Amphipoda of the Northeast Pacific (Equator to Aleutians, intertidal to abyss): III.

Aoroidea - a review. Donald B. Cadien, LACSD

22 July 2004 (revised 15May2015)

Preface

The purpose of this review is to bring together information on all of the species reported to occur in the NEP fauna. It is not a straight path to the identification of your unknown animal. It is a resource guide to assist you in making the required identification in full knowledge of what the possibilities are. Never forget that there are other, as yet unreported species from the coverage area; some described, some new to science. The natural world is wonderfully diverse, and we have just scratched its surface.

Introduction to the Aoroidea

Stebbing (1899) introduced the concept of this group uniting the Aoridae and Unciolidae, but not at the superfamily level. Myers & Lowry (2003) in their review of the corophioids accorded that level to the two family group, creating the current concept of the Aoroidea. For much of the last quarter-century this group was considered to lie within the bounds of the family Corophiidae following J. L. Barnard's synonymization of Aoridae, Isaeidae and Photidae with that family (1973). This action generated much discussion and dissent, and Alan Myers, among others, failed to accept this view of the group. Berge et al (2000) in their cladistic analysis, found Corophiidae sensu Barnard distributed among three different clades. Conlan and Bousfield (1982) monographed the family regionally, although the allocation of genera within families did not match that later employed by Myers & Lowry (2003) closely. Apparent convergence in many character states between families has led to almost continual realignment of generic position for at least some of the corophioid genera. Movement between Photidae and Aoridae has been particularly persistent as genera are reinterpreted by different observers. The placements proposed by Myers & Lowry (2003) and followed on WoRMS (Horton 2015) are used here.

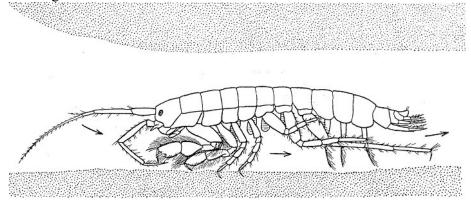
Diagnosis of the Aoroidea

"Head rectangular, anterodistal margin recessed, lateral cephalic lobe weakly extended, eye, if present, situated proximal to lobe; anteroventral margin weakly recessed, moderately excavate. Mandible palp 3-articulate or absent, article 3, when present, asymmetrical, distally rounded, with setae extending along most of posterodistal margin, or approximately parallel-sided with distal setae only; posterior margin with setae of variable length, or with comb of short setae and few long, slender setae. Gnathopod 1 enlarged in males and females, or only in males; coxa 1 enlarged, larger than coxa 2. Gnathopod 2 merus not enlarged. Pereopods 5-7 without accessory spines on anterior margin. Pereopod 7 longer or much longer than pereopod 6. Urosomites not coalesced. Uropods 1 and 2 without dense array of robust setae. Uropod 3 peduncle relatively short, length usually 2 times or less breadth; with 2, 1, or no rami. Telson without hooks or denticles." (Myers and Lowry 2003).

Ecological Commentary

As in other corophioid clades, the Aoroidea typically built tubes (Dixon & Moore 1997). They reported on three species of aorid tubes, Aora gracilis, A. spinicornis, and Lembos websteri. The tubes of both Aora species were flimsy thin constructs of amphipod silk with some admixture of sediment and/or detrital particles. Occupied tubes of both species were observed in situ during examination of kelp holdfasts. Although no in situ observations of occupied Lembos websteri tubes were made, animals released into aquaria rapidly formed similar tubes from materials on the bottom. These were attached their full length to the bottom, and were roughly 11/2 x the animal length. J. L. Barnard (1961) indicates that *Paramicrodeutopus schmitti* constructs tubes on hard surfaces. Myers (1981), while not explicitly discussing tubicoly in each species, describes the Family Aoroidae as a whole as being composed of tube building forms. J. L. Barnard (1961) agreed, stating that all agrids build "stout silty tubes attached to hard bottoms or hard fragments mixed with soft soils". His description of tubes clashes with those provided by others (i.e. Shillaker & Moore 1987) for specific aorids, and seems to be an over-generalization. Some aoroids, such as Aora seem able to construct tubes with or without addition of debris, while *Grandidierella* requires debris for tube construction, and will not form amphipod-silk tubes in its absence (Barnard et al 1989)

Enequist (1949) reported that *Aora typica*, *Microdeutopus gryllotalpa*, *M. propinquus*, and *Lembos longipes* all build silk-lined horizontal burrows in soft bottoms. His aquarium observations do not always reflect the typical field behavior of the animals, which have some behavioral plasticity. In the absence of an algal or other firm attachment site, for instance, a normally tube forming species may resort to a lined burrow of its own construction for protection and/or feeding. The observed feeding activity of *L. longipes*, suggests that at least for that species a lined burrow is probably representative. He actually tested this with the *Aora* and *Microdeutopus* species, finding that on coarser bottoms, where burrowing was difficult or impossible, tubes were constructed and attached to either the aquarium sides or to algae. Dixon & Moore (1997) also report observations of *Aora typica* using the tubes of *Ericthonius punctatus* rather than constructing their own.



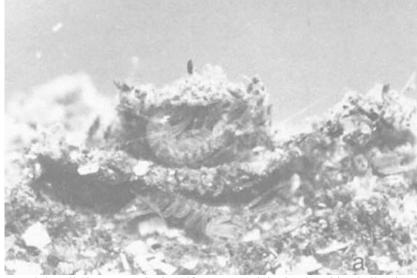
Lembos longipes feeding in its burrow. Arrows indicate pleopod generated current (from Enequist 1949)

Records of tubicoly are available from other sources for *Microdeutopus* gryllotalpa (DeWitt 1985; Borowsky 1981, 1983), but at least one other member of *Lembos* is reported to form neither tubes nor burrows. Munguia et al (2007) during experimental observations of population dynamics in three species, one of which was

Lembos unicornis, saw tube formation only in *Neomegamphopus hiatus*. While settling and development of many juvenile *L. unicornis* was followed, none were seen to burrow or form tubes.

Despite abundant material of several species and repeated collection, no mention of tubes or tubicoly for the genus *Aoroides* is provided by Conlan & Bousfield (1982). They also did not mention tubes for the species of *Lembos* they discussed (actually now a *Bemlos*). Ariyama (2004) in reviewing *Aoroides* in Japan and the NWP, made no mention of the presence of tubes, or of their absence. He saw each of the species alive and described their live coloration, so if tubes had been present they should have been noted. His habitat descriptions refer to specimens being "attached" to various substrates. This might be interpreted as being attached in tubes, but could as easily be a word choice for "clinging to". It is unclear if 1.) *Aoroides* species lack tubes; 2.) They construct flimsy tubes which do not survive field collection; or 3.) The animals flee their tubes so readily that the two have not yet been connected. The recorded habitat is amongst intertidal and shallow subtidal algae. I suspect that the third option above is correct, and that eventually observations on living specimens in situ will confirm their tube building. Indeed J. L. Barnard (1961) indicates *Aoroides columbiae* (present species assignment uncertain) constructs tubes on hard substrates without providing detail.

