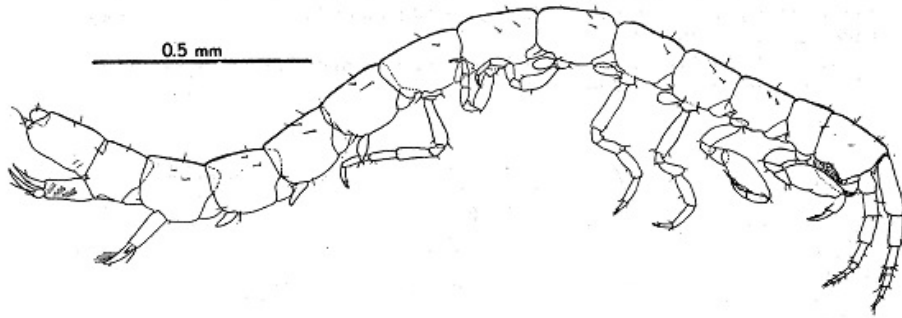


Amphipoda of the Northeast Pacific (Equator to Aleutians, intertidal to abyss): I.
Suborder Ingolfiellidea – a review Donald B. Cadien , LACSD 30Apr2015

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.



Ingolfiella putealis, a brackish groundwater species from the Caribbean (from Stock 1977)

Introduction to the Ingolfiellidea

A group of highly modified interstitial amphipods. They are laterally compressed, elongate and vermiform, and in other respects conform to the demands of their interstitial habitat. Very broadly distributed, the suborder contains two families, only one of which is represented in the Northeast Pacific, and that by few individuals and occurrences. None of the described species are known to occur in the region, and it is highly likely that the records reflect an undescribed taxon or taxa. While the Suborder placement of the group is accepted in WoRMS (Horton 2015), it has been criticized and rejected by some other workers (Dahl 1977, Lowry & Poore 1989). In particular, the latter authors considered the structure deemed an eyescale elsewhere to be analogous with the anterior cephalic corner of some gammarids, and viewed the group as nesting within the gammaroids. Their work seems well grounded, and echoes the observations of others (Dojiri & Sieg 1987, Ruffo & Vigna Taglianti 1989) concerning this structure. It is really the only character which prevents placement of the ingolfiellids within the gammaroids, all other characters being either typical of the interstitial habitat, or also found in some gammaroid groups. Vonk & Schramm (2003) revisit these points and reevaluate the evidence, concluding that the characters used to create the suborder are defensible and sufficient. Ruffo & Vigna Taglianti saw closest relationships with structure in the leucothoid amphipods, and presumably would place the group as a separate superfamily within the Leucothoidea. This issue may eventually be resolved by molecular evidence, but even attempts at morphology based phylogeny (i.e. Berge et al 2000) placed the Ingolfiellids with other gammaroid groups. It was used as an outgroup for the other taxa considered, but ended up firmly ensconced in a heterogeneous clade which included a number of gammaroid families and the caprellids (at that time also considered a separate suborder).

None of the existing molecular based phylogenies of the amphipods have included taxa from the Ingolfiellidea (Englisch 2001; English & Koenemann 2001; English et al 2003; Costa et al 2007, 2009; Hou et al 2007), but future studies will eventually have broader taxon sampling and should address this issue. Until such evidence becomes available, the “traditional” placement as a separate Suborder is followed.

Based on various evidence stygobiont members of the group (and thus the group as a whole) are viewed as originating at least as early as the Miocene-Tertiary boundary, and distributed in a pattern of Tethyan vicariance (Stock 1995). The distribution of the non-stygobiont members seem to conform to this as well. With that in mind it is difficult to explain the occurrence of ingolfiellids in the NEP temperate/boreal region except by vicariance on drifting terrains now accreted to the West Coast of North America.

Definition of the Ingolfiellidea

Diagnosis: “*Body filiform, with the basal joint of the thoracic legs small, not developed as "epimeral" plates. Separate eye-lobes (without eyes) developed from the antero-lateral margin of the head. The antennule with accessory flagellum. The mandible with elongate styliform acute molar process. The first joint of the well-developed palp of the maxillule longer than the second. The maxillipeds only with the major part of their first joints coalesced with each other; the third joint without lobe. The first segment of the thorax more closely connected with the head than with the second segment. The two anterior pairs of thoracic legs with a well-developed hand formed of the fifth segment, while the rest of these legs is claw-shaped; the prehensile hand of the first pair larger than the following pair. The third and fourth pairs of thoracic legs with a thin claw inserted on a much broader seventh joint. The abdomen long, with all the segments well separated from each other; the terminal joint of the sympod of the pleopods developed as a triangular plate without vestige of rami, hairs, or coupling-hooks. The two anterior pairs of uropods normal; the third pair reduced. The telson thick, rounded.*” (from Hansen 1903 as diagnosis of the family)

