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 Pontoporeioidea

J. L. Barnard and Karaman (1991) did not separate this group of families from the Superfamily Phoxocephaloidea. We follow Bousfield (1979) in treating the two groups of families as separate at the superfamily level. Only two of the four families included in this superfamily are represented in the NEP fauna; the Pontoporeiidae and the Haustoriidae. In both cases the NEP houses a few species in very few genera. The Zobrachoidae and the Urohaustoriidae are families occurring in the Southern Ocean (J. L. Barnard & Karaman 1991), and are unrepresented in the NEP. J. L. Barnard and C. M. Barnard (1983) treated this entire superfamily as part of the Gammaroidea s. 1., segregating it as cluster k of their gammaroid group. Erection of the subclass Senticaudata (Lowry & Myers 2013) has modified the placement of this group relative to the gammaroids. They include the gammaroids, including nearly all the “traditional” gammaroid families in their new subclass. The pontoporeioids, however, are united with the Phoxocephalooids outside the Senticaudata, or any as yet created subclass in the Infraorder Phoxocephaliida. While no subclass group currently exists, the informal group of “natant” families (Bousfield 2001) could serve as a temporary home. This is construed here to include two infraorders of “hyperiids”, and three benthic infraorders: Lysianassida, Synopiida, and Phoxocephaliida.

 Diagnosis of the Pontoporeioidea

“Plesiomorphic, generally smooth bodied, weakly rostrate, fossorial gammarideans; dimorphic terminal pelagic male often suppressed (lacking in Haustoriidae) but, when present, bearing plate calceoli and usually brush setae on flagella of both antenna 1 and 2; accessory flagellum short; mouthparts basic, with strong mandibular molar and palp; plates of maxillae 1 and 2 strongly setose and spinose; maxilliped plates and palp well developed and strongly setose; lower lips with distinct inner lobes; coxal plates deep, 4th moderately excavate behind; coxa 5 anteriorly or equi-lobate, coxae 6 and 7 posteriorly lobate; gnathopods 1 and 2 weakly amplexing, unlike, subchelate or simple; peraeopods 5-7 adactylate (or nearly so), markedly heteropodous; brood plates sublinear to broad; coxal gill lacking on peraeopod 7; sternal gills occasionally present (some Pontoporeia); pleopods normal to very powerful; uropods sublinear or lanceolate, rami of 1 and 2 subequal; uropod 3 foliaceous to spinose, outer ramus usually 2-segmented; telson lobes variously separated or fused, apices with spines or setae.” (Bousfield 1979).
Ecological Commentary

Pontoporeoids are burrowing animals, and bear the typical morphological adaptations seen in other groups which “swim” through sandy sediments (Bousfield 1970). Like phoxocephalids, urothoids, and platyischnopids, members of the pontoporeoid families bear fairly robust appendages, and robust antennae. In some areas of the world they are important in energy flow within communities (Elmgren et al 1990, Cavaletto et al 1996, Gardner et al 1990), but in the NEP they usually have less central roles in community function.

They are primarily found in fully marine, or brackish waters, but some live in freshwaters. To some extent this follows family lines, with members of the Haustoriidae, Zobrachoidae, and Urohaustoriidae typically marine, and Pontoporeiidae primarily brackish or fresh. While most species are found in only one of these salinity regimes, others have some tolerance of salinity fluctuations (Filipov 2006). Members of the genus Pontoporeia (including Monoporeia and Diporeia) are among the best known of glacial relict taxa, with holarctic distributions reflecting vicariant events associated with glaciation (Segerstråle 1971a, 1971d, 1977; Bousfield 1989).

Species in pontoporeoid families preferentially inhabit well oxygenated sediments in shallow waters, and many are very active, forced by waves to constantly reestablish their position (Lindström 1991). While some frequent silty sands, most inhabit clean sandy sediments. These characteristics, along with known tolerances in temperature fluctuation (Segerstråle 1978b) and oxygen levels (Johannson 1997) make them useful as bioassay animals (Sundelin 1983, 1984; Eriksson Wiklund et al 2002).

