Melphidippoidea of the NEP (Equator to Aleutians, intertidal to abyss): a review
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Introduction to the Melphidippoidea

Bousfield (1977) proposed the superfamily, based around Stebbings family Melphidippidae. He included that family and two informal family groups which are now recognized as the Hornelliidae and the Megaluropidae. The composition of the superfamily has not changed since except for the addition of the Phreatogammaridae by Bousfield in 1982. While he considered this family of somewhat uncertain affinities, he felt that it was most probably melphidippoid. It is, however, atypical for the group in being brackish to freshwater, with some hypogean members. J. L. Barnard and Karaman (1991) suggest that the Iciliidae and the Maxillipidae have melphidippoid affinities, but their placement remains in dispute, and they are not here treated as members of the superfamily. Both are from western Pacific waters. Bousfield characterizes the superfamily as "marine coastal and shelf, epibenthic and pelagic, mainly in tropical and temperate continental regions" (Bousfield 1979).

Diagnosis of the Melphidippoidea

"Apomorphic, rostrate, abdominally processiferous marine gammaroideans, usually with pelagic terminal male stage; brush setae on elongate peduncle of antennae 1 and 2; calceoli lacking; accessory flagellum present, variable; eyes reniform, lateral; mouthparts more or less basic; upper lip slightly notched distally; lower lip, inner lobes variously developed; mandibular molar strong, palp slender; inner plates of maxillae normally setose, outer plate of maxilla 1 with 9 spine teeth; maxilliped plates strong, inner margin of outer plate with strong spine-teeth, palp somewhat reduced; coxal plates shallow (Deep in fossorial forms), 4th weakly excavate; coxae 5-7 anteriorly lobate; gnathopods 1 and 2 weakly excavate; coxae 5-7 anteriorly lobate; gnathopods 1 and 2 weakly amplexing (Strongly so where terminal pelagic male lacking), dissimilar, subcheate or simple; peraeopods 5-7 heteropodous, basis variously expanded; brook plates linear; coxal gills simple, lacking on peraeopod 7; pleopods normal; uropods langeolate, rami of 2 unequal, tips spinose; uropod 3 peduncle elongate, rami weakly foliaceous, outer ramus 1-segmented or minutely 2-segmented; telson lobes distally separated, apices with broad notch and spine(s)." (Bousfield 1979)

Ecological Commentary

Melphidippoids, with their elaborate spination and elongate slender legs, are at least partially epifaunal. For several studied forms normal orientation is upside down in a sling created by the elongate pereopods 5-7. These are held reflexed over the dorsum (below it in life configuration), forming a suspensory cradle within which the animal lays (Enequist 1950). Feeding was observed to be largely passive suspension feeding, with particle capture by the second antennae, and the 3rd and 4th legs. Collected particulates from these appendages are combed free by the gnathopods, and then passed to the mouthparts for maceration and ingestion (Enequist 1950). Enequist also observed larger organic particles encountered by the posterior reflexed legs being tossed into the water column to be captured by the antennae and legs, but suspected that this was an unnatural action not or seldom required in natural situations. Water movement created by pleopod ventilatory motion apparently played no part in feeding. His observations were of species of *Melphidippa* and *Melphidippella* from northern Europe. Similar posture is apparently adopted by some melphidippids in southern waters (De Broyer et al 2001, and see photo above), although one member of an undescribed melphidippoid genus was observed to walk upright on the sediment surface. This form was judged to be a macrophagous deposit feeder, rather than a passive suspension feeder such as *Melphidippa antarctica* or the forms observed by Enequist (1950). While melphidippids live on soft bottoms, the posession of fully prehensile pereopods in one species suggests that their habitus may be on either another organism itself, or on a biogenic structure built by another organism (Udekem d'Acoz 2006). In forms lacking prehensile pereopods, this is not likely, but is probably the case for the species mentioned above. Prehensility in melphidippoids is very atypical, and violates the family description of Lowry and Springthorpe (2001) which stipulates that no pereopods are prehensile.