Ecological Comments

All small ingolfiellids are interstitial, although a few of the largest forms may be crevice dwellers, or reside on or under rocks (Griffiths 1991). Even so they occupy an extraordinarily broad range of habitats (Vonk & Schramm 2003). Representatives of the group are found in completely fresh groundwaters, in brackish waters of island wells (Stock 1977) and in fully marine conditions. Freshwater forms may be found at 2000m elevation in the Andes, to low elevation riverine bottoms, or in shallow caves or groundwaters. Within the marine realm they range from intertidal sands (Noodt 1959, Martinez & Poore 2003) to abyssal oozes (Mills 1967). Where sediments are coarse, providing abundant space between particles and penetration of oxygenated waters into the sediment column, they may occur deep under the surface (Spooner 1960).

Ruffo and Vigna-Taglianti (1989) observe that the presence and size of the eyelobe in various species seems directly related to the salinity of the waters in which it lives. Marine species all have well developed lobes, those in transitional waters of reduced salinity have reduced lobes, or have lost them; and freshwater species always lack lobes. This suggests the intriguing possibility that these lobes are not, as originally perceived “eyelobes”. It also offers an alternative hypothesis on their nature and function to that offered by Vonk & Schramm (2003). The latter authors suggested that these lobes served to close the gap between the

antennal bases, preventing fine particulates from entering. This is one potential explanation, but does not seem to be supported by the evidence. The largest lobes are found in marine forms, some of which live in muddy sediments, but others of which live in clean shell-sands or gravels. The posited function would not be needed by these forms, and would provide no benefit. If we postulate that these are actually glandular organs whose purpose is to control salt absorption/excretion, the variability in their size in relation to ambient salinity suddenly follows a sensible pattern. So far no evidence of such function is available, and the SEM examinations of Vonk & Schramm (loc. cit.) did not show pores that might be expected to accompany salt-regulatory function. This hypothesis is put forward because the function suggested by Vonk & Schramm is not convincing, and does not seem well-supported by evidence.

Observations on predators of ingolfiellids are virtually non-existent: the interstitial habitat making such observations extremely difficult. Ianilli et al (2008) mention observation of predation on *Ingolfiella alba* by palpigrade arachnoids. Although the pedipalps of these animals are not modified as grasping organs, those authors observed one holding a half-eaten ingolfiellid. This would appear to be conclusive evidence of predation, despite morphological limitations.

Feeding in ingolfiellids remains undescribed, although the strong incisor, lacinia mobilis and mandibular raker row suggest that predation is not impossible. Strongly setose mouthparts of anterior pereonites are not seen in the group, so filter feeding is unlikely. Based on their habits either detritivory or micropredation would seem the most likely nutritive mode. There are currently no observations of feeding in the group, and these are merely suppositions based on morphology.

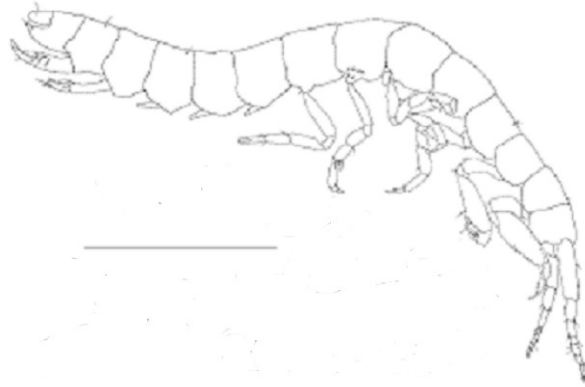
Reproduction in the group has been little studied, as have most aspects of the biology of ingolfiellids. Vonk & Nijman (2006) examined sex ratios and the degree of sexual dimorphism in various species. They found sex ratios to be female skewed, with more females than males, and only restricted sexual dimorphism. Ruffo & Vigna-Taglianti (1989) also comment on the size of the oostegites, which are small and restricted to only a few pereonites. It is unlikely that they can be used to retain eggs or young, so it is likely that eggs are very few and large relative to the animal. This would suggest very limited reproductive potential unless the animals were strongly multivoltine, reproducing constantly with many broods during a year. Mention of eggs or even oostegites are not common, however, so this is unlikely based on the lack of frequent observation of gravid females.

