesopleustes abyssorum (Stebbing, 1888)

P (ORE deep)

#### Subfamily Pleustoidinae Bousfield & Hendrycks, 1994a

Pleustoides carinatus (Gurjanova, 1972)

P (BER?)

#### Subfamily Atylopsinae Bousfield & Hendrycks, 1994a, emend Cadien & Martin, 1999

Myzotarsa anixiphilius Cadien & Martin, 1999

P(SCAL)

#### Subfamily Eosymtinae Bousfield & Hendrycks, 1994a

Eosymytes minutus Bousfield & Hendrycks, 1994a

P(BC)

#### Subfamily Stenopleustinae Bousfield & Hendrycks, 1994a

Arctople	ustes glabricauda (Dunbar, 1954)	A-At (UNG)
Stenopleustes gracilis (Holmes, 1905)		At (AC-DEL) G (FL?)
S.	inermis Shoemaker, 1949	At (AC-DEL)
S.	latipes M. Sars, 1858)	At (ST L, slope)
Sympleustes olricki Hansen, 1887		Α

# Subfamily Pleusymtinae Bousfield & Hendrycks, 1994a

Pleusymtes coquillus Barnard, 1971		P (ORE-CAL)
<i>P</i> .	glaber (Boeck, 1861)?	P(CAL), A-At(AC)
Р.	glabroides (Dunbar, 1954)	A-At (LABR)
<i>P</i> .	pulchella (G. O. Sars ,1876)	A-At (AC?)
<i>P</i> .	subglaber (Boeck, 1871)	P (CAL)
Pleustomesus medius (Goes, 1866)		P?, A-At (ST L, slope)

# Subfamily Pleusirinae Bousfield & Hendrycks, 1994a

Pleusirus secorrus Barnard, 1969

P(AL-CAL)

# Subfamily Dactylopleustinae Bousfield & Hendrycks, 1994a

Dactylopleustes echinoides Bousf. & Hendrycks, 1995b

## Subfamily Neopleustinae Bousfield & Hendrycks, 1994a

P (BC-CAL)

Neopleustes pulchellus (Kroyer, 1846)	At-A (ST L, slope) A-At
"Parapleustes" bicuspis (Kroyer, 1838)	
"P. " assimilis (Sars, 1895)	A-At
"P." gracilis Buchholz, 1874	At (G)
Pleustostenus displosus Gurjanova, 1972	P (BER?)
"Sympleustes" cornigerus Shoemaker, 1964	P-A (BAR)

# Subfamily Parapleustinae Bousfield & Hendrycks, 1994a

Chromopleustes johanseni Bousfield & Hendrycks, 1995ab	P (BER)
C. oculatus (Holmes, 1908).	P (AL-CAL)
C. lineatus Bousfield & Hendrycks, 1995ab	P (SE AL- N CAL)
Incisocalliope aestuarius (Watling & Maurer, 1973)	At (V); G (FL?)
I. karstensi J. L. Barnard, 1959.	Α
Micropleustes nautilus (Barnard, 1969)	P (AL-CAL)
M. nautiloides Bousfield & Hendrycks, 1995b	P (BC-CAL)
Parapleustes americanus Bousfield & Hendrycks, 1995b	P (AL-BC)
Gnathopleustes pugettensi (Dana, 1853)	P (SE AL-CAL)
G. serratus Bousfield & Hendrycks, 1995b	P (SE AL-CAL)
G. pachychaetus Bousfield & Hendrycks, 1995b	P (SE AL-ORE)
G. trichodus Bousfield & Hendrycks, 1995b	P (BC)
G. simplex Bousfield & Hendrycks, 1995b	P (BC)
G. den (Barnard, 1969)	P (CAL)
Trachypleustes trevori Bousfield & Hendrycks, 1995b.	P (AL-BC)
T. vancouverensis Bousfield & Hendrycks, 1995b	P (BC)
Commensipleustes commensalis (Shoemaker, 1952)	P (CAL)
Incisocalliope aestuarius (Watling & Maurer, 1973)	G (FL?)
I. newportensis Barnard, 1959	P (S CAL)
I. bairdi (Boeck, 1871)	P (S CAL)
I. makiki (Barnard, 1970)	P (HAW)

## **Superfamily Stenothoidea Bousfield (2001)**

# Family Amphilochidae Boeck, 1871

## Subfamily Amphilochinae Barnard & Karaman, 1991

Amph.	ilochoides odontonyx (Boeck, 1871)	A-At (shell)
Apolo	chus barnardi Hoover & Bousfield, 2001	P(CAL)
A.	casahoya (McKinney, 1978)	G (FL-TEX)
<i>A</i> .	delacaya (McKinney, 1978)	G.
<i>A</i> .	litoralis (Stout, 1912)	P (SE AL-CAL)
<b>A</b> .	manudens (Bate, 1862)	At (ST L)
<b>A</b> .	picadurus (Barnard, 1962)	P (CAL)
<i>A</i> .	staudei (Hoover & Bousfield, 2001)	P (BC-WA)

<i>A</i> .	pillai Barnard & Thomas, 1983	G (FL)
<i>A</i> .	tenuimanus Boeck, 1871	A-At (ST L, slope)
Gitana abyssicola Sars, 1892		A-At (ST L, deep)
G.	calitemplado Barnard, 1962	P(CAL)
G.	ellisi Hoover & Bousfield, 2001	P(BC)
Gitanopsis arctica Sars, 1892		A-At ST L)
G.	bispinosa (Boeck, 1871)	A-At (ST L)
G.	inermis (Sars, 1882)	A-At (ST L, slope)
Hoursto	nius vilordes (Barnard, 1962)	P (SE AL-CAL)
Н.	laguna (McKinney, 1978)	G (FL-TEX)
Н.	tortugae (Shoemaker, 1933)	G (FL)

# Subfamily Cyproideiinae Barnard & Karman, 1991

Haplopheonoides obesa Shoemaker, 1956

G(FL)

# Family Stenothoidae Boeck, 1871

Mesometopa esmarki (Boeck, 1871)       P (CAL)         M. neglecta Barnard, 1966       P (CAL)         M. sinuata Shoemaker, 1964       P (ORE-CAL)         Metopa alderi (Bate ,1857)       A-At         M. abyssalis Stephensen, 1931.       A (G-EM)         M. boecki Sars, 1892       A-At         M. borealis Sars, 1882       A-At         M. bruzelii (Goes, 1866)       A-At (ST L)         M. cistella Barnard, 1969       P (CAL)         M. clypeata (Kroyer, 1842)       A-At         M. glacialis (Kroyer, 1842)       P (CAL)         M. glacialis (Kroyer, 1842)       P (BER), A-At (ST L)         M. groenlandica (Hansen, 1887)       A-At (ST L)         M. invalida G. O. Sars, 1892       At (ST L)
M.       sinuata Shoemaker, 1964       P (ORE-CAL)         Metopa alderi (Bate, 1857)       A-At         M.       abyssalis Stephensen, 1931.       A (G-EM)         M.       boecki Sars, 1892       A-At         M.       borealis Sars, 1882       A-At         M.       bruzelii (Goes, 1866)       A-At (ST L)         M.       cistella Barnard, 1969       P (CAL)         M.       clypeata (Kroyer, 1842)       A-At         M.       glacialis (Kroyer, 1842)       P (BER), A-At (ST L)         M.       groenlandica (Hansen, 1887)       A-At (ST L)         M.       invalida G. O. Sars, 1892       At (ST L)
Metopa alderi (Bate ,1857)       A-At         M. abyssalis Stephensen, 1931.       A (G-EM)         M. boecki Sars, 1892       A-At         M. borealis Sars, 1882       A-At         M. bruzelii (Goes, 1866)       A-At (ST L)         M. cistella Barnard, 1969       P (CAL)         M. clypeata (Kroyer, 1842)       A-At         M. dawsoni Barnard, 1962       P (CAL)         M. glacialis (Kroyer, 1842)       P (BER), A-At (ST L)         M. groenlandica (Hansen, 1887)       A-At (ST L)         M. invalida G. O. Sars, 1892       At (ST L)
M.       abyssalis Stephensen, 1931.       A (G-EM)         M.       boecki Sars, 1892       A-At         M.       borealis Sars, 1882       A-At         M.       bruzelii (Goes, 1866)       A-At (ST L)         M.       cistella Barnard, 1969       P (CAL)         M.       clypeata (Kroyer, 1842)       A-At         M.       dawsoni Barnard, 1962       P (CAL)         M.       glacialis (Kroyer, 1842)       P (BER), A-At (ST L)         M.       groenlandica (Hansen, 1887)       A-At (ST L)         M.       invalida G. O. Sars, 1892       At (ST L)
M.       boecki Sars, 1892       A-At         M.       borealis Sars, 1882       A-At         M.       bruzelii (Goes, 1866)       A-At (ST L)         M.       cistella Barnard, 1969       P (CAL)         M.       clypeata (Kroyer, 1842)       A-At         M.       dawsoni Barnard, 1962       P (CAL)         M.       glacialis (Kroyer, 1842)       P (BER), A-At (ST L)         M.       groenlandica (Hansen, 1887)       A-At (ST L)         M.       invalida G. O. Sars, 1892       At (ST L)
M.       bruzelii (Goes, 1866)       A-At (ST L)         M.       cistella Barnard, 1969       P (CAL)         M.       clypeata (Kroyer, 1842)       A-At         M.       dawsoni Barnard, 1962       P (CAL)         M.       glacialis (Kroyer, 1842)       P (BER), A-At (ST L)         M.       groenlandica (Hansen, 1887)       A-At (ST L)         M.       invalida G. O. Sars, 1892       At (ST L)
M.       cistella Barnard, 1969       P (CAL)         M.       clypeata (Kroyer, 1842)       A-At         M.       dawsoni Barnard, 1962       P (CAL)         M.       glacialis (Kroyer, 1842)       P (BER), A-At (ST L)         M.       groenlandica (Hansen, 1887)       A-At (ST L)         M.       invalida G. O. Sars, 1892       At (ST L)
<ul> <li>M. clypeata (Kroyer, 1842)</li> <li>M. dawsoni Barnard, 1962</li> <li>M. glacialis (Kroyer, 1842)</li> <li>M. groenlandica (Hansen, 1887)</li> <li>M. invalida G. O. Sars, 1892</li> <li>A-At</li> <li>A-At</li> <li>A-At (ST L)</li> <li>At (ST L)</li> </ul>
M.dawsoni Barnard, 1962P (CAL)M.glacialis (Kroyer, 1842)P (BER), A-At (ST L)M.groenlandica (Hansen, 1887)A-At (ST L)M.invalida G. O. Sars, 1892At (ST L)
M.glacialis (Kroyer, 1842)P (BER), A-At (ST L)M.groenlandica (Hansen, 1887)A-At (ST L)M.invalida G. O. Sars, 1892At (ST L)
<ul> <li>M. groenlandica (Hansen, 1887)</li> <li>M. invalida G. O. Sars, 1892</li> <li>A-At (ST L)</li> <li>At (ST L)</li> </ul>
M. invalida G. O. Sars, 1892 At (ST L)
,
14 1
M. leptocarpa G. O. Sars, 1882 A-At (ST L)
M. longicornis Boeck, 1870 A-At (ST L)
M. norvegica (Lilj, 1950?) At ST L)
M. propinqua G. O. Sars, 1892 A-At (ST L)
M. pusilla G. O. Sars 1892 At (ST L)
M. robusta Sars, 1892 A-At (ST L)
M. samsiluna Barnard, 1962 P (CAL)
M. sinuata Sars, 1892 A-At-(ST L)
M. solsbergi Schneider, 1884 At (ST L)
M. spinicoxa Shoemaker, 1955 A (AC)
M. spitzbergensis Brüggen, 1909 A-At (St L)
M. sporpis Barnard, 1969 P (CAL, deep)
M. tenuimana Sars, 1892 A-At (ST L)
Metopella aporpis Barnard, 1962 P (CAL)
M. carinata (Hansen, 1887) A-At
M. longimana (Boeck 1871) A-At
M. nasuta (Boeck, 1871) A-At
Metopelloides micropalpa (Shoemaker, 1930)  At (AC)