Feeding within pontoporeoid families primarily involves particle capture, either from suspended particles in the water, or sedimentary deposits. None seem to have evolved raptorial modifications allowing a predatory life style. Like some phoxocephalids, however, some pontoporeiids may be selective deposit feeders with a taste for the larvae of other invertebrates (Oakden 1984, Oliver et al 1982, Oliver & Slattery 1985). The authors cited view this as micropredatory activity, but without specialized adaptations to prey (even larval prey) capture, this is perhaps more accurately viewed as selective deposit feeding. Enequist (1950) does not report on the behavior of any Pontoporeia species, but does describe feeding and locomotory behavior in both Bathyporeia and some species in Haustoriidae. He reports the animals suction feed on fine particulates while burrowing in, and moving forward through the sediments. The broad body form and setose appendages help maintain the lateral walls of the feeding “tube” formed by the forward excavation. It is within this space that the suctorial particle capture takes place. He also mentions the capture of larger organic aggregates, potentially including larvae of infaunal species. In his examination of Eohaustorius sencillus guts Slattery (1985) found only an organic paste and diatom frustules, but opportunistic consumption of encountered larvae remains possible although undocumented.

Fresh-water pontoporeiids rely on diatoms either in sediments or in bottom water for their nutrition. Post bloom consumption of settled phytoplankton leads to variable lipid concentrations in pontoporeiids in a predictable seasonal cycle (Autio et al 2003; Hill et al 1992; Johnson 1987; Lehtonen 1996, 2004). Much of the annual productivity in these species centers on the food stores gathered in the spring post-bloom feast (Goedkoop 2004, Goedkoop & Johnson 2001). Lipids stored in the body see the animals
through the much leaner summer, fall and winter months. In areas where the bloom is restricted, stores are not adequate, and the life cycle is annual. Where plankton bloom derived food is abundant, some of the population will overwinter, living two years. Although other food sources are utilized (i.e. bacterial flora) this contributes little to the energy budget of the animals (Goedkoop & Johnson 1994). Reproductive problems in these amphipods are a consequence of inadequate nutrition (Sundelin et al 2008).

Availability of food can be limiting to pontoporeiid populations, and many exhibit either intrapopulation competition (Elmgren et al 2001), or interspecies competition between co-occurring Monoporeia affinis, and Pontoporeia femorata (Lopez & Elmgren 1989, Uitto & Sarvala 1991). These two species partition their habitat to minimize conflict (Busdosh et al 1982, Hill & Elmgren 1987), and respond differently to physical factors (Steele & Steele 1978, Johansson 1997). In addition to the food competition mentioned above, pontoporeiids also are involved in interference competition with other members of the benthos. The inverse relationship between abundances of Monoporeia affinis and the bivalve Macoma balthica has been known for many years (Segerstråle 1973, 1978a; Elmgren et al 1986). The burrowing activities of pontoporeiids also have a profound impact on the meiofauna (Olafsson & Elmgren 1991).

Pontoporeiids serve as food for other animals, and form a significant link connecting the benthic and pelagic portions of lacustrine food webs (Goedkoop & Johnson 1996, Gardner et al 1990). They are also consumed by benthic predators such as worms (Abrams et al 1990) and isopods (Hill & Elmgren 1992). They are even consumed at the very top of the food chain by whales (Hazard & Lowry 1984).

Reproduction is linked to availability of food through vision. Pontoporeiids have good vision (Donner 1971) which is used to synchronize their actions to seasonal changes in day length (Segerstråle 1970, 1971b, 1971c, 1971e, Donner et al 1987). As these are also linked to the timing of the phytoplankton bloom which forms the majority of the annual nutritional input to pontoporeiid populations, vision is critical to their lipid content and reproductive condition.

Conlan (1991) classes both Pontoporeiidae and Haustoriidae as non-mate guarding groups that do not engage in precopulatory grasping. Males find females either with pelagic searching (pontoporeiids) or benthic searching (haustoriids), the latter not apparently involving chemosensory mate location (Conlan 1991). During their swimming excursions male Pontoporeia femorata are classed as major suprabenthic swarvers by Sainte-Marie and Brunel (1985). At the superfamily level (using data from a number of Pontoporeiidae and Haustoriidae), pontoporeoids were found to have an average lifespan of 18.8 months, with an expected lifetime fecundity of 34.2 embryos/female (Sainte-Marie 1991). While endocrine disruptors have been shown to have an impact on reproduction in the group (Jacobson & Sundelin 2006), the primary variable affecting reproductive output of pontoporeiids is apparently food (Sundelin et al 2008).
**NEP Pontoporeioidea** from McLaughlin *et al.* (2005)

* = Taxa on the SCAMIT Ed. 9 list (Cadien and Lovell 2014).

Valid taxa **bolded**, synonyms not.

