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**The North Atlantic genus *Heteromesus*  
(Crustacea: Isopoda: Asellota: Ischnomesidae)**

MARINA R. CUNHA & GEORGE D.F. WILSON



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## The North Atlantic genus *Heteromesus* (Crustacea: Isopoda: Asellota: Ischnomesidae)

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## Abstract

Sixteen species of *Heteromesus* Richardson are reviewed, additional terms are introduced to account for special morphologies in the Ischnomesidae, the diagnosis of the genus is updated and a key to species is given. Twelve species, which have previously been recorded from the Atlantic Ocean, are redescribed and four new species are described, *H. calcar*, *H. ctenobasius*, *H. inaffectus* and *H. oryktus*. *Heteromesus similis* Richardson is illustrated for the first time and *H. bifurcatus* Menzies, *H. dentatus* Hansen, *H. frigidus* Hansen, *H. greeni* (Tattersall), *H. granulatus* Richardson, *H. schmidtii* Hansen, *H. spinescens* Richardson and *H. spinosus* (Beddard) are reillustrated from the type material. The morphological features and ecology of the genus are discussed. The specimens of the new species *H. calcar* and *H. ctenobasius*, collected from Lucky Strike (Mid-Atlantic Ridge), are the first record of *Heteromesus* from hydrothermal vent habitats. Finally, the biogeography of the genus is reviewed and confirms that *Heteromesus* is a deep-sea genus restricted primarily to the North Atlantic and Arctic Seas. Data on unpublished records of undescribed *Heteromesus* spp. allows us to predict a much more diverse composition of the genus and sets the southern limit of its distribution at around 23°S in the Eastern South Atlantic off Africa (Walvis Bay).

**Keywords:** *Heteromesus*, Ischnomesidae, Isopoda, Asellota, deep-sea, North Atlantic Ocean, hydrothermal vents, mid-Atlantic Ridge

## Introduction

The endemic deep-sea genus *Heteromesus* Richardson, 1908 repeats a biogeographic pattern noted by Wilson (1983) for the *Eurycope complanata* complex (Munnopsidae Eurycopinae): a restriction to the North Atlantic and Arctic Oceans. To date, the genus includes twelve described species from depths between 698 and 4077 m. Wolff (1979) mentions one undescribed species from the Northern Caribbean Sea at 4417 m and two undescribed species from Puerto Rico Trench at 7430–8330 m. No species of *Heteromesus* have been reported from other oceans or from the South Atlantic Ocean. Therefore, increasing our knowledge of the species this genus will offer an opportunity to evaluate the biogeography of the North Atlantic. In this paper, we re-describe and re-illustrate many of the existing species because the species concepts are weakly established in the literature. Except for *H. bifurcatus* Menzies, 1962, *H. drachi* Chardy, 1974 and *H. wolffi* Chardy, 1974, other species of the genus were described much earlier, so many characters cannot be adequately assessed in the original descriptions and illustrations. We re-illustrate the type of *H. bifurcatus*, but the two species from Chardy (1974) were found to be adequately illustrated after examining the types. *H. similis* Richardson, 1911 is illustrated

for the first time and *H. spinosus* (Beddard, 1886), *H. greeni* Tattersall, 1905, *H. granulatus* Richardson, 1908, *H. spinescens* Richardson, 1908, *H. dentatus*, Hansen, 1916, *H. frigidus*, Hansen, 1916, *H. schmidtii* Hansen, 1916 and *H. bifurcatus* Menzies, 1962 are re-illustrated from the type material. The type of *H. longiremis* Hansen, 1916 was not available. We provide descriptions to 4 new species: two new species also provide more faunal information on the unique habitats surrounding the hydrothermal vent fields of the Mid Atlantic Ridge, following on from Cunha and Wilson (2003), one new species was recently collected from the canyon bordering the Fylla Structural Complex (West Greenland) and another one was selected among the abundant material collected by the Woods Hole Oceanographic Institution in a transect off Cork, Ireland. Although we have not described all species of *Heteromesus* (other new species are known to us from the Gulf of Mexico and from Woods Hole Oceanographic Institution (WHOI) collections in the Atlantic), reviewing scattered taxonomic works will allow a more thorough treatment of the systematics of the genus and the biogeography of the Atlantic deep sea.

### Generic type status

*Heteromesus* Richardson, 1908 was established for three species previously included in the genus *Ischnosoma*, *I. thomsoni* Beddard, 1886, *I. spinosum* Beddard, 1886, and *I. greeni* Tattersall, 1905, and two new species, *H. spinescens* and *H. granulatus*. Birstein (1960) and Wolff (1962: 87, 265) clearly placed *I. thomsoni* in *Haplomesus* but Menzies (1962) designated this species as the type species for *Heteromesus*. This action effectively made *Heteromesus* a subjective synonym of *Haplomesus*. Because Wolff's (1962) authoritative revision has taken precedence over Menzies (1962), no later taxonomic work on the Ischnomesidae (e.g., Kussakin 1988: 472–473), has recognised the establishment of the type species of *Heteromesus* by Menzies (1962). In order to preserve current usage and avoid instability or confusion, Merrin and Poore (2002: Case 3198) proposed to conserve the generic name *Heteromesus* Richardson, 1908 by designating *Heteromesus granulatus* Richardson, 1908 as the type species. The ruling of the ICZN commission (2004: Opinion 2062) set aside all previous fixations of type species for *Heteromesus* Richardson, 1908 and designated *Heteromesus granulatus* Richardson, 1908 as the type species. We further solidify the generic concept by redescribing *H. granulatus* and providing a new diagnosis for the genus.

### Material and methods

#### *Study sites*

The Lucky Strike segment is located at the Mid-Atlantic Ridge (MAR) southwest of the Azores (Fouquet *et al.* 1994). The hydrothermal field, centred at 37°17.5'N 32°16.5'W,

is one of the largest currently known in the MAR and develops around a lava lake at approximately 1700 m in a depression surrounded by three volcanic cones. The lava lake, the first discovered in a slow spreading ridge (Fouquet *et al.* 1995) is characterised by typical lobate and draped lavas, lava flows and lava pillars. The volcanoes are mostly composed of pillow lavas and volcanic breccia. Many chimneys and other edifices, most of which are inactive or only mildly active, surround the lava lake. Near large chimneys, diffuse venting occurs through unconsolidated sediments. In west Greenland, the studied canyon extends from the upper continental slope into the deep-water basin from 1700 to 2400 m deepening to the south and bordering the western margin of the Fylla Structural Complex. From the canyon flanks was recovered a wide range of rocks from weathered Precambrian gneiss to sub-recent marly mudstone (Dalhoff *et al.* 2004).

#### *Source of specimens*

Specimens from Lucky Strike were collected during a geological survey of the vent field (2000) by a joint program of the Geological and Mining Institute of Portugal, Moscow State University and University of Aveiro (TTR-10, IOC-UNESCO). Specimens from the canyon bordering the Fylla Structural Complex were collected during a geological survey (2003) by a joint program of the Geological Survey of Denmark and Greenland (GEUS) and Moscow State University (TTR-13, IOC-UNESCO). A deep benthic sampling transect off Ireland conducted by WHOI (1972) under the direction of Howard Sanders, Robert Hessler and J. Frederick Grassle, provided the specimens from Cork (CHAIN cruise n°106; WHOI).

Preparation and illustration of specimens, measurements and reporting of ratios follows the methods outlined in Wilson (1989). Some specimens or interesting parts thereof were dehydrated in an ascending ethanol gradient and critical point dried. The material mounted on stubs was sputter-coated with gold-palladium and observed and photographed with a scanning electron microscope. The descriptions of species were generated from the program DELTA (Dallwitz 1980; Dallwitz *et al.* 2000a,b) and uses the terminology of Wilson (1989) and Kavanagh *et al.* (2006).

#### *Morphological terms and characters in the Ischnomesidae*

For this study, we introduce terms additional to the glossary in Wilson (1989) to account for special morphologies in the Ischnomesidae. Because of the distinctive rugose ornamented cuticle of *Heteromesus* species, new terms for spine shapes are necessary.

##### *Cuticular ornamentation*

*Spine*: outpocketing of cuticle that is confluent with the cuticle at its base (not articulated).

*Tubercle*: a small round outpocketing of cuticle, approximately hemispherical, length < width (alternatively a small round firm swelling or nodule on the surface of body or limbs).

*Simple spine*: a pointed (acute or conical) spine, with or without terminal simple seta.

*Bifid spines*: a spine with 2 terminal points; sometimes looking like an anvil.

*Pedestal spine*: sub-cylindrical spine (usually slightly enlarged at its base), topped by a simple or a robust seta.

*Rook spine*: sub-cylindrical spine with distal “embattlement” of denticles, usually topped with a simple seta. We call these “rook spines” owing to their similarity to the chess piece. Often rook or bifid spines will be accompanied by simple spines.

*Spine size*: short, stout and long refers to the ratio between length and width (L/W)  $\approx 1$ , 1–2, >2, respectively.

*Robust setae*: distinctly broad at base, are thick through most of their length and generally have a subdistal sensillum.

*Simple or fine setae*: narrow bases, tapering rapidly and not thick, appear to be flexible, and often curled or coiled distally.

*Ornamentation not serially homologous*: each segment of Ischnomesidae (in particular) has ornamentation that independently assorts on the somites. As a result, all such characters are treated somite by somite, rather than having single characters that cross somite boundaries (e.g., “anterolateral spines on pereonites 1–3” as a single character).

#### *Head*

*Labrum knobs*: rounded, spiny or conical anterolateral projections of the labrum (see arrow heads on Fig. 9).

*Lateral lobes*: broadly rounded ventral projections of the head surface that overlap the insertion of the mandibles.

#### *Pleotelson*

*Dorsal surface axial ridge*: refers to the division of the pleotelson into sections, in dorsal view; although this character may describe a continuum from a fully smoothly arched dorsal surface to a strongly convoluted dorsal surface, the three states can be clearly distinguished using the demarcation between the lateral fields and the central ridge. The first state is a simple vaulted surface with no indentation; the second state includes parallel axial indentations between the central ridge and the lateral fields, but they are smoothly curving and not deep; in the third state, the parallel axial indentations are angular and show as distinct lines in dorsal view.

*Posterolateral margin at uropod insertion*: many *Heteromesus* and other species have a distinctly produced insertion of the uropod, so that the uropod emerges from a ring of cuticle that is distinct from the line of the posterolateral margin. Some *Haplomesus* species have a large posterolateral spine adjacent to the uropods but the margin in the insertion of the uropod is not distinctly produced and can be said to be uninflected. Sometimes the uropod of *Haplomesus* species is set in a distinct concavity.

#### *Antennula*

*Article 2 insertion on article 1*: The position of insertion of article 2 varies within the Ischnomesidae from anterodorsal to dorsal. Many species, such as in *Heteromesus*, appear

to insert more or less on near the posterior margin of article, viewed in dorsal view. This character should not be confused with the direction of the second article's projection, which can be modified by a strong bend in the article near the insertion, as in *Heteromesus*.

*Distal articles including article 3.* Antennula articles 3 and 4 (if present) are not flagellar, and one could argue that article 5 was not flagellar as well, owing to a distinct difference between this article and distal true flagellar articles in many isopods. Nevertheless the basal two articles are different from the distal articles in many ischnomesids, they are sometimes referred to as "flagellar articles" because they appear to be "flagellar." We have avoided referring to the "flagellum" in the antennula.

#### *Pereopods*

*Shaft:* elongated part of the basis.

*Shoulder:* proximal part of the shaft of the basis, often armed with simple, bifid or rook spines.

*Neck:* connection between the hemispherical proximal part of the basis that inserts into the coxa and the shaft of the basis.

#### *Pereopod I*

*Palm:* The ventral margin of the carpus opposes the propodus (in asellotan propodocarposubchelate taxa). In this family, the palm is the margin that is distal to one or more large elongate robust setae on the ventral margin. The length of the palm varies considerably across the Ischnomesidae, from long palms in *Ischnomesus*, to fairly short palms in *Heteromesus*. Some taxa, like *Haplomesus*, have undeveloped palms and the first pereopod is nearly walking leg like. If several long setae are present, then the palm will be the region defined by opposition to the propodus. Setae tend to occur in two distinctly different sizes in many Ischnomesidae, with the elongate robust setae defining the proximal margin of the palm.

*Carpus proximal ventral margin:* This region is proximal to the palm on the ventral margin of the carpus.

*Strongly carposubchelate:* This describes a pereopod I that is distinctly shorter than more posterior pereopods and the propodus and dactylus reflex against an elongate carpus, with a well developed major hinge between the carpus and propodus. Many Ischnomesidae have an additional flexure between the dactylus and propodus. "Weakly carposubchelate" is used for first pereopods where the limb is distinctly shorter than more posterior pereopods and the propodus and carpus have a major hinge. It differs from strongly carposubchelate because the carpus is largely tubular, weakly setose and has no distinctly enlarged or projecting parts of the ventral margin. In such limbs, the propodus-dactylus flexure is similar to that for the carpus-propodus articulation.

#### *Pleopods*

*Lateral hoods:* paired projections of the male's pleopod I distal margin; they form a seat for the distal tip of the pleopod II stylet.



*Abbreviations*

Figure Annotations. Figures use descriptive abbreviations to minimise the figure captions. **Hd**, cephalon or head; **P1–P7**, pereonite 1–7; **PL1**, pleonite 1; **PLn**, pleotelson or pleon; **Au**, antennula; **An**, antenna; **La**, Labrum; **Mnd**, mandible; **Pg**, paragnath; **Mu**, maxillula; **Mx**, maxilla; **Mxp**, maxilliped; **PI–PVII**, pereopod I–VII; **PLI–PLV**, pleopod I–V; **Apm**, appendix masculina (distal part of endopod of male pleopod II); **Op**, operculum (female pleopod II); **Ur**, uropod; **En**, endopod; **Ex**, exopod; **Vn**, ventral view; **Ds**, dorsal view; **Lt**, lateral view; **Fn**, frontal view; **rt**, right side; **lf**, left side.

Institutional abbreviations. AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; DBUA, Department of Biology, University of Aveiro (Biological Research Collection), Portugal; NHM, Natural History Museum London (previously BMNH, British Museum of Natural History, London); MNHN, Muséum national d'Histoire naturelle, Paris; USNM, United States National Museum of Natural History, Washington; WHOI, Woods Hole Oceanographic Institution; ZMUC, Zoologisk Museum, University of Copenhagen, Denmark

*Implicit attributes*

Unless indicated otherwise, the following attributes are implicit throughout the descriptions, except where the characters concerned are inapplicable. These implicit characters substantially reduce the size of the descriptions (see also Just & Wilson 2004; Kavanagh *et al.* 2006).

## Description

*Body* elongate, with broad and subcylindrical regions, smooth; with only scattered setae; *head* embedded in and fused with pereonite 1; *pereonite 5* freely articulated with pereonite 6, *pereonite 6* fused with pereonite 7, *pereonite 7* fused with pleon, *pleonite 1* fused with pleotelson; *pereonites 4 and 5* elongate, produced backwards and forwards, respectively; *pereonites 5–7* narrowing posteriorly; *pereonite 7* length not reduced, similar to pereonite 6; tergites not projecting. *Head* dorsal surface without bulges or protuberances; antennae emerging directly from head; in female with no spines or tubercles. *Pereonites 1–3* in female with no median dorsal tubercle or spine, no paired dorsal spines or tubercles, no anterolateral spines, no lateral spines or tubercles. *Pereonite 4* in female with no median dorsal spine or tubercle, no paired dorsal spines or tubercles, no anterolateral spines, no posterolateral spines or tubercles. *Pereonite 5* with no spines or tubercles; no posterodorsal spines or tubercles, no posterolateral spines or tubercles; in female with no lateral row of spines or tubercles. *Pereonites 6–7* with no dorsal spines or tubercles; no lateral spines or tubercles. *Pleonite 1* region of pleotelson with no dorsal spines or tubercles; no lateral spines or tubercles. *Pleotelson* dorsal surface axial ridge medially smoothly arched; with no dorsal spines or tubercles; with no lateral spines or tubercles; posterolateral margin anterior to uropods without spines or tubercles; terminal margin with no spines or tubercles.

*Antennula* article 1 squat and globular, with no spines; article 2 length greater than 3.0 length of article 1, strongly curved at proximal insertion, distal tip not produced distally, next article inserting apically; lateral margin without row of robust setae. *Antennula* terminated with aesthetasc. *Antenna* article 2 with no lateral spines, no ventromedial spines; article 3 length at least twice article 4 length, cuticle granulate, with no distal spines, no ventral spines, no ventromedial spines and no dorsal spines.

*Mandible* palp absent. *Maxilliped endite* with 3 receptaculi; *palp* shorter than basis, at widest point width narrower than endite, with articles 1–3 wider than articles 4–5, articles 2 and 3 width subequal, epipod setae absent.

*Pereopod bases* with conspicuous neck connecting shaft to coxal articulation, proximal part of shaft projecting dorsally above shoulder; proximal shoulder with no spines. *Pereopod I* strongly carposubchelate, differs from *pereopod II*; *carpus* ventral margin without pectinate setae, with 1 elongate robust seta. *Pereopod I* with one dactylar claw. *Pereopod VII* present, as long as *pereopod VI*. *Pereopods II–VII bases* smooth, with no spines; *ischia* without spines.

*Pleopod III* exopod length more than half endopod length, endopod with 3 plumose setae. *Pleopod IV* without exopod.

*Male specific characters.* *Head* with no spines or tubercles. *Pereonites 1–3* with no median dorsal tubercle or spine, no paired dorsal spines or tubercles, no anterolateral spines, no lateral spines or tubercles. *Pereonite 4* with no median dorsal spine or tubercle, no paired dorsal spines or tubercles, no anterolateral spines, no posterolateral spines or tubercles. *Pereonite 5* with no lateral row of spines or tubercles. *Pleotelson* posterolateral margin anterior to uropods with no spines or tubercles. *Antenna* article 3 with no distal spines, no ventral spines, no ventromedial spines, no dorsal spines; flagellum decreasing in width distally, articles, tubular, longer than wide. *Pleopod I* length more than twice proximal width, with no setae on distal margins, without simple setae on lateral margins, lateral margins indented midway along length. *Pleopod II* protopod with setae on lateral and distal margin.

## Systematics

### *Heteromesus* Richardson, 1908

*Heteromesus* Richardson 1908: 81; Hansen 1916: 66; Gurjanova 1932: 44; Wolff 1956: 141; Menzies 1962: 121; Wolff 1962: 84; Birstein 1971: 200; Chardy 1974: 1543; Kussakin 1988: 472.

Type species. *Heteromesus granulatus* Richardson, 1908

### Diagnosis

*Pereonite 5* freely articulated with *pereonite 6*, articulations not expressed between

pereonite 6, pereonite 7, pleonite 1 and pleotelson. *Pereonite 4* produced posteriorly but always broader than long (L/W less than 0.70 in female and 0.85 in male). *Pleotelson* dorsal surface axial ridge strongly vaulted, separated from lateral fields by distinct indented lines; posterolateral margin at uropod insertion produced from margin. *Antennula* article 1 globular, article 2 inserting dorsally; article 2 strongly curved anteriorly at proximal insertion; articles distal to article 2 reduced to 1–3 articles, distal articles altogether tiny, length less than 0.3 article 2 length. *Mandible* palp absent. *Pereopod bases* with conspicuous neck connecting shaft to coxal articulation, proximal part of shaft projecting dorsally into shoulder. *Pereopod I* carpus distally expanded, widest point distal to midpoint of carpus, with 1 elongate robust seta and a proximal shorter robust seta. *Pleopod II* female operculum with narrow proximal neck, almost circular posteriorly, with plumose setae. *Pleopod III* exopod with plumose setae and fringe of fine setae. *Pleopod V* absent. *Uropod* uniramous, with single article, conical, tapering distally; extending beyond posterior margin of pleotelson.

#### Remarks

Among the Ischnomesidae, species of *Heteromesus* are most easily recognised by their tiny to rudimentary antennular articles distal to article 2, a pereonite 4 that is always near the same length as the anterior pereonites, an often elongate tapering distally uropod and a typically rugose cuticle, with many short spines or tubercles. *Heteromesus* species lack long spines on pereonites 5–7, and pereonite 4 is never elongate as it often is among other Ischnomesidae. All species of *Heteromesus* that we have examined also lack pleopod V, a common trait for many Ischnomesidae. This, however, is not a general feature for the family because a small oval pleopod V is present in *Haplomesus celticensis* Kavanagh, Wilson & Power, 2006.

Regarding the antennula, we prefer to not use the term “flagellum” because, technically speaking, article 3 is not flagellar but is part of the protopod. Therefore, the tiny distal articles on the antennula may not be homologous to the true flagellar articles, that is, articles distal to article 3. An additional problem emerges here as well: we don't know the exact composition of the distal articles because podomere loss (i.e., of article 3) could be one path for reduction, but non-expression of the articulations between antennular articles could be an alternative pathway. On the basis of the evidence available here, one cannot decide. This problem requires a broader understanding of the antennular patterns across the family.

#### Key to species of *Heteromesus*

Users of this key should be aware that many species included here are incompletely known, either from only one sex or from fragments. Several species (e.g., *H. longiremis* and *H. bifurcatus*) appear several times in the key because of this incompleteness. *H. longiremis* also appears either as *H.*

*longiremis* Hansen, 1916 or *H. longiremis* sensu Chardy, 1974 because the specimens described by Chardy (1974) are at variance with Hansen's original description. Undescribed species of *Heteromesus* are known to us, so specimens from localities different than the current species may not key out accurately. As a result, a successful identification from this key should be compared with the descriptions below to ensure that the correct choice has been made.