M. tattersalli Gurjanova, 1938	A (BAR)
Parametopa alaskensis Holmes, 1904)	P(AL)
P. crassicornis Just, 1980	A-At (ST L)
Parametopella cypris (Holmes 1905)	At (V-C) G (W FL)
P. inquilina Watling, 1976	At (C-V) G (FL)
P. ninis Barnard, 1962	P(CAL)
P. texensis McKinney et al, 1978	G(WFL)
P. cf. texensis McKinney, Kalke & Holland, 1978	G (FL)
Proboloides holmesi Bousfield, 1973	At (V)
P. nordmanni (Stephensen, 1931)	A-At
P. pacifica (Holmes, 1908)	P (CAL, deep)
P. tunda Barnard, 1962	P (CAL)
Raumajara carinata (Shoemaker, 1955)	P, A (BAR)
Stenothoe alaskensis Holmes, 1904	P (BER)
S. brevicornis Sars, 1882	A-G?
S. estacola Barnard, 1962	P(CAL)
S. frecanda Barnard, 1962	P(CAL)
S. georgiana Bynum & Fox, 1977	At (C); G (FL)
S. gallensis Walker, 1904	G (FL)
S. marina Bate, 1857	P (CAL?) - At?
S. minuta Holmes, 1905	G (FL)
S. monoculoides Montagu, 1815	At (ST L)
S. symbiotica Shoemaker, 1956	G (FL)
S. valida Dana, 1852	P (CAL)
Stenothoides bicoma Barnard, 1962	P(CAL)
S. burbancki Barnard, 1969	P (CAL)
Stenula incola Barnard, 1969	P (CAL)
S. modosa Barnard, 1962	P(CAL)
S. nordmanni (Stephensen, 1931)	P (BAR), A-At (ST L)
S. peltata (S. I. Smith, 1874)	A-At (ST L, slope)
Zaikometopa erythrophthalmus (Coyle & Mueller, 1981)	P(AL)

# Superfamily Iphimedioidea Lowry & Myers, 2000

## Family Epimeriidae Boeck, 1871 (=Paramphithoidae Sars, 1895)

Epim	eria cora Barnard, 1971	P (deep)
E.	longispinosa K.H. Barnard, 1916	At (E FL deep)
<i>E</i> .	loricata G.O Sars, 1879	A-At (G-BF)
<i>E</i> .	obtusa Watling, 1981	At (C -E FL)
<i>E</i> .	yaquinae McCain, 1971	P (ORE, deep)
Para	mphithoe hystrix Ross, 1835	P-A-At (G, N,slope)
<i>P</i> .	polyacantha (Murdoch, 1885)	Α
Usha	koviella echinophora Gurjanova, 1955	P (BER-SE AL)

# Family Iphimedidae Boeck, 1871

Acar	nthonotozoma inflatum (Kroyer, 1842)	A-At
<b>A</b> .	monodentatus Kudrjaschov, 1965	P (BER?)
<b>A</b> .	rusanovae Bryazhgin, 1974	P (BC-AL), At (ST L)

Acanthonotozoma serratum (Fabricius, 1780)	A-At (ST L)
A. sinuatum Just, 1978	A-At (ST L)
Coboldus hedgpethi (Barnard, 1969)	P(CAL)
Curidia debrogania Thomas, 1983	G (FL)
Iphimedia rickettsi Shoemaker, 1931	P(AL)
I. zora Thomas & Barnard, 1991	G (FL)

## Family Odiidae Coleman & Barnard, 1991

Cryptodius kelleri (Bruggen, 1907)	P (BC-CAL)
C. unguidactylus Moore, 1992	P (BC)
Imbrexodius oclairi Moore, 1992	P (BC)

#### Incerta sedis

#### Family Lafystiidae Sars, 1895

Lafystius acuminatus Bousfield, 1987	AT (V), G (FL?)
L. frameae Bousfield, 1987	AT (V), G (FL?)
L. morrhuana Bousfield, 1987	A-At (AC)
L. sturionis Kroyer, 1842	A-At (AC)
Paralafystius mcallisteri Bousfield, 1987	P (SE AL-BC)
Protolafystius madillae Bousfield, 1987	P (BC)

## Superfamily Dexaminoidea Bousfield, 1979

#### Family Atylidae G. O. Sars, 1882

## Subfamily Atylinae Boeck, 1871; revised Bousfield & Kendall 1994

Atylus carinatus (Fabricius, 1793)		P (BER)-A-At (ST L)
<i>A</i> .	atlassovi (Gurjanova, 1951)	P (BER)-A
<i>A</i> .	borealis Bousfield & Kendall, 1994	P (SE AL-WA)
<i>A</i> .	bruggeni (Gurjanova, 1938)	P (BER)-A
<i>A</i> .	collingi (Gurjanova, 1938)	P (BER)-A
<i>A</i> .	georgianus Bousfield & Kendall, 1994	P (BC-ORE)
<i>A</i> .	melanops (Oldevig, 1959)	A
<b>A</b> .	nordlandicus Boeck, 1871	Α
<i>A</i> .	rylovi (Bulycheva, 1952)	P (W PAC)
<i>A</i> .	tridens (Alderman, 1936)	P (BC-CAL)

# Subfamily Nototropinae Bousfield & Kendall, 1994

Aberratylus aberrantis (J. L. Barnard, 1962)		P(CAL?, deep)
Nototr	opis minikoi (Walker, 1905)	At (V-C), G (E F1?)
<i>N</i> .	smithi Goes, 1866	A, At?
<i>N</i> .	swammerdamii (Milne-Edwards, 1830)	AT (AC-V), G?
<i>N</i> .	urocarinatus McKinney, 1980	G (FL-TEX)

# Subfamily Lepechinellinae Schellenberg, revised Barnard & Karaman 1991

Lepechinella bieri Barnard, 1957

P(CAL, deep)

# Subfamily Anatylinae Bulycheva, 1955; revised Bousfield & Kendall, 1994

Kamehatylus nani Barnard, 1970

P (HAW)

#### Family Dexaminidae Leach, 1813/14

# Subfamily Polycheriinae Bousfield & Kendall, 1994

Polycheria osborni Calman, 1898		P (SE AL-CAL)
<i>P</i> .	carinata Bousfield & Kendall, 1994	P(BC)
Р.	mixillae Bousfield & Kendall, 1994	P(BC)

#### **Subfamily Prophliantinae Nicholls, 1939**

Guernea nordenskioldii (Hansen, 1887)

G. reduncans (Barnard, 1958)

A-At (AC)
P (BC-CAL)

# Subfamily Dexamininae Leach, 1813/14; revised Bousfield & Kendall, 1994

Dexamine thea Boeck, 1861

At (AC)

# Superfamily Ampeliscoidea Bousfield, 1979

#### Family Ampeliscidae Costa, 1857

Ampeli	sca abdita Mills,1964	At (ST L, V-C), G (?)
<i>A</i> .	aequicornis Bruzelius, 1859	At-A (AC)
<i>A</i> .	agassizi (Judd, 1896A)	P (CAL)-At (V), G (E-FL)
	(= A. vera Barnard, 1954)	
<i>A</i> .	amblyops Sars, 1891	At (FL, deep)
<i>A</i> .	amblyopsoides J. L. Barnard, 1960	P (CAL)
<i>A</i> .	bicarinata Goeke & Heard, 1983	G (FL-MI)
A.	birulai Brüggen, 1909	P (BER), A
<i>A</i> .	brachycladus Roney, 1990	P (CAL?)
<i>A</i> .	brevisimulata Barnard, 1954	P (ORE-BC)
<i>A</i> .	burkei Barnard & Thomas, 1989	G (FL)
<i>A</i> .	careyi Dickinson, 1982	P (BC-ORE)
<b>A</b> .	ciego Barnard, 1966	P(CAL)
<b>A</b> .	coeca Holmes, 1908	P (S CAL)
<i>A</i> .	cristata Holmes, 1908	P (BC-ORE)
<i>A</i> .	cristoides Barnard, 1954	P(S CAL)
<b>A</b> .	declivitatus Mills, 1967	At (deep) (ST L)
<i>A</i> .	eoa Gurjanova, 1951	P (BER)
<i>A</i> .	erythrorhabdota Coyle & Highsmith, 1989	P (BER)
<b>A</b> .	eschrichti Kroyer, 1842	P (BER?)-A-At (ST L)
<i>A</i> .	fageri Dickinson, 1982	P (ORE)
	(= A. schellenbergi Shoemaker, 1933	
<i>A</i> .	furcigera Gurjanova, 1936	P (BER)
<b>A</b> .	gibba Sars, 1882	At (ACdeep)
<b>A</b> .	hancocki Barnard, 1954	P (BC-ORE)
<b>A</b> .	hessleri Dickinson, 1982	P (ORE)
<b>A</b> .	holmesi Pearse, 1908	G (FL-MI