Tube construction of *Grandidierella bonnieroides* was observed in Florida aquaria by J. L. Barnard et al (1991), and found to follow a standard path. Bottom detritus (typically plant debris) was stitched into a blanket with silk secreted by the amphipod which lay on its side on the detritus. The animal then rolled over, dragging the detrital blanket across its body. Continued construction either united the top and bottom detrital blankets into a single ovoid tube, or the amphipod rolled the partial tube against the aquarium glass and tacked it there with amphipod silk.



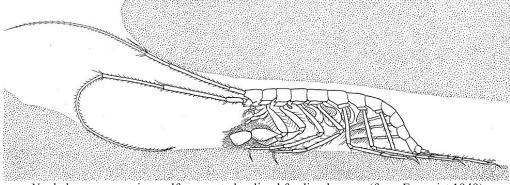
Grandidierella bonnierioides in self-constructed detritus/amphipod-silt tubes against an aquarium wall (from J. L. Barnard et al 1989)

The tubes were then lengthened, eventually reaching five times the animal length. Males were found to be less adept at construction than females, who began the tube in only a few minutes, and could complete it within 10 minutes. Males took substantially longer to initiate and complete tube building, but did engage in theft of completed female

tubes. Larger males could displace smaller females and capture their tubes, then adapting them to their own dimensions. Some other process is employed in *G. japonica* tube construction, as their tubes are muddier, and vertical in the sediments when undisturbed in the field (Cadien, pers. obs., Newport Bay, California). They were not found either attached to objects or flat on the sediment surface as where those of *G. bonnieroides*. No mention of tubes, their position, or nature is provided in the original description of *G. japonica* (Stephensen 1938), or in the review of Ariyama (1996) of four Japanese species, including *G. japonica*. Chapman & Dorman (1975) describe the tube as ushaped, with two surface openings, and often occupied by male/female pairs.

Unciolids may or may not be tubicolous. Observations on *Unciola planipes* (Stephensen 1929) indicate it does not build tubes. Similarly Enequist (1949) found *Neohela monstrosa* to inhabit neither tubes nor lined burrows, making feeding burrows instead, which were soon abandoned in search of a new excavation/feeding site. The delicate elongate legs and antennae of this form make this seem unlikely, but it is what he observed. Another variant behavior is reported for *Unciola irrorata*, which occupies tubes, but only those created by others (Bousfield 1973). He also reported *Unciola serrata* as living in tubes, but did not indicate if they were self-constructed. Several other *Unciola* species were also discussed, with no mention of tubes. Shoemaker (1945) did not discuss either presence or absence of tubes for any of the *Unciola* species he considered (including *U. irrorata* and *U. serrata*).

J. L. Barnard (1969), in his erection of the unciolid genus *Rildardanus* makes no mention of either tubes or the presence of tube-associated morphology. He recorded his material as from sand bottoms with algae, not unlike the habitat of several tubicolous aorids. Similarly *Zoedeutopus* was not recorded as associated with a tube. His habitat note for that species indicates the collection via "rock-washes". This practice involves use of either dilute alcohol or formalin as a dip to induce crevice dwellers and other hard bottom associates to flee their refuge. Had a tube been involved, it is very doubtful that connection would be established after the wash. At least for the subfamily Acuminodeutopinae tube building seems to occur, if not often noted. J. L. Barnard (1961) indicates that both *Acuminodeutopus heteruropus* and *Rudilemboides stenopropodus* construct tubes on hard substrates without providing detail on tube construction. He did, however, indicate that neither genus was found on hard artificial substrates or in the fouling community. They are typically associated with vegetation; eelgrass, algal turfs over soft bottoms, drift algal debris, etc.



Neohela monstrosa in a self-excavated unlined feeding burrow (from Enequist 1949)

Tube emergence behaviour and frequency has been described by several workers (see Shillaker & Moore 1987), and considerable interest has been expressed in the relative frequency of tube emergence by sex. Sex ratios and uneven predation on emerged males have been considered, as males appear to vacate the tube on female-finding excursions. These are more frequent at night, but visual predators may have some effect on day-time tube emergent individuals. Emergence is usually in response to water-born pheromone like chemicals secreted by molting females (Borowsky 1984, Borowsky et al 1987). Such emergence is combined with swimming activity in all cases; crawl-away males have not been reported. While swimming in aorids seems quite facile, that of unciolids (or at least the elongate *Neohela*) is ungainly and caprellid-like. Swimming in *Rildardanus*, *Zoedeutopus*, *Acuminodeutopus*, and *Rudilemboides* is not yet reported.

Aside from male swimming for mate-finding there is little evidence of frequent swimming by aoroids. Saint-Marie & Brunel (1985) recorded only the unciolid *Neohela monstrosa* in their study of swimming behavior of northwest Atlantic amphipods. It was taken infrequently in the lowest sampled level off the bottom.

Conlan (1991) characterized aorids as "mate guarding attenders". This classification refers to species where the male seeks out pre-molt females and defends them against competing male attempts at fertilization. Attenders do not carry the female, as some amphipods do, but stay in close proximity on guard. In *Microdeutopus gryllotalpa* this translates into occupation of a females tube by a male during the immediate pre-molt period (Borowsky 1980, 1983). The female releases a chemical signal into the water to indicate her readiness to molt and copulate (Borowsky 1984, Borowsky et al 1987). A male will follow this signal, enter the tube and cohabit for the premolt period, then leave after copulation (although Myers 1971 reports males remain during incubation). Male/female pairs were also observed in *Grandidierella japonica* tubes by Chapman & Dorman (1975), but it is not clear if this was persistent or temporary.

Moore (1981) found ovigerous females of *Lembos websteri* throughout the year, suggesting continual reproduction. He identified five different cohorts in his samples, with few ovigerous females in the one which overwintered. These were very large, and Moore (*loc. cit.*) suggests they may have produced one or two broods during the preceding autumn. They apparently die after the over-wintering spawn. Females thus may live slightly more than 1 year, with males living a shorter time. Myers (1971) reported female *Microdeutopus gryllotalpa* live much shorter lives, most dying after two months. During that period, however, they produced broods at 6-8 day intervals, reaching eleven broods within their survival period in some cases. Drake & Arias (1995) found a maximum of 5 broods per year in their Italian lagoonal populations. Weszlawski & Legezynska (2002) report spent females of *Neohela monstrosa* and small juveniles of *Unciola leucopis* in July. These arctic species may only be able to bear a single brood during the year when waters are warmest.