1. Pleotelson terminal margin with no spines or tubercles ..... 2
- Pleotelson terminal margin with pedestal spines ..... 15
- 2(1). Pleonite 1 region of pleotelson and pleotelson with no dorsal spines or tubercles .... 3
- Pleonite 1 region of pleotelson and pleotelson with dorsal rook spines .....  
     ..... *Heteromesus dentatus* Hansen, 1916
- Pleonite 1 region of pleotelson and pleotelson with dorsal tubercles ..... 14
- 3(2). Pereopods II–VII bases with no spines ..... 4
- Pereopods II–VII bases with simple spines..... 12
- Pereopods II–VII bases with pedestal spines ..... 13
- 4(3). Pleotelson posterolateral margin anterior to uropods without spines or tubercles .... 5
- Pleotelson posterolateral margin anterior to uropods with simple spines .....  
     ..... *Heteromesus bifurcatus* Menzies, 1962
- 5(4). Pereonite 5 in female length up to 2.54 width ..... 6
- Pereonite 5 in female length 2.55 width or more ..... 10
- 6(5). Antennula with up to 3 articles altogether ..... 7
- Antennula with 5 articles altogether..... 8
- 7(6). Pereonite 1 in female with no median dorsal tubercle or spine, no paired dorsal spines or tubercles and no lateral spines or tubercles; pereonite 2 in female with no lateral spines or tubercles..... *Heteromesus frigidus* Hansen, 1916
- Pereonite 1 in female with median tubercle and dorsal tubercles and with paired lateral simple spines; pereonite 2 in female with paired lateral tubercles .....  
     ..... *Heteromesus schmidtii* Hansen, 1916
- 8(6). Antennula article 3 short and tubular, length near width, length similar to article 4 ..  
     ..... *Heteromesus oryktus* sp.nov.
- Antennula article 3 squat, wider than long, longer than article 4 ..... 9
- 9(8). Antennula article 2 with 3 elongate stiff ventromedial setae; antennula article 2 distal tip produced distally beyond insertion of next article, distal article inserting subapically; antenna article 2 with no ventromedial spines; pereopod I carpus palm length distinctly less than proximal region length .....  
     ..... *Heteromesus longiremis* sensu Chardy, 1974
- Antennula article 2 with 4 elongate stiff ventromedial setae; antennula article 2 distal tip not produced distally, next article inserting apically; antenna article 2 with 1 ventromedial spine; pereopod I carpus palm length near proximal region length .....  
     ..... *Heteromesus greeni* (Tattersall, 1905)

- 10(5).Pereonite 5 length in male up to 5.94 width .....  
 ..... *Heteromesus longiremis* sensu Chardy, 1974  
 Pereonite 5 length in male 5.95 width or more ..... 11
- 11(10).Pereonite 2 in female with no median dorsal spine or tubercle, no paired dorsal spines or tubercles and no anterolateral spines; pereonite 3 in female with no median dorsal spine or tubercle .....*Heteromesus inaffectus* sp.nov.  
 Pereonite 2 in female with median tubercle and dorsal tubercles and with 1 pair of anterolateral simple spines; pereonite 3 in female with median tubercle .....  
 ..... *Heteromesus longiremis* Hansen, 1916
- 12(3).Antennula with up to 3 articles altogether, article 2 with 4 elongate stiff ventromedial setae, article 3 squat, wider than long .....  
 .....*Heteromesus granulatus* Richardson, 1908  
 Antennula with 5 articles altogether, article 2 with 3 elongate stiff ventromedial setae, article 3 elongate and tubular, much longer than wide .....  
 ..... *Heteromesus spinescens* Richardson, 1908
- 13(3).Antennula with up to 3 articles altogether; antenna article 3 with distomedial and distolateral spines and no ventromedial spines .....*Heteromesus calcar* sp.nov.  
 Antennula with 5 articles altogether; antenna article 3 with no distal spines; antenna article 3 in male with ventromedial spines.....*Heteromesus similis* Richardson, 1911
- 14(2).Pleopod II protopod apex narrow, tapering; pleopod II stylet tapering and pointed not extending to distal margin of protopod; antennula article 2 with 3 elongate stiff ventromedial setae.....*Heteromesus wolffi* Chardy, 1974  
 Pleopod II protopod apex rounded; pleopod II stylet thick and blunt extending beyond distal margin of protopod; antennula article 2 with 4 elongate stiff ventromedial setae ..... *Heteromesus drachi* Chardy, 1974
- 15(1).Pereonite 4 in female with no anterolateral spines; pereonite 1 in female with median pedestal spine and with dorsal pedestal spines; pereonite 1 anterolateral spines in female length distinctly less than length of pereonite 1 .....  
 ..... *Heteromesus ctenobasius* sp.nov.  
 Pereonite 4 in female with 1 pair of anterolateral simple spines, with median rook spine and dorsal rook spines; pereonite 1 anterolateral spines in female length near pereonite 1 length ..... *Heteromesus spinosus* (Beddard, 1886)

### Species of *Heteromesus*

#### *Heteromesus bifurcatus* Menzies, 1962

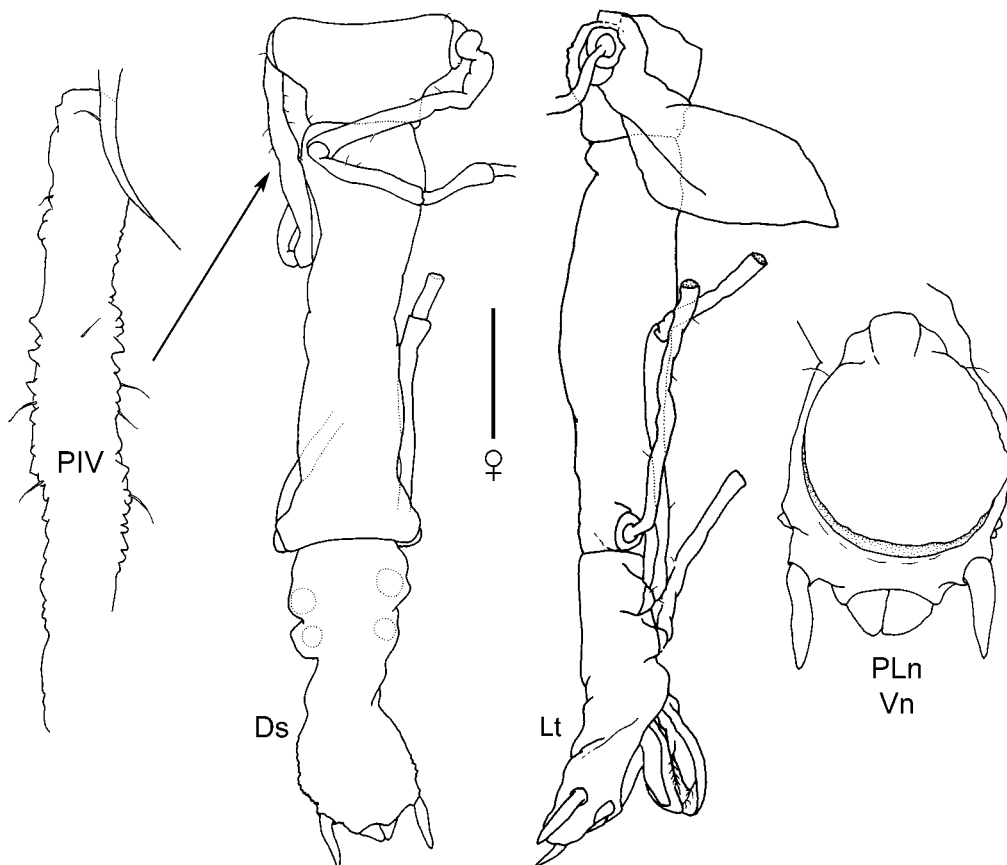
(Figure 1)

*Heteromesus bifurcatus* Menzies 1962: 122, fig. 22C; Wolff 1962: 85, 265.

*Material examined*

*Holotype*: brooding female (fragment, 4 mm), North Atlantic, Caribbean, Colombia Abyssal Plain, 14°05'N, 75°25'W, 7 Nov 1958, R/V Vema stn V-15-9 (Biotrawl n°94), 4077 m (AMNH 12061).

*Remarks on type material*: The holotype is a headless fragment of a brooding female (pereonites 4–7 and pleotelson with some incomplete pereopods). The fragment is deformed and decalcified (almost transparent). The suture between pereonite 5 and 6 is evident. The spine on each side of the pleon that was drawn and described by Menzies (1962: 122, fig. 22C) is not evident in dorsal view, but can be seen in ventral view. The spines, however, are damaged and present only as stubs in this specimen.



**FIGURE 1.** *Heteromesus bifurcatus* Menzies, 1962. Holotype female, AMNH 12061: Pereopod IV basis; habitus dorsal and lateral; pleotelson ventral. Scale bar 0.5 mm.

*Diagnosis (Female only)*

Pereonite 5 length 2.8 width. Pleotelson pleonite 1 region with no dorsal spines or tubercles; posterolateral margin anterior to uropods with simple spines. Pereopod bases proximal shoulder with no spines; pereopods II–VII bases granulate, with no spines. Uropods length 0.40–0.45 length of pleotelson.

*Description (Female characters only)*

Body length 4 mm (approximately; fragment); granular. *Pereonite 4* length 0.60 width. *Pleotelson* length 1.15 width; posterolateral margin at uropod insertion produced from margin; posterolateral margin anterior to uropods with low and broad posterolateral spines (damaged, possibly with distal seta).

*Distribution*

North Atlantic, Caribbean, Columbia Abyssal Plain, 4077 m.

*Remarks*

Menzies (1962: 122) commented that *H. bifurcatus* is similar to *H. dentatus*, but differs from it by having an incision in the pleotelson. This is in error because the pleotelson is not incised and only the anal plates are seen in dorsal view. Ischnomesidae have anal openings and the associated plates close to the terminus of the pleotelson. This condition is similar to that of the Munnidae where the anus and anal plates are completely terminal. Ischnomesids, however, have the anus somewhat covered by the dorsal surface of the pleotelson and the anus itself is somewhat angled under the body. Some badly preserved specimens, as in this case, will show the anal plates in dorsal view.

In fact, *H. bifurcatus* is unlike other species that also have spines on the posterolateral margin of the pleotelson, because it apparently lacks other distinctive features such as dorsal rook spines (as in *H. dentatus*), or elongate spines on the pereopods (as in *H. spinosus*). The male and the head of the female, however, are unknown, so this species remains poorly characterised.

***Heteromesus calcar* sp. nov**

(Figs 2–6)

*Etymology*

*Calcar* means spur, and is used as a noun in apposition.

*Material examined*

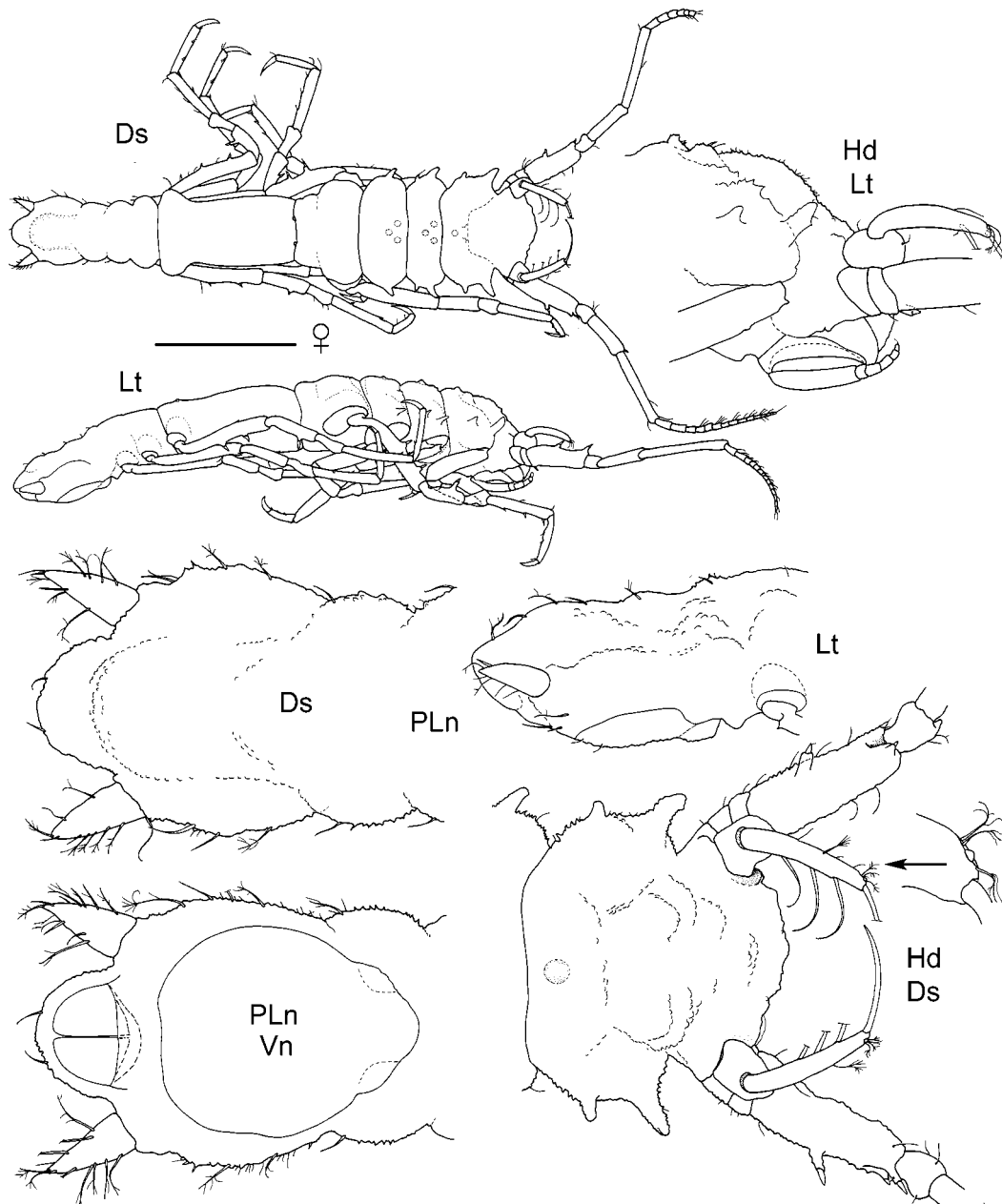
*Holotype*: female (3.7 mm), North Atlantic, Mid-Atlantic Ridge, Lucky Strike, 37°17.4'N, 32°16.6'W, 10 Aug 2000, R/V Prof Logachev, TTR10 stn AT-265-GR, 1685 m (ZMUC CRU-9878).

*Paratypes*: male (3.2 mm), same data as holotype (ZMUC CRU-9879); 1 male (3.0 mm) same data as holotype, (dissected, mouthparts on slide AM P 72117); 3 females, 1 male, 1 intersex, 2 fragments (heads), same data as holotype (AM P 72118).

*Other material*: 1 female, same locality as holotype, 37°17.5'N, 32°16.9'W, 11 Aug 2000, R/V Prof Logachev, TTR10 stn AT-271-GR, 1712 m (DBUA 786.01); 2 females, 1 manca, same locality as holotype, 37°17.4'N, 32°16.6'W, 11 Aug 2000, R/V Prof Logachev, TTR10 stn AT-273-GR, 1675 m (DBUA 786.02).

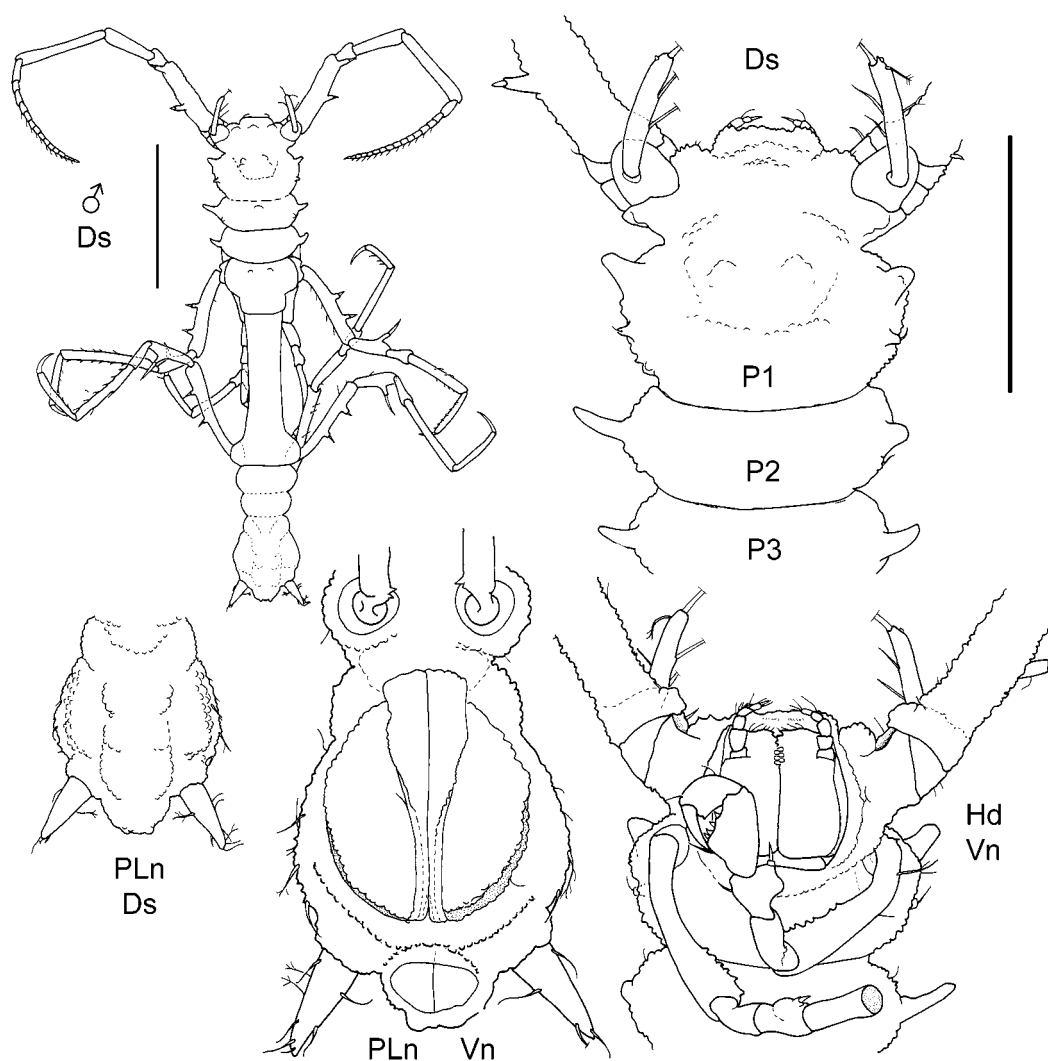
*Diagnosis*

Pereonites 1–3 with anterolateral spines. Pereonite 2 in female with no paired dorsal spines or tubercles. Pereonite 5 in female length 2.0 width, in male 6.3 width. Antennula with 3 articles altogether. Pereopods IV–V bases with pedestal spines; ischia with elongate pedestal spines.



**FIGURE 2.** *Heteromesus calcar* sp. nov. Holotype female, ZMUC CRU-9878: Habitus dorsal and lateral; head lateral and dorsal; pleotelson dorsal lateral and ventral. Scale bar 1.0mm.

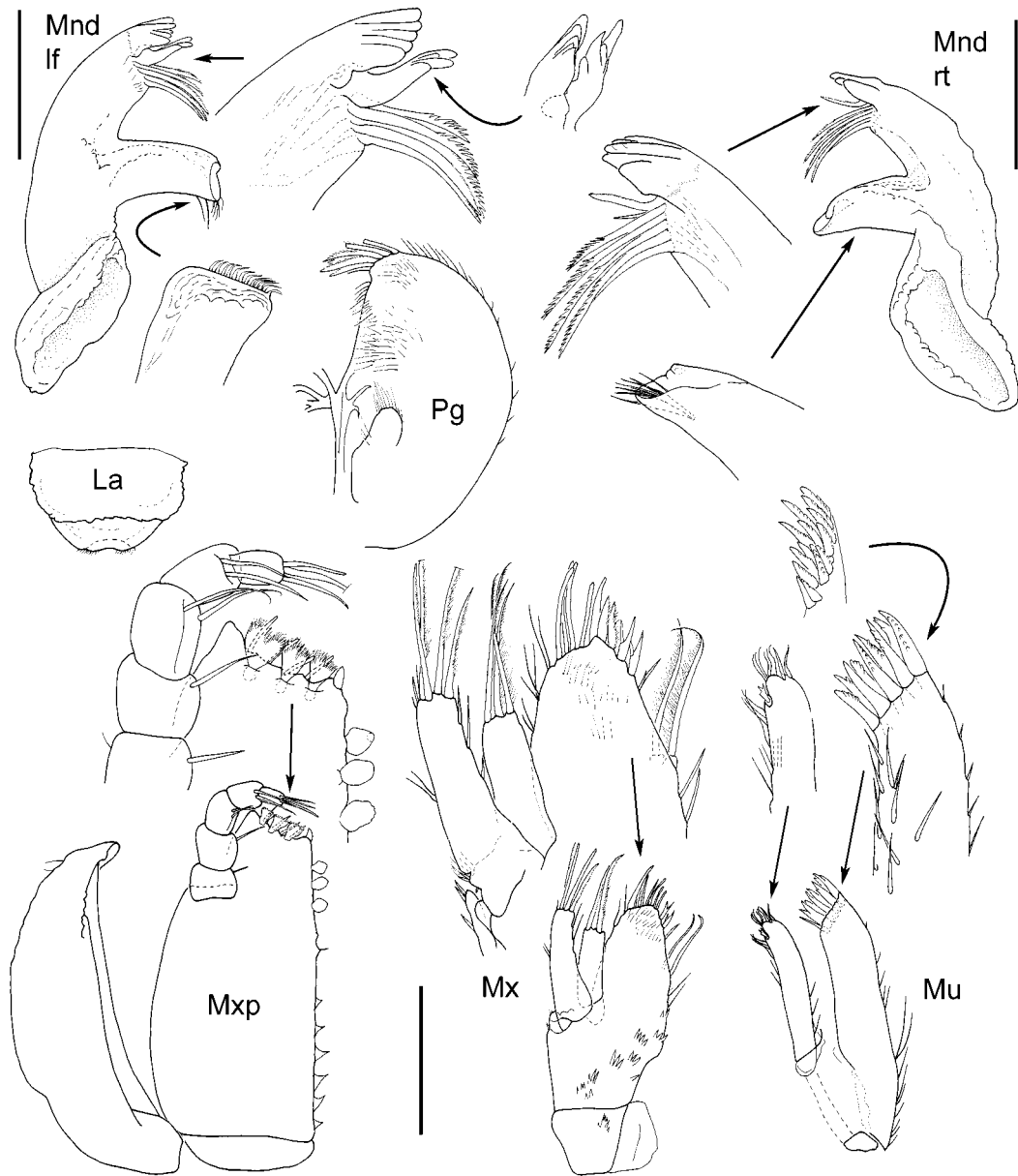




**FIGURE 3.** *Heteromesus calcar* sp. nov. Paratype male, ZMUC CRU-9879: Habitus dorsal, scale bar 1.0mm; head dorsal and ventral, scale bar 0.5mm; pleotelson dorsal and ventral.

#### *Description*

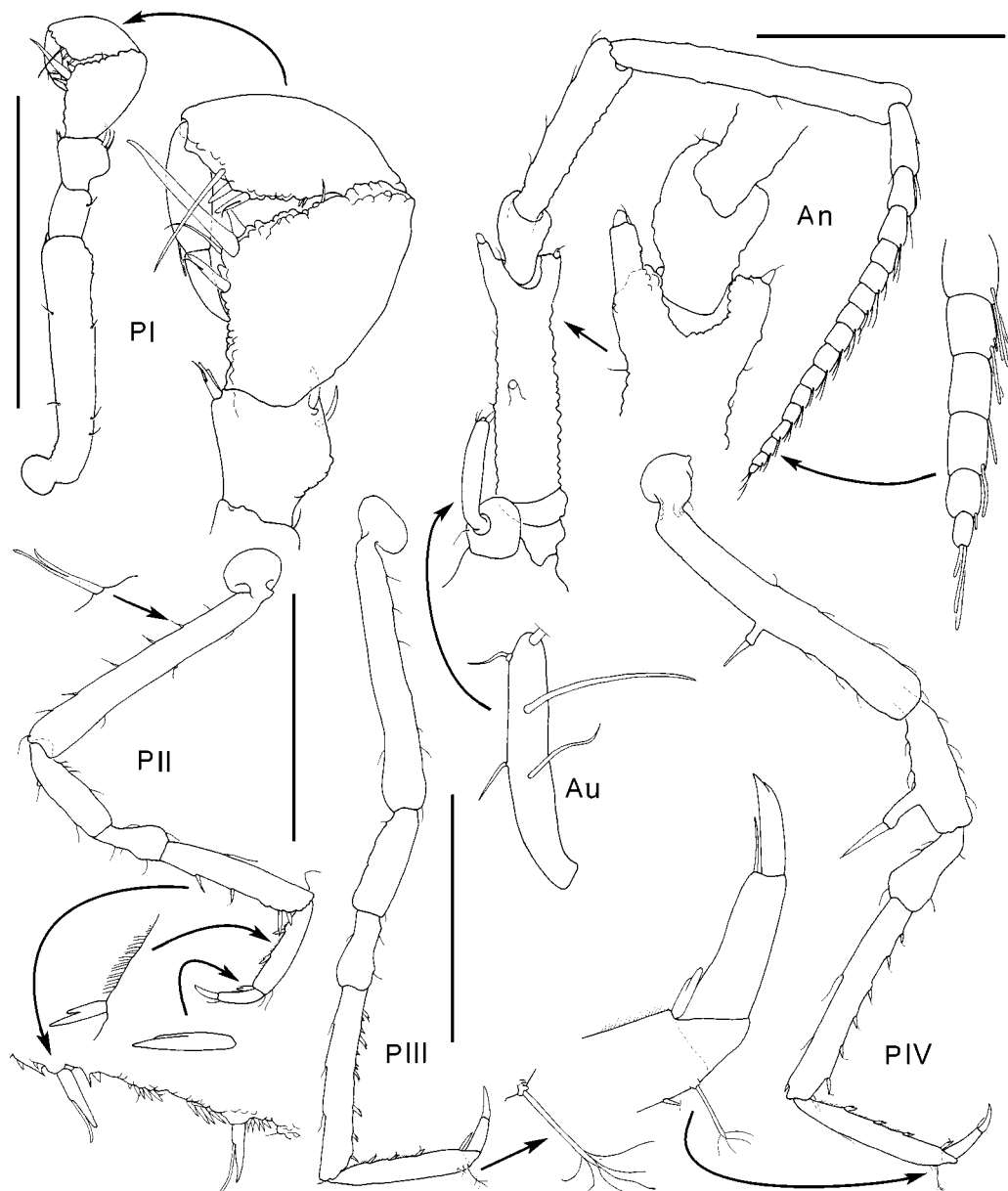
*Body* length in female 3.7 mm; granular. *Head* in female length 0.95 width; dorsal surface with pair of cephalic bullae; lobe on ventrolateral margin present in lateral view; dorsal cuticle tubercular granulation. *Pereonite 1* in female width 0.2 total body length; with median tubercle, 1 pair of anterolateral simple spines, 1 pair of lateral simple spines. *Pereonite 2* in female with median tubercle, 1 pair of anterolateral simple spines, 1 pair of lateral spines. *Pereonite 3* in female with median tubercle, 1 pair of anterolateral simple spines. Female pereonites 1–3 anterolateral simple spines stout to long decreasing in length from pereonite 1 to 3, anterolateral spines length distinctly less than length of pereonite 1, lateral simple spines short. *Pereonite 4* in female length 0.65 width. *Pereonite 5* in female length 0.25 total body length. *Pleotelson* in female length 1.35 width; terminal margin without distal tubercles (only in male).