List of Ingolfiellidea reported in the NEP. McLaughlin et al (2005) record no members of the Suborder occurring on the Pacific Coast of North America. Cadien & Lovell (2014) have a listing for Ingolfiellidae, but without identification below family. There are grey literature records of an *Ingolfiella* sp from Prince William Sound, taken during the sampling after the Exxon Valdez oil spill. That sampling was double blind so actual location and depth were not revealed to the taxonomists. Consequently the only recorded taxon is:

Family Ingolfiellidae

Ingolfiella sp. – Prince William Sound, Gulf of Alaska to Northern Channel Islands, SCB: depth? but shallow

Discussion by Family



Ingolfiella azoriensis from surface sediments in 10-15m depth. Scale=0.5mm (from Rubal & Larsen 2013)

Family Ingolfiellidae – The family currently contains five genera (Lowry 2015), but only *Ingolfiella* is believed to occur in the NEP. A single record of a member of the family, presumed to belong to the genus, came from 2008 regional monitoring sampling in the Northern Channel Islands. Otherwise the only record is from environmental monitoring samples taken in Prince William Sound, Alaska following the Exxon Valdez Oil Spill investigations. Several members of the family are known from the NWP, and further to the south on the western margin of the Pacific, but the only published records in the Eastern Pacific are from Chile.

Description. “*Head free, not coalesced with peraeonite 1; exposed; longer than deep, or deeper than long; anteroventral margin straight; rostrum present or absent, short; eyes present, well developed or obsolescent; not coalesced; 1 pair; not bulging. Body cylindrical; cuticle smooth.*

Antenna 1 shorter than antenna 2, or subequal to antenna 2, or longer than antenna 2; peduncle with sparse robust and slender setae; 3-articulate; peduncular article 1 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; antenna 1 callynophore absent. Antenna 2 present; short; 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; lacinia mobilis present on both sides; accessory setal row without distal tuft; molar present, medium, non-tritulative; palp present or absent. Maxilla 1 present; inner plate present, weakly setose apically; 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 or reduced, separate; **outer plates absent**; palp 4-articulate, article 3 without rugosities. Labium smooth.*

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

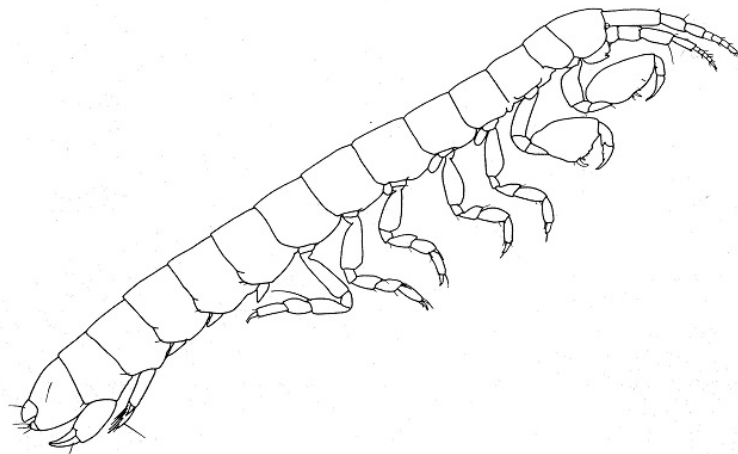
Coxae 1-7 well developed, none fused with peraeonites. Coxae 1-4 broader than long, discontinuous, coxae not acuminate. Coxae 1-3 not successively smaller, none vestigial. Coxae 2-4 none immensely broadened.

Gnathopod 1 not sexually dimorphic; smaller (or weaker) than gnathopod 2, or subequal to gnathopod 2; vestigial; 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; carpochebate;

coxa vestigial; ischium short; merus not fused along posterior margin of carpus or produced away from it; carpus/propodus not cantilevered, carpus elongate, longer than 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 vestigial**, as long as broad; carpus subequal to propodus or longer than propodus, not produced; dactylus minute, or well developed with cylindrical bifid unguis. Coxa vestigial, 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, or subequal in length to peraeopod 6; coxa vestigial, without posterior lobe; basis linear, subrectangular, without posteroventral lobe; merus/carpus free; carpus weakly expanded, or 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 slightly expanded or linear, without dense slender setae; dactylus without setae. **Pleon.** Pleonites 1-3 without transverse dorsal serrations, without dorsal carina; without slender or robust dorsal setae. Epimera 1-3 absent.*