<i>A</i> .	indentata Barnard, 1954	P (CAL)
A.	latipes Stephensen, 1925	At (ST L-AC)
A. A.	lobata Holmes, 1908	P(AL)
71.	(= A. articulata Stout, 1913)	, ,
<i>A</i> .	macrocephala Liljeborg, 1852	P (BER)-A-At (AC)
A.	mexicana Barnard, 1954	P (S CAL)
л. <b>A</b> .	milleri Barnard, 1954	P (CAL)
A. A.	pacifica Holmes, 1908	P(CAL)
A. A.	plumosa Holmes, 1908	P(AL)
A. A.	pugetica Stimpson, 1864	P (BC-WA)
A. A.	romigi Barnard, 1954	P (CAL)
A. A	schellenbergi (see Coyle & Highsmith, 1989)	
A.	shoemakeri Barnard, 1954	P (CAL)
л. <b>А</b> .	typica (Bate, 1856)	AT (AC)
A. A.	uncinata Chevreux, 1887	At (AC, deep)
A. A.	unsocolae Barnard, 1960	P(ORE)
A. A.	vadorum Mills, 1963	At (G, V)(E FL?)
A. A.	venetiensis Shoemaker, 1916	P (CAL)
A. A.	verrilli Mills, 1967	At (V-C?)(E FL?)
	barbarensis Barnard, 1960	P (CAL)
B.	bathyalis Barnard, 1966	P (CAL)
В. В.	brevirama Dickinson, 1983	P (ORE),- A
В.	crassicornis Metzger, 1875	P (BER?)
В.	frigidis Coyle & Highsmith, 1989	P (BER)
В.	gaimardii (Kroyer, 1846)?	P (BER?)-A-At (AC)
В.	longispina Dickinson, 1983	P(BC)
B.	medialis Mills, 1971	At (AC, deep)
B.	millsi Dickinson, 1983	P(BC)
В.	mulleni Dickinson, 1983	P (ORE)
В.	pearcyi Dickinson. 1983	P (BER),- A
B.	robustus Coyle & Highsmith, 1989	P (BER)
B.	serrata S. I. Smith, 1873	At (V), G (E FL?)
B.	tannerensis Barnard, 1966	P(CAL)
<i>B</i> .	teres (see C. & H., 1989)	P (BER)
В. В.	thyabilis Barnard, 1971	P (ORE)
B.	veleronis Barnard, 1954	P (BC-CAL)
	ops fundiensis Wildish & Dickinson, 1982	At (AC)
<i>H</i> .	laevis Hoek, 1882	P (CAL)-A-At (ST L)
Н.	sibirica Gurjanova, 1929	A
Н.	lodo Barnard, 1961	P (CAL?)
Н.	setosa Boeck, 1871	P(ER), At(AC)
Н.	similis Stephensen, 1925	At (AC, shelf to deep)
H.	spinosa Shoemaker, 1931	At (AC)
Н.	tubicola Liljeborg, 1856	P (BER)-A-At (ST L)

# Superfamily Melphidippoidea Bousfield, 1979 [= cheirocratids Barnard & Barnard, 1983 (part)]

## Family Melphidippidae Stebbing, 1899

Casco bigelowi (Blake, 1929)		At (ST L-AC-DEL)
Melphisana bola Barnard, 1962		P (AL-CAL)
Melphidipe	lla macer (Norman, 1869)	P (BC)
Melphidipp	a amorita Barnard, 1966	P (CAL)?
<i>M</i> .	borealis Boeck, 1971	P-A?-At (ST L)
М.	goesi Stebbing, 1899	A-At (AC)
<i>M</i> .	macrura G. O. Sars, 1894	At (ST L)

#### Family Hornelliidae Bousfield, 1982

Hornell	ia (Metaceradocus) tequestaeThomas & Barnard, 1986	G (FL)
Н.	occidentalis (Barnard, 1959)	P (S CAL)

## Family Megaluropidae Thomas & Barnard, 1986

Megaluropus longimerus Schellenberg, 1925?	P (BC-CAL)
Gibberosus devaneyi Thomas & Barnard, 1986	P (S CAL?)
G. myersi (McKinney, 1980)	P (CAL?); G (FL-TEX)
G. visendus (Barnard, 1969)	P (B CAL)
Resupinus coloni Thomas & Barnard, 1986	P (CAL)

# Superfamily Liljeborgioidea, Bousfield, 1979

## Family Liljeborgiidae Stebbing, 1899

Idunella aequicornis (Sars, 1876)		A-At (ST L)
I.	bowenae Karaman, 1979	At (V, shelf)
I.	smithi Lazo-Wasem, 1985	At (V), G (E FL?))
Liljebo	rgia bousfieldi McKinney, 1979	G (FL-TEX)
L.	cota Barnard, 1962	P (ORE-CAL, deep)
L.	fissicornis M. Sars, 1858?)	A-At (N, slope)
L.	geminata Barnard, 1969	P (CAL?)
L.	pallida (Bate, 1857)	P (CAL)? G (FL)
Listrie	lla albina Barnard, 1959	P (ORE-CAL, deep)
L.	barnardi Wigley, 1966	At (V-C), G (W FL)
L.	carinata McKinney, 1979	G (FL-TEX)
L.	clymenellae Mills, 1962	At (V-C), G (FL?)
L.	diffusa Barnard, 1959	P (CAL)
L.	eriopisa Barnard, 1959	P(S CAL)
L.	goleta Barnard, 1959	P (ORE-CAL)
L.	melanica Barnard, 1959	P (CAL)
L.	quintana McKinney, 1979	G (TEX)

## Family Sebidae Walker, 1908

## **Subfamily Sebinae Holsinger1980**

Seba aloe Karaman, 1971		G (W FL)
S.	profunda Shaw, 1989	P (BC, deep)

## Subfamily Seborgiinae Karaman, 1992

Relictoseborgi	ia hershleri (Holsinger, 1992b)	FW (TEX)
?R.	relicta (Holsinger, 1980)	FW (TEX)

## Family Colomastigidae Stebbing, 1899

Colomastix bousfieldi	LeCroy 1995	G (FL-TEX)
C	camura LeCroy, 1995	At (C), G (FL-TEX)
<i>C</i> .	cornuticauda LeCroy, 1995	G (W FLA)
<i>C</i> .	denticornis LeCroy,1995	G (W FL)
<i>C</i> .	falcirama LeCroy, 1995	G (FL)
<i>C</i> .	gibbosa LeCroy, 1995	G (FL)
<i>C</i> .	halichondriae Bousfield, 1973	At, G (FL-TEX)
<i>C</i> .	heardi LeCroy, 1995	AT (C), G (FL-YUC)
<i>C</i> .	irciniae LeCroy, 1995	G (FL)
<i>C</i> .	janiceae Heard & Perlmutter, 1977	G (FL-YUC), At (C)
<i>C</i> .	tridentata LeCroy, 1995	At (C), G (FL-YUC)

# Superfamily Crangonyctoidea Bousfield 1973 [= crangonyctoids Barnard & Barnard, 1983 (part)]

# Family Crangonyctidae Bousfield 1973 (revised Holsinger 1977)

Bactrurus brachycaudus Hubricht & Mackin, 1940		FW
В.	hubrichti Shoemaker, 1945	FW
В.	mucronatus (Forbes, 1876)	FW
Crange	onyx aberrans D. Smith, 1983	FW
<i>C</i> .	alpinus Bousfield, 1963	FW (P)
<i>C</i> .	anomalus Hubricht, 1943	FW
<i>C</i> .	antennatus Packard, 1881	FW
<i>C</i> .	dearolfi Shoemaker, 1942	FW
<i>C</i> .	floridanus Bousfield, 1963	FW
<i>C</i> .	forbesi (Hubricht & Mackin, 1940)	FW
<i>C</i> .	gracilis Smith, 1871	FW
<i>C</i> .	grandimanus Bousfield, 1963	FW
<i>C</i> .	hobbsi Shoemaker, 1941	FW
<i>C</i> .	minor Bousfield, 1958	FW
<i>C</i> .	obliquus (Hubricht & Mackin, 1940)	FW
<i>C</i> .	packardi S. I. Smith, 1888	FW
<i>C</i> .	pseudogracilis Bousfield, 1958	FW
<i>C</i> .	richmondensis richmondensis Ellis, 1940	FW
<i>C</i> .	r. occidentalis Hubricht & Harrison, 1941	FW (P)
C	r. laurentianus Bousfield, 1958	FW
C	rivularis Bousfield, 1958	FW
<i>C</i> .	serratus (Embody, 1911)	FW
<i>C</i> .	setodactylus Bousfield, 1958	FW
<i>C</i> .	shoemakeri (Hubricht & Mackin, 1940)	FW
Stygonyx courtneyi Bousfield & Holsinger, 1989		FW (P)
Stygobromus abditus Holsinger, 1978 FW		FW
S.	ackerlyi Holsinger, 1978	FW
S.	alabamensis alabamensis (Stout, 1911)	FW

C	a and destalia (Walsiman, 1967)	TAV
S.	a. occidentalis (Holsinger, 1967)	FW
S.	allegheniensis (Holsinger, 1967)	FW
S.	araeus (Holsinger, 1969)	FW
S.	arizonensis Holsinger, 1974	FW
S.	balconis (Hubricht, 1943)	FW
S.	baroodyi Holsinger, 1978	FW
S.	barri (Holsinger, 1967)	FW
S.	barryi Holsinger, 1978	FW
S.	bifurcatus (Holsinger, 1967)	FW
S.	biggersi Holsinger, 1978	FW
S.	borealis Holsinger, 1978	FW
S.	bowmani (Holsinger, 1967)	FW
S.	canadensis Holsinger, 1980	FW
S.	carolinensis Holsinger, 1978	FW
S.	clantoni (Creaser, 1934)	FW
S.	coloradensis Ward, 1977	FW
S.	conradi (Holsinger, 1967)	FW
S.	cooperi (Holsinger, 1967)	FW
S.	cumberlandus Holsinger, 1978	FW
S.	dejectus (Holsinger, 1967)	FW
S.	dicksoni Holsinger, 1978	FW
S.	elatus (Holsinger, 1967)	FW
S.	elliotti Holsinger, 1974	FW
S.	emarginatus (Hubricht, 1943)	FW
S.	ephemerus (Holsinger, 1969)	FW
S.	estesi Holsinger, 1978	FW
S.	exilis Hubricht, 1943	FW
S.	fecundus Holsinger, 1978	FW
S.	ferausoni Holsinger, 1978	FW
S.	finleyi Holsinger, 1978	FW
S.	flagellatus (Benedict, 1896)	FW
S.	franzi Holsinger, 1978	FW
S.	gracilipes (Holsinger, 1967)	FW
S.	gradyi Holsinger, 1974	FW
S.	grahami Holsinger, 1974	FW
S.	grandis Holsinger, 1978	FW
S.	hadenoecus (Holsinger, 1966)	FW
S.	harai Holsinger, 1974	FW
S.	hayi (Hubricht & Mackin, 1940)	FW FW
S.	heteropodus Hubricht, 1943	FW FW
S.	•	
S.	hoffmani Holsinger, 1978	FW
	holsingeri Ward, 1977	FW
S.	hubbsi Shoemaker, 1942	FW
S.	indentatus (Holsinger, 1967)	FW
S.	inexpectatus Holsinger, 1978	FW
S.	interitus Holsinger, 1978	FW
S.	iowae Hubricht, 1943	FW
S.	kenki Holsinger, 1978	FW
S.	lacicolus Holsinger, 1974	FW
S.	leensis Holsinger, 1978	FW
S.	longipes (Holsinger, 1966)	FW