**Family Pontoporeiidae**

*Diporeia erythrophthalma* (Waldron 1953) – Lake Washington, freshwater

*Monoporeia affinis* (Lindstrom 1855) – distribution uncertain in NEP; in brackish to freshwater

Pontoporeia affinis Lindstrom 1855 (see *Monoporeia affinis*)

Pontoporeia affinis erythrophthalma Waldron 1953 (see *Diporeia erythrophthalma*)

**Pontoporeia femorata** Krøyer 1842 – distribution uncertain in NEP; in brackish to freshwater

**Family Haustoriidae**

*Acanthohaustorius n. sp.* Dexter 1974 – Costa Rica to Columbia; intertidal

*Eohaustorius barnardi* Bousfield and Hoover 1995 – Pt. Conception to San Diego, Ca; 5-20m

*Eohaustorius brevicuspis* Bosworth 1973 – Strait of Juan de Fuca, Puget Sound, Washington to Crescent City, Ca; 0-1m

*Eohaustorius eous* (Gurjanova 1951) – Kamchatka to Aleutians; 5-25m

*Eohaustorius estuarius* Bosworth 1973 Crescent Beach Washington to Sooes Estuary, Oregon; 0-1m in brackish waters

*Eohaustorius sawyeri* Bosworth 1973 – British Columbia to Carpinteria, Ca.; 2-22m

*Eohaustorius sencillus* J. L. Barnard 1962 – Southern Oregon to SCB; 1-20m

*Eohaustorius washingtonianus* (Thorsteinson 1941) – Prince William Sound, Alaska to Central California; 0-2m

Haustorius eous Gurjanova 1951 (see *Eohaustorius eous*)

Haustorius washingtonianus Thorsteinson 1941 (see *Eohaustorius washingtonianus*)

**Family Zobrachoidae** – no representatives in the NEP

**Family Urohaustoriidae** - no representatives in the NEP

**Comments by Family**

**Family Pontoporeiidae** – The family Bathyporeiidae, created by Bousfield (1979) from within the Pontoporeiidae, has since been recombined with the latter family. McLaughlin *et al.* (2005), the amphipod portion of which was organized and directed by Bousfield, no longer separates the two. The family apparently has a number of previously unrecognized forms, apparently divergent glacial relict populations, throughout North America. Bousfield (Ed Hendrycks, pers. comm.) is currently working on the family and has already identified a number of new genera, and numerous additional species.

Diagnosis: “The body is medium or slender, or rarely broad; the urosome (and occasionally the pleon) often is toothed or setose dorsally. The rostrum is weak. The eyes are small, ovate, and few-faceted, or rarely lacking. Antenna 1 often is geniculate at peduncle 1, which may form a pseudorostrum with the opposite member. Sexual
dimorphism is pronounced, usually with a (smaller) terminal pelagic male. In antenna 1 the flagellum is occasionally calceolate (male) or rarely elongate (Pontoporeia). In antenna 2 the peduncular segments are little expanded, and the flagellum is short in the female or usually elongate and calceolate in the male. The mouthparts are basic and setose; the maxillae are normal, and the maxilliped palp is dactylate (four-segmented). The gnathopods are weakly subchelate, subsimilar or dissimilar (Bathyporeia), weakly (rarely strongly) sexually dimorphic, and amplexing in males. Peraeopods 3-7 have dactyls, which are small and masked by spines; the bases of peraeopods 5-7 (especially 7) are very broadly expanded, the distal segments are moderately so, and the coxae are equally or anteriorly lobate; peraeopod 5 often is geniculate at segment 4. The pleopods are normal, and the rami are subequal. Uropod 3 is large, and the rami dimorphic. Sternal gills are present in some Pontoporeia. The telson lobes are separate or fused basally. The brood plates usually are large, and the margins are richly setose.” (Bousfield 1982).

Steele (1991), points out that all three types of brood plates are present in the pontoporeiids despite Bousfield’s characterization of “large” as the usual state for the family. He indicates the differences in brood plate morphology may be useful in tracing evolutionary divergence within the group. Genera within the family were reevaluated by Bousfield (1989) who separated Pontoporeia into three genera; Pontoporeia s.s., Monoporeia, and Diporeia. All three are reported from the NEP, although, due to nomenclatural confusion in the identity of the animals, some of the historic distributional records may not be accurate. The genus Priscillina is also reported from the NEP, but only from Arctic portion above the Aleutians. None of the other genera in the family are known from the NEP.