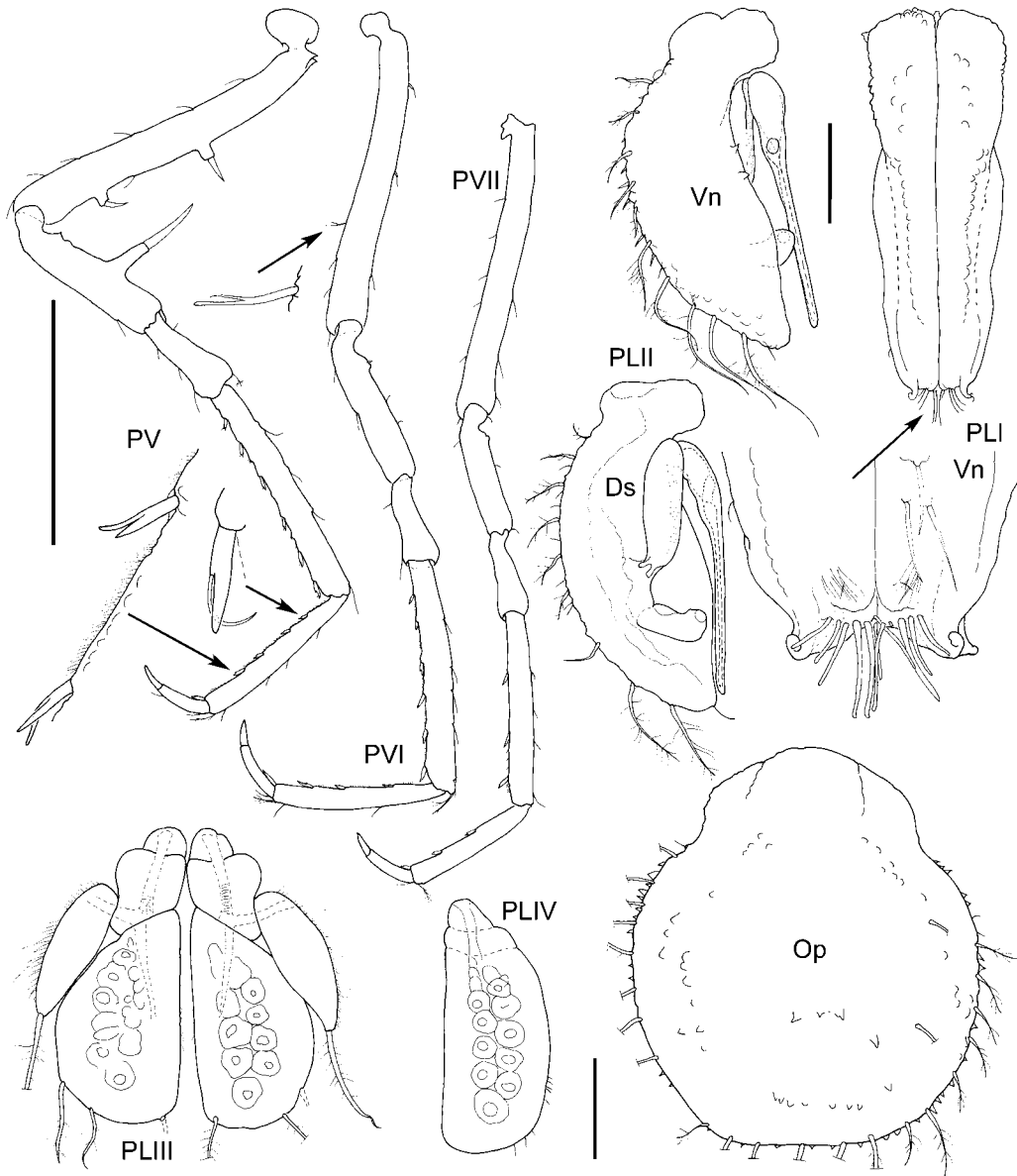
**FIGURE 4.** *Heteromesus calcar* sp. nov. Paratype male dissected, AM P 72117: mandible left and right; labrum; paragnath; maxilliped; maxilla; maxillula. Scale bars 0.1 mm.

*Antennula* with 3 articles altogether; article 2 length in female 0.65 head width, with 4 elongate stiff ventromedial setae, distal tip produced distally beyond insertion of next article, distal article inserting subapically; article 3 terminal, squat, wider than long. *Antenna* in female length 2.7 anterior body length; article 2 with 1 ventromedial pedestal spine; article 3 length 0.28 anterior body length, length 2.6 width, with distomedial and

distolateral pedestal spines and 1 dorsal pedestal spine placed midlength; article 5 length 0.15 anterior body length; article 6 length 0.31 anterior body length; flagellum with 15 articles, flagellum length 0.37 total antenna length.



**FIGURE 5.** *Heteromesus calcar* sp. nov. Holotype female, ZMUC CRU-9878: Pereopods I to IV; antenna; antennula. Scale bars 0.5mm.



**FIGURE 6.** *Heteromesus calcar* sp. nov. Holotype female, ZMUC CRU-9878. Pereopods V to VII, scale bar 0.5mm; operculum, scale bar 0.1mm. Paratype male dissected, AM P 72117: pleopods I–IV, scale bar 0.1mm.

*Labrum* knobs low. *Maxilliped* palp article 2 wider than 3.

*Pereopod* bases proximal shoulder with simple spines only. *Pereopod I* *merus* dorsal margin with 2 distinctly robust setae, placed distally; *carpus* palm length near proximal region length, with 1 robust seta on palm distal to elongate seta; *propodus* ventral margin with 2 robust setae. Pedestal spines only on dorsal margin of bases and ischia of pereopods IV and V, 1–2 long pedestal spines topped by long robust seta on basis and 1 pedestal spine on ischium.

*Uropods* in female extending near posterior margin of pleotelson; length 0.25 length of pleotelson.

*Male specific characters.* Body length 3.2 mm. Head length 1.0 width; with 4 tubercles. *Pereonite 1* width 0.20 total body length; with 1 pair of anterolateral simple spines, 1 pair of lateral simple spines. *Pereonite 2* with median tubercle, 1 pair of anterolateral simple spines, 1 pair of lateral spines. *Pereonite 3* with median tubercle, 1 pair of anterolateral simple spines. *Pereonite 4* with 1 pair of dorsal tubercles. *Pereonite 1–3* anterolateral simple spines stout to long decreasing in length from pereonite 1 to 3, lateral simple spines short. *Pereonite 4* length 0.75 width. *Pereonite 5* length 0.40 total body length. *Pleotelson* length 1.25 width; terminal margin with 1 pair of distal tubercles. *Antennula* article 2 length 0.47 head width. *Antenna* length 2.0 anterior body length; article 3 length 0.40 anterior body length, length 4.5 width, with distomedial and distolateral pedestal spines and 1 dorsal pedestal spine placed midlength; article 5 length 0.27 anterior body length; article 6 length 0.47 anterior body length; flagellum length 0.32 total antennal length, flagellum with 15 articles. *Pleopod I* distal tip with lateral horns. *Pleopod II* protopod apex rounded, stylet tapering and pointed, not heavily calcified, extending beyond distal margin of protopod. *Uropods* length 0.35 length of pleotelson.

#### *Distribution*

North Atlantic: Mid-Atlantic Ridge, Lucky Strike hydrothermal field, 1675–1712 m, on hydrothermal sulphide deposits, sulphide rubble and volcanic rocks, close to active hydrothermal chimneys, known only from type locality.

#### *Remarks*

*Heteromesus calcar* **sp. nov.** is similar to *H. frigidus*, *H. granulatus*, *H. inaffectus* and *H. schmidti* in having altogether 3 antennular articles, and by the tubercular granulation and inconspicuous ornamentation (few spines) of the body. It differs from these species in having anterolateral spines on pereonites 1–3. The most distinctive feature is the presence of long pedestal spines only on dorsal margin of the basis and ischium of pereopods IV and V (also seen in *H. spinosus* and *H. ctenobasius*).

#### ***Heteromesus ctenobasius* sp. nov.**

(Figs 7–12)

#### *Etymology*

The name pertains to the comb-like basis of the pereopods.

#### *Material examined*

*Holotype:* female (4.3 mm), North Atlantic, Mid-Atlantic Ridge, Lucky Strike, 37°17.4'N, 32°16.6'W, 10 Aug 2000, R/V Prof Logachev, TTR10 stn AT-265-GR, 1685 m (ZMUC CRU-9874).

*Paratypes:* male (4.3 mm), same data as holotype (ZMUC CRU-9875); 2 females, 1 fragment, same data as holotype (AM P 72119).

*Other material:* female, same locality as holotype, 37°17.3'N, 32°16.5'W, 8 Aug 2000, R/V Prof Logachev, TTR10 stn AT-250-GR, 1704 m (SEM stub AW575, AM P 72120); 1 female, same locality, 37°17.5'N, 32°16.9'W, 10 Aug 2000, R/V Prof Logachev, TTR10 stn AT-262-GR, 1720 m (DBUA 787).

*Remarks on type material.* Male pereonites 2 and 3 damaged.

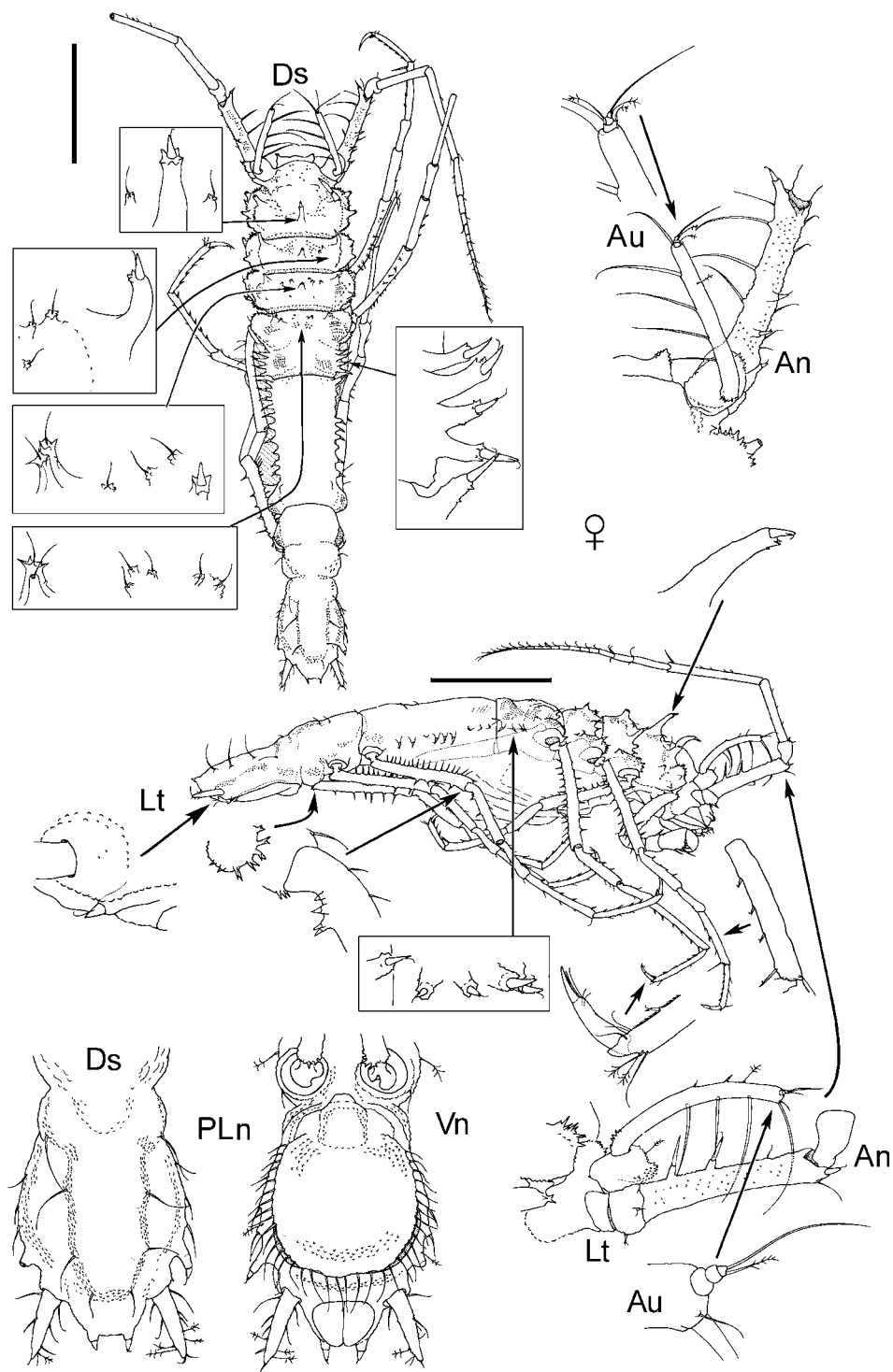
#### *Diagnosis*

Pereonite 1–3 median pedestal spines. Pereonites 4–5 in female with lateral pedestal spines. Pereonite 5 in female length 2.3 width, in male 4.1 width. Pleotelson terminal margin with pedestal spines. Antennula with 5 articles altogether. Pereopod II–VII bases and ischia with pedestal spines.

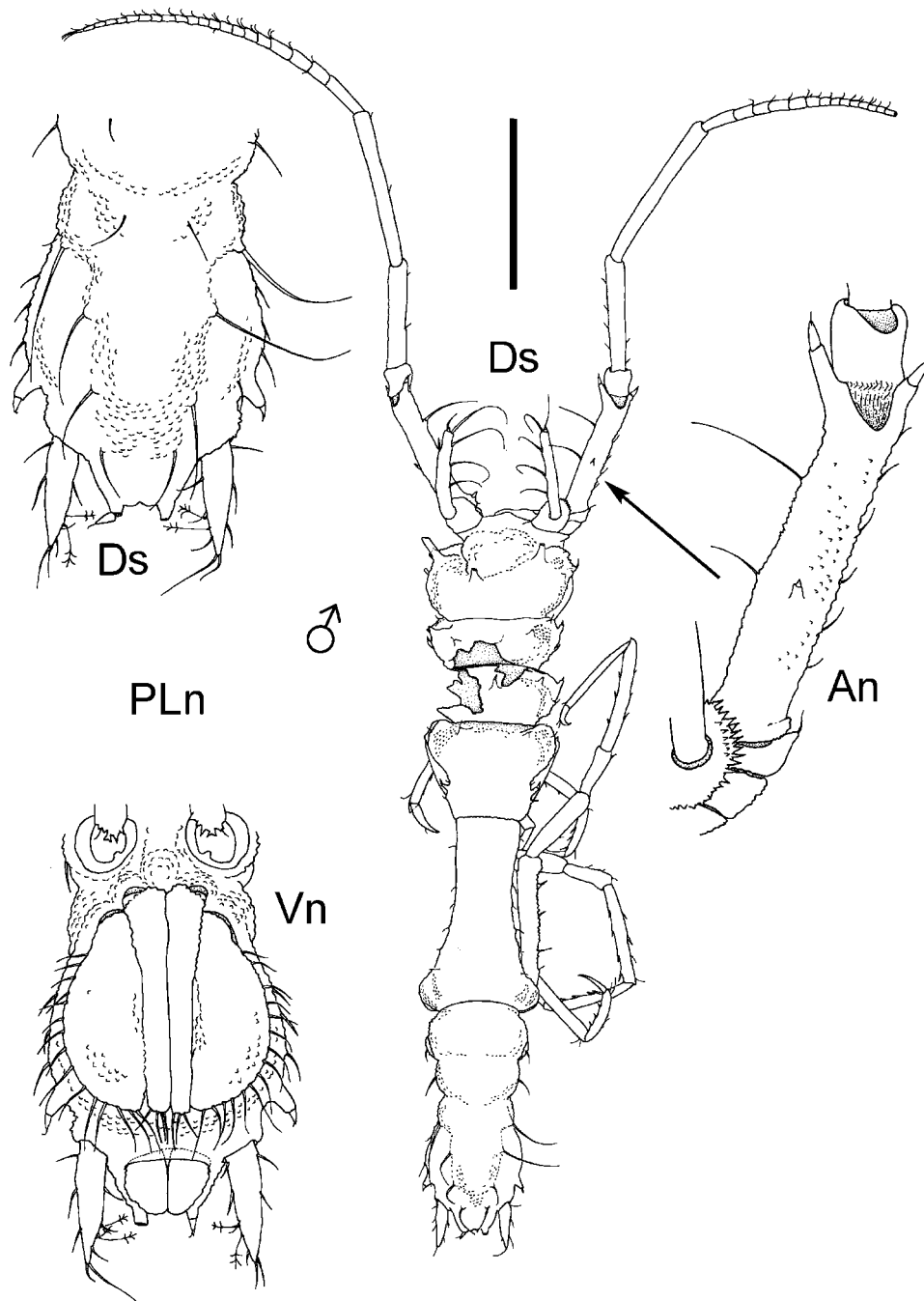
#### *Description*

*Body* length in female 4.3 mm; granular. *Head* in female length 0.75 width; lobe on ventrolateral margin present in lateral view; dorsal cuticle fine tubercular granulation. *Pereonite 1* in female width 0.2 total body length; with median pedestal spine, 1 pair of dorsal pedestal spines, 1 pair of anterolateral pedestal spines, 1 pair of lateral pedestal spines. *Pereonite 2* in female with median pedestal spine, 1 pair of dorsal pedestal spines, 1–2 pair of dorsal rook spines, 1 pair of anterolateral pedestal spines, 1 pair of lateral pedestal spines. *Pereonite 3* in female with median pedestal spine, 3–4 pairs of dorsal rook spines, 1 pair of anterolateral rook spines, 1 pair of lateral rook spines. *Pereonite 4* in female length 0.65 width; with 3–4 pair of dorsal rook spines, posterolateral margins with row of 4 long pedestal spines topped by stout robust setae. *Pereonites 1–4* in female with pedestal spines stout to long topped by short robust setae decreasing in length from pereonite 1 to 3, anterolateral spines length distinctly less than length of pereonite 1, rook spines short to stout. *Pereonite 5* in female length 0.25 total body length; with lateral row of 10–11 stout to long pedestal spines topped by stout to long robust seta. *Pereonite 7* in female with 1 pair of short pedestal spines topped by simple seta. *Pleotelson* in female length 1.55 width; posterolateral margin anterior to uropods with 1 pair of posterolateral stout pedestal spines topped by short robust setae; terminal margin with one pair of distal short pedestal spines topped by stout robust setae.

*Antennula* in female article 1 with 1 penicillate seta; article 2 length 0.88 head width, with 5 elongate stiff ventromedial setae; article 3 length similar to article 4, squat, wider than long, terminal article shorter than penultimate article, aesthetascs absent. *Antenna* in female length 1.9 anterior body length; article 2 with 1 lateral pedestal spine and 1 ventromedial pedestal spine; article 3 length 0.33 anterior body length, length 5.5 width, with 1 distomedial pedestal spine and 1 short distolateral pedestal spine placed somewhat ventrally (not visible in dorsal view: antenna slightly rotated as shown) and 2–3 stout



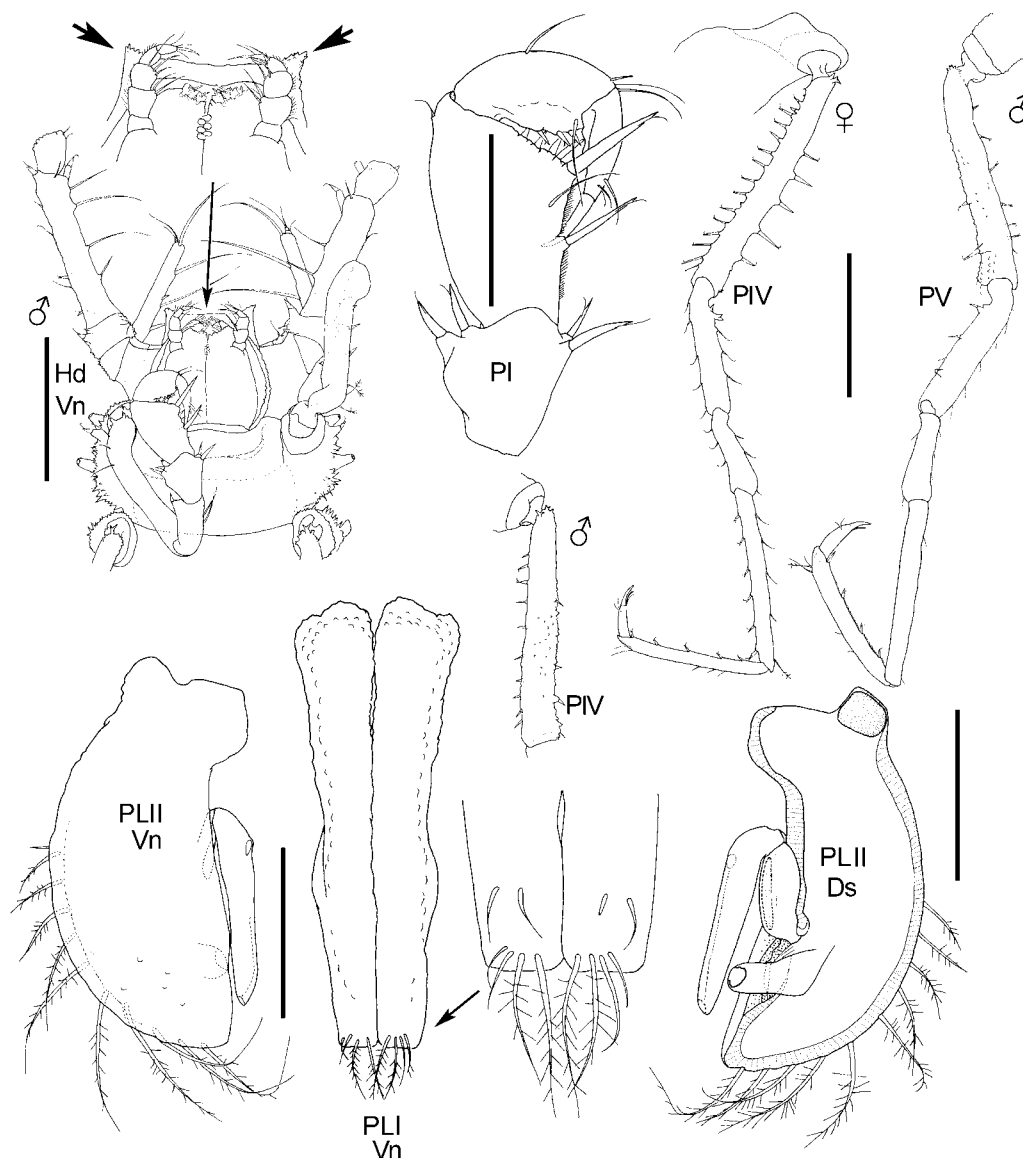
**FIGURE 7.** *Heteromesus ctenobasius* sp. nov. Holotype female, ZMUC CRU-9874: habitus dorsal and lateral; details on pedestal and rook spines on pereonites 1–4; antennula; antenna; pleotelson dorsal and ventral. Scale bar 1.0mm.



**FIGURE 8.** *Heteromesus ctenobasius* sp. nov. Paratype male, ZMUC CRU-9875: habitus dorsal, scale bar 1.0mm; antenna; pleotelson dorsal and ventral.

dorsal pedestal spines placed proximally and at midlength; article 5 length 0.31 anterior body length; article 6 length 0.42 anterior body length; flagellum with 14 articles, flagellum length 0.39 total antenna length.

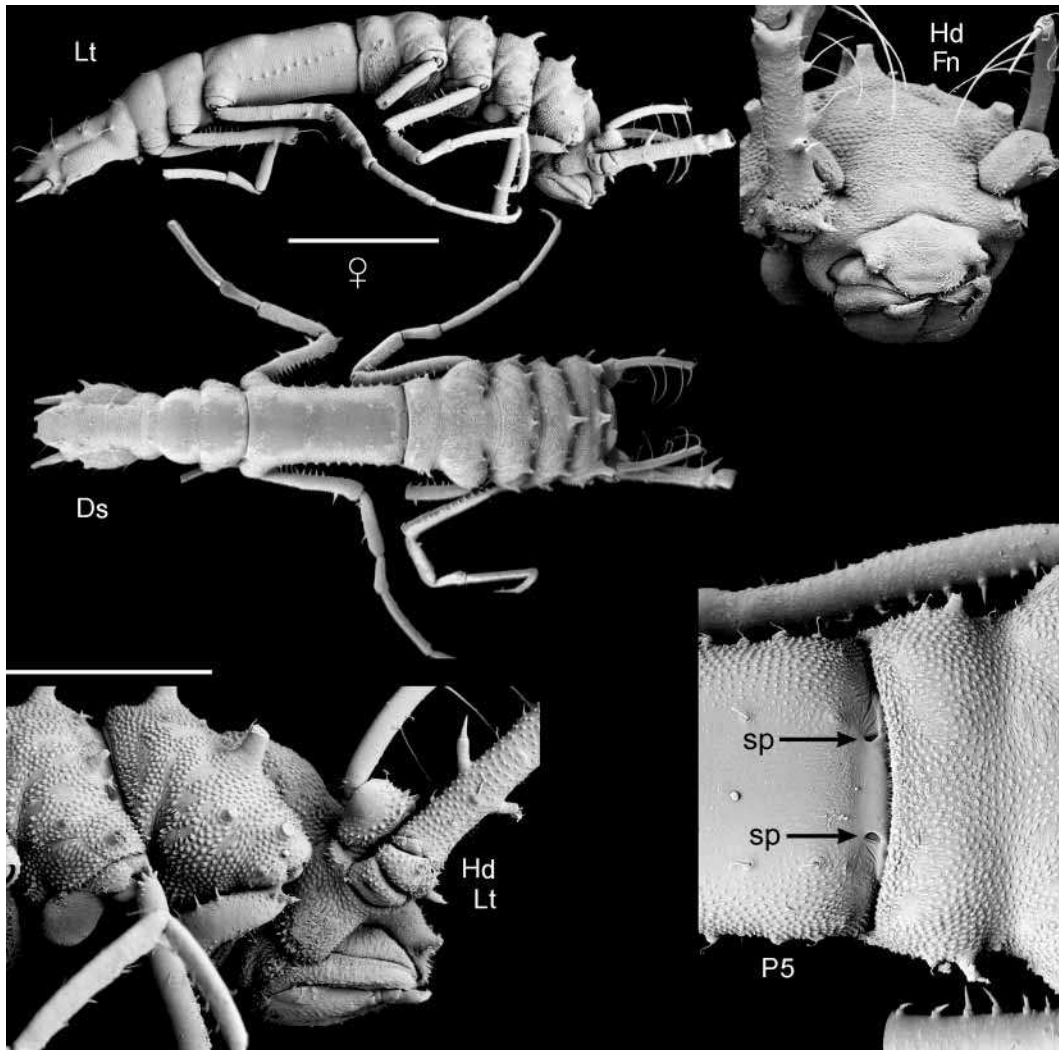




**FIGURE 9.** *Heteromesus ctenobasius* sp. nov. Paratype male, ZMUC CRU-9875: head ventral, arrowheads indicate "labrum knobs" scale bar 0.5mm, pereopod I, scale bar 0.2mm; pereopods IV and V, pleopods I and II, scale bars 0.2mm. Holotype female, ZMUC CRU-9874: pereopod IV.