S.	lucifugus (Hay, 1882)	FW
S.	mackenziei Holsinger, 1974	FW
S.	mackini Hubricht, 1943	FW
S.	minutus Holsinger, 1978	FW
S.	montanensis Holsinger, 1974	FW
S	montanus (Holsinger, 1967)	FW
S.	morrisoni (Holsinger, 1967)	FW
S.	mundus (Holsinger, 1967)	FW
S.	mysticus Holsinger, 1974	FW
S.	nanus Holsinger, 1978	FW
S.	nortoni (Holsinger, 1969)	FW
S.	obrutus Holsinger, 1978	FW
S.	obscurus Holsinger, 1974	$\mathbf{F}\mathbf{W}$
S.	onondagaensis (Hubricht & Mackin, 1940)	FW
S	oregonensis Holsinger, 1974	FW
S.	ozarkensis (Holsinger, 1967)	FW
S.	parvus (Holsinger, 1969)	FW
S.	pecki (Holsinger, 1967)	FW
S.	pennaki Ward, 1977	FW
S.	phreaticus Holsinger, 1978	FW
S.	pizzinii (Shoemaker, 1938)	FW
S.	pollostus Holsinger, 1978	FW
S.	pseudospinosus Holsinger, 1978	FW
S.	putealis (Holmes, 1909)	FW
S.	puteanus Holsinger, 1974	FW
S.	quatsinensis Holsinger & Shaw, 1987	FW
S.	redactus Holsinger, 1978	FW
S.	reddelli (Holsinger, 1966)	FW
S.	russelli (Holsinger, 1967)	FW
S.	secundus Bousfield & Holsinger, 1981	FW
S.	sheldoni Holsinger, 1974	FW
S.	sierrensis Holsinger, 1974	FW
S.	mithi Hubricht, 1943	FW
S.	sparsus Holsinger, 1978 (1969?)	FW
S.	spinatus (Holsinger, 1967)	FW
S.	spinosus (Hubricht & Mackin, 1940)	FW
S.	stegerorum Holsinger, 1978	FW
S.	stellmacki (Holsinger, 1967)	FW
S.	subtilis (Hubricht, 1943)	FW
S.	tahoensis Holsinger, 1974	FW
S.	tenuis tenuis (S. I. Smith, 1874)	FW
S.	t. potomacus (Holsinger, 1967)	FW
S.	tritus Holsinger, 1974	FW
S.	vitreus Cope, 1872	FW
S	wengerorum Holsinger, 1974	FW
Synp	leonia pizzini Shoemaker, 1941	FW (At)
	rella chamberlaini Shoemaker,1936?	FW (At - FL)
S.	bifurca (Hay, 1882)	FW FW
S.	chamberlaini (Ellis, 1941)	FW
S.	dentata Hubricht, 1943	FW
S.	johanseni Shoemaker, 1920	FW (P)
	•	(*)

# Superfamily Talitroidea Bulycheva, 1957

# Family Hyalidae Bulycheva, 1957

Apohyal	le pugettensis (Dana, 1853)	P (SE AL-CAL)
A	anceps (Barnard, 1969)	P (CAL-BC)
<i>A</i> .	californica (Barnard, 1969)	P (BC-CAL)
Hyale m	nedia (Dana, 1853)	G (FL)
H. ni	ilssoni Rathke 1843	At (AC)
Н. ос	culata Bousfield, 1981	P (BC)
H. pe	erieri (Lucas, 1846)	G (FL)
Leptohy	ale longipalpa Bousfield 1981	P (BC)
Parallo	rchestes ochotensis (Brandt, 1851)	P (AL-BC)
Р.	brevicornis Bousfield, 1981	P (AL-BC)
<i>P</i> .	minor Bousfield, 1981	P (BC)
<i>P</i> .	spinosa Bousfield, 1981	P (BC)?
<i>P</i> .	subcarinata Bousfield, 1981	P (SE AL-WA)
<i>P</i> .	supracarinata Bousfield, 1981	P (BER)
Р.	trispinosa Bousfield, 1981	P(BC)
<i>P</i> .	nuda Bousfield, 1981	P (BC)
<i>P</i> .	americana Bousfield, 1981	P(AL)
<i>P</i> .	minima Bousfield, 1981	P (BC)
<i>P</i> .	occidentalis Bousfield, 1981	P (BC)
<i>P</i> .	subcarinata Bousfield, 1981	P (SE AL-WA)C
Parhyal	e hawaiensis (Dana,1853)	G (FL)
Р.	fascigera Stebbing, 1897	G (FL)
Plumulo	phyale plumulosa (Stimpson, 1857)	P(BC-CAL), At(V), G(FL?)
Protohy	ale frequens (Stout, 1913)	P (BC-CAL)
<i>P</i> .	canalina Barnard, 1979	P(SCAL?)
<i>P</i> .	nigra (Haswell, 1879)	P (CAL)
Р.	lagunae (Stout, 1913)	P (S CAL)
Р.	intermedia (Bousfield, 1981)	P (SE AL-ORE)
<i>P</i> .	seticornis (Bousfield, 1981)	P (SE AL-CAL)
<i>P</i> .	oclairi (Bousfield, 1981)	P (SE AL-WA)
<i>P</i> .	spinosa (Bousfield, 1981)	P (SE AL-BC)

# Family Hyalellidae Bulycheva, 1957

# Subfamily Hyalellinae Bousfield, 1996

Allorchestes an	ngusta Dana, 1853	P (AL-CAL)
<i>A</i> .	bella bella Barnard, 1974	P (BER-CAL)
A	pacifica Bousfield, 1981	P(BC)
<i>A</i> .	parva Bousfield, 1981	P(BC)
<i>A</i> .	subcarinata Bousfield, 1981	P(AL)
<i>A</i> .	urocarinata Bousfield, 1981	P (SE AL-BC)
<i>A</i> .	carinata Iwasa, 1939 (Bousfield, 1981)	P (BER)
Hyalella (Hyalella) azteca (Saussure, 1858)		FW
Н.	(H.) inermis S. I. Smith, 1974	FW
Н.	(H.) longicornis Bousfield, 1996	FW
Н.	(H.) muerta Baldinger, Shepard, & Threloff 2000	FW

Hyalella	(H.) montezuma Cole & Watkins, 1977	FW
H.	(H.) sandra Baldinger, Shepard, & Threloff 2000	FW
Н.	(H.) texana Stevenson & Peden, 1973	FW
Parhyalella wh	elpleyi (Shoemaker, 1933)	G (FL)

### Family Dogielinotidae Gurjanova, 1953

Proboscinotus loquax (Barnard, 1968)

P(ORE-WA)

### Family Najnidae J. L. Barnard, 1972

Najna consiliorum Derzhavin, 1937		P (BER)
<i>N</i> .	kitimati Barnard, 1979	P (CAL)
<i>N</i> .	lessoniophilum Bousfield, 1981	P (CAL)
<i>N</i> .	rugosum Bousfield, 1981	P (AL-BC)
<i>N</i> .	setosum Bousfield, 1981	P (BC-ORE?)
<i>N</i> .	plumulosum Bousfield, 1981	P (BC-ORE?)

### Family Eophliantidae Sheard, 1936

Lignophliantis pyrifera Barnard, 1969

P(SCAL)

#### Family Phliantidae Stebbing, 1899

Pariphinotus	(Heterophlias) escabrosus (Barnard, 1969)	P (BC-CAL)
<i>P</i> .	(H.) seclusus (Shoemaker, 1933)	At (C), G (FL)

### Family Talitridae Rafinesque, 1815

### (a) Palustral subgroup (pragmatic subfamily group, Bousfield, 1984)

Uhlorchestia uhleri (Shoemaker, 1930)		At (C-FL)), G (FL-TEX)
U.	spartinophila Bousfield & Heard, 1986	At (V-C), G (FL)

### (b) Beachflea subgroup (Bousfield, 1984)

Orchestia gammarella (Pallas, 1766)	At (AC)
Orcheslia grillus Bosc, 1802	At (AC-V); G (FL-TEX)
Paciforchestia klawei (Bousfield, 1959)	P (S CAL- B.C)
Platorchestia chathamensis Bousfield, 1982	P (BC)
P. platensis (Kroyer, 1845)	At (AC-V), G (FL-TEX)
Tethorchestia sp 1 (= tropica Shoemaker MS)	G (FL)
Tethorchestia brevipleopoda (Bousfield MS)	G (FL)
Traskorchestia traskiana (Stimpson, 1856)	P(Al -CAL)
T. georgiana (Bousfield, 1958)	P (CAL -BC)
T. ochotensis (Brandt, 1851)	P (ALEUT)
Transorchestia enigmatica (Bousfield & Carlton, 1968)	P (CAL, intr.)

### (c) Sandhopper subgroup (Bousfield, 1984)

Americord	chestia longicornis (Say, 1818)	At (AC-V), G
A.	barbarae Bousfield, 1992	G (TEX)

Americorchest	tia heardi Bousfield, 1992	G (FL-LA)
<i>A</i> .	megalophthalma (Bate, 1862)	At (AC-C)
<i>A</i> .	salomani Bousfield, 1992	G (FL-LA)
Megalorchesti	a californiana (Brandt, 1851)	P
М.	columbiana (Bousfield, 1958)	P
<i>M</i> .	minor (Bousfield, 1957)	P (S CAL)
<i>M</i> .	dexterae Bousfield, 1982	P (S-B CAL)
М.	pugettensis (Stimpson, 1856)	P
М.	corniculata (Stout, 1912)	P (CAL)
<i>M</i> .	benedicti (Shoemaker, 1936)	P(CAL)

## (d) Landhopper subgroup (Bousfield, 1984)

Arcitalitrus sylvaticus (Haswell, 1879)	P (CAL, intr.)
Talitroides topitotum (Burt, 1934?)	P (CAL, intr.), G (FL-MI, intr.)
T. alluaudi (Chevreux, 1896)	P (BC - CAL), At (intr.), G (FL)

## Superfamily Pontoporeioidea Bousfield, 1979 [= Haustorioidea Barnard & Drummond, 1982 (part)]

## Family Bathyporeiidae Bousfield, 1978

Amphiporeia gigantea Bousfield, 1973	At (AC)
A. lawrenciana Shoemaker, 1929	At (AC)
A. virginiana Shoemaker, 1933	At AC), G (E FL?)
Bathyporeia parkeri Bousfield, 1973	At (V-C) G (E FL)
B. quoddyensis Shoemaker, 1949	At (AC-V)