Diporeia - A single species is known from the NEP, *D. erythrophthalma* from the freshwaters of Lake Washington near Seattle. Originally described as a subspecies of *Pontoporeia affinis* (Waldron 1953), it has since been transferred to *Diporeia* (in the revision of Bousfield 1989), and raised to full specific status. Chapman (2007) provides information on the animal, and a key separating it from *Monoporeia*. No collections from either brackish or marine waters have yet been reported.

Diagnosis:” *Urosome 1 with weak dorsal hump (or lacking); posterior pleosome and urosome often dorsally setulose (Fig. 1B). Lateral head lobe not produced, subacute.*
Antenna 1, accessory flagellum 3-4 segmented. Antenna 2, peduncular segments 4 and 5 normal, with one major fanwise group of lateral facial spines; segment 5, antero-distal process very weak, spine group weak.

Gnathopod 1, propod deeply ovate; palm with group of three postero-distal spines; carpus longer than deep, hind lobe shallow, unevenly rounded below. Gnathopod 2 weakly parachelate; propod medium, about two-thirds length of carpus; palm relatively strong, postero-distal angle with two to three spines.


Uropod 1, rami sparsely spinose, especially outer margin of inner ramus. Uropod 2, rami with long slender marginal spines except on inner margin of outer ramus. Uropod 3, rami short, outer ramus lacking terminal segment.

Telson squared, about as wide as long, lobes cleft to base, apices with long and short slender spines. Sternal gills double on peraeon segments 3-5, single on segment 2.”

(from Bousfield 1989)

Monoporeia affinis, gravid female (Photo: Rasmus Neideman)

Monoporeia – A single member of this genus is reported from the boreal portion of the NEP, Monoporeia affinis. As reported by Bousfield (1989) there is good reason to suspect that the species identified as M. affinis in the NEP differs from that known from other boreal and arctic records, particularly in Europe. His earlier report of the species from numerous locations across the continent (Bousfield 1958) stresses uncertainty over the meaning of the “varietal” names he synonymized there under M. affinis. He suggested that the records he listed might not apply to Lindstrom’s species. This contention was further supported by the results of later molecular work (Väinölä and Varvio 1989). Chapman (2007) reports only Monoporeia sp. Despite the probability that previous records refer to one or more undetected cryptic species in the genus, the possibility of circumarctic distribution for M. affinis cannot yet be ruled out. It is
Pontoporeia femorata (from Bousfield 1973)

Pontoporeia – The species Pontoporeia femorata is recorded from coastal fresh/brackish waters in Alaska, but is otherwise not known from the NEP. Like Monoporeia, this form may prove to be an unrecognized locally distributed species rather than Pontoporeia femorata as known from Europe.

Diagnosis: “Antenna 1 not geniculate; mandibular palp not on basal process, molar ridged; outer plate of maxilla 2 not enlarged; maxillipedal palp 4-articulate; coxae 1-2 of normal size, rounded-quadrate below; gnathopod 1 subchelate, articles 5-6 subequal in length, gnathopod 2 slightly chelate; at least pereopods 1, 2, 5 dactylate; rami of uropod 3 equal in length; telson cleft halfway or more.“ (from J. L. Barnard 1969)

Family Haustoriidae - Haustoriids are particularly well represented in the Northwest Atlantic (Bousfield 1965, 1970, 1973) where they have extensively diversified, with representatives of Acanthohaustorius, Haustorius, Lepidactylus, Neohaustorius, Protohaustorius, and Pseudohaustorius. Several investigations of the autecology of these species are available (Croker 1967a,b; Dexter 1967, 1971; Sameoto 1969a,b,c). In the
NEP the family is represented only by the genus *Eohaustorius*, which is not among the large NW Atlantic haustoriid contingent (McLaughlin *et al* 2005). *Eohaustorius* is a North Pacific endemic genus, with representatives in both the NWP and NEP. It appears to be most closely related to the NWA *Pseudohaustorius*, and likely resulted from migration west of NWA precursors prior to the Miocene formation of the Isthmus of Panama (Bousfield & Hoover 1995).