Feeding habits of some aorids are known. *Microdeutopus gryllotalpa*, for instance, is an herbivore (Hecksher et al 1996), as is *Aora typica* (Taylor & Brown 2006). The observations of Enequist (1949) suggest that the unciolid *Neohela monstrosa* and the aorid *Lembos longipes* are selective surface deposit feeders, sifting the sediments they manipulate within their burrow/feeding excavations. In situations where tubes are

constructed, *L. longipes* and *Microdeutopus propinquus* both appear to feed on suspended particulates. Since tube-building behavior is somewhat plastic in several species, it is likely that feeding behavior is also plastic, and that the most easily available nutritive source is utilized in any given situation.

While aoroids are often characterized as algal associates, they seem to have few associations with other animals. Myers & Moore (1983) report a species of *Aora* associated with sponges in New Zealand. A second species is reported associated with majid crabs in the Falkland Islands, but as yet based only on a single individual (Vader & Krapp (2005). An undescribed *Aora* has been taken in association with hermit crabs in Australia according to unpublished notes of Vader (Vader & Krapp 2005) One instance of parasitism has been reported (Costello & Myers 1989) where a brood parasitic copepod afflicts *Aora typica*. The same authors summarize earlier reports of similar parasites on species of *Lembos* and *Lemboides*.

Several species of aoroids have been subject to anthropogenic transport from their native habitats into new areas. *Grandidierella japonica* was transported from brackish waters in Japan to embayments in the NEP (Chapman & Dorman 1975), presumably as ride-alongs with the transplantation of oysters. It is now widely distributed in the NEP, ranging south at least to San Diego Bay. No records from further south are available (Garcia Madrigal 2007). The species is also now recorded from the British Isles (Ashelby 2006). The arrival of Microdeutopus gryllotalpa from the Atlantic or Mediterranean is more mysterious. It must have taken place sometime before 1980, when it was first detected on the mudflats of Humboldt Bay in Northern California (Boyd et al 2002). The species is now more widely distributed into at least Central California (Chapman 2007). It has not yet been recorded from further south, in the SCB, but its spread into further range is likely. No mechanism of introduction is currently known, although oyster culture and the transport of European oysters to the NEP is a possibility. Ballast water introduction in the busy commercial port of Eureka on Humboldt Bay is another. The natural history if this species in its new range has been examined (Greenstein & Tiefenhaler 1997) and it is now used for bioassay (Nipper et al 1987).



Grandidierella japonica, an introduced species in California bays (from calacademy.org)

Both male and female can be recognized by their short urosome.

Key to NEP Aoroid families and genera, (separation of families from Myers & Lowry 2003) generic key modified from Conlan & Bousfield 1982)

- dbcadien 15 May 2015

1. Pereopod 7 disproportionately longer than pereopod 6	Aoroidae 6
Pereopods 5, 6, and 7 in regular length progression	Unciolidae 2
2. Uropods 1 and 2, inner ramus vestigial	Rildardanus
Uropods 1 and 2, inner ramus well developed	3
3. Uropod 3 uniramous, inner ramus absent	Neohela
Uropod 3 biramous, inner ramus either reduced or norma	al4
4. Head lobe acutely produced, uropod 3 outer ramus uniar	ticulate5
Head lobe rounded, uropod 3 outer ramus biarticulate	Zoedeutopus
5. Uropod 3 less than half the length of the outer	Acuminodeutopus
Uropod 3 rami subequal in length	Rudilemboides
6. Uropod 3 uniramous	Grandidierella
Uropod 3 biramous	7
7. Uropod 3 outer ramus uniarticulate	8
Uropod 3 outer ramus biarticulate	9
8. Peduncular distal spine present on uropods 1 & 2	Columbaora
Peduncular distal spine present only on uropod 1	Microdeutopus
9. Accessory flagellum vestigial, a minute button	Aoroides
Accessory flagellum of 3 articles	Paramicrodeutopus
Accessory flagellum of 8 articles	Bemlos

NEP Aoroidea from McLaughlin et al (2005) augmented by known provisionals *= Taxa on SCAMIT Ed. 9 list (Cadien & Lovell 2014).

Valid taxa Bolded, synonyms not.

Family Aoridae

- *Aoroides columbiae Walker 1898 Amchitka Id., Aleutians, Alaska to SCB: 0-322m
- *Aoroides exilis Conlan & Bousfield 1982 Southeastern Alaska to Northern Baja California, Mexico: 0-82m
- *Aoroides inermis Conlan & Bousfield 1982 British Columbia, Canada to SCB: 0-102m
- *Aoroides intermedia Conlan & Bousfield 1982 Baranof Id., Alaska to SCB: 0-305m
- *Aoroides secundus Gurjanova 1938 NWP to SCB: 0-3.4m
- *Aoroides spinosa Conlan & Bousfield 1982 Prince William Sound, Alaska to SCB: 0-84m
- *Aoroides sp A SCAMIT 1996§ SCB: 0-196m

Bemlos achire (J. L. Barnard 1979) – Costa Rica to Galapagos: 0-6m

*Bemlos audbettius (J. L. Barnard 1962) – Goleta to Baja California, Mexico: 0-196m

*Bemlos concavus (Stout 1913) – SCB: 0-51m

Bemlos edentulus (J. L. Barnard 1967) – off Northern Baja California, Mexico: 791-842m

*Bemlos macromanus Shoemaker 1925 – Hawaii, Philippines; Cayucos, California to Galapagos Ids.: 0-61m

Bemlos tehuecos (J. L. Barnard 1979) - Gulf of California, Mexico: 0-1m

*Columbaora cyclocoxa Conlan & Bousfield 1982 – Southeastern Alaska to Goleta: 0-29m

*Grandidierella japonica Stephensen 1938 – Japan; Humboldt Bay to SCB: 0-10m

Grandidierella nottoni Shoemaker 1935 – Mazatlan, Mexico: 0-4m

Lembos achire J. L. Barnard 1979 (see Bemlos achire)

Lembos audbettius J. L. Barnard 1962 (see Bemlos audbettius)

Lembos edentulus J. L. Barnard 1967 (see Bemlos edentulus)

Lembos tehuecos J. L. Barnard 1979 (see Bemlos tehuecos)

Microdeutopus gryllotalpa Costa 1853 – North Atlantic and Mediterranean; introduced to the NEP, Humboldt Bay: 0-150m

Microdeutopus hancocki Myers 1968 (see Paramicrodeutopus hancocki)

Microdeutopus schmitti Shoemaker 1942 (see Paramicrodeutopus schmitti)

Microdeutopus trichopus Myers 1968 (see Paramicrodeutopus trichopus)

Paramicrodeutopus hancocki (Myers 1968) – Costa Rica to Ecuador: 0-18m

*Paramicrodeutopus schmitti (Shoemaker 1942) – Humboldt Bay, Northern California to Costa Rica:0-221m

Paramicrodeutopus trichopus (Myers 1968) — Galapagos Ids.: 0m Family Unciolidae

Subfamily Acuminodeutopinae

*Acuminodeutopus heteruropus J. L. Barnard 1959 – Seal Beach to Costa Rica: 1.3-59m

Acuminodeutopus periculosus J. L. Barnard 1969 – Gulf of California, Mexico: 0-38m

*Rudilemboides stenopropodus J. L. Barnard 1959 – Gaviota to Gulf of California, Mexico: 1-68m

*Rudilemboides sp A SCAMIT 1998§ - SCB to Bahia Todos Santos, Mexico: 12-196m

Subfamily Unciolinae

Neohela intermedia Coyle and Mueller 1981- Gulf of Alaska: depth?