*Labrum* knobs present, conical.

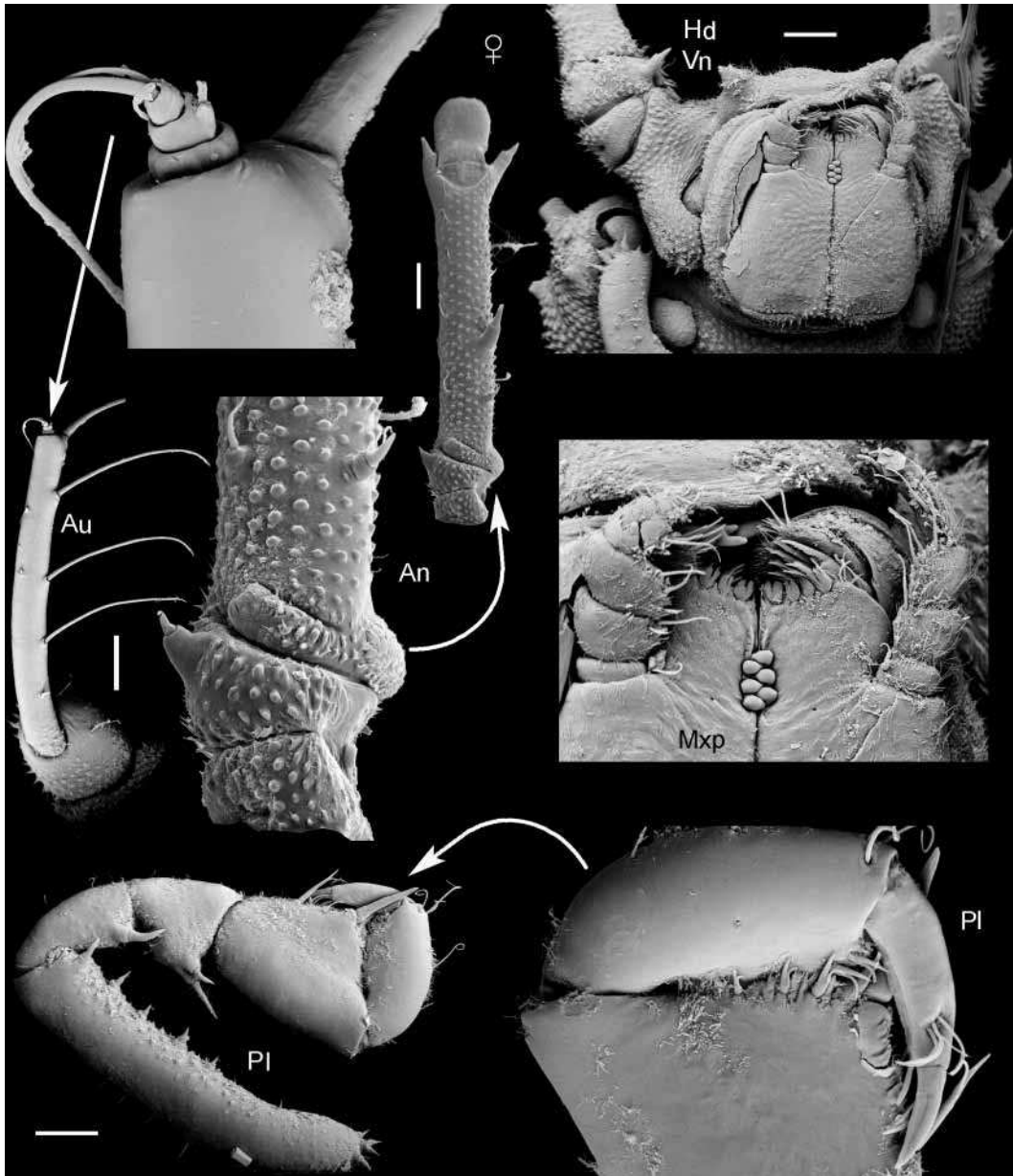
*Pereopod* bases proximal shoulder with bifid spines. *Pereopod I* carpus palm length distinctly less than proximal region length, with 4 robust setae on palm distal to elongate seta; *propodus* ventral margin with 3 robust setae. *Pereopods II–VII* bases granulate, with short pedestal spines, topped with long robust seta, on dorsal and ventral margins, 2–6 spines dorsally, 10–15 ventrally; *ischia* with 2–3 short pedestal spines topped with long robust seta, on dorsal margin only.



**FIGURE 10.** *Heteromesus ctenobasius* sp. nov. Paratype female, AM P 72120: SEM micrographs, habitus lateral and dorsal, scale bar 1.0mm; head frontal and lateral, scale bar 0.5 mm; pereonite 5, arrows indicate dorsal opening to spermathecal ducts.

*Uropods* in female length 0.25–0.30 length of pleotelson.

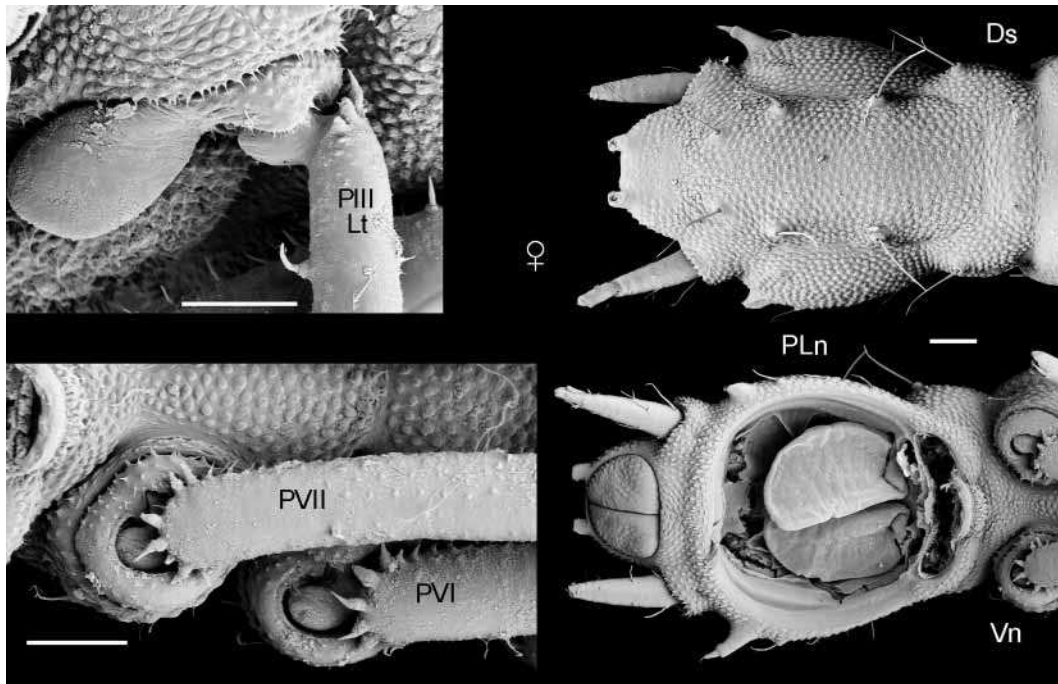
*Male specific characters.* Body length 4.3 mm. Head length 0.65 width. *Pereonite 1* width 0.20 total body length; with median pedestal spine, 1 pair of dorsal pedestal spines, 1 pair of anterolateral pedestal spines, 1 pair of lateral pedestal spines. *Pereonite 2* with median pedestal spine, 1 pair of dorsal pedestal spines, 1–2 pairs of dorsal rook spines, 1 pair of anterolateral pedestal spines, 1 pair of lateral pedestal spines. *Pereonite 3* with median pedestal spine, 1–2 pairs of dorsal rook spines, 1 pair of anterolateral rook spines, 1 pair of lateral rook spines. *Pereonite 4* length 0.75 width; with 2 pairs of dorsal rook spines, 1 pair of anterolateral rook spines, posterolateral margins with 2 pedestal spines. *Pereonite 1–4* pedestal spines stout to long topped by short robust setae, median and dorsal



**FIGURE 11.** *Heteromesus ctenobasius* sp. nov. Paratype female, AM P 72120: SEM micrographs, antennula; antenna, head ventral; maxillipeds; pereopod I. Scale bars 0.1mm.

spines decreasing in length from pereonite 1 to 3, anterolateral spines length distinctly less than length of pereonite 1, rook spines short to stout. *Pereonite 5* length 0.25 total body length; with row of approximately 8 simple setae (some topping short pedestal spines). *Pleotelson* length 1.35 width; posterolateral margin anterior to uropods with 1 pair of stout pedestal spines topped by short robust setae; terminal margin with 1 pair of distal short pedestal spines topped by stout robust setae. *Antennula* article 2 length 1.1 head width.

*Antenna* length 1.9 anterior body length; article 3 length 0.33 anterior body length, length 5.5 width, with distomedial and distolateral pedestal spines and 1 dorsal pedestal spine placed at midlength; article 5 length 0.23 anterior body length; article 6 length 0.44 anterior body length; flagellum length 0.37 total antennal length, flagellum with 15 articles. *Pleopod I* distal tip without lateral horns. *Pleopod II protopod* apex rounded, *stylet* thick and blunt, heavily calcified, not extending to distal margin of protopod. *Uropods* length 0.35 length of pleotelson.



**FIGURE 12.** *Heteromesus ctenobasius* sp. nov. Paratype female, AM P 72120: SEM micrographs, pereopods III, VI and VII; pleotelson dorsal and ventral (operculum removed). Scale bars 0.1mm.

#### *Distribution*

North Atlantic: Mid-Atlantic Ridge, Lucky Strike hydrothermal field, 1685–1720 m, on volcanic rocks, close to active hydrothermal chimneys, known only from type locality.

#### *Remarks*

*Heteromesus ctenobasius* sp. nov. is similar to *H. spinosus* in the heavy ornamentation of the body (many spines) and pereopods by both pedestal and rook spines and in having posterolateral and distal spines on the pleotelson. Both species have 5 antennular articles altogether. The most distinctive feature of *H. ctenobasius* is the dorsal median pedestal spine on peronites 1–3. The female shows conspicuous pedestal spines arranged along the lateral margin of pereonites 4 and 5.

***Heteromesus dentatus* Hansen, 1916**

(Figs 13–14)

*Heteromesus dentatus* Hansen 1916: 66–68, pl. V, figs. 6a–d, pl. VI, figs. 1a–c; Gurjanova 1932: 45, tabl. XV-54, 1933: 411; Menzies 1962: 122; Wolff 1962: 85, 217, 259; Kussakin 1988: 474–475, fig. 387.

*Material examined*

*Syntypes*: 2 males (posterior fragments, fragment illustrated 3.0 mm), 1 female (anterior fragment illustrated 1.7 mm), 2 heads and 1 pleotelson of undetermined sex, North Atlantic: southwest of Iceland, 60°37'N, 27°52'W, 1895–1896, R/V Ingolf stn 78, 1505 m (799 Danish fathoms) (ZMUC CRU-6258).

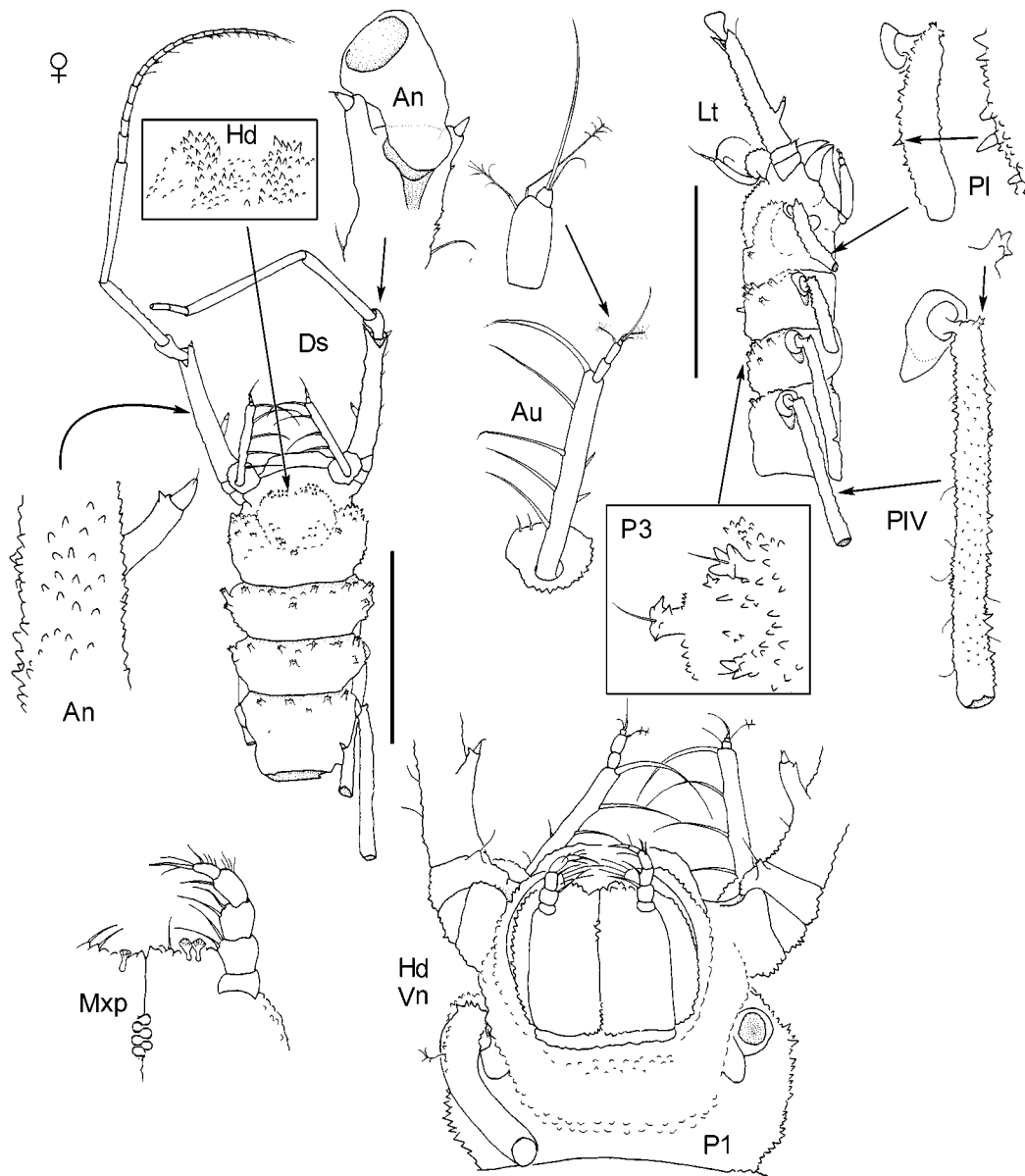
*Remarks on type material*. Specimens in ZMUC CRU-6258, are considered to be syntypes. We do not designate a lectotype here because all specimens are fragmentary. The mutilated and fragile specimens illustrated by Hansen were identified and re-illustrated (preparatory female: anterior fragment with head and pereonites 1–4, both pereopods I are missing; male: posterior fragment from pereonite 2 to pleotelson, right uropod missing). Male pleopods I and II were illustrated from a third specimen (male: posterior fragment P5-pleotelson).

*Diagnosis*

Pereonite 1 in female with 1–3 pairs of dorsal rook spines; pereonite 5 in male with posterodorsal rook spines; pereonite 6 in male with dorsal rook spines; pereonite 7 in male with lateral rook spines. Pereonite 5 in male length 5.5 width. Pleotelson (only male known) with posterolateral rook spines. Antennula with 5 articles altogether.

*Description*

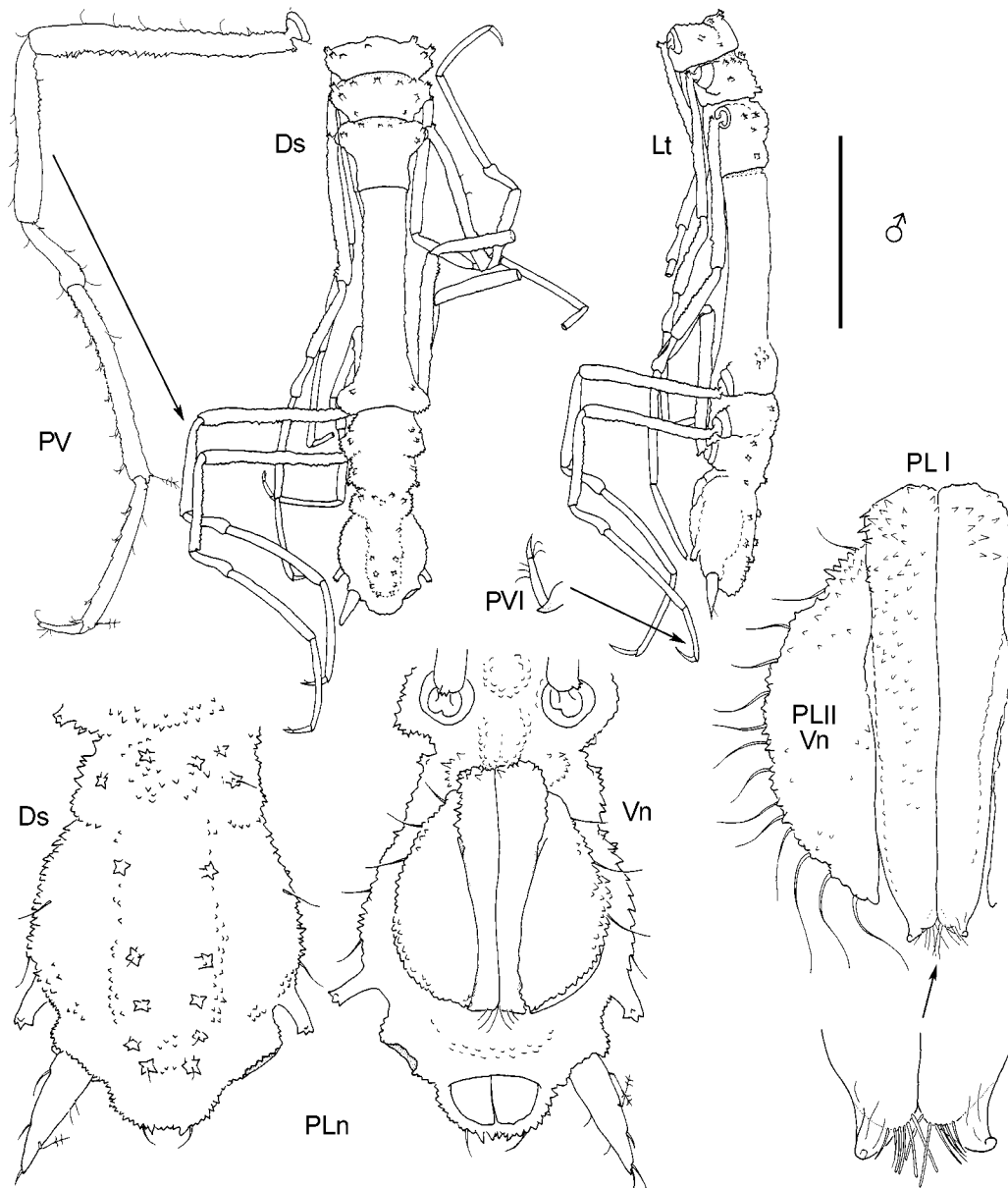
*Body* granular. *Head* in female length 0.75 width; dorsal surface with pair of cephalic bullae; lobe on ventrolateral margin present in lateral view; dorsal cuticle fine spinous granulation. *Pereonite 1* in female with median rook spine, 1–3 pairs of dorsal rook spines, 1 pair of anterolateral simple spines, 1 pair of lateral simple spines. *Pereonite 2* in female with median rook spine and median tubercle, 2–3 pairs of dorsal rook spines, 1–2 pairs of dorsal tubercles, 1 pair of anterolateral rook spines, 1 pair of lateral rook spines. *Pereonite 3* in female with median rook spine and median tubercle, 2–3 pairs of dorsal rook spines, 1 pair of anterolateral rook spines, 1 pair of lateral rook spines. *Pereonite 4* in female length 0.70 width; with median rook spine, 2 pairs of dorsal rook spines. *Pereonites 1–4* dorsal and median rook spines short to stout placed along anterior margin, anterolateral rook spines short to stout, length distinctly less than length of pereonite 1, male and female similar (*pereonites 5–7* with male only).



**FIGURE 13.** *Heteromesus dentatus* Hansen, 1916. Syntype female, ZMUC CRU-6258: habitus dorsal and lateral (anterior fragment); antennula; antenna; head ventral and maxilliped; pereopods I and IV bases; details on cuticular structure of head and rook spines on pereonite 3. Scale bars 1.0mm.

*Antennula* in female article 2 length 0.73 head width, with 5 elongate stiff ventromedial setae; article 3 length similar to article 4, elongate and tubular, much longer than wide, terminal article shorter than penultimate article. *Antenna* in female length 2.2 anterior body length; article 2 with 1 ventromedial short pedestal spine; article 3 length

0.44 anterior body length, length 7.5–8.0 width, with stout distomedial pedestal spine and short distolateral pedestal spine, 1 long ventromedial pedestal spine placed proximally, length near distal article width; article 5 length 0.28 anterior body length; article 6 length 0.38 anterior body length; flagellum with 20 articles, flagellum length 0.37 total antenna length.



**FIGURE 14.** *Heteromesus dentatus* Hansen, 1916. Syntype male, ZMUC CRU-6258: habitus dorsal and lateral (posterior fragment); pleotelson dorsal and ventral; pereopod V and dactylus of pereopod VI; pleopods I and II. Scale bar 1.0mm.

*Labrum* knobs absent.

*Pereopod bases* proximal shoulder with rook spines. *Pereopod I* (Hansen, 1916: fig. 6d) *carpus* palm length distinctly less than proximal region length, with 2 elongate robust setae, with 1 robust seta on palm distal to elongate seta; *propodus* ventral margin with 2 robust setae. *Pereopods II–VII bases* denticulate, sometimes sharply toothed.

*Male specific characters.* (Head and pereonite 1 only with female) *Pereonite 2* with median rook spine and median tubercle, 2–3 pairs of dorsal rook spines, 1 pair of dorsal tubercles, 1 pair of anterolateral rook spines, 1 pair of lateral rook spines. *Pereonite 3* with median rook spine, 2–3 pairs of dorsal rook spines, 1 pair of anterolateral rook spines, 1 pair of lateral rook spines. *Pereonite 4* length 0.80 width; with median rook spine, 2–3 pairs of dorsal rook spines. *Pereonite 5* with lateral row of unobscured tubercles. *Pereonites 5–7* rook spines short to stout, 1 pair in pereonite 5 and 2 pairs in each of pereonites 6 and 7. *Pleotelson* length 1.45 width. *Pleonite 1* region of pleotelson with 1 median and 2 pairs of dorsal rook spines short to stout. *Pleotelson* with 5 pairs of dorsal rook spines short to stout arranged in 2 median longitudinal rows; posterolateral margin anterior to uropods with paired elongate curved rook spines; terminal margin with 1 pair of distal short simple spines. *Pleopod I* distal tip with lateral horns. *Pleopod II protopod* apex narrow, tapering, *stylet* tapering and pointed, not heavily calcified, extending to distal margin of protopod. *Uropods* length 0.30 length of pleotelson.