Diagnosis: “The body is medium to very broad, smooth and narrowing and/or reflexed (often strongly) at the urosome. The appendages are very strongly fossorial. Sexual dimorphism is weak, and a terminal pelagic male is lacking. The rostrum is moderate. The eyes are very small and weakly (or not) pigmented. In the antennae the peduncular segments (especially of antenna 2) are broadly expanded behind and strongly spinose and setose; the flagella are short and lack calceoli; the accessory flagellum is two- to five-segmented. The mouthparts are basic, but specialized for filter feeding. The mandibular molar is strong, and the incisor is weak. In the lower lip the outer lobes lack a mandibular process, and the inner lobes are elongate proximally. The maxillae are very setose; in maxilla 2 the plates are often very large and bale-shaped; in the maxilliped the palp is three-segmented (the dactyl is lacking). Gnathopod 1 is simple, and 2 is microchelate; both are richly setose and alike in the male and female (2 is large and carpochelate in the Neohaustorius male). Peraeopods 3-7 lack dactyls, and the distal segments are expanded, strongly spinose, and often plumose-setose. Peraeopods 3 and 4 occasionally are unlike (*Eohaustorius*). Peraeopods 5-7 are dissimilar; segments 4 and 5 are variously expanded and spinose; the bases are broadly expanded; the coxae typically are posteriorly lobate. The pleopods are very powerful, the peduncles are cylindrical, and setose at the joints. The telson lobes are short, and variously fused to a V-cleft, or widely separated. On segment 6 (*Eohaustorius*), sternal gills are lacking. The brood plates are medium broad.” (Bousfield 1982).

*Acanthohaustorius millsii*, a western Atlantic species (from Bousfield 1973)

*Acanthohaustorius* – The presence of an unidentified and presumably new species in this genus was reported from Costa Rica and northern Pacific Columbia by Dexter (1974). No description of this animal is available to date. It is included here to bring attention to the presence of the genus in the NEP. Otherwise, genera other than *Eohaustorius* are unrepresented in the NEP.

Eohaustorius washingtonianus (from Bousfield and Hoover 1995)

**Eohaustorius** – An endemic North Pacific genus, with representatives on both the western and eastern margins of that ocean. Living either intertidally or subtidally on exposed sandy shores, species of *Eohaustorius* are active burrowing detritivores. Ecology and population characteristics of *Eohaustorius sencillus* were evaluated by Slattery (1985) in Monterey Bay. The zoogeographic analysis of Bousfield and Hoover (1995) show this as one of three species recorded from southern California, described by J. L. Barnard (1962) from material taken near Point Conception. Earlier records of a fourth species, *E. washingtonianus*, were allocated to *E. barnardi* when that species was described as new (Bousfield & Hoover 1995). It was described from the Puget Sound area (Thorsteinson 1941), and is common north of central California. The third southern
California taxon is *E. sawyeri*, described initially by Bosworth (1973) from central California, but ranging at least as far south as Carpinteria in the Santa Barbara Channel (personal obs.). All of these species are currently listed on the SCAMIT Edition 9 listing.

Four species are known from the northern part of the NEP above the SCB: *E. eous*, *E. estuarius*, *E. washingtonianus*, and *E. brevicuspis*. The first of these only ranges from the Sea of Okhotsk through western Alaska, while the next two range from Southeastern Alaska down to Central California. *Eohaustorius brevicuspis* has a narrower range, being known only between British Columbia and Central California. Original descriptions of these four are available in Gurjanova (1951), Bosworth (1973), and Thorsteinson (1941), but all are redescribed by Bousfield and Hoover (1995). All seven NEP species can be separated using the genus key provided by Bousfield & Hoover (1995, p.37).

Diagnosis: “Head broad, broadest in middle, lateral margins subparallel, rostrum strong. Accessory flagellum 2-articulate. Article 5 of peduncle on antenna 2 broad but scarcely lobate ventrally. Mandible with incisor. Outer plate of maxilla 2 little larger than inner, not lunate. Palp article 3 of maxilliped clavate. Anterior pereonites without pronounced lobes just above coxae. Coxae 1-2 much smaller than 3-4, disjunct in size from 3-4. Pereopod 4 distinctly smaller than and unlike pereopod 3. Posterodorsal border of pleonite 3 slightly decurved, strongly reflexed, forming lobe overhanging urosome. Epimeron 3 with posterior process. Urosome short, lappet absent; dorsal margin of urosomite 2 short, not occluded, about equal to urosomite 3. Uropod 1 slender, both rami armed with both spines and setae (mostly); rami subequal, distally expanding. Uropod 2 strong biramous. Article 2 on outer ramus of uropod 3 medium. Telsonic lobes widely separated at base; lobes slender-setose.” (from J. L. Barnard and Karaman 1991)

**Literature Cited**


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