Rildardanus tros J. L. Barnard 1969 – Bahia de Los Angeles, Gulf of California, Mexico: 9-16m

Zoedeutopus cinaloanus J. L. Barnard 1979 – Gulf of California, Mexico: 0-1m

Comments by Family

<u>Family Aoridae</u> – With six genera reported from the NEP, this is a well represented family in the region. Some of the species are relatively abundant, but for the most part NEP aorids are present sparingly over a broad range. Several unique endemic taxa are known from the subtropical portion of the region. Conlan and Bousfield (1982) provide a

key to the genera of the Aoridae then known from the region. This also includes members of the Unciolidae, which was still combined with the Aoridae at the time. While their key is generally serviceable, several changes have taken place which reduce effectiveness. The genus *Paramicrodeutopus* was erected to house some forms previously placed in *Microdeutopus*, and a valid *Microdeutopus* was reported as introduced to the region. *Bemlos* is not represented in their key, but for all purposes their *Lembos* can be interpreted as *Bemlos*. The key also does not include *Zoedeutopus*, which was considered extralimital to their treatment. A comprehensive key to the genera covered was presented earlier.

Description: "Head free, not coalesced with peraeonite 1; exposed; as long as deep, or longer than deep; anteroventral margin weakly recessed or moderately recessed or strongly recessed or concave or oblique, anteroventral margin deeply excavate or shallowly excavate or moderately excavate, anteroventral corner rounded or subquadrate or hooked; rostrum present or absent, short; eyes present, well developed or obsolescent, or absent; not coalesced; 1 pair; not bulging. Body laterally compressed, or subcylindrical; cuticle smooth.

Antenna 1 subequal to antenna 2, or longer than antenna 2; peduncle with sparse robust and slender setae; 3-articulate; peduncular article 1 shorter than article 2, or subequal to article 2, or longer than article 2; antenna 1 article 2 longer than article 3; peduncular articles 1-2 not geniculate; accessory flagellum present, or absent; antenna 1 callynophore absent. Antenna 2 present; short, or medium length, or long; articles not folded in zigzag fashion; without hook-like process; flagellum shorter than peduncle; less than 5-articulate, or 5 or more articulate; not clavate; calceoli absent.

Mouthparts well developed. Mandible incisor dentate; lacinia mobilis present on both sides; accessory setal row without distal tuft; molar present, small or medium, triturative; palp present or absent. Maxilla 1 present; inner plate present, strongly setose along medial margin or weakly setose apically; palp present, not clavate. Maxilla 2 inner plate present; outer plate present. Maxilliped inner and outer plates well developed or reduced, palps present, well developed or reduced; inner plates well developed, separate; outer plates present, large or small; palp 4-articulate, article 3 without rugosities. Labium smooth.

Peraeon. Peraeonites 1-7 separate; complete; sternal gills absent; pleurae absent.

Coxae 1-7 well developed or reduced, none fused with peraeonites. Coxae 1-4 longer than broad or as long as broad or broader than long, overlapping or discontiguous, coxa 1 anteroventrally acuminate or coxae not acuminate. Coxae 1-3 not successively smaller, none vestigial or coxa 1 reduced. Coxae 2-4 none immensely broadened.

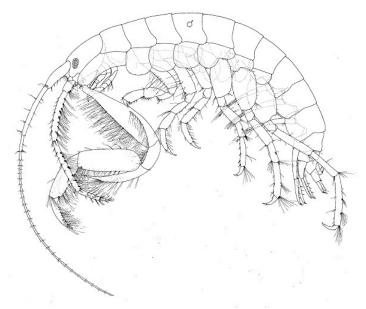
Gnathopod 1 sexually dimorphic, or not sexually dimorphic; smaller (or weaker) than gnathopod 2, or subequal to gnathopod 2, or larger (or stouter) than gnathopod 2; smaller than coxa 2, or subequal to coxa 2, or larger than coxa 2; gnathopod 1 merus and carpus not rotated; gnathopod 1 carpus/propodus not cantilevered; shorter than propodus, or subequal to propodus, or longer than propodus; gnathopod 1 strongly produced along posterior margin of propodus, or not produced along posterior margin of propodus; dactylus large. Gnathopod 2 sexually dimorphic, or not sexually dimorphic; simple, or subchelate,

or parachelate; coxa smaller than and mostly hidden by coxa 3, or subequal to but not hidden by coxa 3, or larger than coxa 3; ischium short; merus not fused along posterior margin of carpus or produced away from it; carpus/propodus not cantilevered, carpus short or elongate, shorter than propodus or subequal to propodus or longer than propodus, not produced along posterior margin of propodus.

Peraeopods heteropodous (3-4 directed posteriorly, 5-7 directed anteriorly) or heteropodous (3-5 directed posteriorly, 6-7 directed anteriorly), some or all prehensile or none prehensile. Peraeopod 3 well developed. Peraeopod 4 well developed. 3-4 with glandular basis; 3-7 without hooded dactyli, 3-7 propodi without distal spurs. Coxa well developed, longer than broad or as long as broad or broader than long; carpus shorter than propodus or subequal to propodus or longer than propodus, not produced; dactylus well developed. Coxa subequal to coxa 3, not acuminate, without posteroventral lobe; carpus not produced. Peraeopods 5-7 with few robust or slender setae; dactyli without slender or robust setae. Peraeopod 5 well developed; shorter than peraeopod 6; coxa subequal to coxa 4 or larger than coxa 4, with posterodorsal lobe or without posterior lobe; basis expanded or slightly expanded or linear, subrectangular or subquadrate, without posteroventral lobe; merus/carpus free; carpus linear; with a few subterminal setae or setae absent. Peraeopod 6 shorter than peraeopod 7, or subequal in length to peraeopod 7; merus/carpus free; dactylus without setae. Peraeopod 7 with 6-7 well developed articles; longer than peraeopod 5, or immensely elongate; similar in structure to peraeopod 6; with 7 articles; basis expanded or slightly expanded or linear, with long dense slender setae or without dense slender setae; dactylus with a few subterminal setae or without setae.

Pleon. Pleonites 1-3 without transverse dorsal serrations, without dorsal carina; with slender or robust dorsal setae, or without slender or robust dorsal setae. Epimera 1-3 present. Epimeron 1 well developed. Epimeron 2 setose, or without setae.