#### *Distribution*

North Atlantic, southwest of Iceland, 1505 m.

#### *Remarks*

The “spiniform tubercles” on the pereonites and pleotelson of *Heteromesus dentatus* described by Hansen (1916: 67) are complex, each consisting of a short pedestal ending in around four (3–5) denticles usually with one seta in the centre herein designated as “rook spines”. *H. dentatus* is distinctive among the other species in the genus because of its abundant rook spines on most dorsal surfaces, and particularly on the lateral margin of pereonite 7. Male pleopod I appears to have a different shape in the two illustrated specimens (Fig. 14) because it is embedded laterally in pleopod II on the more intact specimen and, in the enlargement from a fragment, it is partially exposed, showing the lateral margins. Pereonite 7 in the males also has a ventral rounded tubercle.

*Heteromesus dentatus* is similar to *H. greeni* and *H. oryktus* in having spinous granulation of the body, 5 antennular articles altogether and inconspicuous ornamentation of the pereopods (in which these species differ from *H. spinosus* and *H. ctenobasius* that also have 5 antennular articles) that are characterised, however, by the presence of rook spines on the proximal “shoulders” of the bases. The most distinctive features of *H. dentatus* are the rook spines arranged in dorsal rows in the pereonites and pleotelson, the anterolateral rook spines on pereonites 2 and 3 and posterolateral rook spines on the pleotelson.



***Heteromesus drachi* Chardy, 1974**

*Heteromesus drachi* Chardy 1974: 1546–1549, figs. 6–7.

*Material examined*

*Holotype*: male (5.6 mm), North Atlantic: off Ivory coast, 4°21.2'N, 4°35.2'E, 1971, R/V Jean Charcot, Campagne Walda stn 36 DS 28, 1261 m, (MNHN IS-3362).

*Remarks on type material*. The holotype was dissected (apparently by Chardy), and some parts were found loose in the vial.

*Diagnosis (Male only)*

Pereon without rook spines. Pereonite 5 length 4.7 width. Pleotelson pleonite 1 region with low dorsal tubercles. Pleotelson with low dorsal tubercles; posterolateral margin anterior to uropods without spines or tubercles. Antennula with 4 articles altogether; article 3 short and tubular, length near width.

*Description (Male characters only)*

*Body* length 5.6 mm, granular. *Head* length 0.70 width, dorsal cuticle tubercular granulation, lobe on ventrolateral margin present in lateral view. *Pereonite 1* width 0.20 total body length; with one median simple spine, 1 pair of anterolateral simple spines and 1 pair of lateral simple spines. *Pereonite 2* with one median simple spine and 1 pair of anterolateral simple spines. *Pereonite 3* with one median simple spine, 1 pair of anterolateral simple spines. *Pereonites 1–3* median spines stout, anterolateral spines long to short, decreasing in size from pereonite 1 to 3, length distinctly less than pereonite 1 length, additional lateral spines short. *Pereonite 4* length 0.60 width. *Pereonite 5* length 0.35 total body length. *Pleonite 1* region of pleotelson with 1 median and 2 dorsal pairs of tubercles. *Pleotelson* length 1.35 width, with 2 pairs of dorsal tubercles.

*Antennula* article 2 length 1.2 head width, with 4 elongate stiff ventromedial setae; article 3 longer than article 4; terminal article shorter than penultimate article, aesthetascs absent. *Antenna* length 2.0 anterior body length; article 2 with 1 ventromedial spine; article 3 length 0.39 anterior body length, length 5.0 width, with distomedial spine and 1 ventral stout spine; article 5 length 0.32 anterior body length; article 6 length 0.41 anterior body length; flagellum length 0.37 total antennal length, flagellum with 18 articles.

*Labrum* knobs absent. *Maxillula* medial lobe without robust dentate setae. *Maxilla* without long medially-projecting pectinate setae on medial lobe.

*Pereopod bases* proximal shoulder with simple spines only. *Pereopod I carpus* palm length near proximal region length, with 2 robust setae on palm distal to elongate seta; *propodus* ventral margin with 2 robust setae.

*Pleopod I* distal tip with lateral horns. *Pleopod II protopod* apex rounded; *stylet* thick and blunt, extending beyond distal margin of protopod (with hook-like lateral curve under posterior margin of protopod). *Uropods* length 0.30 length of pleotelson.

*Distribution*

North Atlantic, off Ivory Coast, 1261–3109 m.

*Remarks*

Chardy (1974) did not describe the female of *H. drachi* and made no comments on sexual dimorphism for this species. A pleotelson with a few paired tubercles (and nowhere else on the body) is the most distinctive feature of *Heteromesus drachi*. *H. spinosus* and *H. dentatus* also have rook spines on the pleotelson but they are arranged in longitudinal rows. It also differs from the former in having midline spines on the anterior pereonites. The elongate, curved appendix masculina has not been seen in other members of *Heteromesus*. With regard to the distal articles in the antennula, Chardy (1974: 1546) stated “Flagellum ... constitué de 3 segments” as illustrated in his fig. 6 but our examination of the holotype finds only 2 distal articles.

***Heteromesus frigidus* Hansen, 1916**

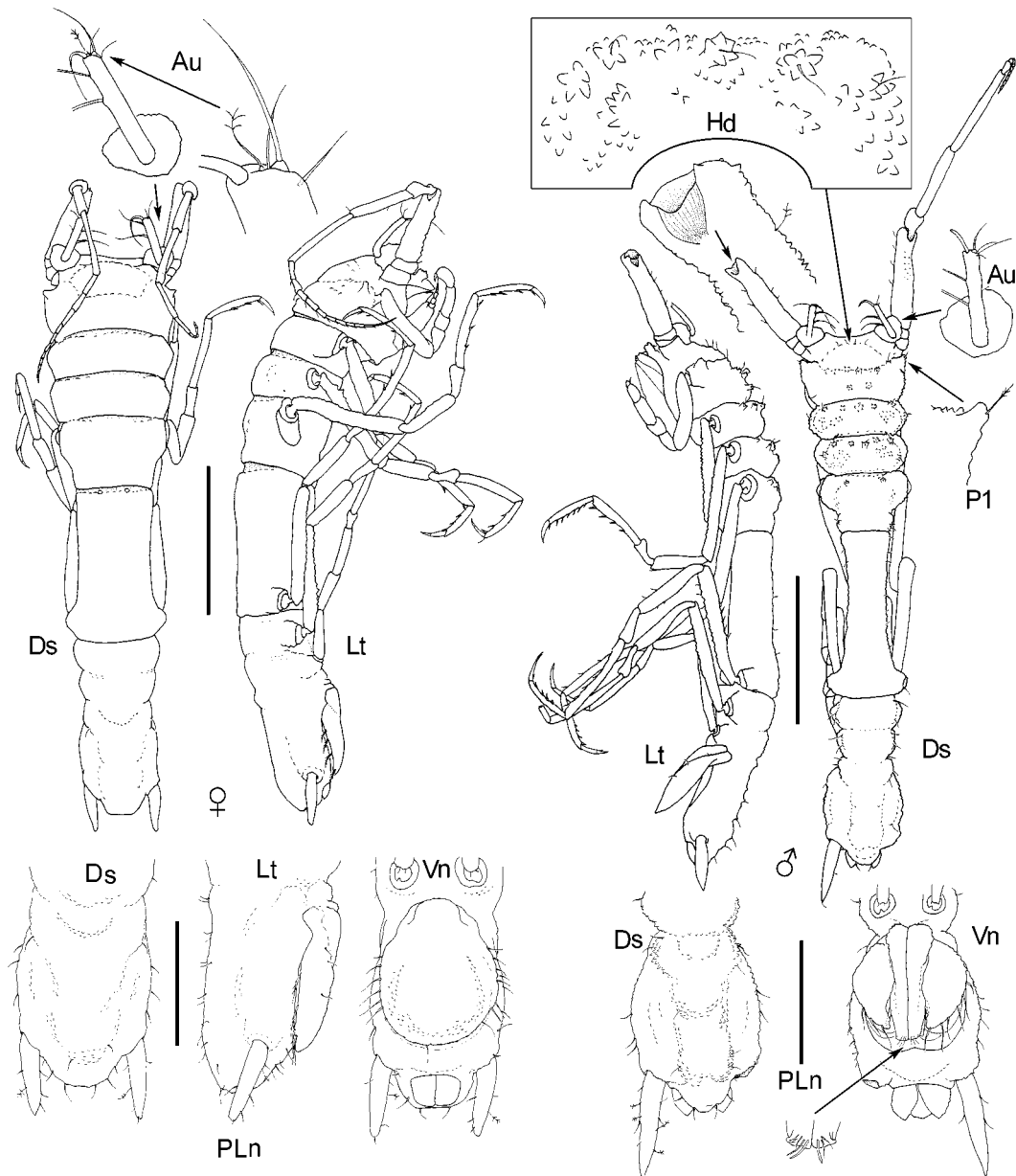
(Figs 15–16)

*Heteromesus frigidus* Hansen 1916: 71–72, pl. VI, figs 4a–t; Gurjanova 1932: 46, tabl. XVI, 57, 1933: 411, 1964: 259; Menzies 1962: 122; Wolff 1962: 73, 85, 216, 260; Svavarsson 1984: 35; Kussakin 1988: 478–480, figs. 391–392.

*Material examined*

*Syntypes*: 12 females, 2 males, 1 manca III male, 6 manca, Norwegian Sea, north of the Faeroes, 63°36'N, 7°30'W, 1895–1896, R/V Ingolf, stn 139, 1322 m (702 Danish fathoms) (ZMUC CRU-9234); 1 female, 1 manca III female, 2 manca III males, 11 manca, several fragments, same locality, 63°22'N, 6°58'W, 1895–1896, R/V Ingolf, stn 141, 1279 m (679 Danish fathoms) (ZMUC CRU-9235); 1 female, Norwegian Sea, East of Iceland, 66°23'N, 12°05'W, 1895–1896, R/V Ingolf, stn 101, 1012 m (537 Danish fathoms) (ZMUC CRU-9236). 1 female, 1 manca, same locality, 66°23'N, 10°26'W, 1895–1896, R/V Ingolf, stn 102, 1413 m (750 Danish fathoms) (ZMUC CRU-6468); 1 female, same locality, 65°34'N, 7°31'W, 1895–1896, R/V Ingolf, stn 105, 1435 m (762 Danish fathoms) (ZMUC CRU-3764); 5 females, 4 manca, 1 fragment (head), Norwegian Sea, North of Iceland, 67°40'N, 15°40'W, 1895–1896, R/V Ingolf, stn 124, 932 m (495 Danish fathoms) (ZMUC CRU-9233).

*Remarks on type material.* Numerous syntype specimens, mostly mancae and females and only two males in CRU-9234. Several females and mancae were intact but most were mutilated or fragmented specimens. The male illustrated here is lacking part of the left antenna and the right uropod. The other male lacked pleopods; these were possibly removed by Hansen for illustration. An intact female from the same sample (CRU-9234) was selected for the illustration.

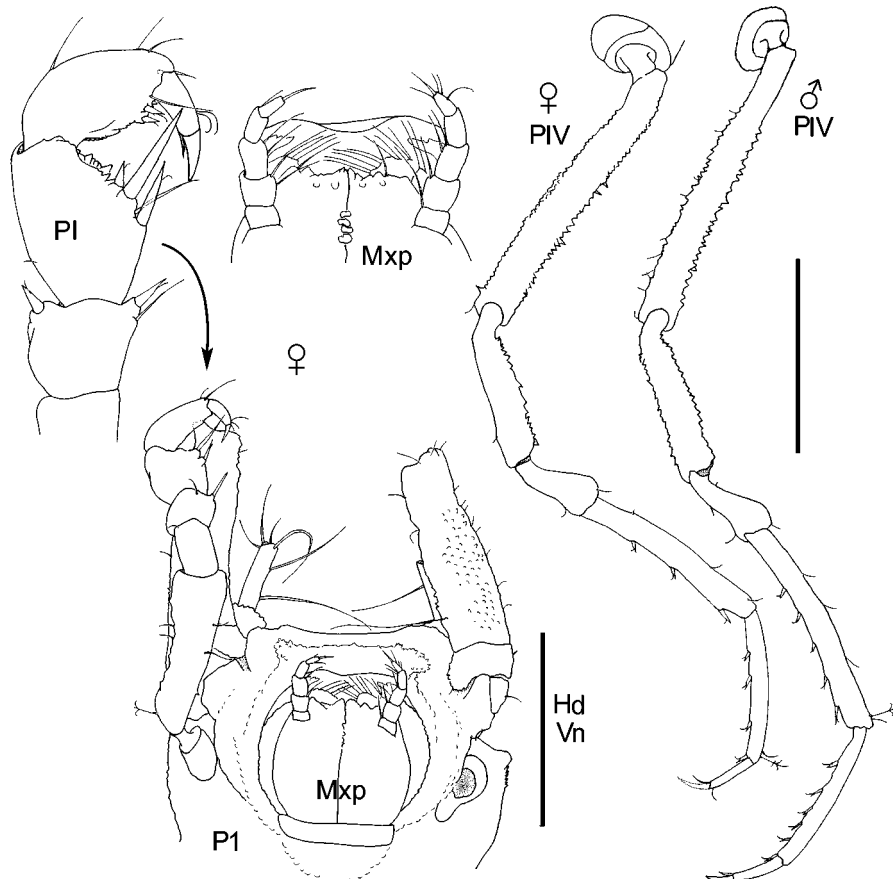


**FIGURE 15.** *Heteromesus frigidus* Hansen, 1916. Syntype female, ZMUC CRU-9234: habitus dorsal and lateral; antennula; pleotelson dorsal, lateral and ventral. Syntype male, ZMUC CRU-9234: habitus dorsal and lateral; detail on head cuticular structure and rook spines; antennula; anterolateral spine on pereonite 1; pleotelson dorsal and ventral. Scale bars: habitus 1.0mm; pleotelson 0.5mm.

*Diagnosis*

Pereonite 1 in female with no median dorsal tubercles or spines; pereonite 5 in female length 2.2 width. Male with rook spines on pereonites 1–4. Pereonite 5 in female length 2.2

width, in male length 4.4 width. Pleotelson posterolateral margin anterior to uropods without spines or tubercles. Antennula with 3 articles altogether. Pereopods II–VII bases denticulate, sometimes sharply toothed. Uropods in male longer than in female, length 0.60 pleotelson length.



**FIGURE 16.** *Heteromesus frigidus* Hansen, 1916. Syntype female, ZMUC CRU-9234: head ventral; maxilliped; pereopods I and IV. Syntype male: pereopod IV. Scale bar 0.5mm.

#### *Description*

*Body* length in female 3.7 mm; heavy blunt tubercular granulation. *Head* in female length 0.30 width; dorsal cuticle tubercular granulation. *Pereonite 1* in female width 0.25 total body length; with 1 pair of anterolateral simple spines, short to stout, length distinctly less than length of pereonite 1. *Pereonite 4* in female length 0.65 width. *Pereonite 5* in female length 0.30 total body length. *Pleotelson* in female length 1.4 width.

*Antennula* in female article 2 length 0.51 head width, with 3 elongate stiff ventromedial setae, distal tip produced distally beyond insertion of next article, distal article inserting subapically; article 3 terminal, squat, wider than long, aesthetascs absent.

*Antenna* in female length 1.7 anterior body length; article 3 length 0.35 anterior body length, length 3.7 width; article 5 length 0.27 anterior body length; article 6 length 0.34 anterior body length; flagellum with 11–12 articles, flagellum length 0.31 total antenna length.

*Labrum* knobs present, distally truncate, denticulate.

*Pereopod I carpus* palm length near proximal region length, with 3 robust setae on palm distal to elongate seta; *propodus* ventral margin with 2 robust setae. *Pereopods II–VII bases* denticulate, sometimes sharply toothed.

*Uropods* in female length 0.35–0.4 length of pleotelson.

*Male specific characters.* *Body* length 3.6 mm. *Head* length 0.45 width. *Pereonite 1* width 0.20 total body length; with median rook spine, 3–4 pairs of dorsal rook spines, 1 pair of anterolateral simple spines, short to stout, length distinctly less than pereonite 1 length. *Pereonite 2* with median rook spine, 2 pairs of dorsal rook spines, 1 pair of lateral rook spines. *Pereonite 3* with median rook spine, 3 pairs of dorsal rook spines. *Pereonite 4* length 0.70 width; with 1 pair of dorsal rook spines, 1 pair of posterolateral rook spines. *Pereonites 1–4* with heavy granulations arranged in rosettes developing into stout rook spines. *Pereonite 5* length 0.30 total body length. *Pleotelson* length 1.3 width. *Antennula* article 2 length 1.1 head width. *Antenna* article 3 length 0.50 anterior body length, length 4.5 width; article 5 length 0.38 anterior body length; article 6 length 0.48 anterior body length; flagellum with 10–11 articles. *Pleopod I* distal tip without lateral horns. *Pleopod II protopod* apex narrow, tapering; *stylet* thick and blunt, heavily calcified, extending beyond distal margin of protopod.

#### *Distribution*

Norwegian Sea, north of the Faeroes, east and north of Iceland, North Polar Sea, 539–2024 m (Hansen 1916; Gurjanova 1964; Svavarsson 1984; Ólafsdóttir & Svavarsson 2002), epibenthic (Svavarsson 1984; Ólafsdóttir & Svavarsson 2002).

#### *Remarks*

*Heteromesus frigidus* Hansen shows high sexual dimorphism, males having several rook spines (sets of 4–5 large tapering granulations or short spines arranged in the shape of a star or flower with one seta in the centre) on pereonites 1–4, uropods much longer than in females and juveniles and propodus of pereopods with 5–6 robust setae (3–4 in female). The material from Ingolf stations labelled as *H. frigidus* by Hansen is abundant and the specimens show some morphological variability. Among these, some manca III male specimens have developing spines (anterolateral on pereonites 1–3 and one additional lateral pair on pereonite 1); one female with oostegites (smaller than the other females) has 1 additional pair of lateral spines on pereonite 1 and one pair of anterolateral spines on pereonite 2.

This species is similar to *H. granulatus*, *H. inaffectus* and *H. schmidtii* in having 3

antennular articles altogether, in having one pair of anterolateral spines only on pereonite 1 and by the tubercular granulation and inconspicuous ornamentation (few spines) of the body. The male differs from these species in having dorsal rows of rook spines on pereonites 1–4. The female differs from *H. inaffectus* and *H. schmidti* in having short uropods and from *H. inaffectus* and *H. granulatus* by the different proportion of pereonite 5.

***Heteromesus granulatus* Richardson, 1908**

(Fig. 17)

*Heteromesus granulatus* Richardson 1908: 82, figs. 14–18; Menzies 1962: 121–123, fig. 22D; Wolff 1962: 86, 262, 274–275; Kussakin 1988: 485–487, fig. 400.

*Heteromesus granulatus*. –Kussakin 1988: fig. 399 [*lapsus calami*].

*Material examined*

*Holotype*: female (3.2 mm), Northwest Atlantic: off Massachusetts, south of Martha's Vineyard, approximately 39°N, 70°30'W, 1885, USFC Steamer Albatross, stn 2547, 713 m (390 fathoms) (USNM 38969).

*Remarks on type material*. The holotype, an ovigerous female, was in almost perfect condition, the antennae are broken at article 4 (described by Richardson but not found in the vial) and all pereopods are intact except for pereopod VI (both in the left and right sides). The body is more slender than described by Richardson (1908: 82, fig. 14): "Body of female about three and a half times longer than wide", although we measure the body length as 4.2 pereonite 1 width. The antennulae have long setae on article 2 as is typical for members of this genus. Paratypes, determined from Richardson (1908: 83) as 40 additional females and 4 males from the same sample, were not examined.

*Diagnosis*

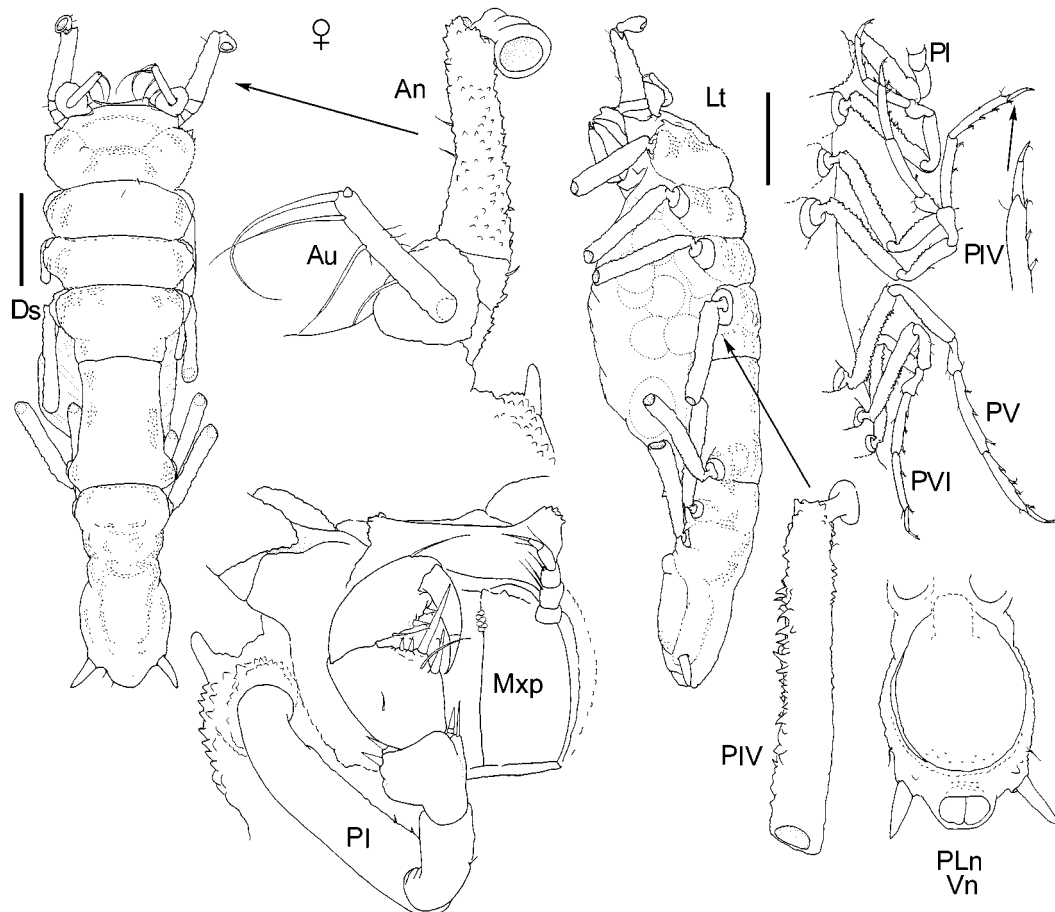
Pereonite 5 length in female 1.6 width, in male 3.7 width. Antennula with 3 articles altogether; article 2 distal tip produced distally beyond insertion of next article, distal article inserting subapically. Pereopods II–VII bases denticulate, sometimes sharply toothed, with simple spines. Uropods length in female 0.25–0.30, in male 0.40 length of pleotelson.

*Description*

*Body* length in female 3.2 mm; granular. *Head* in female length 0.35 width; dorsal cuticle coarse tubercular granulation. *Pereonite 1* in female width 0.20 total body length; with 1 pair of dorsal tubercles, 1 pair of anterolateral simple spines, short, length distinctly less than length of pereonite 1. *Pereonite 4* in female length 0.55 width. *Pereonite 5* in female length 0.20 total body length. *Pleotelson* in female length 1.35 width; posterolateral margin anterior to uropods with posterolateral tubercles inserted ventrally,

not visible in dorsal view.

*Antennula* with 3 articles altogether; article 2 in female length 0.31 head width, with 4 elongate stiff ventromedial setae, distal tip produced distally beyond insertion of next article, distal article inserting subapically; article 3 terminal, squat, wider than long, aesthetascs absent. *Antenna* in female article 3 length 3.0 width, flagellum with 14 articles (Richardson 1908).



**FIGURE 17.** *Heteromesus granulatus* Richardson, 1908. Holotype female, USNM 38969: habitus dorsal and lateral; antennula; antenna; head ventral showing maxilliped and pereopod I; pereopods IV–VI; pleotelson ventral. Scale bars 1.0mm.

*Labrum* knobs present, distally rounded, denticulate, strongly asymmetrical. *Maxillula* medial lobe with 1 robust medially-projecting dentate seta.

*Pereopod* bases proximal shoulder with simple spines only. *Pereopod I* carpus palm length distinctly less than proximal region length, with 2 robust setae on palm distal to elongate seta; propodus ventral margin with 2 robust setae. *Pereopods II–VII* bases with simple spines, stout, on dorsal margin only.

*Male specific characters.* Pereonite 5 length 3.7 width. Pleotelson length 1.55 width.

*Antenna* flagellum with 16 articles.

*Distribution*

Northwest Atlantic, south of Martha's Vineyard, southeast of Georges Bank, south of Block Island, 713–3235 m.

*Remarks*

The male of *Heteromesus granulatus* was scored according to information from original description (pereonite 5 and pleotelson illustrated). Richardson (1908) mentioned collection of abundant material (males and females) from different locations off New England, USA. Given the depth range of the reported localities, these should be examined to test whether they are all conspecific.