Urosome not dorsoventrally flattened; urosomites 1 to 3 free; urosomite 1 subequal to urosomite 2, or longer than urosomite 2; urosome urosomites not carinate; urosomites 1-2 without transverse dorsal serrations. Uropods 1-2 apices of rami without robust setae. Uropods 1-3 similar 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 subequal to outer ramus. Uropod 3 not sexually dimorphic; peduncle short; outer ramus shorter than peduncle or longer than peduncle, 1-articulate, without recurved spines. Telson thickened dorsoventrally; entire; longer than broad, or as long as broad; apical robust setae absent.” (from Lowry & Springthorpe 2001)



Ingolfiella bassiana, a marine species from shell sand at 121m (from Lowry & Poore 1989)

Ingolfiella – The forty-three taxa currently placed here form the majority of the Suborder. A number of different subgenera have been proposed, but many of the species are not clearly referable to one of these. All of the members of the genus are similar in gross appearance, differing mainly in details of the male and female gnathopods, the number of setal rows on the second uropod, and a few other characters. The two records of this genus in the NEP

are both based on application of *Ingolfiella s.l.*, and may perhaps refer to another genus within the family. It is likely, however, that they have been appropriately identified as *Ingolfiella*.

Diagnosis: "Ocular lobes developed. Pleopods present in females (males unknown). Pereopods 3-7 similar; dactyli elongate, with claw long, slender, apically sharp or very minutely bifid only in pereopods 3-4. Oostegites present." (from Ruffo & Vigna-Taglianti 1989)

Literature Cited

- Berge, Jørgen, Geoffrey A. Boxshall, and Wim Vader. 2000.** Phylogenetic analysis of the Amphipoda, with special emphasis on the origin of the Stegocephalidae. *Polskie Archiwum Hydrobiologii* **47**(3-4): 379-400.
- Cadien, Donald B., and Lawrence L. Lovell. 2014.** A Taxonomic Listing of Benthic Macro- and Megainvertebrates from Infaunal & Epifaunal monitoring and research programs in the Southern California Bight. Los Angeles, California, USA: 186.
- Costa, Filipe O., Jeremy R. deWaard, James Boutillier, Sujeevan Ratnasingham, Robert T. Dooh, Mehrdad Hajibabaei, and Paul D. N. Hebert. 2007.** Biological identifications through DNA barcodes: the case of the Crustacea." *Canadian Journal of Fisheries and Aquatic Sciences* **64**: 272-295.
- , **C. M. Henzler, D. H. Lunt, N. M. Whiteley, and J. Rock. 2009.** Probing marine *Gammarus* (Amphipoda) taxonomy with DNA barcodes. *Systematics and Biodiversity* **7**(4): 365-379.
- Dahl, Eric. 1977.** The amphipod functional model and its bearing upon systematics and phylogeny. *Zoologica Scripta* **6**: 221-228.
- Dojiri, Masahiro and Jürgen Sieg. 1987.** *Ingolfiella fuscina*, new species (Crustacea: Amphipoda) from the Gulf of Mexico and the Atlantic coast of North America, and partial redescription of *I. atlantisi* Mills, 1967. *Proceedings of the Biological Society of Washington* **100**(3): 494-505.
- Englisch, Ulricke. 2001.** Analyse der Phylogenie der Amphipoda (Crustacea, Malacostraca) mit Hilfe von Sequenzen des Gens der RNA der kleinen ribosomalen Untereinheit. *Biologie*. Beilefeld, Germany, Ruhr-Universität Bochum. **PhD**: 311pp.
- , **Charles O. Coleman, and Johann W. Wägele. 2003.** First observations on the phylogeny of the families Gammaridae, Crangonyctidae, Melitidae, Niphargidae, Megaluroipidae and Oedicerotidae (Amphipoda, Crustacea), using small subunit rDNA gene sequences. *Journal of Natural History* **37**(20): 2461-2486.
- , **and Stefan Koenemann. 2001.** Preliminary phylogenetic analysis of selected subterranean amphipod crustaceans, using small subunit rDNA gene sequences. *Organisms Diversity & Evolution* **1**: 139-145.
- Griffiths, Charles L. 1991.** A new ingolfiellid (Crustacea: Amphipoda) from subterranean waters in western Namibia. *Cimbebasia* **13**: 75-79.
- Hansen, Holm J. 1903.** The Ingolfiellidae, fam. n., a new type of Amphipoda. *The Journal of The Linnean Society, Zoology* **29**: 117-133.