Urosome dorsoventrally flattened, or not dorsoventrally flattened; urosomites 1 to 3 free, or 1 free, 2 and 3 coalesced; urosomite 1 subequal to urosomite 2, or longer than urosomite 2, or much longer than urosomite 2; urosome urosomites not carinate; urosomites 1-2 without transverse dorsal serrations. Uropods 1-2 apices of rami with robust setae. Uropods 1-3 similar in structure and size. Uropod 1 peduncle without long plumose setae, with 1 or 2 basofacial robust setae or without basofacial robust seta, with ventromedial spur or without ventromedial spur. Uropod 2 well developed; with ventromedial spur or without ventromedial spur, without dorsal flange; inner ramus shorter than outer ramus, or subequal to outer ramus, or longer than outer ramus. Uropod 3 not sexually dimorphic; peduncle short or elongate; outer ramus shorter than peduncle or subequal to peduncle or longer than peduncle, 1-articulate or 2-articulate, without recurved spines. Telson thickened dorsoventrally; emarginate, or entire; longer than broad, or as long as broad, or broader than long; apical robust setae present, or absent." (Lowry and Springthorpe 2001).

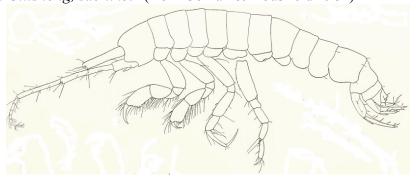


Aoroides intermedia, perhaps the most common aorid in southern California (from Conlan & Bousfield 1982)

Aoroides – A moderately sized genus of eighteen species (Lowry 2015a). centered in the North Pacific, but with a small austral flock as well (Myers 1995, 2009). There is a single provisional species known from the NEP. The animals are strongly sexually dimorphic, and males are more easily identifiable than females in most cases because of their enlarged and modified first gnathopods. Prior to 1982 only a single species was reported from the NEP, Aoroides columbiae of Walker (1898). Conlan and Bousfield (1982) reviewed this supposedly variable taxon and separated it into five species, also reporting *Aoroides secunda* (Gurjanova 1938) from the NEP... Ariyama (2004) reported even more species in the Northwest Pacific. There is also a tropical representative from Hawaii (J. L. Barnard 1970). While color patterns in live or freshly preserved material have had separatory value (Conlan & Bousfield 1982), these patterns are variable in expression, and unreliable in preserved material. The most stable of the colorations reported are the small black pigment dots found in several of the NEP taxa. Conlan & Bousfield (1982) provide a key to the described NEP species. The provisional Aoroides sp A can be differentiated from the other species by several characters presented in comparative character tables, which, along with the voucher sheet, are available on the SCAMIT website. Myers (1981) treated *Aoroides* as a synonym of *Aora*, but this has not been followed subsequently.

Diagnosis: "Body with a pair of short setae on the dorsum of pleon 3 and urosome 1. Sternal bump or process on segment 1. Head lobe medium, not bilobed. Coxal plates shallow, coxa 5 as deep as coxa 4. Cuticle not especially shiny. Antenna I, peduncle 1 lacking a ventrodistal spine; accessory flagellum minute, vestigial. Antenna 2, flagellum of 31/2, segments, first much longer, each segment distally spinose. Mandibular palp slender, cylindrical, segment 2 with 0-2 setae, segment 3 slightly longer, inner margin with 2-7 setae, no setae at base of palp. Maxilla 1 inner plate with 1 seta; outer plate with 10 teeth. Maxilla 2 inner plate much more slender than outer. Maxilliped inner plate teeth serrated, outer plate teeth serrated or smooth; palp segment 2 not extending beyond

the distal end of the outer plate; palp segment 3 with a distal protuberance, dactyl short. Gnathopods strongly sexually dimorphic. Male gnathopod 1 elongate, merochelate; coxa elongating with age to mask laterally the buccal mass; segment 2, anterior, lateral and in some species, posterior margin setose; segment 4 prolonged into a long distal tooth extending to the junction of segments 5 and 6; segment 5 shorter than 6, as broad as 5 in young but slendering with age; never a distal tooth; dactyl serrated in young, losing cusps, elongating and bearing dense marginal setae at maturity; all segments moderately to densely setose. Gnathopod 2, both sexes, subchelate; segment 2, anterior margin setose, posterior margin bare; segment 5 subequal to 6, not broadened distally, margin not densely setose; segment 6, margins not densely setose, palm transverse, obturator spine normal, dactyl overlapping the palm. Peraeopods 3 and 4 slender, segment 5 longer than segment 4 and barely tapered proximally. Peraeopods 5-7, hind margin of segment 2 with or without long setae, lower hind corner marked by a long slender spine; dactyls barely differing in length. Peraeopods 5 and 6, segment 5 with 2 groups of spines. Peraeopod 7, segment 2 slender or moderately expanded. Epimera 1-3, hind corner notched, lateral ridge lacking; lower margin of epimeron 2 bare. Uropod spines slender; peduncular process of uropods 1 and 2 about I/, the length of the longer ramus. Uropod 3 rami with or without lateral spines, both rami terminally setose, outer more so than inner. Outer ramus 2-segmented, distal segment minute. Telson with a few setae at the apical cusps. Gills long, sac-like." (from Conlan & Bousfield 1982)



Bemlos edentulus (from J. L. Barnard 1967)

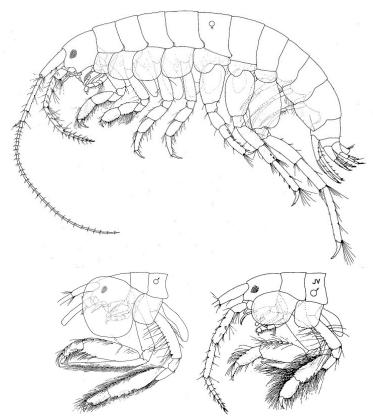
Bemlos – A very large genus of 71 taxa (Lowry 2015c) distributed worldwide in warmer waters but with representatives in cooler boreal and antiboreal waters (J. L. Barnard & Karaman 1991). For years after its creation *Bemlos* was viewed as a synonym of *Lembos* (i.e. J. L. Barnard 1969b), but it was reinstated based on cladistic analysis (Myers 1988a). Most members are shallow-water algal associates, but some deep dwelling taxa are also placed within the genus (such as *Bemlos edentulus* from midbathyal depths in the NEP). That species and five other described forms are known from the NEP. No provisionals are yet reported from the region. J. L. Barnard (1979) provides a key to males of all regional species (as *Lembos*) except *B. edentulus*. A key to the NEP members of the genus is provided below:

Key to NEP Bemlos (both sexes unless otherwise stated) - dbcadien 14May 2015

1.	Lacking eyes, or ocular pigment	B. edentulus
	With pigmented eyes	2
2.	Anterior head lobe truncate, straight	
	Anterior head lobe rounded	5
3.	Telson posterior margin concave	B. macromanus
	Telson posterior margin convex or undescribed	4
4.	Coxa 1 & 2 in male bearing long dense ventral setae	B. tehuecos*
	Coxa 1 & 2 in male bearing short sparse setae ventrally	B. achire*
5.	Epimera 1-3 bearing oblique ridge laterally	B. concavus
	Epimera 1-3 lacking oblique ridge laterally	B. audbettius