*H. granulatus* is similar to *H. inaffectus*, *H. schmidtii* and the female of *H. frigidus* in having 3 antennular articles altogether, and in its nearly complete absence of large spines, denticles or tubercles on the dorsal and lateral surfaces except for short anterolateral spines on the first pereonite. Although Richardson (1908) called attention to the granulation of the cuticle, we find that this is common for many of the species of *Heteromesus*. The most distinctive feature of this species is its compact body shape with a short pereonite 5 (L/W much less than 2.0) and short uropods.

***Heteromesus greeni* (Tattersall, 1905)**

(Fig. 18)

*Ischnosoma greeni* Tattersall 1905: 20–22, 72, pl. IV, figs. 1–6.

*Heteromesus greeni* (Tattersall).– Richardson 1908: 81; Wolff 1962: 86, 217, 260, 274; Kussakin 1988: 483–485, fig. 397.

*Material examined*

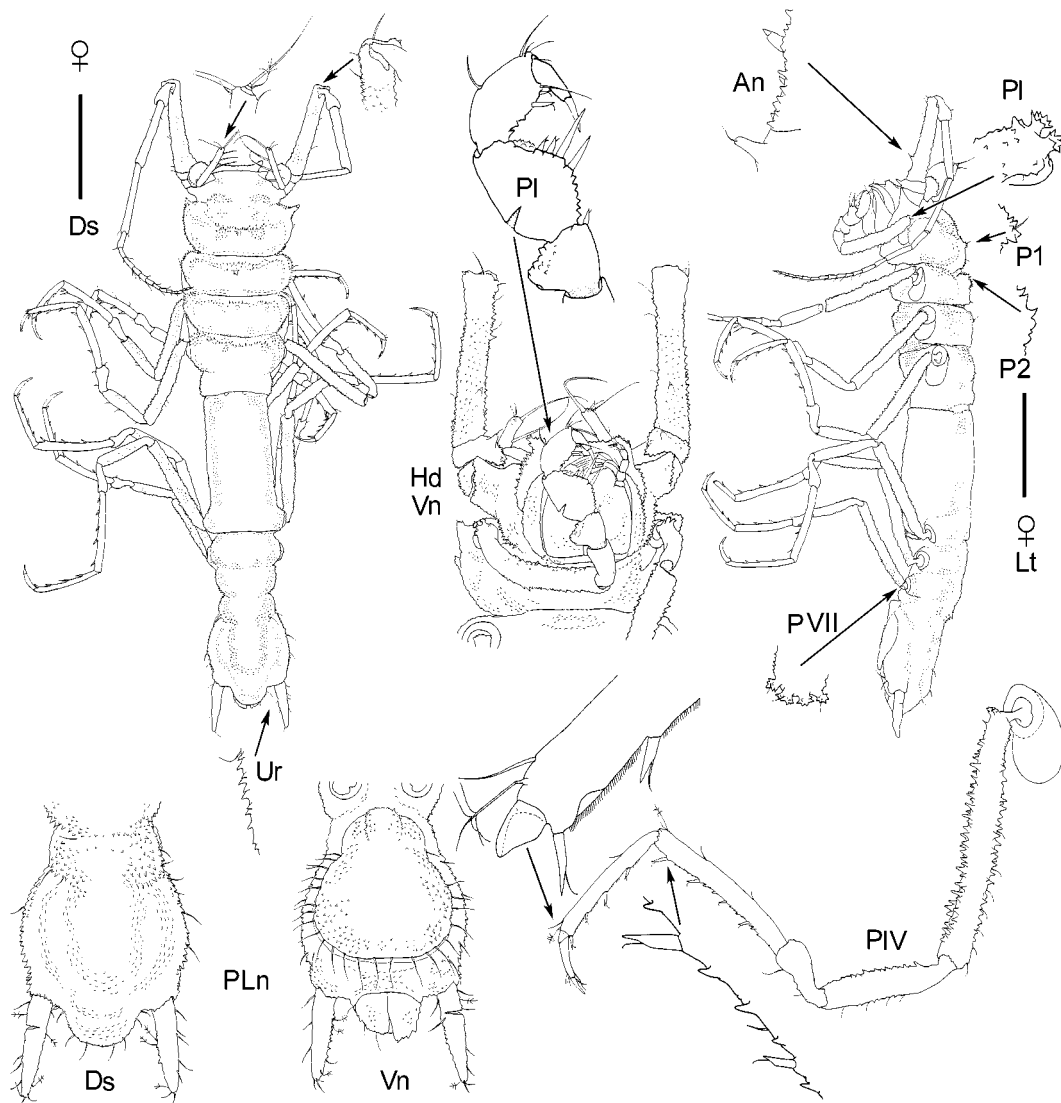
*Holotype*: preparatory female (4.2 mm), North Atlantic: off west coast of Ireland, west of Achill Head, approximately 54°N, 11°W, Aug 1901, R/V Helga, 698 m (NHM 1911.11.8.9599).

*Remarks on type material*. Holotype female was in almost perfect condition.

*Diagnosis (Female only)*

Pereonites 1–3 with median rook spines, but with no paired dorsal spines or tubercles. Pereonite 5 length 2.2 width. Pleotelson posterolateral margin anterior to uropods without spines or tubercles. Antennula with 5 articles altogether, article 2 distal tip not produced distally, next article inserting apically; article 3 longer than article 4, squat, wider than long. Antenna article 2 with 1 ventromedial spine. Labrum knobs present. Pereopod bases proximal shoulder with rook spines.





**FIGURE 18.** *Heteromesus greeni* (Tattersall, 1905). Holotype female, NHM 1911.11.8.9599: habitus dorsal and lateral; head ventral; pleotelson dorsal and ventral; pereopod IV; details on antenna, rook spines on shoulder of pereopods I and VII, uropod medial margin and cuticular structure of pereonites 1 and 2. Scale bars 0.8mm.

*Description (Female characters only)*

*Body* length 4.2 mm; granular. *Head* length 0.7 width; dorsal surface with pair of cephalic bullae; dorsal cuticle coarse spinous granulation. *Pereonite 1* width 0.20 total body length; with median rook spine, 1 pair of anterolateral pedestal spines, 1 pair of lateral simple spines. *Pereonite 2* with median rook spine. *Pereonite 3* with median rook spine. *Pereonites 1–3* rook spines short, pereonite 1 pedestal spines stout topped by short robust seta, length distinctly less than length of pereonite 1. *Pereonite 4* length 0.60 width.

*Pereonite 5* length 2.2 width, 0.25 total body length. *Pleotelson* length 1.2 width.

*Antennula* article 2 length 0.56 head width, with 4 elongate stiff ventromedial setae; article 3 longer than article 4, squat, wider than long; terminal article shorter than penultimate article. *Antenna* length 2 anterior body length; article 2 with 1 ventromedial stout pedestal spine terminated with fine seta; article 3 length 0.42 anterior body length, length 5 width, with 1 ventral stout pedestal spine; article 5 length 0.32 anterior body length; article 6 length 0.32 anterior body length; flagellum with 15 articles, flagellum length 0.37 total antenna length.

*Labrum* knobs present, strongly asymmetric, right side conical, left side rounded, both denticulate.

*Pereopod bases* proximal shoulder with rook spines. *Pereopod I carpus* palm length near proximal region length, with 2 robust setae on palm distal to elongate seta; *propodus* ventral margin with 2 robust setae. *Pereopods II–VII bases* denticulate, sometimes sharply toothed.

*Uropods* medial margin denticulate; length 0.45–0.50 length of pleotelson.

#### *Distribution*

North Atlantic, off North Ireland, 364–700 m.

#### *Remarks*

*Heteromesus greeni* is similar to *H. dentatus* and *H. oryktus* in having spinous granulation of the body, 5 antennular articles altogether and inconspicuous ornamentation of the pereopods showing only rook spines on the proximal "shoulders" of the bases. It is distinctive in its having one rook spine on the dorsal midline of pereonites 1–3.

#### ***Heteromesus inaffectus* sp. nov.**

(Figs 19–23)

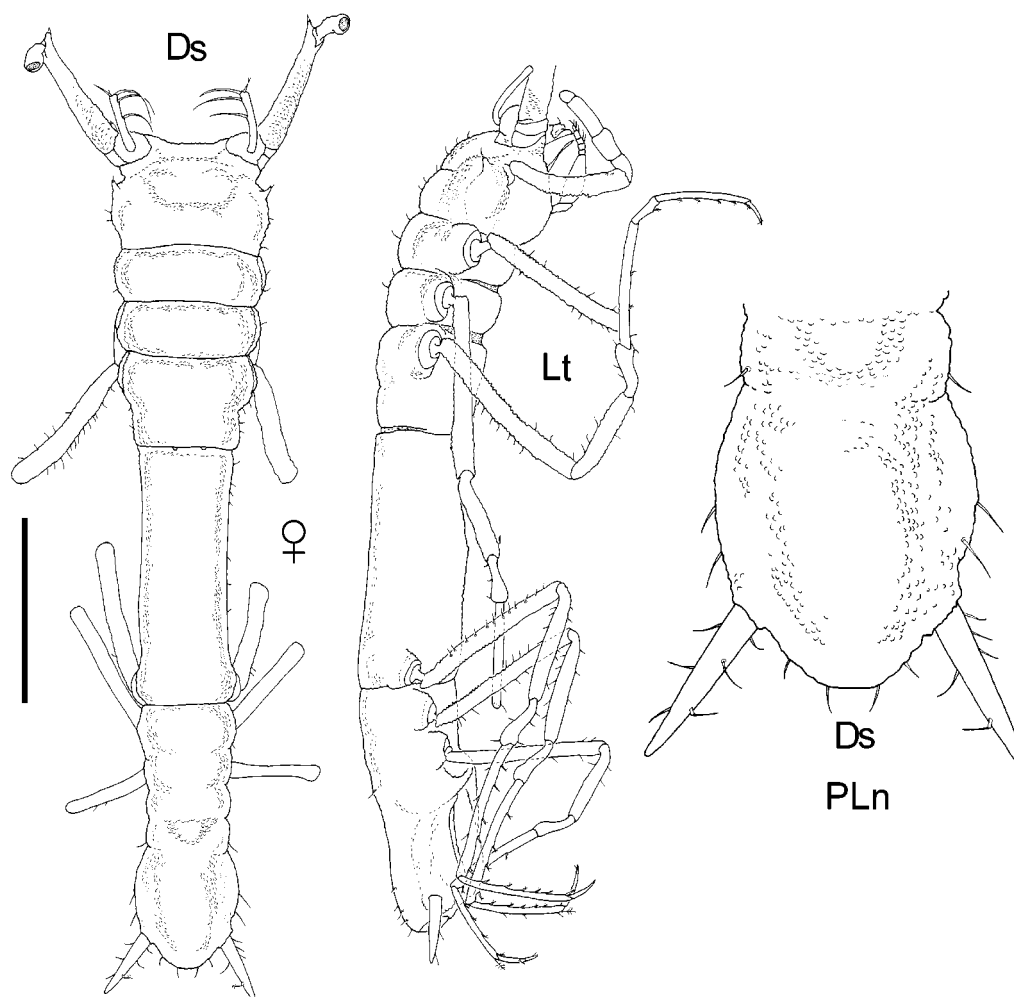
#### *Etymology*

*Inaffectus* means natural or simple.

#### *Material examined*

*Holotype*: female (4.5mm), North Atlantic, offshore of Cork, Ireland, 50°12.3'N, 13°35.8'W, 20 Aug 1972, R/V CHAIN cruise n° 106, stn. WHOI 321, epibenthic sled, 2890–2868 m (ZMUC CRU-9876).

*Paratypes*: male (3.1 mm), same data as holotype (ZMUC CRU-9877); 68 specimens including males, females, mancae and 1 intersex, same data as holotype (AM P 72122); adult male (4.4 mm) same data as holotype (dissected, mouthparts on slide, AM P 72121); preparatory female, same data as holotype (SEM stub AW573, AM P 72245); preparatory female, same data as holotype (SEM stub AW574, AM P 72246).

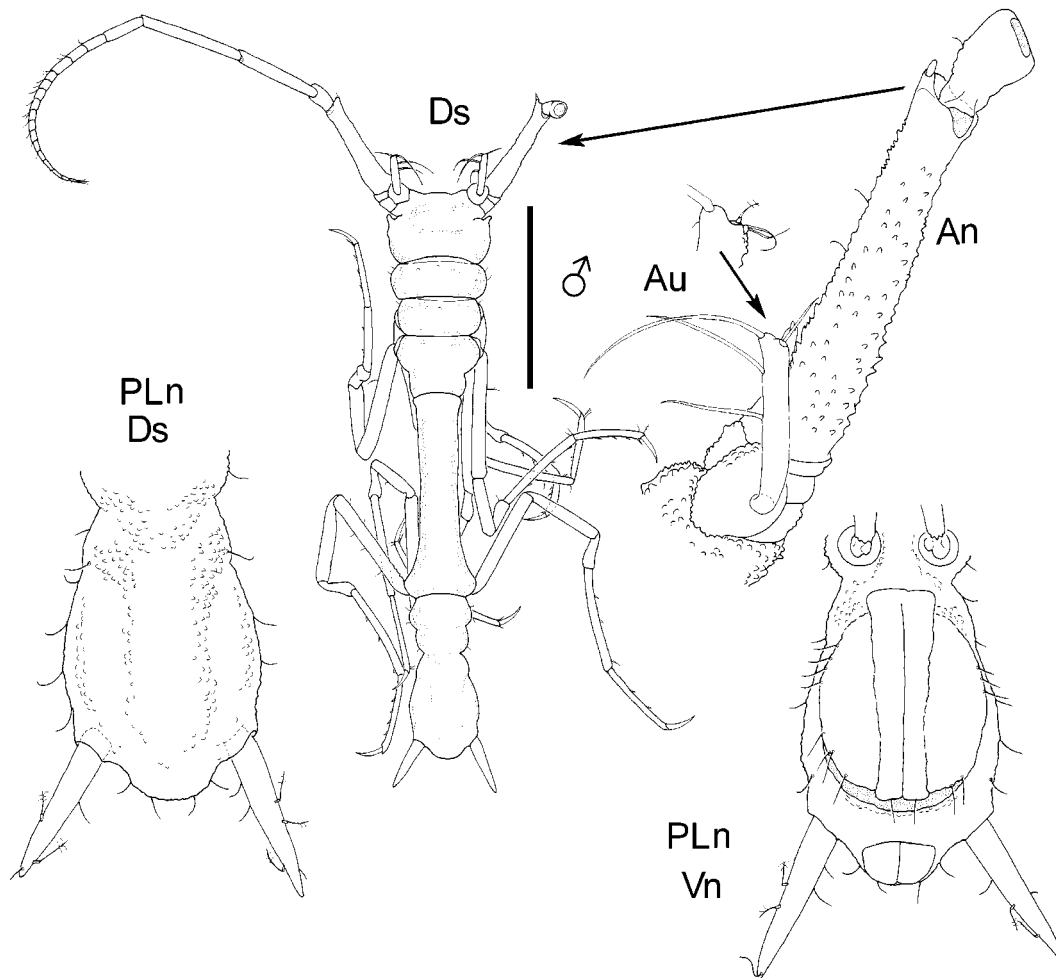


**FIGURE 19.** *Heteromesus inaeffectus* sp. nov. Holotype female, ZMUC CRU-9876: habitus dorsal and lateral; pleotelson dorsal. Scale bars 1.0mm.

*Remarks on type material.* Several specimens in this lot showed developmental oddities. One large specimen that had the female form and obvious pores to the spermathecal ducts, also had somewhat distorted male pleopods. Various asellote species are known to have facultative sex determination, but we suspect that this individual was only a single aberration, perhaps caused by a parasite. Three adult specimens had pereopods in the middle of the pereon that were in a rudimentary state, similar to the limbs of a manca III. Apparently, these limbs were being regenerated in subsequent molts. This species thus shows an ability to lose and regenerate limbs, perhaps as a predation escape mechanism. If the isopod needed to lose a limb, the break could occur at the thin neck between the shaft of the basis and the coxa.

*Diagnosis*

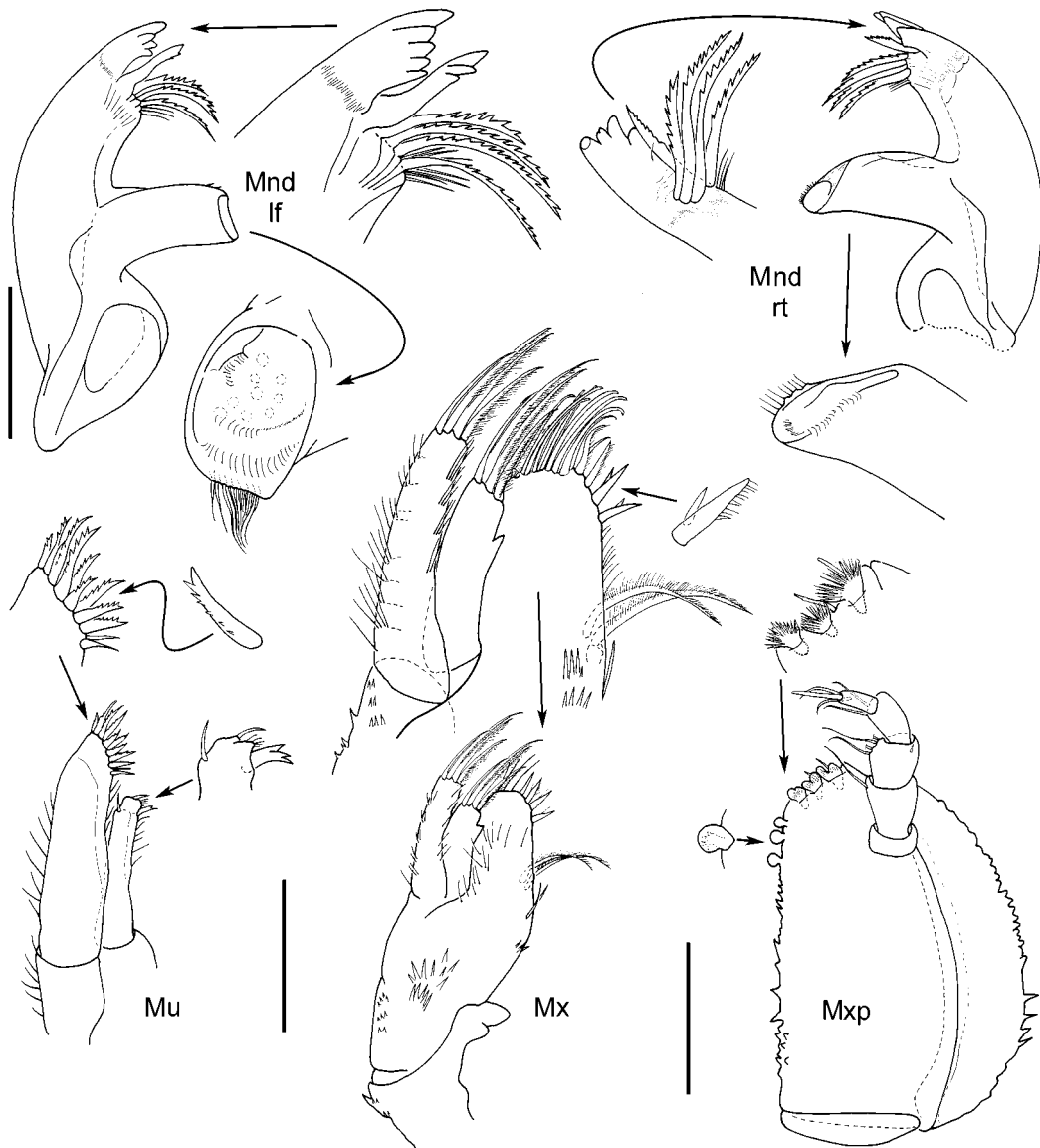
Pereonite 2 in female with no median dorsal spine or tubercle. Pereonite 5 in female length 3.1 width; in male length 6.9 width. Pleotelson posterolateral margin anterior to uropods without spines or tubercles. Antennula with 3 articles altogether. Pereopod bases proximal shoulder with bifid spines. Uropods elongate, length in female 0.50, in male 0.50–0.55 length of pleotelson.



**FIGURE 20.** *Heteromesus inaffectus* sp. nov. Paratype male, ZMUC CRU-9877: habitus dorsal; antennula; antenna; pleotelson dorsal and ventral. Scale bars 1.0mm.

*Description*

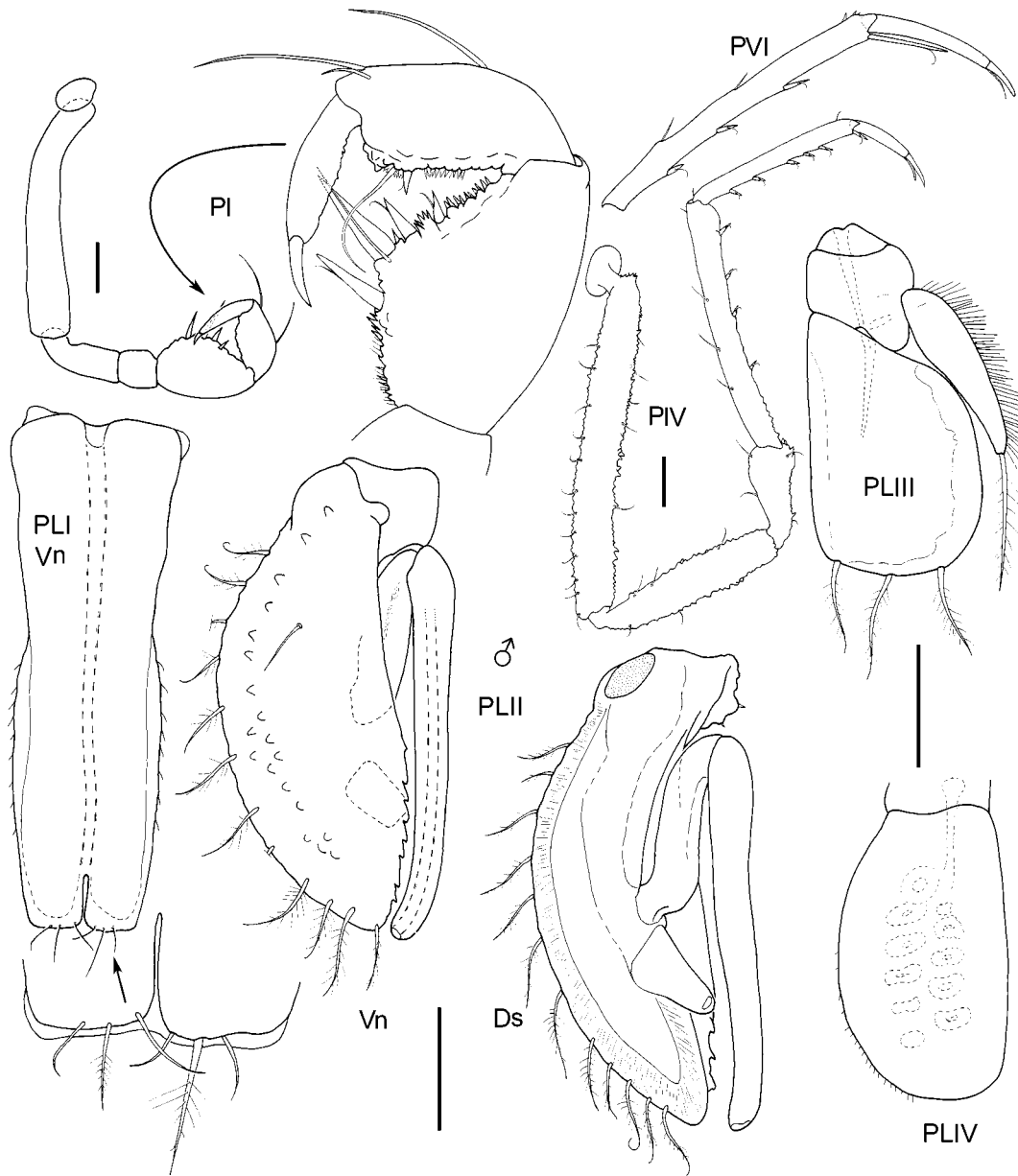
*Body* length in female 4.5 mm; granular. *Head* in female length 0.45 width; dorsal surface with pair of cephalic bullae; lobe on ventrolateral margin present in lateral view; dorsal cuticle tubercular granulation. *Pereonite 1* in female width 0.20 total body length; female with 1 pair of anterolateral simple spines, stout, length distinctly less than length of pereonite 1. *Pereonite 4* in female length 0.65 width. *Pereonite 5* in female length 0.35 total body length. *Pleotelson* in female length 1.4 width.



**FIGURE 21.** *Heteromesus inaffectus* sp. nov. Paratype male dissected, AM P 72121: mandible left and right; maxillula; maxilla; maxilliped. Scale bars 0.1mm.