### Family Pontoporeiidae Dana, 1855

Diporeia brevicornis (Segerstrale, 1937)	FW
D. erythrophthalma (Waldron, 1953)	FW
D. filicornis (Smith, 1974)	FW
D. hoyi (Smith, 1874)	FW
D. intermedia (Segerstrale, 1977)	FW
D. kendalli (Norton, 1909)	FW
Monoporeia affinis (Lindstrom, 1885)	A-At (ST L), P (AL)
Pontoporeia femorata Kroyer, 1842	P (AL-BC)-A-At (ST L-AC)
Priscillina armata (Boeck, 1861)	A-At (ST L - AC)

### Family Haustoriidae Stebbing, 1906

Aca	nthohaustorius bousfieldi Frame, 1982	At (V)
<i>A</i> .	cf. bousfieldi Frame, 1980	G (E FL)
<b>A</b> .	intermedius Bousfield, 1965	At (V-C)
<i>A</i> .	nr. intermedius Bousfield, 1965	G (FL?)
<i>A</i> .	millsi Bousfield, 1965	At (V-C) G (E. FL)
<b>A</b> .	uncinus Foster, 1988	G (FL-MI)
<i>A</i> .	pansus Thomas & Barnard, 1984	G (FL)
<i>A</i> .	shoemakeri Bousfield,1965	At (V-C)
<b>A</b> .	cf. shoemakeri Bousfield 1965	G (NW FL)
<b>A</b> .	similis Frame, 1980	At (V-C)

A. spinosus (Bousfield, 1962)	At (AC-Del)
•	
A. uncinus Foster, 1989	G (FL-MI)
Eohaustorius brevicuspis Bosworth, 1973	P (BC-ORE)
E. eous (Gurjanova, 1951)	P (BER)
E. sencillus Barnard, 1962	P (CAL)
E. washingtonianus (Thorsteinsen, 1941)	P (AL-CAL?)
E. estuarius Bosworth, 1973	P (BC-ORE)
E. sawyeri Bosworth, 1973	P (BFC-ORE)
Haustorius canadensis Bousfield, 1962	At (SW G-V) (G (FL?)
H. jayneae Foster & LeCroy, 1991	G (NE)
Lepidactylus dytiscus Say, 1818	G (E FL)
L. triarticulatus Robertson & Shelton, 1980	G (FL-TEX)
Neohaustorius biarticulatus Bousfield, 1965	At (V-C), G (E FL?)
N. schmitzi Bousfield, 1965	At $(V-C)$ , $G(EFL)$
Parahaustorius attenuatus Bousfield, 1965	At (V)
P. holmesi Bousfield, 1965	At (AC) G (FL?)
P. longimerus Bousfield, 1965	At (V-C) G (FL?)
P. cf. longimerus Bousfield, 1965	G (W. FL)
P. obliquus Robertson & Shelton, 1978	G (FL-TEX)
Protohaustorius bousfieldi Robertson & Shelton, 1978	G (FL-TEX)
P. deichmannae Bousfield, 1965	At (V) G (FL?)
P. wigleyi Bousfield, 1965	At (V) G (FL?)
Pseudohaustorius americanus (Pearse, 1908)	G (FL-MI)
P. borealis Bousfield, 1965	At (V)
P. caroliniensis Bousfield, 1965	At V-CAR-E FL?)

## Superfamily Gammaroidea Bousfield, 1977 [= gammaroid group Barnard & Barnard, 1983 (part]

## Family Gammaridae Leach, 1813

Chaetogammarus stoerensis (Reid, 1938)		At (AC)
<i>C</i> .	ischnus (Sars, 1896)	FW (intr.)(Witt, et al, 1998))
Eulimnogamn	narus obtusatus (Dahl, 1938)	At (AC-ST L)
Gammarus a	cherondytes Hubricht & Mackin, 1940	FW
G. annui	atus S. I. Smith, 1874	At (ST L - AC)
G. boust	ieldi Cole & Minckley 1961	FW
G. daibe	ri Bousfield, 1969	P (CAL, intr.)-At (V-C)-G?
G. despe	ratus Cole, 1981	FW
G. duebe	ni Liljeborg, 1851	At (AC)
G. fascia	tus Say, 1818	FW
G. hyale	lloides Cole, 1976	FW
G. jenne	ri Bynum & Fox, 1977	At (V-C)
G. lacus	ris lacustris Sars, 1864	FW
G. lawre	ncianus Bousfield, 1956	A-At
G. limna	eus S. I. Smith, 1874	FW
G. minus	minus Say, 1818	FW
G. minus	pinicollis Cole, 1976	FW
G. payne	i Delong, 1992	FW
G. pecos	Cole & Bousfield, 1970	FW
G. pseud	olimnaeus Bousfield, 1958	FW
G. tigrin	us Sexton, 1939	At (AC-C)G (FL-LA)

G. troglophilus Hubricht & Mackin, 1940 **FW** G. (Lagunogammarus) oceanicus (Segerstrale, 1947) At (A-AC) G. (L.)setosus Dementieva, 1931 P (AL-BC)-A-At G. (L.)wilkitzkii (Birula, 1897) Α

G. (Mucrogammarus) mucronatus (Say, 1818) At (AC-V-C), G(FL), P (Salton Sea)

G. (M.).palustris Bousfield, 1969 G (FL?) Marinogammarus finmarchicus Dahl, 1938 At (AC-V-C)

#### Family Anisogammaridae Bousfield, 1977

Anisogammarus pugettensis pugettensis (Dana, 1853)	P (AL-CAL)
A. amchitkana Bousfield, 2001	P(AL-)
A. epistomus Bousfield, 2001	P(BC)
A. slatteryi Bousfield, 2001	P (BER-WA)
Barrowgammarus mcginitiei (Shoemaker, 1955)	P-A (BAR)
Carineogammarus makarovi (Bulycheva, 1952)	P(SE AL)
Eogammarus oclairi Bousfield, 1979	P (BC-ORE)
E. confervicolus (Stimpson, 1856)	P (SE AL- CAL)
E. psammophilus Bousfield, 1979	P (ALEUT)
Locustogammarus levingsi Bousfield, 1979	P (SE AL-BC)
L. locustoides (Brandt, 1851)	P (AL-BC)
Ramellogammarus campestris Bousfield & Morino, 1992	FW P (ORE)
R. californicus Bousfield & Morino, 1992	FW P (CAL)
R. columbianus Bousfield & Morino, 1992	FW P (BC-ORE)
R. oregonensis (Shoemaker, 1944)	FW P (ORE)
R. ramellus (Weckel, 1907)	FW P (CAL)
R. similimanus (Bousfield, 1961)	FW P (ORE)
R. setosus Bousfield & Morino, 1992	FW P (ORE)
R. littoralis Bousfield & Morino, 1992	FW P (ORE)
R. vancouverensis Bousfield, 1979	FW P (BC)
Spinulogammarus subcarinatus (Bate, 1862)	P (AL-BC)
Spasskogammarus tzvetkovae Bousfield, 1979	P (BER)

#### Family Gammaroporeiidae Bousfield, 1977

Gammaroporeia alaskensis (Bousfield & Hubbard, 1968) P(SE AL)

#### Family Mesogammaridae Bousfield, 1977

Paramesogammarus americanus Bousfield, 1979 P(SE AL)

### Superfamily Hadzioidea Bousfield, 1977 [= hadzioids Barnard & Barnard, 1983]

#### Family Allocrangoncytidae Holsinger, 1989

Allocranqonyx hubrichti Holsinger, 1971 **FW** pellucidus (Mackin, 1935) **FW** 

#### Family Hadziidae S. Karaman, 1933

## Weckeliid subgroup (Holsinger, 1992) (= weckeliids of Barnard & Barnard, 1983)

Allotexiweckelia hirsuta Holsinger, 1980

FW (TX)

Holsingerius samacos (Holsinger, 1980)	FW
H. smaragdinus Holsinger, 1992b	FW
Mexiweckelia hardeni Holsinger, 1992b	FW
Paramexiweckelia ruffoi Holsinger, 1993	FW
Texiweckelia texensis (Holsinger, 1973)	FW (TEX)
Texiweckeliopsis insolita (Holsinger, 1980)	FW (TEX)

# Hadziid subgroup (= hadziids of Barnard & Barnard, 1983)

Dulzura sal J. L. Barnard, 1969	P (CAL)
Protohadzia sp. Zimmerman & Barnard, 1977	G (FL?)
P. schoenerae (Fox, 1973)	At(C); G(FL)
Metaniphargus beattyi Shoemaker, 1942	G (FL?)
Netamelita barnardi McKinney et al, 1978	G (TEX)
N. brocha Thomas & Barnard, 1991c	G (FL)
N. cortada Barnard, 1962	P(S CAL)
Spathiopsis looensis Thomas & Barnard, 1985	G (FL)

## Gammarellas (=nuuanids Barnard & Barnard, 1983)

Tabatzius muelleri (Ortiz, 1976) G (FL-YUC)
T. copillius (McKinney & Barnard, 1977) G (FL?-YUC)

# Family Melitidae Bousfield, 1973 [= melitids + ceradocids sensu Barnard & Barnard, 1983 (part)}

Abludomelita obtusa (Monatagu, 1813)	P? (WA?), At (ST L)
Anamaera hixoni Thomas & Barnard, 1985	G (FL)
Bathyceradocus torelli (Goes, 1966)	P (bathyal), A-At (ST L, deep)
Ceradocus colei (Kunkel, 1910)	At (V)
C. paucidentatus Barnard, 1952	P (CAL)
C. rubromaculatus (Stimpson, 1856)	P
C. sheardi Shoemaker, 1948	G (W FL)
C. shoemakeri Fox, 1973	At (C); G (FL)
C. spinicauda (Holmes, 1908)	P (BC-CAL)
Denticeradocus sp. (see Barnard, 1952)	P(CAL)
Desdimelita barnardi Jarrett & Bousfield, 1996	P(BC)
D. desdichada (J. L. Barnard, 1962)	P (SE AL-CAL)
D. californica (Alderman, 1936)	P (AL-CAL)
D. microdentata Jarrett & Bousfield, 1996	P (SE AL-ORE)
D. microphthalma Jarrett & Bousfield, 1996	P (SE AL)
D. transmelita Jarrett & Bousfield, 1996	P(BC)
Dulichiella appendiculata (Say, 1818)	P(SCAL);At(C); G(FL-LA)
Elasmopus antennatus (Stout, 1913)	P (SE AL-CAL)
E. balcomanus Thomas & Barnard, 1988	G (FL)
E. bampo Barnard, 1979	P (CAL)
E. holgurus Barnard, 1962	P (CAL)
E. lemaitrei Ortiz, 1994	G (FL? CUBA)
E. levis (S. I. Smith, 1873)	At $(V-C)$ , $G(FL)$
E. mutatus Barnard, 1962	P (WA -CAL)
E. pectenicrus (Bate, 1862)	G (FL)
E. pocillimanus (Bate, 1862)	G (FL)
E. serricatus Barnard, 1969	P (S CAL)
E. thomasi Ortiz, 1994	G (FL - CUBAt)
Eriopisa elongata Bruzelius, 1859	P (CAL) -At (V-C, shelf), G (FL?)