- Horton, Tammy. 2015.** Ingolfiellidea. In: Horton, T.; Lowry, J. & De Broyer, C. (2013 onwards) World Amphipoda Database. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=12671>
- Hou, Zhong, Jinzhong Fu, and Shuqiang Li. 2007.** A molecular phylogeny of the genus *Gammarus* (Crustacea: Amphipoda) based on mitochondrial and nuclear gene sequences. *Molecular Phylogenetics and Evolution* **45**(2): 596-611.
- Iannilli, Valentina, Raffaella Berera, and Vezio Cottarelli. 2008.** Description of the first marine interstitial ingolfiellid from Philippines, *Ingolfiella alba* sp. nov., with some remarks on the systematic of the genus (Amphipoda: Ingolfiellidae). *Zootaxa* (1675): 49-58.
- Lowry, James K. 2015.** Ingolfiellidae Hansen, 1903. In: Horton, T.; Lowry, J. & De Broyer, C. (2013 onwards) World Amphipoda Database. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=101427>
- , **and Gary C. B. Poore. 1989.** First ingolfiellids from the southwest Pacific (Crustacea: Amphipoda) with a discussion of their systematics. *Proceedings of the Biological Society of Washington* **102**(4): 933-946.
- , **and Roger T. Springthorpe (2001 onwards).** Amphipoda: Families and Subfamilies. Version 1: 1 September 2001. <http://crustacea.net/>.
- Martinez, Susana G. and Gary C. B. Poore. 2003.** A new species of ingolfiellid amphipod (Crustacea: Amphipoda) from Western Australia. *Records of the Western Australian Museum* **22**: 75-80
- McLaughlin, P. A., D. K. Camp, M. V. Angel, E. L. Bousfield, P. Brunel, R. C. Brusca, D. B. Cadien, A. C. Cohen, K. Conlan, L. G. Eldredge, D. L. Felder, J. W. Goy, T. A. Haney, B. Hann, R. W. Heard, E. A. Hendrycks, H. H. Hobbs III, J. R. Holsinger, B. Kensley, D. R. Laubitz, S. E. LeCroy, R. Lemaitre, R. F. Maddocks, J. W. Martin, P. Mikkelsen, E. Nelson, W. A. Newman, R. M. Overstreet, W. J. Poly, W. W. Price, J. W. Reid, A. Robertson, D. C. Rogers, A. Ross, M. Schotte, F. R. Schram, C.-T. Shih, L. Watling, and G. D. F. Wilson. 2005.** *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada - Crustaceans*. Bethesda, Maryland, U. S. A.: American Fisheries Society. 565pp.
- Noodt, Wolfram. 1959.** Estudios sobre crustaceos Chilenos de aguas subterranas. I. *Ingolfiella chilensis* n. sp. de la playa marina de Chile Central. (Crustacea, Amphipoda). *Investigaciones Zoológicas Chilenas* **5**: 199-209.
- Rubal, Marcos and Kim Larsen. 2013.** A new species of Ingolfiellidae (Peracarida, Amphipoda, Crustacea) from the Azores, Portugal. *Helgoland Marine Research* **67**(1): 149-154.
- Ruffo, Sandro and Augusto Vigna-Taglianti. 1989.** Description of a new cavernicolous *Ingolfiella* species from Sardinia, with remarks on the systematics of the genus. *Annali del Museo Civico di Storia Naturale "Giacomo Doria"* **87**: 237-261.
- Spooner, G. M. 1960.** The occurrence of *Ingolfiella* in the Eddystone Shell Gravel, with description of a new species. *Journal of the Marine Biological Association of the United Kingdom* **39**: 319-329.
- Stock, Jan H. 1977.** The zoogeography of the crustacean suborder Ingolfiellidea with descriptions of new West Indian taxa. *Studies on the Fauna of Curaçao and other Caribbean Islands* **60**(178): 131-146.

- , 1995. Age of limnic and stygobiont Amphipoda of the Madeira Archipelago and La Gomera, Canary Islands. *Polskie Archiwum Hydrobiologii* **42**(4): 409-415.
- Vonk, Ronald and Vincent Nijman. 2006.** Sex ratio and sexual selection in wormshrimps (Crustacea, Amphipoda, Ingolfiellidea). *Contributions to Zoology* **75**(3/4): 189-194.
- , **and Frederick R. Schram. 2003.** Ingolfiellidea (Crustacea, Malacostraca, Amphipoda): a phylogenetic and biogeographic analysis. *Contributions to Zoology* **72**(1): 1-28.