^{*=} females of these two species cannot be reliably separated

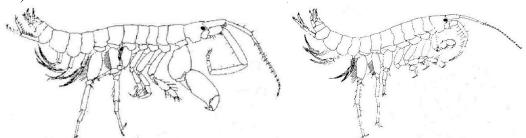
Diagnosis: "Mandible palp article 2 usually less than two thirds length of article 3, weakly setiferous, article 3 generally not markedly falcate, posterior margin with setae of 2 distinct lengths, left molar with well-developed plates, rounded or with primary plate falcate. Maxilla 1 outer plate with 10 spines. Maxilliped without flanges. Male pereon generally with sternal processes. Gnathopod 1 always sexually dimorphic. Gnathopod 2 of similar size in both sexes but sometimes sexually dimorphic. Pereopods 5 and 6 propodus posterior margin with several spines. Uropod 3 rami weakly spinous with very long terminal setae outer ramus with small second article." (from Myers 1988b)



Columbaora cyclocoxa female, male and juvenile male (from Conlan & Bousfield 1982)

Columbaora – A NEP endemic monotypic genus with a unique apomorphy in the male coxa 1. As males mature through several molts the first coxa enlarges, in the end becoming a large oval which covers the eye laterally. This change is accompanied by elongation of the meral protuberance until the terminal male is merochelate. Females undergo no such developmental change, and are most easily separated from females of *Aoroides* species by the accessory flagellum.

Diagnosis: "Body with a pair of short setae on the dorsum of urosome 1. Segment 1 with a sternal hump or process. Head lobe strongly produced in the male, not bilobed. Coxal plates moderately deep, coxa 5 shallower than coxa 4. Antenna 1 accessory flagellum multi-segmented. Antenna 2 flagellum 6-7 segments, lower 3 segments distally spinose. Mandibular palp strong, falcate. Maxilla 1 inner plate with 1 setae; outer plate with 10 teeth. Maxilla 2 inner plate nearly as broad as outer. Maxilliped palp segment 2 not extending beyond the distal end of the outer plate; segment 3 with a distal protuberance, dactyl short. Gnathopods strongly sexually dimorphic. Male gnathopod 1 elongate, merochelate; segment 4 extending the full length of segments 5 and 6 together. Gnathopod 2, both sexes, subchelate, palm oblique, obturator spine small; segment 5 longer than 6, in the male becoming greatly elongate and densely setose. Peraeopods 3 and 4 slender, segment 5 slightly shorter than segment 4 and tapered proximally. Peraeopods 5-7, hind margin of segment 2 without long setae, lower hind corner not spinose, dactyls barely differing in length. Peraeopods 5 and 6, segment 5 with 3 groups of spines. Peraeopod 7, segment 2 with a broad hind lobe. Epimera 1-3, hind corner notched; lateral ridge present; lower margin of epimeron 2 setose. Uropod spines moderately strong; peduncular process of uropods 1 and 2 long, more than half the length of the longest ramus. Uropod 3 both rami spinose and terminally setose. Telson with a few setae at the apical cusps. Gills long, sac-like." (from Conlan & Bousfield 1982)



Grandidierella japonica male (left) and female (right) (from Chapman & Dorman 1975)

Grandidierella – Two species in this genus are known from the NEP, although the genus is much more speciose worldwide (43 valid taxa – Lowry 2015d). All members of the genus are shallow shelf forms, none occurring deeper than 80m (J. L. Barnard & Karaman 1991). A number of these are normally encountered in brackish or even freshwater habitats. Of the two species known from the study area, one is native (*G. nottoni* from west Mexico) and one introduced (*G. japonica*). Chapman & Dorman (1975) suggest that the introduction of this species into California waters took place well before the first collection in 1966. They suspect that the introduction was effected with transplant of oysters from Japan, an effort that began in 1928 and continues. Although most recorded collections in the NEP are from areas of reduced salinity, the species is

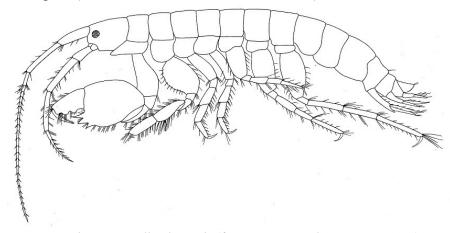
also taken in fully saline embayments. It was very common in portions of Newport Bay, with large colonies forming dense incrustations on the intertidal muds of Balboa Island. These were of closely approximated, mostly vertical tubes (Cadien, pers. obs.). Stephensen (1938) reported "stridulating organs" in males of this species. These are formed by ridges on the dorsal lobe of the carpus, which can be rubbed against the basis. Chapman & Dorman (1975) noted individual males wandering in aquaria to rapidly scrape these ridges against the sharp anterior edge of the basis. The result of such action is uncertain, but could produce a pressure wave sensible to others of the species. They did not indicate that any vibration so produced could be detected outside the aquarium. No others in the genus have been suggested to have such specialization.

Diagnosis: "Body subcylindrical, slightly depressed, smooth, urosomites free, 1 ordinary. Rostrum short, ocular lobes short, blunt; antennal sinus weak. Eyes small to medium. Antennae elongate, 1 slender, antenna 2 weakly stout; peduncular article 3 of antenna 1 much shorter than 1, article 2 slightly longest, accessory flagellum 1.25-articulate. Antenna 2 peduncular article 3 scarcely elongate, peduncle slightly stout in male, flagellum much shorter than article 5 of peduncle, with 4-13 articles. Epistome unproduced anteriorly. Labrum subrounded, entire or weakly incised. Mandible normal, palp weak, very slender, article 1 elongate (or short, thus variable), article 3 rectolinear or clavate, scarcely longer, often shorter than 2. Labium with entire outer lobes, with well-developed inner lobes, mandibular lobes long, pointed. Inner plate of maxilla 1 vestigial, without setae, outer plate with 10-11 spines, palp 2-articulate. Plates of maxilla 2 ordinary, inner plate with mediofacial row of setae. Inner plate of maxilliped with distal spines, outer plate normal, not reaching apex of palp article 2, with thin spines only on medial margin, palp with 4 articles, article 2 long, article 3 unlobed, article 4 very short, with short nail and setae.

Coxae very small, relatively short, mostly contiguous in type, discontiguous in other species, of various sizes and shapes, progressively shorter from 1 or 2 to 4, coxa 1 not dilated, not produced forward, or rarely with angular cusp, coxa. 2 smaller or larger than 1, coxa 4 shorter than coxa 1, not lobed, coxa 5 usually longer than 4, coxa 7 much smaller than anterior coxae. Gnathopods 1-2 diverse, both with sublinear articles, often densely setose, gnathopod 1 greatly larger than 2, in male simple or with false palmar boss, carpochelate, article 4 enlarged, inflated, incipiently merochelate, extended and fused distally along posterior margin of article 5, article 5 long, thick, lobed, article 6 short, very narrow, dactyl large. Gnathopod 2 subchelate, feeble, palm transverse (type), linear, with article 4 slightly inflated and setose, article 5 longer than 6, unlobed, article 6 more slender than 5, dactyl ordinary.