E incisa McKinney, Kalke & Holland, 1978	G (TEX)
E. schoenerae Fox, 1973	G (FL?)
Eriopisa sp. (Barnard, 1952)	P(S CAL)
Jerbarnia americana Watling 1981	At (C-E FL)-,G (FL)
Lupimaera lupana (Barnard, 1969)	P(CAL)
Maera danae (Stimpson, 1853)	P-At (AC)
M. cf. danae Krapp-Schickel & Jarrett. 2000	P(AL-SE AL)
M. loveni (Bruzelius, 1859)	P(Al-WA)-A-At(N)
M. fusca (Bate, 1864)	P(AL-WA)
M. nelsonae Krapp-Schickel & Jarrett, 2000	P (BER-CAL)
M. bousfieldi Krapp-Schickel & Jarrett, 2000	P (BC-CAL)
M jerrica Krapp-Schickel & Jarrett, 2000	P (SE AL- ORE)
M. similis Stout, 1913	P (BC-MEX)
Maera diffidentia J. L. Barnard, 1969	At (NC-G (FL)
M rathbunae Pearse, 1908	G (FL-MI)
Maera sp. (nr. rathbunae) Krapp-Schickel & Jarrett, 2000	P (BC - At (NC)
M. grossimana (Montagu, 1808)?	P (BC-ORE)
M. prionochira Bruggen, 1907	P(AL)
M. quadrimana (Dana, 1853)	G (CUBA-FL)
M. reishi Barnard, 1979	P (CAL?)
M. serrata Schellenberg, 1938	G (CUBA-FL?)
M. sulca (Stout, 1913)	P(S CAL)
M. williamsi Bynum & Fox, 1977	At (C); G (FL)
Megamoera amoena (Hansen, 1887)	<b>A</b>
M. bowmani Jarrett & Bousfield, 1996	P(SEAL)
M. borealis Jarrett & Bousfield, 1996	P(SEAL)
M. dentata (Kroyer, 1842)	P-A-At
M. glacialis Jarrett & Bousfield, 1996	P (SE AL)
M. kodiakensis (Barnard, 1964)	P(SE AL)
M. mikulitschae (Gurjanova, 1953)	P (BER)
M. rafiae Jarrett & Bousfield, 1996	P(SEAL)
M. subtener (Stimpson, 1856)	P (BC-CAL)
M unimaki Jarrett & Bousfield, 1996	P (ALEUT)
Melita alaskensis Jarrett & Bousfield, 1996	P(AL)
M. intermedia Sheridan, 1980	G (W FL)
M. elongata Sheridan, 1979	G (W FL)
M. longisetosa Sheridan, 1979	At (V-C). G (W FL)
M. nitida (S. I. Smith, 1874)	P (intr.)-At, G (E FI)
M. oregonensis Barnard, 1954	P (BC-CAL)
M. shoemakeri (= M. nitida Shoemaker, 1936)	G (YUC)
M. sulca (Stout, 1913)	P(S CAL)
Melitoides makarovi Gurjanova, 1934	P (BER
M. valida (Shoemaker, 1964)	P (BER)
Quadrimaera carla Krapp-Schickel & Jarrett, 2000	P (BC - CAL)
?Q. vigota Barnard, 1969	P(CAL)
Quasimelita quadrispinosa (Vosseler, 1889)	PA (SE AL)-A-At (ST L)
Q. formosa (Murdoch, 1885)	A (AL)-At (ST L)
Spathiopus looensis Thomas & J. L. Barnard, 1985	G (FL)

# Superfamily Bogidielloidea Bousfield, 1977 [= bogidiellids Barnard & Barnard,, 1983 (part)]

# Family Atesiidae Holsinger & Longley, 1980

Artesia welbourni Holsinger, 19	992b	FW TEX
Artesia weidourni Hoisinger, 1.		TWITTY
A. subterranea Holsinger,	1980	FW TEX

## Family Bogidiellidae Hertzog 1936

Parabogidiella americana Holsinger, 1980 FW TEX

# Superfamily Corophioidea Barnard & Barnard, 1983 (revised)

## Family Ampithoidae Stebbing, 1899

	1 1029	P (AL-ORE)
-	e dalli Shoemaker, 1938	G (FL Keys)
<i>A</i> .	divisura Shoemaker, 1933	P (AL-BC))
<i>A</i> .	kussakini Gurjanova, 1955	P?-At (V), G (W FL)
<i>A</i> .	longimana (S. I. Smith, 1873)	• •
<i>A</i> .	lacertosa Bate, 1858	P (AL-S CAL)
<i>A</i> .	plumulosa Shoemaker, 1938	P (BC-S CAL)
<i>A</i> .	ramondi Audoin, 1828 (= A. divisura?)	P?, G (FL)
<i>A</i> .	rubricata (Montague, 1808)	At (AC)
<i>A</i> .	rubricatoides Shoemaker, 1938	P (BER)
Α.	sectimanus Conlan & Bousfield, 1982	P (SE AL-ORE)
Α.	simulans Alderman, 1936	P (AL-ORE)
<i>A</i> .	valida S. I. Smith, 1873	P(BC-CAL), At(V)), G(FL)
A.	volki Gurjanova, 1938	P (BER?)
	usa compta (S. I. Smith, 1873)	AT (V), G (W FL)
C.	filosa Savigny, 1816	G (FL)
С. С.	uncinata (Stout, 1912)	P (BC-CAL)
	phithoe eoa (Barnard, 1954)	P (BER?)
P eramp	femorata (Kroyer, 1845)	P-At?
Р.	humeralis (Stimpson, 1864)	P (SE AL-S CAL)
г. Р.	mea (Gurjanova, 1938)	P (ALEUT)
	lindbergi (Gurjanova, 1938)	P (BER-CAL)
<i>P</i> .		P (SE AL-CAL)
<i>P</i> .	stypotrupetes Conlan & Chess, 1992	P (BC-CAL)
<i>P</i> .	plea (Barnard, 1965)	P (SE AL-S CAL)
<i>P</i> .	tea (Barnard, 1965)	P(S CAL)
Pleonexes aptos Barnard, 1969		G (FL?, CUBA)
Pseuda	mphithoides bacescui Ortiz, 1976	At (offshore), G
Sunam	phitoe pelagica (Milne-Edwards, 1830)	At (Olishole), O

## Family Biancolinidae J. L. Barnard, 1972

Biancolina brassiacephala Lowry, 1974 G

## Family Aoridae Stebbing, 1899

Arctolembos arcticus (Hansen, 1887)	Α
Acuminodeutopus heteruropus Barnard, 1959	P (CAL)
Aoroides columbiae Walker, 1898	P (BER-CAL)

<b>A</b> .	exilis Conlan & Bousfield, 1982	P (SE AL-CAL)
<i>A</i> .	inermis Conlan & Bousfield, 1982	P (BC-CAL)
<b>A</b> .	intermedius Conlan & Bousfield, 1982	P (BC)
<i>A</i> .	spinosus Conlan & Bousfield, 1982	P (SE AL-ORE)
	los audbettius Barnard, 1962	P (CAL)
В.	concavus (Stout, 1913)	P (CAL)
В.	mackinneyi Myers, 1978	G (FL)
В.	macromanus Shoemaker, 1925	P (S CAL)
В.	sanmartini Ortiz, Lalana & Lopez, 1992?	
Colu	mbaora cyclocoxa Conlan & Bousfield, 1982	G (FL - CUBA ) P (SE AL-S CAL)
Grai	ndidierella bonnieroides Stephensen, 1948	G (W FI-TEX)
G.	notoni Shoemaker, 1935	G? (YUC?)
G.	japonica Stephensen, 1938	P (CAL-BC, intr.)
Lemi	bos (Arctolembos) arctica Hansen, 1887	A-P (BER)
L.	(Globosolembos) francanni Reid, 1951	G (FL)
L.	(Globosoolembos) smithi (Holmes, 1905)	G (FL-YUC)
L.	borealis Myers, 1976	,
L.	bruneomaculatus brunneomaculatus Myers, 1977	At (G-S)
L.	brunneomaculatus mackinneyi Myers, 1978	G (FL)
L.	dentischium Myers, 1977	G (FL-TEX)
L.	hypacanthus (K. H. Barnard, 1916)	G (FL)
L.	kunkelae Myers, 1977	G (E FL) G (FL)
L.	minimus Myers, 1977	` '
L.	ovalipes Myers, 1979	G (FL) G (W FL)
L.	rectangulatus Myers, 1977	G (W FL)
L.	setosus Myers, 1978	G (VFL)
L.	smithi (Holmes 1905)	At (V-C)
L.	spinicarpus spincarpus (Pearse, 1912)	G (FL)
L.	spinicarpus inermis Myers, 1979	G (W FL)
L.	tigris Myers, 1981	G (W FL)
L.	tigrinus Myers, 1979	G (W FL)
L.	tempus Myers, 1981	G (W FL)
L.	unicornis Bynum & Fox, 1977	At $(C)$ , $G$ $(FL)$
L.	unifasciatus unifasciatus Myers, 1977	G (FL)
L.	unifasciatus reductus Myers, 1979	G (W FL)
L.	websteri Bate, 1856	At (ST L; V), G (E FL?)
Lepto	cheirus pinguis (Stimpson, 1853)	A-At (AC)
L.	plumulosus Shoemaker, 1932	At (V), G (E FI)
L.	rhizophorae Ortiz, 1981	G (FL - CUBA)
Liocui	na caeca Myers, 1981	G (W FL)
Micro	deutopus anomalus (Rathke, 1843)	At (V)
<i>M</i> .	gryllotalpa Costa, 1853	At (V)
<i>M</i> .	myersi Bynum & Fox, 1977	At (C-FL), G (FL)
	la monstrosa Boeck, 1861	A-At (ST L)
<i>N</i> .	intermedia Coyle & Mueller, 1981	P(W AL)
<i>N</i> .	pacifica Gurjanova, 1953	P(CAL?)
Param	sicrodeutopus schmitti (Shoemaker, 1942)	P(S CAL)
Pseudunciola obliquua (Shoemaker, 1949)		At (AC-V, shelf)
Pterunciola spinipes Just, 1977		At (off NC, deep)
Rildardanus laminosa (Pearse, 1912)		At (HAT)-G (W FL-AL)
Rudile	mboides naglei Bousfield, 1973	At (V-C), G (FL)
		/