Melphidippa antarctica assuming the epibenthic "cradle" position (Photo © Gauthier Chapelle, IRSNB)

In the megaluropid genera *Gibberosus* and *Resupinus* a similar upside down position is adopted, but the animals are at least partially buried while in it (J. L. Barnard, Thomas and Sandved 1989). In these animals the U shape adopted by the melphidippids observed by Enequist was modified by anterior extension of the urosome until it nearly contacted the mouthparts. Ths small gap left apparently serves as a particle trap for organic particles moved by bottom currents. Both suspended and saltatory particles fall into the dead space in front of the mouthparts. The buried animals are capable of slow lateral motions within the unconsolidated sandy bottoms on which they live. J. L. Barnard et al also observed that the configuration of the coxae in these animals allowed the anterior legs to be raised above (or extended below in life position) the main body of the amphipod (see whole body figure of *Resupinus spinicaudatus* in Thomas and J. L.

Barnard 1986, figure 2). This would allow access to the surrounding sediments and might provide an additional source of organic detrital particles for the animals nutrition.

Both swimming and burial in these animals was extremely fast, virtually invisible in real time, but visible in video tape recordings. *Gibberosus* used its chromatophores to mimic the coloration of the bottom sands while on the bottom. The chromatophores were contracted while swimming, making the animal nearly glass-clear. On the bottom the white chromatophores joined pink and purple pigment spots on the exoskelton to provide excellent camouflage against a bottom of white coraligenous sands speckled with colored foraminiferan tests.

Megaluropids are often caught in light traps suspended over sandy bottoms at night. Whether this reflects attraction or only random catch from a large swimming population is not known. It is possible that the burial activities observed for *Gibberosus* in Florida (J. L. Barnard et al 1989) reflect attempts to escape from visual predators during daylight periods. Perhaps at night much of the population emerges, frequently swimming, to feed on the surface. The presence of pronounced efforts at camouflage would tend to support an expectation of significant visual predation pressure on the population. Large eyes in both male and female megaluropids and melphidippids also support the liklihood of a well-developed visual system, which in these suspension feeding animals could only serve as predator (or perhaps mate) detection.

Ecological information available on hornelliids is scant. Thomas and J. L. Barnard (1991), however, illustrate a new species of *Metaceradocus* from Florida in a posture similar to that for the megaluropid genus *Gibberosus*, and suspect that the behavior and life position of the species is similar to that of melphidippids and megaluropids. The cheirocratids, which are viewed as closely related to the hornelliids by J. L. Barnard and C. M. Barnard (1983), are here considered to be in the family Hornelliidae. Information on several members of this group is available. The upside down cradle posture of most other melphidippoids seems not to be used by the cheirocratids (based on observations reported by Krapp-Schickel and Vader (2002). Enequist (1950) reports that the feeding of *Cheirocratus sundevalli* is like that of some melitoids, and involves surface excavation of the sediments followed by sediment resuspension by vigorous pleopod beating and gnathopod seiving of the suspensate. The burrowing behavior of another cheirocratid, *Casco bigelowi* from the northwest Atlantic, is also similar to that of some melitoids, involving construction of relatively deep burrows for both feeding and protection (Thiel et al 1997). Within these the animals confer extended parental care on their young, who remain in the adult burrow well past the manca stage.

Key to NEP Melphidippoid genera (modified from J. L. Barnard and C. M. Barnard 1983, and Thomas and J. L. Barnard 1986) - dbcadien 17 Sept 2007

1. Rami of uropod 3 flabellate.................... (Megaluropidae).............................2
Rami of uropod 3 lanceolate...4
2. Merus of gnathopod 2 strongly lobate distally................................*Gibberosus*
Merus of gnathopod 2 not strongly lobate..3
3. Uropod 1 peduncle with interramal spine.......................Megaluropidae n. gen.
Uropod 1 peduncle lacking interramal spine....................................*Resupinus*

4. Peduncle of uropod 3 shorter than peduncle of uropod 1....................*Hornellia*
   Peduncle of uropod 3 longer than peduncle of uropod 1..................................5
5. Accessory flagellum long, 2+articulate..*Melphidippa*
   Accessory flagellum short, 1 articulate...6
6. Telson cleft...*Melphidipella*
   Telson entire or emarginate..*Melphisana*

NEP Melphidippoidea from McLaughlin et al. (2005) augmented by known provisionals *= Taxa on SCAMIT Ed. 5 list. Valid species **bolded**, synonyms not.