*Antennula* in female article 2 length 0.48 head width, with 3 elongate stiff ventromedial setae, distal tip produced distally beyond insertion of next article, distal article inserting subapically; article 3 terminal, squat, wider than long. *Antenna* in female length 0.49 anterior body length; article 3 length 0.43 anterior body length, length 4.9 width, with 1 stout distomedial pedestal spine and 1 ventromedial stout pedestal spine placed proximally.

*Labrum* knobs present, low, rounded.

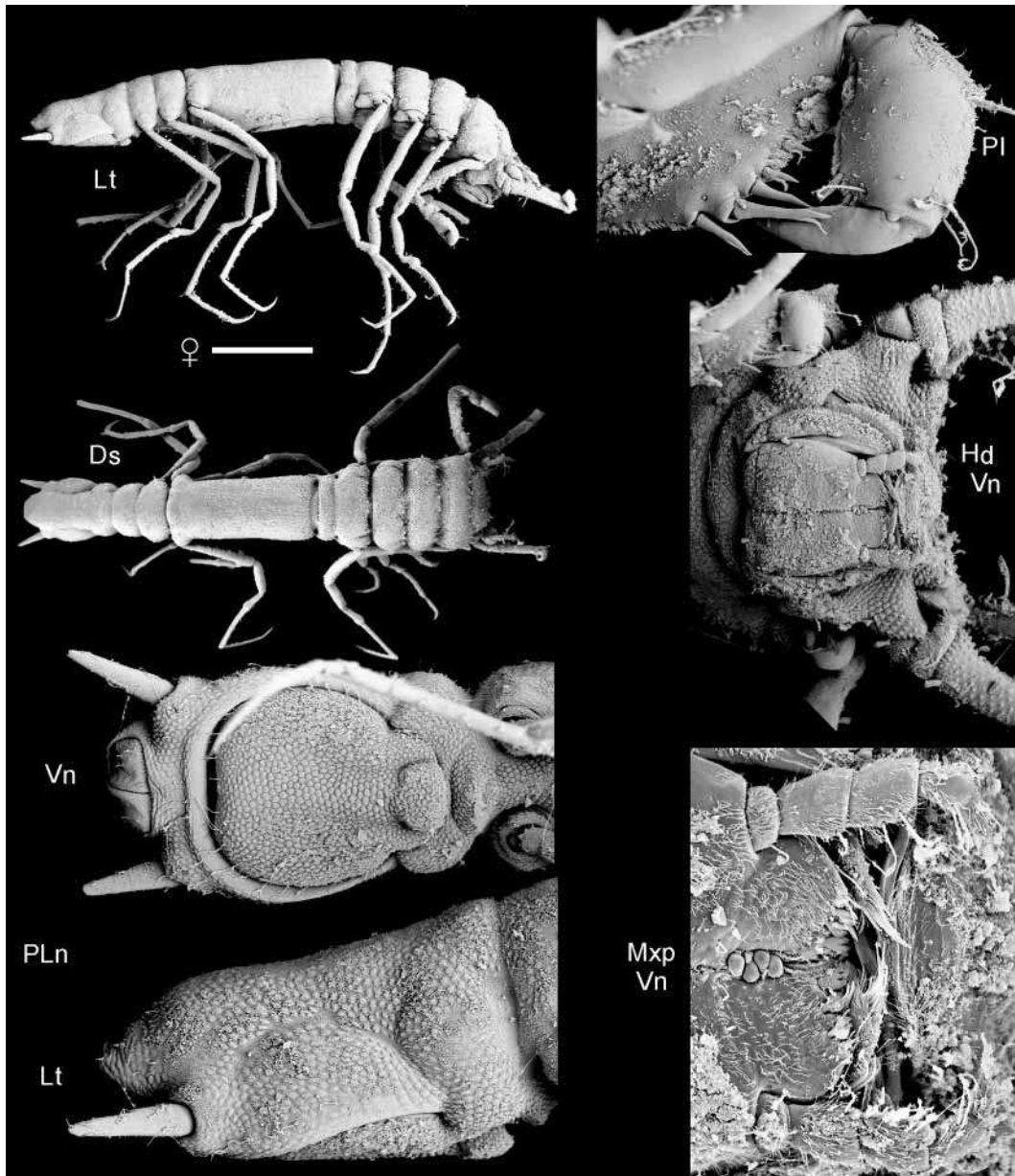


**FIGURE 22.** *Heteromesus inaeffectus* sp. nov. Paratype male dissected, AM P 72121: pereopods I, IV and VI; pleopods I to IV. Scale bars 0.1mm.

*Pereopod bases proximal shoulder with bifid spines. Pereopod I carpus palm length near proximal region length, with 3 robust setae on palm distal to elongate seta; propodus ventral margin with 1 robust seta. Pereopods II–VII bases granulate.*

*Male specific characters. Body length 3.1 mm. Head length 0.45 width. Pereonite 1 width 0.20 total body length; with median tubercle, 1 pair of anterolateral simple spines, stout, length distinctly less than pereonite 1 length. Pereonite 2 with median tubercle, 1 pair of dorsal tubercles. Pereonite 3 with median tubercle. Pereonite 4 length 0.70 width. Pereonite 5 length 0.45 total body length. Pleotelson length 1.45 width. Antennula article*

2 length 0.50 head width. *Antenna* length 2.8 anterior body length; article 3 length 0.51 anterior body length, length 4.4 width, article 3 with distomedial spine; article 5 length 0.42 anterior body length; article 6 length 0.52 anterior body length; flagellum length 0.42 total antennal length, flagellum with 17 articles. *Pleopod I* distal tip without lateral horns. *Pleopod II protopod* apex rounded, *stylet* thick and blunt, heavily calcified, extending beyond distal margin of protopod.



**FIGURE 23.** *Heteromesus inaeffectus* sp. nov. Paratype female, AM P 72245: SEM micrographs, habitus lateral and dorsal; pereopod I; head ventral; pleotelson ventral and lateral; maxilliped. Scale bar 1.0mm.

*Distribution*

North Atlantic Ocean: Celtic Sea, South-West of Ireland, 2890–2868 m.

*Remarks*

*Heteromesus inaffectus* **sp. nov.** differs from similar *Heteromesus* species (*H. granulatus*, the female of *H. frigidus* and *H. schmidtii*) in having an elongated pereonite 5 and long uropods both in the male and female. In some specimens (females and males) we can observe 3–5 pairs of dorsal tubercles arranged in a transverse row near to the anterior margins of pereonites 1–4. These are not easily detected in optical microscopy but are relatively conspicuous in the female specimen used for SEM micrographs (Fig. 23).

***Heteromesus longiremis* Hansen, 1916**

*Heteromesus longiremis* Hansen 1916: 68–69, pl. VI, fig. 2a–f; Gurjanova 1932: 45, tabl. XV, 55; Menzies 1962: 122, fig. 22A–B; Wolff 1962: 85, 217, 262, 275, 289; Kussakin 1988: 481–483, fig. 394–396.

Not *Heteromesus longiremis*.– Chardy 1974: 1549–1551, fig. 8–9.

*Material examined*

None, data taken from Hansen (1916).

*Remarks on type material.* Syntypes mentioned in original description: female fragment (3.5 mm), male fragment (3.7 mm), North Atlantic: Davis Strait, 61°50'N, 56°21'W, 1895–1896, R/V Ingolf, stn 36, 2702 m (1435 Danish fathoms). Type material was missing from ZMUC, but according to Hansen (1916), it consisted of one mutilated female without head and pereonite 1, and one mutilated male without head and pereonites 1–4.

*Diagnosis*

Pereonite 2 in female with median tubercle, with 1 pair of anterolateral simple spines, with no lateral spines or tubercles. Pereonite 5 in female length 4.0 width, in male length 6.2 width. Pleotelson posterolateral margin anterior to uropods without spines or tubercles. Pereopod bases without spines. Uropods length in female 0.50, in male 0.65 length of pleotelson.

*Description*

*Body* granular. *Pereonite 2* in female with median tubercle, 2–3 pairs of dorsal tubercles, 1 pair of anterolateral simple spines. *Pereonite 3* in female with median tubercle, 2 pairs of dorsal tubercles. *Pereonites 2–3* in female with dorsal tubercles arranged in transverse row, anterolateral simple spines short, length distinctly less than length of pereonite 1. *Pereonite 4* in female length 0.55 width. *Pleotelson* in female length 1.35 width.



*Male specific characters.* Pleotelson length 1.3 width. Pleopod II protopod apex rounded.

#### *Distribution*

North Atlantic: Davis Strait, 2702 m. Wolff (1962: 262) mentions 2 localities (at 698 and 2702 m); not in accordance with Hansen (1916: 69).

#### *Remarks*

*Heteromesus longiremis* was scored according to original description by Hansen (1916), measurements having been obtained from his illustrations. This species is poorly characterised but is distinct from other species based on the following combination of features: pereopods II–VII bases lacking spines; female pereonite 5 length 4.0 width, 6.2 in male; and male uropods being longest of any recorded species, length 0.65 pleotelson length.

#### ***Heteromesus longiremis* sensu Chardy, 1974**

*Heteromesus longiremis* sensu Chardy 1974: 1549–1551, fig. 8–9.

#### *Material examined*

None; male measurements taken from Chardy (1974: 1549–1552; figs. 8–9). Reported localities from the North Atlantic, Atlantic Abyssal Plain, Campagne Noralante R/V Jean Charcot, August–October 1971: 1 male illustrated, stn 8, E03 (52°10.4'N 45°32.3'W, 4100 m); 1 female, stn 5, E02 (54°21.6'N 23°00.2'W, 3178 m), 1 damaged specimen, stn 16, E06 (58°47.7'N 52°56.5'W, 3610 m); 2 females, stn 21, E07 (38°28.2'N 43°03'W, no indication of depth).

#### *Diagnosis (Male only)*

Pleotelson posterolateral margin anterior to uropods without spines or tubercles. Pereonite 5 length 4.6 width. Antennula with 5 articles altogether (Chardy, 1974:1549), article 2 distal tip produced distally beyond insertion of next article, distal article inserting subapically, article 3 longer than article 4. Uropods length 0.50–0.55 length of pleotelson.

#### *Description (Male characters only)*

Body length 5.7 mm, granular. Head length 0.45 width, with 2 tubercles on dorsal surface posterior to antennulae, cuticular structure fine tubercular granulations. *Pereonite 1* width 0.20 total body length; with median tubercle, 4–5 pairs of dorsal tubercles, 1 pair of anterolateral simple spines. *Pereonite 2* with median tubercle, 4 pairs of dorsal tubercles, 1 pair of anterolateral simple spines. *Pereonite 3* with median tubercle, 2 pairs of dorsal tubercles. *Pereonite 4* length 0.65 width; with median tubercle, 2 pairs of dorsal

tubercles. *Pereonites 1–4* dorsal tubercles arranged in transverse row along anterior margin, pereonite 1 with 1 additional pair of dorsal tubercles close to anterolateral spine, anterolateral simple short spines decreasing in size from pereonite 1 to 2, length distinctly less than pereonite 1 length (Chardy (1974, fig. 8) drew median tubercles as short spines, but in Hansen (1916, Pl. VI, fig. 2a) these were drawn in female as tubercles). *Pereonite 5* length 0.30 total body length. *Pleotelson* length 1.3 width.

*Antennula* article 2 length 0.50 head width with 3 elongate stiff ventromedial setae (and one proximal shorter seta), distal tip produced distally beyond insertion of next article, distal article inserting subapically; article 3 squat, wider than long; terminal article shorter than penultimate article, aesthetascs absent. *Antenna* length 2.6 anterior body length; article 3 length 0.47 anterior body length, length 4.1 width, article 3 with distomedial spine; article 5 length 0.31 anterior body length; article 6 length 0.51 anterior body length; flagellum length 0.41 total antennal length, flagellum with 17 articles.

*Maxillula* medial lobe without robust dentate setae. *Maxilla* with 2 long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe.

*Pereopod I merus* dorsal margin with 2 distinctly robust setae (short), placed distally; *carpus* palm length distinctly less than proximal region length, with 2 robust setae on palm distal to elongate seta, shorter setae directly adjacent to elongate seta on palm ventral margin; *propodus* ventral margin with 1 robust seta, placed proximally to elongate fine seta and distally to several fine setae and fine denticles on proximal margin.

*Pleopod I* distal tip without lateral horns. *Pleopod II protopod* apex rounded, *stylet* thick and blunt, heavily calcified (assumed), extending beyond distal margin of protopod.

#### *Distribution*

North Atlantic: Atlantic Abyssal Plain, 3178–4100 m.

#### *Remarks*

Because the original types of *H. longiremis* Hansen, 1916 are missing, we cannot fully evaluate Hansen's specimens of this species. We suspect that the specimens of Chardy (1974) may be a different species, but have not inspected them. Thus, we cannot reclassify Chardy's specimens. The male scored from Chardy (1974) and measurements obtained from the illustrations (his figs. 8–9) are at variance with Hansen's original. *Pereonite 5* length to width ratio in the male is 4.6, which is distinctly smaller than Hansen's (1916) male specimen, 6.2. The uropod is smaller (length 0.50–0.55 length of pleotelson in Chardy's specimen and 0.65 in Hansen's). Pereonite 4 has dorsal tubercles in Chardy's male and Hansen's female lacks them (Hansen's male is a fragment lacking head and P1–4). The pleotelson length to width ratio, however, is similar. Chardy mentioned the collection of 1 male, 2 females and 1 mutilated specimen but described only the male. Given the large geographic spread of the reported specimens, we are also unsure whether Chardy's (1974) specimens are all conspecific. *Heteromesus longiremis* sensu Chardy is

similar to *H. schmidtii* but the two species can be identified using the number of antennular articles. Chardy (1974: 1549) reports that the antennula has 3 terminal articles, and his illustration (his fig. 8D) shows that the two distal articles are minute. Given the difficulties in interpreting these articles in other species by the original authors, some uncertainty remains on this point.

***Heteromesus oryktus* sp. nov.**

(Figs 24–25)

*Etymology*

*Oryktos* means "digger" (Greek, masculine) because this species was collected from mudstone burrows possibly made by the animals.

*Material examined*

*Holotype*: female (6.1 mm), North Atlantic: off West Greenland, canyon bordering the western margin of the Fylla Structural Complex, 63°14.1'N, 55°26.0'W, 18.Aug 2003, R/V Prof Logachev, TTR13 stn AT-457-GR, 2140 m (ZMUC CRU-9872)

*Paratype*: male (5.7 mm), same data as holotype (ZMUC CRU-9873).

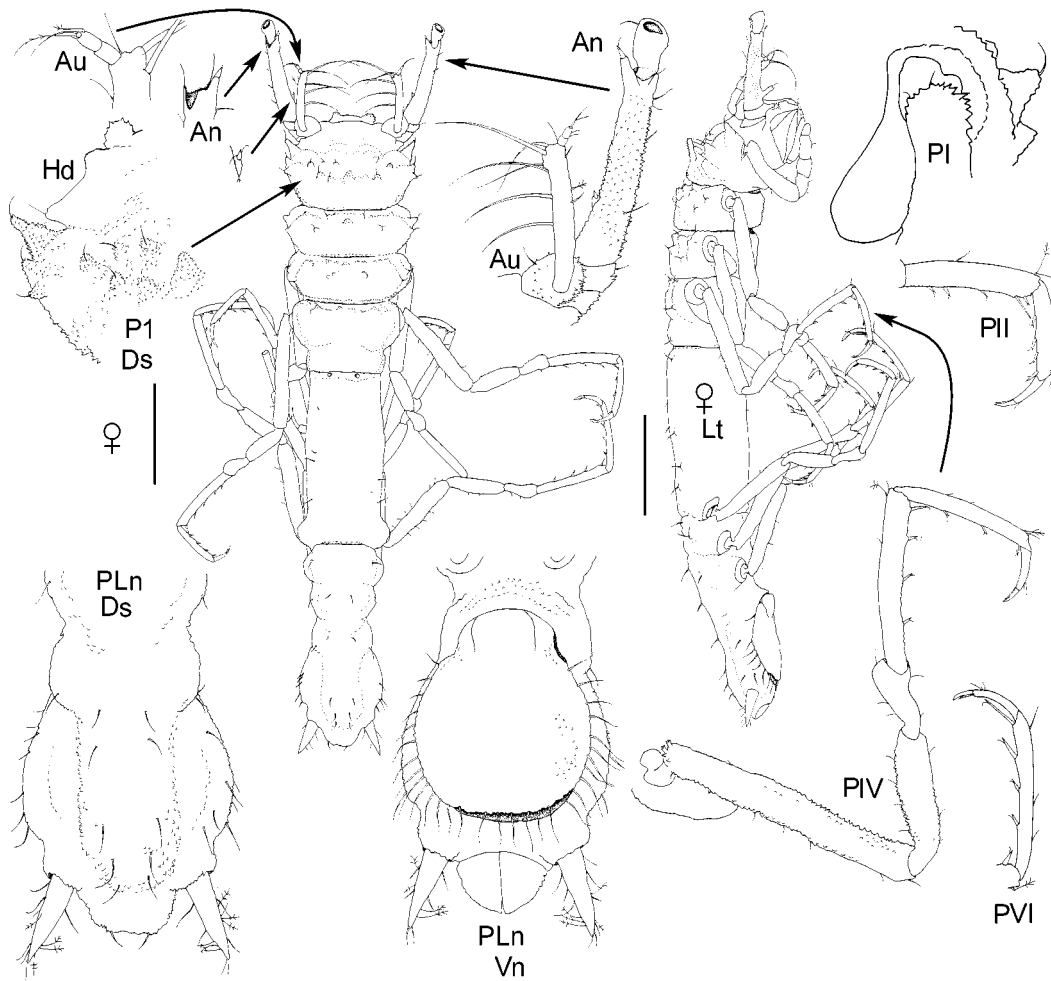
*Diagnosis*

Pereonites 1–3 with anterolateral denticulate spines; pereonites 1–4 with median and paired lateral denticulate spines arranged in dorsal rows. Pereonite 1 of male with paired lateral rook spines. Pereonite 5 in female length 2.2 width, in male 4.1 width. Pleotelson posterolateral margin anterior to uropods without spines or tubercles. Antennula with 5 articles altogether; article 3 length similar to article 4. Uropods in male length 0.45 length of pleotelson.

*Description*

*Body* length in female 6.1 mm; granular. *Head* in female length 0.60 width, with 1–2 pairs of simple spines, cuticular structure fine spinous granulations, lobe on ventrolateral margin absent in lateral view. *Pereonite 1* in female width 0.20 total body length; with median simple spine, 2–3 pairs of dorsal simple spines, 1 pair of anterolateral simple spines, 2 pairs of lateral simple spines. *Pereonite 2* in female with median simple spine, 2 pairs of dorsal rook spines, 2 pairs of lateral simple spines. *Pereonite 3* in female with median simple spine, 2–3 pairs of dorsal simple spines, 1 pair of lateral simple spines. *Pereonite 4* length 0.65 width; with 2 pairs of dorsal simple spines. *Pereonites 1–4* in female with spines stout to short, denticulate and topped by setae; anterolateral spines decreasing in length from pereonite 1 to pereonite 3, length distinctly less than length of pereonite 1. *Pereonite 5* in female length 0.25 total body length. *Pereonite 5* with lateral row of setae. *Pleotelson* in female length 1.5 width.

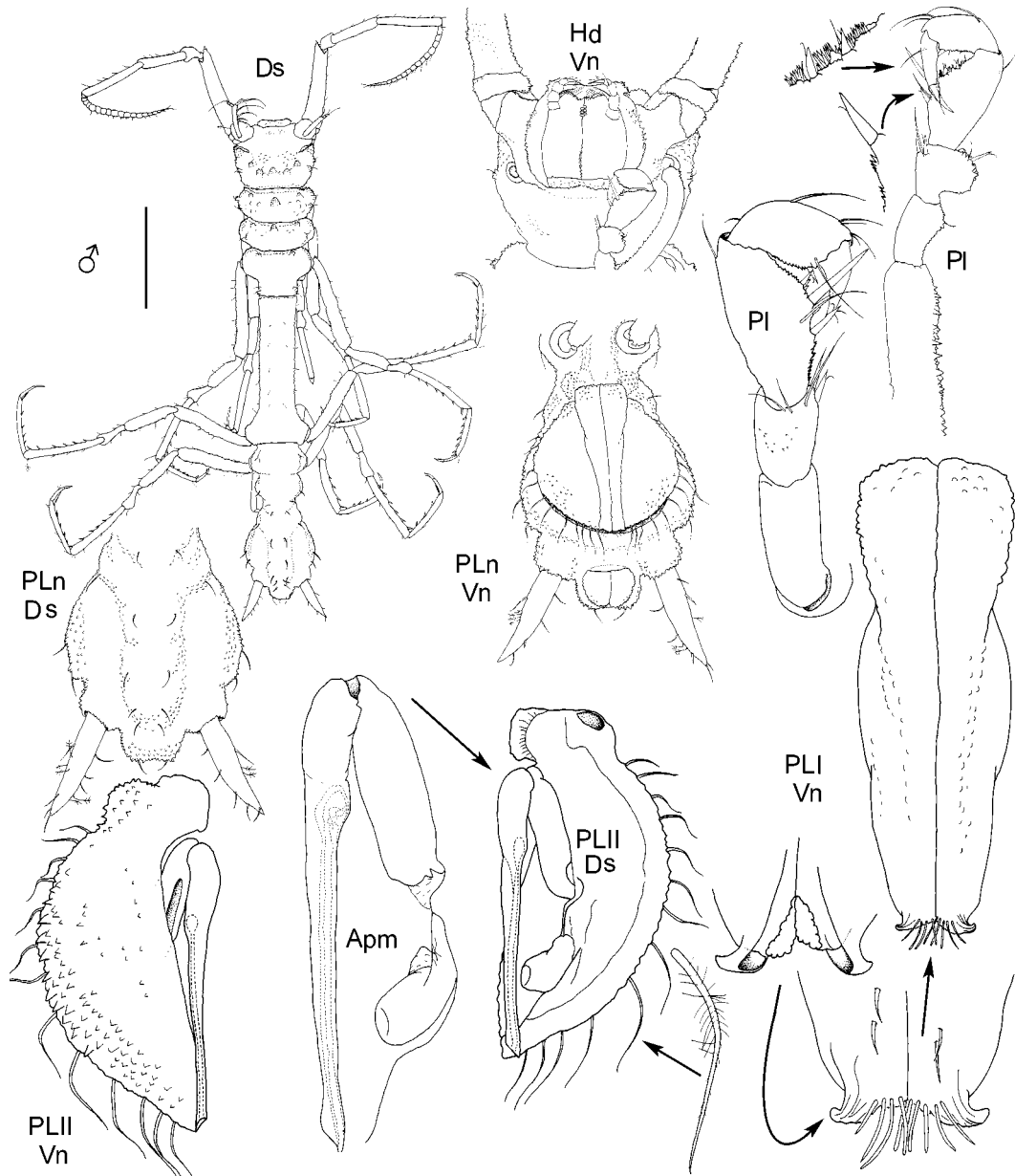
*Antennula* in female article 2 length 0.58 head width, with 4 elongate stiff ventromedial setae (and 2 distal shorter setae); article 3 short and tubular, length near width, terminal article shorter than penultimate article, aesthetascs absent. *Antenna* in female article 2 with 1 ventromedial spine (in female only); article 3 length 0.35 anterior body length, length 3.4 width, with 1 distomedial stout pedestal spine and 1 ventral long pedestal spine placed in proximal third of article.



**FIGURE 24.** *Heteromesus oryktus* sp. nov. Holotype female, ZMUC CRU-9872: habitus dorsal and lateral; head and detail of dorsal denticulate spines on pereonite 1; antennula; antenna; pleotelson dorsal and ventral; pereopod IV and details on pereopods I, II and VI. Scale bars 1.0mm.

*Labrum* knobs present, low, rounded, sharply denticulate.

*Pereopod* bases proximal shoulder with rook spines. *Pereopod I* carpus palm length near proximal region length, with 2 robust setae on palm distal to elongate seta; *propodus* ventral margin with 1 robust seta. *Pereopods II–VII* bases granulate.



**FIGURE 25.** *Heteromesus oryktus* sp. nov. Paratype male, ZMUC CRU-9877: habitus dorsal; head ventral; pleotelson dorsal and ventral; pereopod I; pleopods I and II; appendix masculina. Scale bars 1.2mm.

*Uropods* in female length 0.25–0.30 length of pleotelson.

*Male specific characters.* Body length 5.7 mm. Head length 0.70 width; cuticular structure with spinous granulations. *Pereonite 1* width 0.15 total body length; with median simple spine, 2 pairs of dorsal simple spines, 1 pair of anterolateral simple spines, 2 pairs

of lateral rook spines. *Pereonite 2* with median simple spine, 1 pair of dorsal rook spines. *Pereonite 3* with median simple spine, 1 pair of lateral rook spines. *Pereonite 4* length 0.65 width; with 1 pair of dorsal rook spines, 2 pairs of posterolateral rook spines. *Pereonites 1–4* simple spines stout to short, denticulate and topped by setae; anterolateral spines decreasing in length from pereonite 1 to pereonite 3, length distinctly less than length of pereonite 1. *Pereonite 5* length 0.30 total body length. *Pleotelson* length 1.35 width. *Antennula* article 2 length 0.60 head width. *Antenna* length 1.8 anterior body length; article 3 length 0.46 anterior body length, length 3.9 width, with distomedial pedestal spine; article 5 length 0.28 anterior body length; article 6 length 0.38 anterior body length; flagellum length 0.30 total antennal length, flagellum with at least 17–18 articles. *Pleopod I* distal tip with lateral horns. *Pleopod II protopod* apex rounded; *stylet* thin with medial blade, extending beyond distal margin of protopod. *Uropods* much longer than in female; length 0.45 length of pleotelson.