Pereopods 3-4 normal, similar, with slender article 2, article 4 scarcely dilated, dactyls long. Pereopods 5-7 similar to each other, progressively longer, with almost linear, heavily setose article 2, pereopod 5 much shorter than pereopod 7, article 2 less setose, dactyl of pereopods 5-7 medium to long, curved. Sternal processes of thorax often present. Coxal gills [undescribed]. Pleopods with short peduncle, longer than broad, outer ramus shortened. Epimeron 3 not bisinuate. Uropods 1-2 biramous, normal, rami slightly unequal, longer than peduncle, peduncle with ventrodistal process, that of uropod 2 (rarely 1) smaller or obsolescent. Uropod 3 of medium length, uniramous, single ramus long, I-articulate, obtuse distally, narrow, tapering and with few armaments mostly apical, often with vestigial article 2, peduncle shorter than rami, very short,

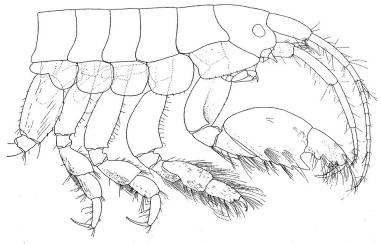
dilated medially. Telson entire, short, broader than long, pentagonal or trapezoidal, with 2 hooked apical cusps." (from J. L. Barnard & Karaman 1991)



Microdeutopus gryllotalpa male (from J. L. Barnard & Karaman 1991)

Microdeutopus – Although all members of the genus *Paramicrodeutopus* were originally placed in *Microdeutopus*, no NEP endemic species remain there. The only *Microdeutopus* known from the region is the introduced *M. gryllotalpa* from the Mediterranean/North Atlantic. According to Chapman (2007) this species has been detected in Humboldt Bay since 1980 (see Boyd et al 2002). The genus currently contains a dozen species considered valid with many earlier attributions either synonymized or transferred into genera introduced by Myers in his revision of the Aorinae (1988a). *Microdeutopus gryllotalpa* can be recognized among NEP aorids by the characters of the key to genera.

Diagnosis: "Mandibular palp article 3 longer than article 2, posterior margin distally concave, proximally straight; left mandibular molar with complex plates, primary plate triangular, the posterior margins straight or weakly convex, secondary, tertiary, and quaternary plates of similar shape; maxilliped anterior margin with or without wing-like flanges; male gnathopod 1 carpochelate, carpus much larger than propodus; uropod 3 peduncle elongate, not markedly expanded, rami relatively short with marginal spines, hut no marginal setae, outer ramus with small second article." (from Myers 1988a)



Paramicrodeutopus schmitti; anterior of male (from Shoemaker 1942)

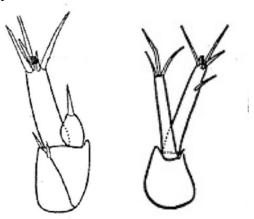
Paramicrodeutopus - Created by Myers in his revision of the subfamily (1988a), the genus still consists of the four species originally placed there. Three of these are NEP distributed (Myers 1968), and the fourth (a likely cognate) is from the southwest Atlantic (Bynum & Fox 1977). Only one of the NEP forms reaches into the Californian province, the others being Panamic. Myers (1969) provides a key to the three NEP species (as *Microdeutopus*) as part of his key to male *Microdeutopus* of the world. Males of these three species can be distinguished using characters in couplets 10-12, which also include *Microdeutopus gryllotalpa* conveniently.

Mandibular palp articles longer than article 2, posterior margin distally concave, proximally straight; left mandibular molar with complex plates, primary plate triangular or sub-triangular, secondary plate reduced or absent, tertiary and quaternary plates missing; maxilliped without wing-like flanges on anterior margin; male gnathopod 1 carpochelate, carpus larger than propodus; uropod 3 peduncle shortened, a little expanded, rami with spines but no marginal setae, outer ramus with small second article." (from Myers 1988a)

Family Unciolidae – Five unciolid genera are reported to occur in the NEP, in two different subfamilies. The Acuminodeutopinae contains the regional genera *Acuminodeutopus* and *Rudilemboides*, while the Unciolinae contains the genera *Neohela*, *Rildardanus*, and *Zoedeutopus*. Most of these genera are shallow living, the exception being *Neohela*, which frequents bathyal depths. Myers (1981) treated *Acuminodeutopus* and *Rudilemboides* as synonyms, but this has not been followed by subsequent workers, including Myers himself (Myers & Lowry 2003).

Diagnosis: "Head anteroventral margin moderately excavate, or strongly excavate for reception of enlarged antenna 2. Pereopod 7 not very elongate, entire propodus not extending beyond pereopod 6." (Myers and Lowry 2003).

Subfamily Acuminodeutopinae

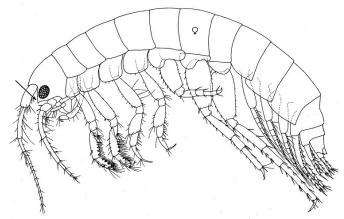


Although *Acuminodeutopus* and *Rudilemboides* are similar, their 3rd uropods differ. *Acuminodeutopus heteruropus* (left) and *Rudilemboides stenopropodus* (right) (from J. L. Barnard & Reish 1959)

Acuminodeutopus – A NEP endemic genus with two members, *A. heteruropus* from the SCB, and *A. periculosus* from the Gulf of California. The two are very closely

related, differing in some details of proportion and setal placement. The most obvious difference is the presence of an additional tooth on the carpochelate G1 "palm" formed by article 5 in the male.

Diagnosis: "Lateral lobes of head acutely produced; accessory flagellum short; gnathopod 1 in male with a large distal tooth on article 5 (complexly chelate); outer ramus of uropod 3 longer than peduncle, inner ramus quite short; article 6 of male gnathopod 1 much narrower and shorter than article 5." (from J. L. Barnard & Reish 1959)



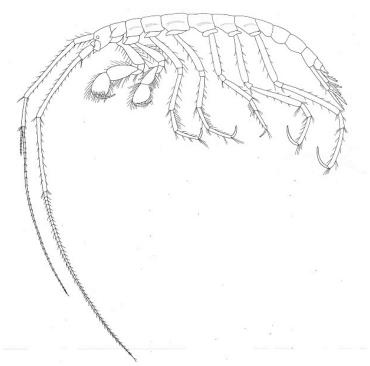
Rudilemboides naglei from the Northwest Atlantic. Arrow indicates acute eyelobe (from Bousfield 1973)

Rudilemboides – A genus of only two described species, *R. naglei* from the Western Atlantic, and *R. stenopropodus* from the NEP. A third provisional member, *Rudilemboides* sp A, is known from the SCB. All are relatively shallow living, none extending beyond shelf depths. The two NEP representatives can be separated by characters listed in the voucher sheet for the provisional on the SCAMIT website.