Family Melphidippidae
- Atylus macer Norman 1869 (see Melphidippella macra)
- **Melphidippella macra** (Norman 1869) – North Atlantic, NWP, boreal NEP;10-200m
- **Melphidippa amorita** J. L. Barnard 1966 – Santa Maria Basin, Central California to Tanner Canyon; 299-496m
- **Melphidippa borealis** Boeck 1870 – North Atlantic, Japan, to Santa Maria Basin, Central California; 32-360m
- *__Melphisana bola__ J. L. Barnard 1962 – Santa Maria Basin, central California to San Cristobal Bay, Baja California; 12-130m

Family Hornelliidae
- *__Hornellia occidentalis (__J. L. Barnard 1959) – Pt. Conception, California, to Ensenada, Baja California; 2-31m
- Metaceradocus occidentalis J. L. Barnard 1959 (see Hornellia occidentalis)

Family Megaluropidae
- *__Gibberosus devaneyi__ Thomas and J. L. Barnard 1986 – Santa Cruz Id., California to Peru; 0-18m
- **Gibberosus falciformis** (J. L. Barnard 1969) – Bahia de Los Angeles, Gulf of California; 2m
- *__Gibberosus myersi__ (McKinney 1980) – Tropical West Atlantic, NEP from British Columbia to Peru; 0-29m
- *__Megaluropidae genus A sp A__ Paquette 1989§ - Oceanside California to Bahia de San Cristobal, Baja California; 50-98m
- Megaluropus agilis report of J. L. Barnard 1963 (see Resupinus coloni and/or Megaluropidae genus A sp A)
- Megaluropus longimerus record of J. L. Barnard 1962 (see Gibberosus myersi)
- Megaluropus longimerus falciformis J. L. Barnard 1969 (see Gibberosus falciformis
- Megaluropus visendus J. L. Barnard 1969 (see Resupinus visendus)
- **Resupinus coloni** Thomas and J. L. Barnard 1986 – Bahia San Cristoba, Baja California to Culebra Id., Panama; 0-9m
- **Resupinus visendus** (J. L. Barnard 1969) Bahia de Los Angeles, Gulf of California to Pacific Panama; 0-17m

Family Phreatogammaridae – no representatives in the NEP

Comments by Family

Family Melphidippidae – Description:" **Head** free, not coalesced with peraeonite 1; exposed; as long as deep; rostrum present, short; eyes present, well developed or obsolescent; not coalesced; 1 pair; bulging, or not bulging. Body laterally compressed, or subcylindrical; cuticle smooth, or processiferous and dorsally carinate.

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; antenna 1 article 2 longer than article 3; peduncular articles 1-2 not geniculate; accessory flagellum present; antenna 1 callynophore absent. **Antenna 2** present; ***long***; articles not folded in zigzag fashion; without hook-like process; flagellum shorter than peduncle; 5 or more articulate; not clavate; *calceoli* absent.

Mouthparts well developed. *Mandible* incisor dentate; accessory setal row without distal tuft; molar present, medium, triturative; palp present. *Maxilla 1* present; inner plate present, strongly setose along medial margin; palp present, not clavate, 2 - articulate. *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, 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, none fused with peraeonites. *Coxae 1-4* broader than long, overlapping, coxae not acuminate. *Coxae 1-3* not successively smaller, none vestigial. *Coxae 2-4* none immensely broadened.

Gnathopod 1 sexually dimorphic; smaller (or weaker) than gnathopod 2, or subequal to gnathopod 2; subequal to coxa 2; gnathopod 1 merus and carpus not rotated; gnathopod 1 carpus/propodus not cantilevered; longer than propodus; gnathopod 1 not produced along posterior margin of propodus; dactylus large. *Gnathopod 2* sexually dimorphic; simple, or subchelate; coxa subequal to but not hidden by coxa 3; ischium short, or elongate; merus not fused along posterior margin of carpus or produced away from it; carpus/propodus not cantilevered, carpus elongate, subequal to propodus, not produced along posterior margin of propodus.

Peraeopods heteropodous (3-4 directed posteriorly, 5-7 directed anteriorly), none prehensile. *Peraeopod 3* well developed. *Peraeopod 4* well developed. 3-4 not glandular; 3-7 without hooded dactyli, 3-7 propodi without distal spurs. Coxa well developed, broader than long; carpus 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; subequal in length to peraeopod 6; coxa subequal to coxa 4, without posterior lobe; basis linear, subrectangular, with posteroventral lobe; merus/carpus free; carpus linear; 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; subequal to peraeopod 5, or longer than peraeopod 5; similar in structure to peraeopod 6; with 7 articles; basis linear, without dense slender setae; dactylus without setae.