Unicola crassipes Hansen 1887		A-At (N, slope)
U.	dissimilis Shoemaker 1945	At (V-C), G (E FL?)
U.	inermis Shoemaker 1945	A-At (AC-CHES)
U.	irrorata Say, 1818	At (AC-V)
U.	laticornis Hansen, 1887	A-At (AC-CV, deep)
U.	leucopis (Kroyer, 1845)	A-At (AC)
U.	serrata Shoemaker, 1945	G (FL-AL)
U.	spicata Shoemaker, 1945	At,- G

# Family Cheluridae Allman, 1847

Chelura terebrans Philippi, 1839	P (CAL, intr.), At (AC), G
Tropichelura gomezi Ortiz, 1976	G. (FL- CUBA)
T. insulae Barnard, 1959	G (FL)

# Family Isaeidae Stebbing, 1906

Ampelisciphotis podophthalma (J L. Barnard, 1958)	P (CAL)
Audulla chelifera Chevreux, 1901	G (FL)
Cheirimedia macrocarpa america Conlan, 1983	P (BC-ORE)
C. macrodactyla Conlan, 1983	P (BER)
C. similicarpa Conlan, 1983	P (AL-BC)
C. zotea (Barnard, 1962)	P (BC-CAL)
Cheirophotis megacheles (Giles, 1885)	P (CAL)
Chevalia aviculae Walker, 1904	P (BC); G (FL)
C. carpenteri Barnard & Thomas, 1987	G (FL)
C. inaequalis (Stout, 1913)	G (FL)
C. mexicana Pearse, 1913	G (FL-LA)
Gammaropsis atlantica Stebbing, 1888	G (FL)
G. effrena (Barnard, 1964)	P (CAL)
G. ellisi Conlan, 1983	P (C-CAL)
G. inaequistylis Shoemaker, 1930	A-At (ST L shelf)
G. maculatus (Johnston, 1827)	A-At (N)
G. mamola (Barnard, 1962)	P (CAL)
G. martesia (Barnard, 1964)	P(CAL)?
G. melanops G. O. Sars, 1882	At (G)
G. nitida (Stimpson, 1853)	A-At (AC)
G. ocellatus Conlan, 1994	P (CAL, deep)
G. ociosa (J. L. Barnard, 1962)	P (CAL)
G. shoemakeri Conlan, 1983	P (BC- S. CAL)
G. sophiae (Boeck, 1861)	A-At (AC slope)
G. spinosa (Shoemaker, 1942)	P (BC-S.CAL)
G. sutherlandi Nelson, 1981	AT (N C), G (SE FL)
G. thompsoni (Walker, 1898)	P (SE AL-S CAL)
Microprotopus raneyi Wigley, 1966	At (C), G (W FL)
M. shoemakeri Lowry, 1972	At (V-C), G (E. FL- LA)
Pareurystheus alaskensis (Stebbing, 1910)	P(AL)
P. dentatus (Holmes, 1908)	P (BER-BC)
P. tzvetkovae (Conlan, 1983)	P(AL)
Photis bifurcata Barnard, 1962	P (WA-CAL)
1 10 10	P (AL-CAL)
P. brevipes Shoemaker, 1942	

Р.	californica Stout, 1913	P(CAL)
Р.	chiconola Barnard, 1962	P (deep)
Р.	conchicola Alderman, 1936	P (WA-CAL)
Р.	dentata Shoemaker, 1945	At (V) G (FL)
P.	elephantis Barnard, 1962	P(CAL)
Р.	fischmanni Gurjanova, 1938	P (BER)
Р.	kurilica Gurjanova, 1955	P (BER-ORE)
P.	lacia J. L. Barnard, 1962	P (BC-CAL)
<b>P</b> .	linearmanus Conlan, 1994	P(CAL)
Р.	longicaudata (Bate & Westwood, 1862)	G (FL)
Р.	macromana McKinney et al, 1978	G (FL-W TEX)
Р.	macinerneyi Conlan, 1983	P (BC-WA)
Р.	macrocoxa Shoemaker, 1945	At (AC-V)
Р.	macrotica Barnard, 1962	P(CAL)
Р.	melanica McKinney, 1980	G (FL-TEX)
P.	oligochaeta Conlan, 1983	P (SE AL -BC)
Р.	pachydactyla Conlan, 1983	P (SE AL-BC)
P.	parvidons Conlan, 1983	P (BC -WA)
Р.	pugnator Shoemaker, 1945	At (C-FL), G (FL)
Р.	reinhardi Kroyer, 1842	P?-A-At (AC-BF)
P.	spasskii Gurjanova, 1951	P(AL-BC)
P.	spinicarpa Shoemaker, 1942	P(CAL)?
<i>P</i> .	tenuicornis G. O. Sars, 1882	A-At (G-I, C)
<i>P</i> .	trapherus Thomas & Barnard, 1991b	G (FL)
<i>P</i> .	typhlops Conlan, 1994	P (CAL, deep)
<i>P</i> .	viuda J. L. Barnard, 1962	P(S CAL)
	ceropsis amchitkensis Conlan, 1983	P(AL)
<i>P</i> .	angustimana Conlan, 1983 (= G. ociosa?)	P (BC)
<i>P</i> .	barnardi (Kurjaschov & Tzvetkova, 1975)	P (BER -BC)
<i>P</i> .	chionoecetophila Conlan, 1983	P (ALEUT-ORE)
<i>P</i> .	setosa Conlan, 1983	P(AL)
	medeia articulata Barnard, 1962	P (ORE-S CAL)
<i>P</i> .	fasciata Kroyer, 1842?	P? (WA), A-At
<i>P</i> .	grandimana Bruggen, 1905	P (BER-BC)A-At
<i>P</i> .	penates Barnard, 1966	P (BC CA)
<i>P</i> .	prudens Barnard, 1966	P (BC-S CAL)
Р.	stephenseni Shoemaker,1955	A-At (ST L)
		• •

# Family Neomegamphopidae Myers, 1981

Neomegamp	hopus heardi Barnard & Thomas, 1987	G (FL)?
<i>N</i> .	hiatus Barnard & Thomas, 1987	G (FL).
<i>N</i> .	kalanii Barnard & Thomas, 1987	G (E FL)
<i>N</i> .	pachiatus Barnard & Thomas, 1987	G(SFL)?
<i>N</i> .	roosevelti Shoemaker, 1942	G (FL)

## Family Ischyroceridae Stebbing, 1899 (contains subfamilies Cerapiinae Budnikova and Ischyrocerinae Stebbing)

Bonnierella linearis californica Barnard, 1966

P (OR-deep)

Cerapus tubularis Say, 1818	At (V-C)
C. benthophilus Thomas & Heard, 1979	G (FL)
C. cudjoe Lowry & Thomas, 1991	G (FL)
Ericthonius brasiliensis (Dana, 1853)	P (intr.?), G (FL)
E. difformis Milne-Edwards, 1830	P(WA?), A-At
E. fasciatus (Stimpson, 1853)	AT (ST L-V)
E. rubricornis (Stimpson, 1853)	P (BER-CAL),- At
E. tolli Bruggen, 1909	A-At (ST L)
Ischyrocerus anguipes (Kroyer, 1838)	P-A-At (to DEL) (not FL!)
I. claustris (Barnard, 1969)	P (CAL)
I. commensalis Chevreux, 1900	A-At (ST L)
I. gurjanovae Kudrjaschov, 1975	P (BER)
I. latipes Kroyer, 1842	A-At (ST L, slope)
I. malacus Barnard, 1964	P (CAL, deep)
I. megalops G. O. Sars, 1894	At (G-EM)
I. nanoides (Hansen, 1887)	P(WA?), At (ST L)
I. parvus Stout, 1913	P(S CAL)
I. pegalops Barnard, 1962	P (CAL)
I. serratus Gurjanova, 1938	P (AL?)
I. tuberculatus (Hoek, 1882) Gurjanova	P (BER)
I. tzvetkovae Kudrjaschov, 1975	P (BER)
Jassa borowskyae Conlan, 1990	P (AL-CAL)
J. carltoni Conlan, 1990	P(CAL)
J. marmorata Holmes, 1903	P - At (ST L -V-C)- G (E FL),
J. morinoi Conlan, 1990	P (BC-CAL)
J. myersi Conlan, 1990	P (CAL)
J. oclairi Conlan, 1990	P (AL-BC
J. shawi Conlan, 1990	P (BC-CAL)
J. slatteryi Conlan, 1990	P (BC-CAL)
J. staudei Conlan, 1990	P (SE Al - BC, ORE)
Microjassa bahamensis Conlan, 1995	At (E FL?)
M. boreopacifica Conlan, 1995	P (SE AL-BC)
M. barnardi Conlan, 1995	P (ORE-CAL)
M. bousfieldi Conlan, 1995	P (CAL)
M. floridensis Conlan, 1995	G (FL)
M. litotes Barnard, 1954	P (BC-CAL)
M. macrocoxa Shoemaker (1942)	AT (AC-G?)
M. micropalpa Shoemaker (1942)	At (V-C?)
M. tetradonta Conlan, 1995	P(CAL?) G(FL)
Parajassa angularis Shoemaker, 1942	P(CAL?)
Ventojassa ventosa (Barnard, 1962)	P (CAL, deep)
Neoischyrocerus claustris (J. L.Barnard, 1969)	P (CAL)

# Family Corophiidae Dana, 1849

## Subfamily Corophiinae Bousfield & Hoover, 1997

Americorophium spinicorne (Stimpson, 1957)		P (AL-CAL)
<i>A</i> .	aquafuscum (Heard & Sikora, 1972)	At (C), G (FL-MI)
<i>A</i> .	brevis (Shoemaker, 1949)	P (SE AL-CAL)
A.	ellisi Shoemaker, 1943	G (FL-LA)

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<i>A</i> .	salmonis (Stimpson, 1857)	P (SE AL-WA)
<i>A</i> .	stimpsoni (Shoemaker, 1941)	P (CAL)
Apocorophi	um acutum (Chevreux, 1908)	P(CAL, intr), At (V-C). G(FL)
<i>A</i> .	lacustre (Vanhoffen, 1911)	At (V). G (E FL)
Apocorophi	um simile (Shoemaker, 1934)	At (C-E FL)
<i>A</i> .	louisianum (Shoemaker, 1934)	G (FL-LA)
Corophium	volutator (Pallas, 1776)	At (AC)
Crassicorop	hium crassicorne (Bruzelius, 1859)	P-A-At (tAC-CHES)
<i>C</i> .	clarencense (Shoemaker, 1949)	P-A (BER)
<i>C</i> .	bonelli (Milne Edwards, 1830)	P-A-At (AC)(not FL!)
-	um baconi (Shoemaker, 1934)]	P (AL-CAL) (not FL!)
Monocoropl	nium insidiosum (Crawford, 1937)	P (BC-CAL, intr?), At (ST L; V) (FL?)
<i>M</i> .	acherusicum (Costa, 1857)	P (AL-CAL) A-At (CHES), G (FL)
М.	californianum (Shoemaker, 1934)	P (BC-CAL)
<i>M</i> .	carlottensis Bousfield & Hoover, 1997	P (BC-SE AL)
<i>M</i> .	oaklandense (Shoemaker, 1949)	P (CAL)
<i>M</i> .	steinegeri (Gurjanova, 1951)	P (BER)
<i>M</i> .	uenoi (Stephensen, 1932)	P (CAL, intr.)
<i>M</i> .	tuberculatum (Shoemaker, 1934)	At (V-C), G (FL)
Sinocorophi	um alienensis (Chapman, 1988)	P(CAL, intr.)