Diagnosis: "Antenna 1, accessory flagellum as long as peduncular article 3; article 4 of male gnathopod 1 small, not produced, article 5 much larger than 6, not produced, article 6 rectangular, elongate, scarcely subchelate; mandible, palp article 3 blunt; gnathopod 2 scarcely subchelate; uropod 3, rami much longer than peduncle" (from J. L. Barnard & Reish 1959).

Subfamily Unciolinae

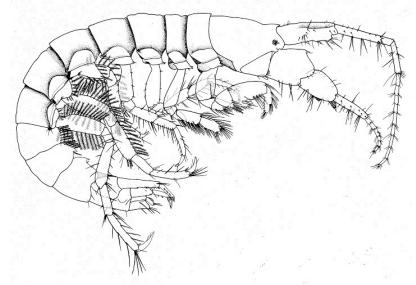
Neohela – The genus, containing five species (Lowry 2015b), is predominantly Arctic/sub-Arctic and deep water. McLaughlin et al (2005) have a questionable report of *N. pacifica* as occurring in the NEP. This remains unconfirmed, and based on available records the species is presumed restricted to the NWP. *Neohela monstrosa* is reported from various portions of the Arctic, but does not occur in the NEP study area. The sole local representative is *N. intermedia* (Coyle & Muller 1981) from the Gulf of Alaska. Udekem d'Acoz (2007) recently considered the genus, describing a new species.



Neohela monstrosa (from J. L. Barnard & Karaman 1991)

Diagnosis: "Body cylindrical, depressed, provided with humps, urosomites 1-2 free, 1 slightly elongated, 3 coalesced with telson. Rostrum short, ocular lobes short, pointed, antennal sinus weak to moderate., Eyes absent. Antennae hugely elongate, 1 shorter than 2, both slender, peduncular article 3 of antenna as long as 1, article 2 greatly longest, accessory flagellum pluriarticulate. Antenna 2 peduncular article 3 scarcely elongate, flagellum greatly elongate. Epistome unproduced anteriorly. Labrum subrounded, incised. Mandible normal, palp strong, very slender, article 3 rectolinear or tapering, scarcely shorter. than 2. Labium with entire outer lobes, with well-developed inner lobes, mandibular lobes short, blunt. Inner plate of maxilla 1 linguiform, with 1. facial seta and 3 apical setae, outer plate with 9 spines, palp 2-articulate. Inner plates of maxilla 2 shortened, with only mediomarginal setae. Inner plate of maxilliped with distal spines, outer normal, not reaching apex of palp article 2, with spines on medial margin, palp with 4 articles, article 2 long, article 3 unlobed, article 4 very long, with medium nail and setae. Coxae very small, short, discontiguous, of various sizes and shapes, progressively shorter from 2 to 4, spiniform, coxa 1 not dilated, produced forward, coxa 2 larger than 1, coxa 4 not longer. than coxa 1, not lobed, coxa 5 somewhat longer than 4, coxae 6-7 not much smaller than anterior coxae. Gnathopods 1-2 alike, of subequal size, medium, densely setose, gnathopod 1 scarcely larger than 2, subchelate, article 5 unlobed, palm short and subtransverse, article 5 of both gnathopods as long as 6, article 6 large, palm sculptured in male, dactyl long. Pereopods 3-4 longer than gnathopods, similar, very elongate, with slender article 2, article 4 not dilated, dactyIs short. .Pereopods 5-7 similar to each other, progressively .longer, with linear article 2, pereopod 5 much shorter than pereopod 7, dactyl of pereopod 5 short, of 6-7 elongate, curved. .Sternal processes of thorax absent. Coxal gills moderately broad, present on segments 2-6. Pleopods normal. Epimeron 3 not bisinuate. Uropods 1-2 biramous,

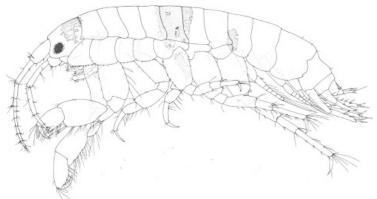
normal, rami slightly unequal, shorter (1) or as long (2) as peduncle, peduncle without ventrodistal process, peduncular and ramal spines very conspicuous. Uropod 3 small, uniramous, single ramus long, pointed distally, peduncle shorter than ramus, not dilated medially, I-articulate, narrow, tapering and with few armaments. Telson entire, fused to urosomite 3, longer than broad, triangular, blunt apically, poorly armed." (from J. L. Barnard & Karaman 1991)



Rildardanus tros (from J. L. Barnard 1969a)

Rildardanus – A monotypic endemic genus in the NEP. J. L. Bernard mentions in his original description (1969a) the similarities to *Corophium* in the second antennae and body, but stresses that the mouthparts preclude placement there. Myers (1981) placed Pearse' species *Unciola laminosum* in *Rildardanus*, but it is currently viewed as being a member of the genus *Pedicorophium* (Lowry 2015e)

Diagnosis: "Antenna 2 strongly ornamented; mandibular palp 3 -articulate; inner plates of maxillipeds broad, flat; gnathopod 1 in male much larger than 2, both pairs subchelate; accessory flagellum uniarticulate, vestigial; inner rami of both uropods 1 and 2 scale-like, vestigial; uropod 3 composed only of a setose peduncle; telson a large subcircular. simple flap." (from J. L. Barnard 1969a)



Zoedeutopus cinaloanus (from J. L. Barnard 1979)

Zoedeutopus – A monotypic NEP endemic genus, known only from sites in the Gulf of California (Garcia Madrigal 2007). It is close to *Acuminodeutopus* and *Rudilemboides*, differing in details of the mandibular palp, uropods, and the anterior head lobe. The genus is also reminiscent of *Microdeutopus*.

Diagnosis: "Lateral cephalic lobes strongly produced, antenna 2 deeply inserted along ventral cephalic margin. Mandibular palp articles 2 and 3 subequal in length to each other, article 3 linear, setose apically, article 1 more than half as long as articles 2-3. Mandibular lobes of lower lip subacute. Inner plate of maxilla 1 broadly expanded, apically rounded, bearing 2 facial setae. Gnathopod 1 larger than gnathopod 2 in female, in male enlarged and of Microdeutopus-form, carpochelate, article 6 shorter and narrower than article 5, gnathopod 2 in male also enlarged and larger than gnathopod 1, weakly carpochelate, article 6 shorter and narrower than article 5, chelate. Rami of uropod 3 subequally long but inner distinctly shorter than outer, latter with distinct article 2. Telson ordinary." (from J. L. Barnard 1979)

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