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

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

NEP melphidippid species typically have bulging eyes that are like hemispheres projecting from the side of the cephalon. This is particularly evident in *Melphisana bola*, the most usually encountered coastal form. In this respect (and no others) they resemble some species of dulichiids. Legs are slender and appear fragile in these forms, and are frequently broken off distally. Antennae are likewise frequently not present on collected specimens. Several NEP melphidippids are described and discussed in Thomas and McCann (1995), who provide a key to three of the four species reported from the region. Their key would, however, need considerable modification to include the fourth species. I suggest that the generic key provided above would suffice, with the two species of *Melphidippa* known from the region separated as described below under that genus.

Melphidippella – A single species in the genus is known from the NEP, *Melphidippella macra*. The species is well illustrated and described in Lincoln (1979). He indicates in his discussion that there is a second species in the genus from Japan, but I can find no record of such a species. J. L. Barnard and C. M. Barnard (1983) list only the type species in the genus. The genus is separated from other members of the family by the structure of the mandibular palp and the accessory flagellum.

Melphidippa – Two species are known from the NEP, *Melphidippa borealis* and *Melphidippa amorita*. The former is a widely distributed boreal form also known from the Atlantic and northwest Pacific. The two can easily be distinguished by the strong posterior serration of the pleonal epimera in *amorita*, lacking in *borealis*, and by the structure of the telson. This is deeply and simply cleft in *M. borealis*, and very shallowly and widely cleft in *M. amorita*. The original description of *M. amorita* is in J. L. Barnard 1966, and *M. borealis* is described and illustrated in Thomas and McCann 1995. Sars (1895, plt. 170.) provides a full body illustration of the species, and additional detail not provided by Thomas and McCann.

Melphisana – Although only a single species is known from the NEP, *M. bola*, there is considerable variability in the telson of the animal. This was sufficient to make separation based on the telson difficult in comparisons with *Melphidippa amorita*, and led to the adoption of a complex designation by SCAMIT in the past. This is no longer used, although the full extent of the variation in *M. bola* remains unresolved. The genus has two species, one on either side of the North Pacific. The original description of *M. bola* by J. L. Barnard (1962) was reprised by Thomas and McCann (1995, pg. 43). Comments by J. L. Barnard and C. M. Barnard (1983) suggest that *Melphisana* is derived from *Melphidippa*, with *M. amorita* a transitional form connecting the two. This partially explains the difficulties and uncertainties in comparison of telsons in *Melphidippa amorita* and *Melphisana bola* locally.

Family Hornelliidae – Description of the hornelliid group:"Peduncle of uropod 3 only weakly elongate; pleonites with transverse serrations dorsally or dorsolaterally; anterior coxae ordinary; hands of one or more gnathopods with weak palm or palms bulging; article 2 of pereopods 5-7 lacking posteroventral lobes; plates of maxilla 2 medially setose; telson cleft more than halfway; outer ramus of uropod 2 shortened." (J. L. Barnard and C. M. Barnard 1983).

Hornellia – A single species in the genus is known from the NEP, *Hornellia occidentalis* (J. L. Barnard 1959). This was originally described as *Metaceradocus occidentalis*, but the two genera have more recently been considered as subgenera of *Hornellia* (Thomas and J. L. Barnard 1986b) although differing in the number of articles in the outer ramus of the third uropod. McLaughlin et al (2005) list them, along with other hornelliids within the family Melphidippidae, but they are separated here, with Hornelliidae recognized as valid. Should the character of the third uropod segmentation be reevaluated as sufficient to validate *Metaceradocus* as a full genus, the NEP species would return to that genus. It can be separated from other members of the genus using the key provided by Thomas and J. L. Barnard (1986b, p. 477). One of the new species described in that paper (*Hornellia atlanticus*) is very similar to *H. occidentalis*, and is a probable Tropical West Atlantic cognate to our NEP species.

Family Megaluropidae – Diagnosis: "Body compressed laterally; all urosomites free. Rustrum small. Eyes lateral, large.