## Subfamily Siphonoecetinae Just, 1983

Siphonoecetes smithianus Rathbun, 1905 At (V, shelf)
Caribboecetes crassicornis Just, 1984 G (FL?)

## Family Podoceridae Leach, 1814

Dulichia rhabdoplastis McLoskey, 1970	P (SE AL-CAL)
D. tuberculata Boeck, 1870	P(WA?)-A-At (ST L)
Dulichiopsis remis (Barnard, 1964)	P(AL?)
Dyopedos arcticus (Murdoch, 1885)	P(WA, CAL)-A-At (ST L)
D. bispinus (Gurjanova, 1930)	P (AL-BC)-At
D. falcata (Bate, 1857)	A-At (ST L, slope)
D. monacanthus (Metzger, 1875)	A-At (ST L - CHES)
D. porrectus Bate, 1857	A-At (ST L)
D. spinosissima Kroyer, 1845	A-At (AC, slope)
D. unispinus (Gurjanova, 1951)	P(BER)
Paradulichia typica Boeck, 1870	PA (Barrow), At (ST L, slope)
Podocerus brasiliensis (Dana, 1853)	P(SCAL), G(FL)
P. chelonophilus Chevreux & DeGuerne, 1888	G (FL)(see Thomas & Barnard, 1992a)
P. cristatus (Thomson, 1879)	P(CAL)
P. fulanus Barnard, 1962	P(S CAL)
P. kleidus Thomas & Barnard, 1992b	G (FI)
P. spongicolus Alderman, 1936	P (BC?-CAL)

## SUBORDER CAPRELLIDEA Leach, 1814

# Superfamily Caprelloidea Laubitz, 1993

# Family Caprogammaridae Kudrjaschov & Vassilenko, 1966, emend McCain, 1970

## Subfamily Caprogammarinae K. & V., 1966

Caprogammarus gurjanovae Kudrjaschov & Vassilenko,1966 WNP

## Family Caprellidae White, 1847, emend McCain, 1970

#### Subfamily Caprellinae Leach, 1814

	Sublaniny Capremnae Leach, 1814	
	angusta Mayer, 1903	P (BC-ORE)
<i>C</i> .	alaskana Mayer, 1903	P (BER-ALEUT-CAL))
<i>C</i> .	andreae (Mayer, 1890)	At (AC)- G
<i>C</i> .	borealis Mayer, 1903	P(AL-WA)
<i>C</i> .	brevirostris Mayer, 1903	P(CAL)
<i>C</i> .	californica Stimpson, 1857	P (BC-CAL)
<i>C</i> .	carina Mayer, 1903	A
<i>C</i> .	ciliata G.O. Sars, 1880?	P(AL)-N At
<i>C</i> .	constantina Mayer, 1903?	P (BER)
<i>C</i> .	cristibrachium Mayer, 1903?	P (BER-ALEUT)
<i>C</i> .	danielevskii Czern. 1868	At (FL)- G
<i>C</i> .	drepanocheir Mayer, 1890	P(AL-WA)
<i>C</i> .	dubia Hansen, 1888	At -A
<i>C</i> .	equilibra Say, 1818	At (V) - G - P (BC-WA intr?)
<i>C</i> .	gracilior Mayer, 1903	P(AL-CAL)
<i>C</i> .	greenleyi McCain, 1969	P (ORE-CAL)
<i>C</i> .	incisa Mayer, 1903	P (SE AL-CAL)
<i>C</i> .	irregularis Mayer, 1890	P (AL-WA)
<i>C</i> .	kincaidi Holmes 1904?	P (BER)
<i>C</i> .	laeviuscula Mayer, 1890?	P (AL-ORE)
<i>C</i> .	linearis L. 1758	A-At-N P
<i>C</i> .	mendax Mayer, 1903	P(BC)
<i>C</i> .	mutica Schurin, 1935	P(CAL)
<i>C</i> .	natalensis Mayer, 1903	P (BC-CAL)
<i>C</i> .	paulina Mayer, 1903	P (BER-ALEUT)
	penantis Leach, 1814	At-G; P (CAL intr?)
	pilidigita Laubitz, 1970	P (BC-WA)
<i>C</i> .	pilipalma Dougherty & Steinberg, 1953	P(CAL)
	pustulata Laubitz, 1970	P (SE AL-ORE)
	radiuscula Laubitz, 1970	P (SE AL-WA)
	rinki Stephensen, 1933	At (deep)
	scabra Holmes, 1904	P(SE AL)
	scaura Templeton, 1836	P(CAL)-At
<i>C</i> .	septentrionalis Kroyer, 1842?	P (BER?), A-At
	striata Mayer, 1903	P(AL-WA?)-A
	trispinus Honeyman, 1889	At (deep)
	ungulina Mayer, 1903	P (BC, deep)
<i>C</i> .	unica Mayer, 1903	At

C.	uniforma La Follette, 1915	P (CAL)
C.	verrucosa Boeck, 1872	P (BC-CAL)
_	acaprella anomala (Mayer, 1903)	P (AL-CAL)
M.	ferresa Mayer, 1903	P (A-CAL)
<i>M</i> .	horrida G. O. Sars, 1880	At-A
М.	kennerlyi (Stimpson, 1864)	P (AL-CAL)

# Subfamily Aeginellinae Vassilenko, 1968

Aeginella spinosa Boeck, 1861	N At (deep)
Aeginina longicornis (Kroyer, 1842)	A-At

# Family Pariambidae Laubitz, 1993

Deutella californica Mayer, 1890 D. abracadabra Steinberg & Dougherty, 1952 D. incerta Mayer, 1903	P (SE AL-CAL) At-G G
Hemiaeginina minuta Mayer, 1890	At, G
Luconacea incerta Mayer, 1903	At (V)
Paracaprella tenuis Mayer, 1903 P. pusilla Mayer, 1890 P. cf. temir (fide Nelson, 1995)	At (V) At G G

## Family Protellidae McCain, 1970, emend Laubitz, 1993

<ul><li>Mayerella limicola Huntsman,1915</li><li>M. banksia Laubitz, 1970</li><li>M. acanthopoda Benedict 1997</li></ul>	At P (AL-CAL) P (S CAL)
Protellina ingolfi Stephensen (1942?)	N At (deep)
Proaeginina norvegica (Stephensen, 1931)	N At
Protoaeginella sp. Laubitz & Mills, 1972	N At
Tritella pilimana Mayer 1903  T. laevis Mayer, 1903  T. tenuissima Doughty & Steinberg 1953	P (AL-ORE) P (BC-S CAL) P (CAL, deep)

## Family Paracercopidae Vassilenko, 1968

Cercops holbolli Kroyer, 1842	Α
C. compactus Laubitz, 1970	P

Paracercops setifer Vassilenko, 1972 P (BER?)

### Family Caprellinoididae Laubitz, 1993

Pseudaeginella biscaynensis (McCain, 1968) Pseudoliropus vanus Laubitz, 1970

At (FL) G P (BC, deep)

## Family Phtisicidae Vassilenko, 1968

### Subfamily Phtisicinae Vassilenko, 1968

Phtisica marina Slabber, 1769

At-G

Perotripus brevls (La Follette, 1915) Hemiproto wigleyi McCain, 1968

P (AL-S CAL) At (G -E FL)

## Infraorder Cyamida Bousfield, 1979

# Family Cyamidae Rafininesque, 1817 (revised Margolis, McDonald, & Bousfield 2000)

Cyamus (Cyamus) ceti (L.) Lamarck, 1801 C. (Cyamus) erraticus R. de Vauzeme, 183 C. (Cyamus) ovalis R. de Vauzeme, 1834 C. (Cyamus) gracilis R. de Vauzeme, 1834 C. (Cyamus) monodontis Lutken, 1873 C. (Cyamus) nodosus Lutken, 1860	P (AL-CAL P (BC)-At P (SE AL)-A P (SE AL)-A P (BER)-A-A	on Balaena glacialis on Balaena glacialis At on B. gracilis
Cyamus (Paracyamus) balaenopterae K. H. Barn	ard, 1931 P-At	on balaenopteae (blue, fin)
C. (Paracyamus) boopis Lutken, 1870)	P (AL-CAL	
Cyamus (Mesocyamus) catodontis Margolis, 1954	P (BC)-At	on Physeter
C. (Mesocvyamus) orubraedon Waller, 1989		on <i>Berardius bairdi</i>
C. (Mesocyamus) mesorubraedon Margolis	et al., 2000 P	on Physeter
Cyamus(Apocyamus) scammoni Dall, 1872	P (AL-CAL	on Eschrichtius
C. (Apocyamus) eschrichtii Margolis et al, 2	000 P	on Eschrichtius
C. (Apocyamus) kessleri Brandt, 1872	P (AL-CAL)	on Eschrichtius
Orcinocyamus orcinus (Leung, 1870)	P (BC+)	on Orcinus orca
Isocyamus delphini (Guerin-Meneville, 1836)	P (AL-CAL)	on porpoises, dolphins
I. globicipitis Lutken, 1973	At	on Globicephalus
I. kogiae Sedlak-Weinstein, 1992	P (CAL?)	on Kogia (pygmy sperm)
Neocyamus physeteris (Pouchet, 1888)	P (SE AL-B	C) on Physeter, Globicephalus
Platycyamus flaviscutatus Waller, 1989	P	on <i>Berardius bairdi</i>
Platycyamus thompsoni (Gosse, 1855) ampullatus	At	on Hyoperodon
Syncyamus pseudorcae Bowman, 1955	At	on Pseudorca
Scutocyamus parvus Lincoln & Hurley, 1974	At	on white-beak dolphin (Cephalorhynchus)

## **NOTES**