Upper lip with ventral notch. Mandibles with projecting, toothed incisors, toothed right and left laciniae mobiles, triturative molars, 3-articulate palps with A(B)DE setae. Lower lip with fleshy inner lobes, long mandibular lobes and facial humps on mandibular lobes. Inner plate of maxilla 1 fully setose medially, with apical nipple-like extension; outer plate with 9+ spines; palp 2-articulare, symmetrical on right and left sides. Plates of maxilla 2 broad, inner with strong olbique facial row of setae. Plates of maxilliped well developed, outer with strong medial spines, palp 4-articulate, dactyl stubby, with large nail.

Anterior coxae diverse, coxa 3 smallest, coxa 2 often smaller than 1, coxa 4 generally trowel-shaped and tapering, posterodorsal excavation small; coxae 5-7 shorter than 4. Gnathopod 1 simple, carpus long but not lobate. Gnathopod 2 sexually diverse, enlarged in male, but basically simple through dactyl closing on undefined palm.

Pereopods 3-4 with bent article 2 so as to emerge from coxal bundle and project above head for walking and perching upside down. Pereopods 5-7 increasingly elongate, article 2 expanded, article 6 of pereopod 7 very elongate (often missing on specimens). Coxal gills unpleated, on coxae 2-6 or 2-7. Oostegites slender, strap-shaped, poorly setose.

Pleopods 1-2 with cusp on posterodistal lateral apex of peduncle, peduncles elongate, rami subequally long and like each other, coupling hooks 2. Epimera broad. At least one pleonite dorsally cuspidate trnasversely, at least pleonite 6 with dorsal spines arranged transversely.

Rami of uropods 1-2 strongly spinose apically, marginal spines sparse, uropod 1 with basofacial spines. Rami of uropod 3 broadly expanded, paddle-shaped, peduncle short. Telson deeply cleft, with at least apical spines." (Thomas and J. L. Barnard 1986a).

Unlike the melphidippids, local megaluropids have eyes that do not bulge, but are either completely or virtually flush with the surface of the head. In some forms the eyes appear to project slightly, because they occur on curved cephalic lobes. The family is briefly discussed and keyed by Chapman (2007).

Gibberosus – A small genus created by Thomas and J. L. Barnard (1986a) to house species previously considered to belong in *Megaluropus*. This latter genus was restricted to the old world (Mediterranean and southern Africa), while *Gibberosus* was mostly new world. The exception to the pattern is *Gibberosus longimerus* from Namibia. The other three members of the genus are from the NEP. They can be separated using the generic key provided by Thomas and J. L. Barnard (1986a, pg. 459).

Megaluropidae genus A – A new genus of megaluropids discovered by Carol Paquette of MBC in material collected off Oceanside with a hyperbenthic sampler. She produced a voucher sheet describing the animal and explaining the characters differentiating it from other megaluropid genera. A manuscript is virtually complete and awaiting publication. J. L. Barnard reviewed it prior to his death, and concurred with Carol's conclusions. The voucher sheet was published in the SCAMIT Newsletter Vol. 6(6) in 1987. The animal appears to live in offshore sandy bottoms along the SCB coast, and off the west coast of Baja California. This latter record is derived from records of the female of the species (reported as *Megaluropus agilis*) by J. L. Barnard 1963. The male he reported under that name belonged to *Resupinus coloni* (see the voucher sheet).

Resupinus – The three members of the genus are all discussed by Thomas and J. L. Barnard (1986a). Two are trans-isthmic cognates; *Resupinus visendus* from the NEP, and *R. spinicaudatus* from the Tropical West Atlantic. The remaining species is *R. coloni*, described from the Pacific coast of Panama, and now known to occur as far north as the outer coast of Baja California. There is as yet no evidence that *R. coloni* also has a Tropical West Atlantic cognate. The species has, in the past, been confused with specimens of the still undescribed new genus and new species discussed above. J. L. Barnard (1963) illustrated the female of that form as *Megaluropus agilis*, while the male he illustrated for *M. agilis* was *R. coloni*. The three *Resupinus* species can be separated with the key provided by Thomas and J. L. Barnard (1986a, p. 445).

Family Phreatogammaridae – A small family of austral amphipods from brackish to freshwaters in New Zealand. Questionably placed in the melphidippoids, and ecologically somewhat distant from other melphidippoideans. The family is not represented in the NEP.

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