#### *Distribution*

North Atlantic: west of Greenland, canyon bordering the western margin of the Fylla Structural Complex, 2140 m, in mudstones; only known from type locality.

#### *Remarks*

*Heteromesus oryktus* **sp. nov.** was found in mudstones collected from the slope of a canyon (female found inside tubular cavity). The mudstones were heavily bored into by sipunculids.

*Heteromesus oryktus* is similar to *H. dentatus* and *H. greeni* (characters already mentioned in the remarks on these species). The most distinctive features of *H. oryktus* are the anterolateral denticulate spines on pereonites 1–3 and median and paired lateral denticulate spines arranged in dorsal rows on pereonites 1–4.

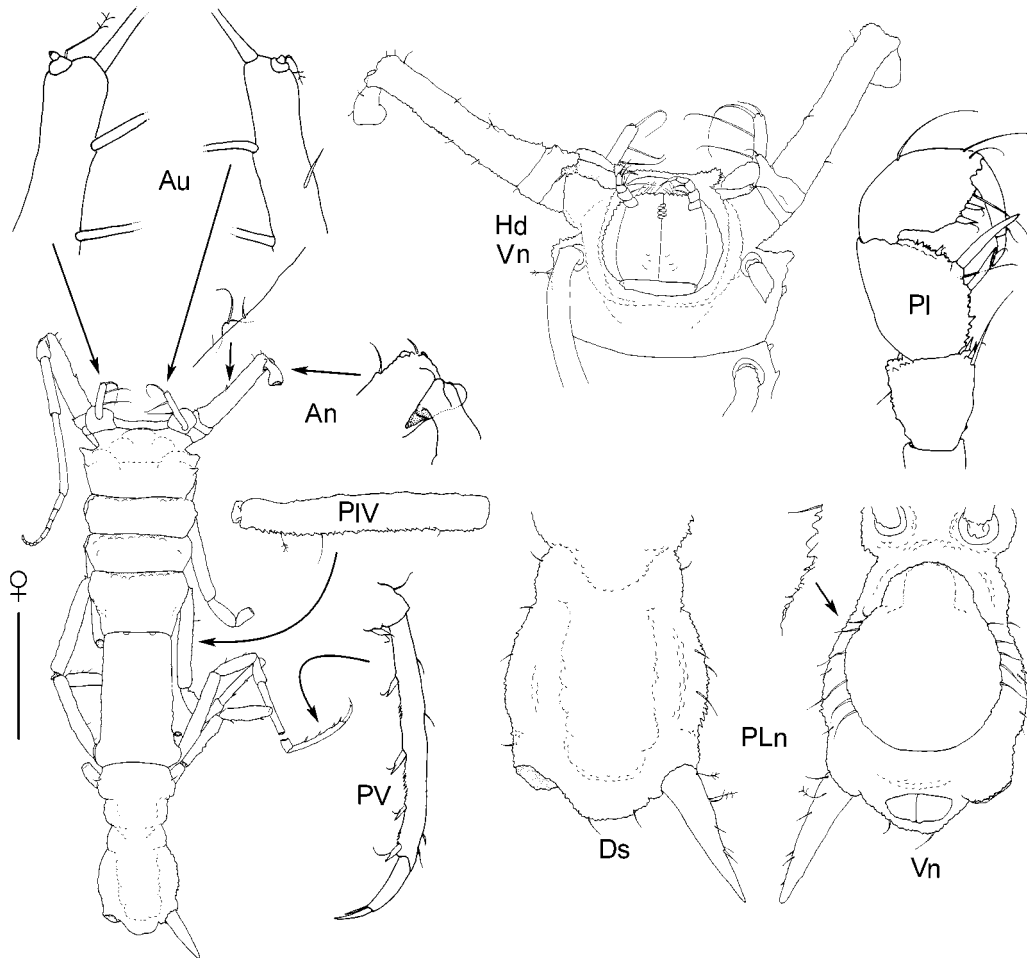
#### ***Heteromesus schmidtii* Hansen, 1916**

(Fig. 26)

*Heteromesus schmidtii* Hansen 1916: 69–70, pl. VI, fig. 3a–e; Gurjanova 1932: 45, tabl. XV, 56, 1933: 411; Menzies 1962: 122; Wolff 1962: 85, 217, 260; Kussakin 1988: 477–478, fig. 390.

#### *Material examined*

*Holotype*: female (4.1 mm), North Atlantic: South of Iceland, 62° 57'N, 19°58'W, 14 Jul 190, R/V Thor, 3956m (508 Danish fathoms) (ZMUC CRU-8027).



**FIGURE 26.** *Heteromesus schmidtii* Hansen, 1916. Holotype female, ZMUC CRU-8027: habitus dorsal; antennulae; antenna detail; head ventral; pereopod I; pereopod IV basis; pereopod V propodus and dactylus; pleotelson dorsal and ventral. Scale bar 1.0mm.

*Remarks on type material.* The holotype is a fragile preparatory female, with most pereopods broken; the left uropod and right pereopod I are also broken but in the vial.

*Diagnosis (Female characters only)*

Pereonite 1 with paired lateral spines; pereonite 4 with median tubercle and paired tubercles. Pereonite 5 length 1.9 width. Antennula with 3 articles altogether, article 2 distal tip produced distally beyond insertion of next article, distal article inserting subapically, article 3 terminal.

*Description (Female characters only)*

Body length 4.5 mm; granular. Head length 0.40 width; dorsal surface with pair of cephalic bullae; dorsal cuticle tubercular granulation. Pereonite 1 width 0.20 total body

length; with median tubercle, 1 pair of dorsal tubercles, 1 pair of anterolateral simple spines, 1 pair of lateral simple spines. *Pereonite 2* with median tubercle, 3–4 pairs of dorsal tubercles, 1 pair of lateral tubercles. *Pereonite 3* with median tubercle, 3–4 pairs of dorsal tubercles. *Pereonite 4* length 0.60 width; with median tubercle, 2–3 pairs of dorsal tubercles. *Pereonites 1–4* tubercles arranged in row along anterior margin, anterolateral spines stout, length distinctly less than length of pereonite 1. *Pereonite 5* length 0.25 total body length. *Pleotelson* length 1.3 width.

*Antennula* article 2 length 0.59 head width, with 3 elongate stiff ventromedial setae; article 3 terminal, squat, wider than long, aesthetascs absent. *Antenna* length 1.6 anterior body length; article 2 with 1 ventromedial spine; article 3 length 0.41 anterior body length, length 4 width, with 1 ventromedial short pedestal spine with thin curved simple seta; article 5 length 0.27 anterior body length; article 6 length 0.39 anterior body length; flagellum with 10 articles, flagellum length 0.22 total antenna length.

*Labrum* knobs present, rounded conical, with spinous granulation.

*Pereopod bases* proximal shoulder with simple spines only. *Pereopod I carpus* palm length distinctly less than proximal region length, with 1 robust seta on palm distal to elongate seta; *propodus* ventral margin with 2 robust setae. *Pereopods II–VII bases* granulate.

*Uropods* length 0.50 length of pleotelson.

#### *Distribution*

North Atlantic, south of Iceland, 956 m.

#### *Remarks*

Hansen (1916: 69) described the antennulae of *Heteromesus schmidtii* as follows: "it has above near the distal end a small tubercle, which in closer examination is seen to consist of three extremely short joints (Pl. VI, fig. 3c)". We find only one reduced article with the proximal part of the long distal seta that is broken. Our drawing (Fig. 26) is similar to Hansen's but he clearly drew 3 articles and a distal seta. The situation with this species is similar to *H. frigidus*, which also has only one article, while Hansen (1916: 71) stated that it has 2 articles.

*H. schmidtii* is distinct from similar species of the genus (*H. granulatus*, *H. inaffectus* and the female of *H. frigidus*) because pereonite 1 has paired lateral spines and pereonite 5 has a different L/W ratio (longer than *H. granulatus* and shorter than *H. frigidus* and *H. inaffectus*).

#### ***Heteromesus similis* Richardson, 1911**

(Fig. 27)

*Heteromesus similis* Richardson 1911: 532–533; Menzies 1962: 123; Wolff 1962: 85, 265.



*Material examined*

*Holotype*: Manca III male (3.5 mm), North Atlantic, Azores, northwest of S. Miguel, 38°38'N, 27°26'W, 22 Aug 1883, R/V Talisman, stn 31, 2995 m (MNHN IS-1775).

*Remarks on type material*. A manca III male with developing pereopods VII: the body is decalcified, the right uropod and both antennulae are missing (except for the first article) and pereopods II–VI are broken.

*Diagnosis (Male manca III only)*

Pereonites 1–4 with transverse rows of pointed tubercles. Pereonite 5 length 4.6 width. Pleotelson with no posterolateral spines. Pereopod bases proximal shoulder with simple spines only. Pereopods II–VII bases denticulate, sometimes sharply toothed, with pedestal spines.

*Description (Male manca III characters only)*

*Body* length 3.5mm, granular. *Head* length 0.75 width, with 2 dorsal tubercles, on frons between antennulae; lobe on ventrolateral margin present in lateral view; dorsal cuticle not evident (specimen decalcified). *Pereonite 1* width 0.20 total body length; with median tubercle, 2 pairs of dorsal tubercles, 1 pair of anterolateral simple spines, 1 pair of lateral simple spines. *Pereonite 2* with median tubercle, 2–3 pairs of dorsal tubercles, 1 pair of anterolateral simple spines, 1 pair of lateral tubercles. *Pereonite 3* with median tubercle, 2–3 pairs of dorsal tubercles, 1 pair of anterolateral simple spines, 1 pair of lateral tubercles. *Pereonite 4* length 0.70 width; with median tubercle, 2–3 pairs of dorsal tubercles, 2 pairs of posterolateral stout rook spines. *Pereonites 1–3* anterolateral spines decreasing in length, length distinctly less than pereonite 1 length, tubercles arranged in transverse row on anterior margin of pereonites. *Pereonite 5* length 0.3 total body length. *Pleotelson* length 1.65 width.

*Antennula* with 5 articles altogether (estimated from original description). *Antenna* article 2 with ventrolateral spine; article 3 length 0.44 anterior body length, length 4.4 width, with distomedial stout pedestal spine and distolateral shorter pedestal spine and 2 medial pedestal spines placed ventrally and dorsally in proximal third of article.

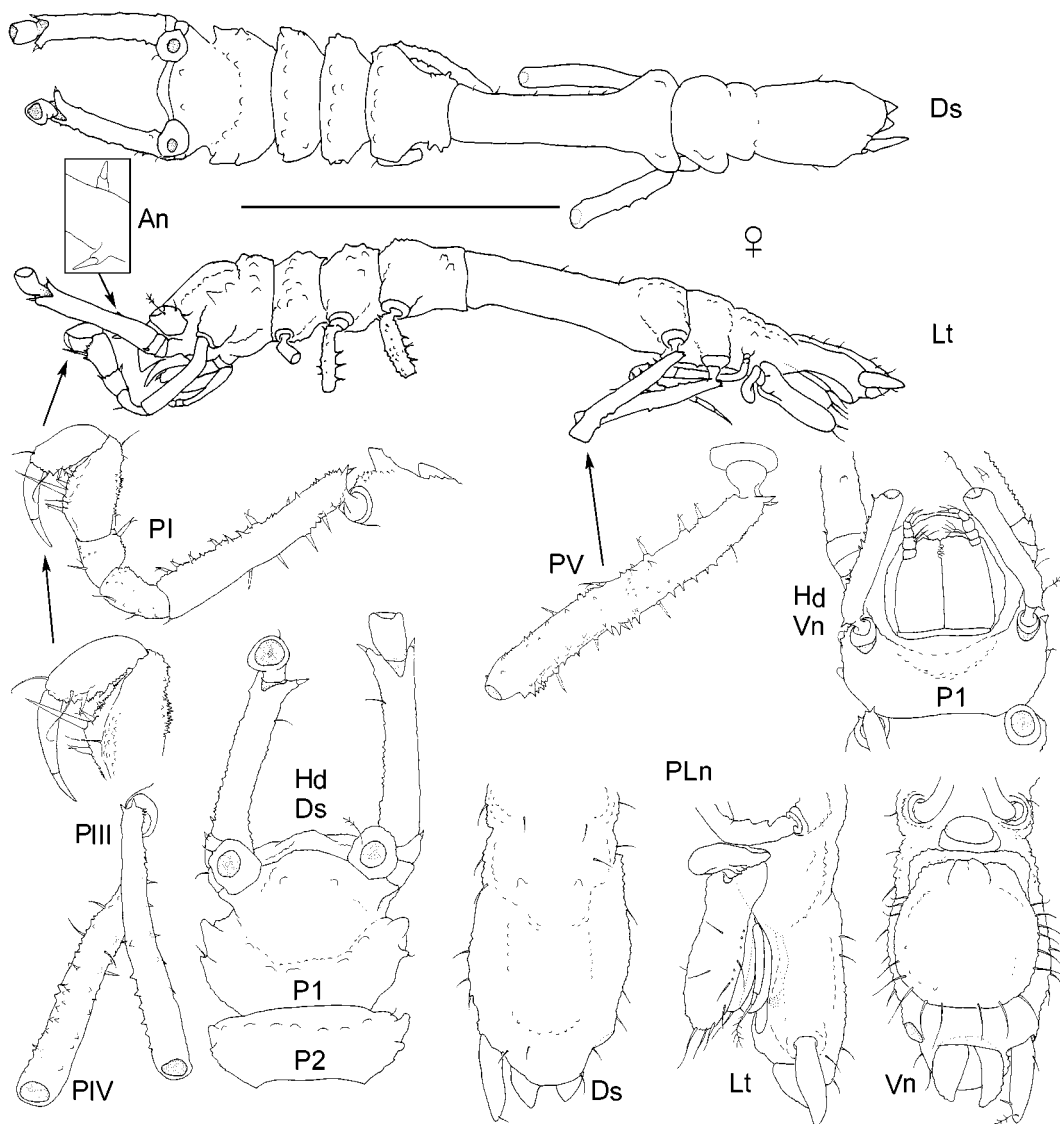
*Labrum* knobs absent.

*Pereopod bases* proximal shoulder with simple spines only. *Pereopod I* carpus palm length near proximal region length, with 3 robust setae on palm distal to elongate seta (decreasing in size distally); *propodus* ventral margin with 2 robust setae. *Pereopods II–VII bases* denticulate, sometimes sharply toothed, with pedestal spines (robust setae on short pedestal with tuberculate shape), positioned more distally on dorsal margin than on ventral margin.

*Uropods* length 0.30 length of pleotelson.

*Distribution*

North Atlantic: northwest of the Azores, 2995 m.



**FIGURE 27.** *Heteromesus similis* Richardson, 1911. Holotype manca III male, MNHN IS-1775: habitus dorsal and lateral; antenna detail; head dorsal and ventral; pereopod I; pereopods III–V bases; pleotelson dorsal, lateral and ventral. Scale bar 1.5 mm.

#### Remarks

Richardson (1911) provided no illustrations of the specimens of *Heteromesus similis*, so this species is often overlooked in compendia on deep-sea isopods (e.g., Kussakin 1988). She described antennulae that are now missing from the holotype, with 4 articles in the “flagellum”, the fourth perhaps being the base of a broken terminal seta; no other *Heteromesus* species has this many articles. This species, although only represented by a manca III, is distinct from other *Heteromesus* species by its joint possession of 1 pair of

lateral spines on pereonite 1, 2 pairs of posterolateral rook spines on pereonite 4 (also seen in the male of *H. oryktus*), and rows of dorsal tubercles on pereonites 1–4.

*H. similis* is similar to *H. spinescens* (the transverse rows of more or less pointed tubercles on the anterior margin of pereonites 1–4 in *H. similis* are not much different from the low spines in *H. spinescens*), but it has a longer pereonite 5 and lacks pleotelson posterolateral spines. Richardson (1911) mentioned posterolateral spines on the pleotelson, but these are absent in the holotype (Fig. 27).

### ***Heteromesus spinescens* Richardson, 1908**

(Figs 28–29)

*Heteromesus spinescens* Richardson 1908: 83–84, fig. 19; Menzies 1962: 123, fig. 22E; Wolff 1962: 85, 265; Kussakin 1988: 480–481, fig. 393.

#### *Material examined*

*Holotype*: male, Northwest Atlantic, off New England, off Virginia, approximately 37°30'N 72°30'W, 1883, USFC Steamer Albatross, stn 2105, 2551 m (1395 fathoms) (USNM 38970).

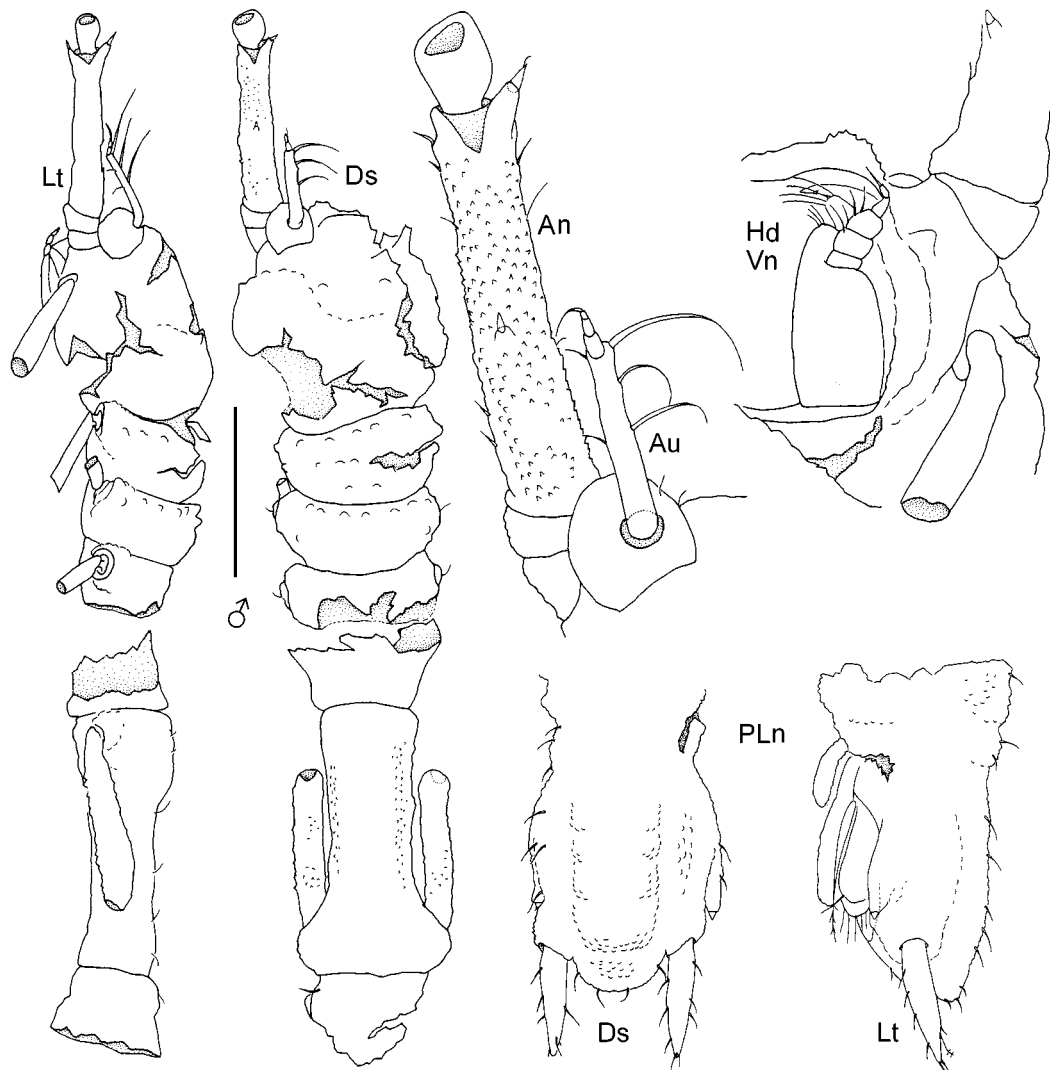
*Remarks on type material*. The holotype male had been severely damaged since Richardson's (1908) description. The body was found to be broken in three parts, several pereonites and the head smashed, both the antennula and the antenna on the right side missing and on the left side the antenna broken at article 4, pereopods I–IV in both sides and pereopods VI and VII on the right side missing (only the basis of some remain). Other material labelled under this species was found to belong to other species.

#### *Diagnosis (Male only)*

Pereonite 5 length 3.3 width. Antennula with 5 articles altogether, article 3 elongate and tubular, much longer than wide. Pereopod bases proximal shoulder with no spines; pereopods II–VII bases denticulate, sometimes sharply toothed with simple spines.

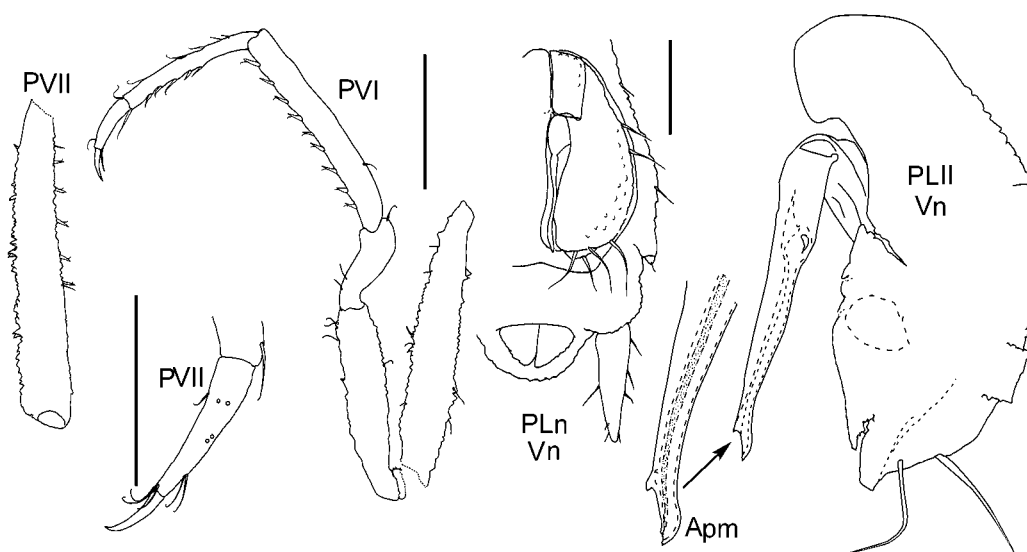
#### *Description (Male characters only)*

*Body granular. Head* with 2 tubercles (low and unelaborated) on dorsal surface near posterior margin of head. *Pereonite 1* width 0.20 total body length; with median simple spine, 6 pairs of dorsal simple spines, 1 pair of anterolateral simple spines, 1 pair of lateral simple spines. *Pereonite 2* with median simple spine, 6 pairs of dorsal simple spines. *Pereonite 3* with median simple spine, 6 pairs of dorsal simple spines. *Pereonite 4* length 0.60 width; with 2 pairs of dorsal simple spines. *Pereonites 1–4* dorsal spines short, arranged in two transverse rows, anterolateral spines stout, length distinctly less than pereonite 1 length. *Pereonite 5* length 0.30 total body length. *Pleotelson* length 1.4 width; posterolateral margin anterior to uropods with pedestal stout spines topped by short robust seta.



**FIGURE 28.** *Heteromesus spinescens* Richardson, 1908. Holotype male, USNM 38970: habitus dorsal and lateral; antennula; antenna; head ventral; pleotelson dorsal and lateral. Scale bar 1.0 mm.

*Antennula* article 2 length 0.42 head width, with 3 elongate stiff ventromedial setae; article 3 longer than article 4; terminal article shorter than penultimate article; aesthetascs absent. *Antenna* article 3 length 0.48 anterior body length, length 4.7 width, with distomedial and distolateral stout pedestal spines, 1 ventromedial and 1 dorsal pedestal spines placed midlength.



**FIGURE 29.** *Heteromesus spinescens* Richardson, 1908. Holotype male, USNM 38970: pereopod VI; pereopod VII basis and dactylus; pleotelson ventral; pleopod II and appendix masculina. Scale bars, left to right: 0.2mm, 0.5mm, 0.3mm.

*Labrum* knobs present, low, rounded, denticulate.

*Pereopods II–VII bases* denticulate, sometimes sharply toothed, with simple spines, scattered, with tuberculate (shorter than broad) shape, with robust sensillate setae, on dorsal and ventral margin.

*Pleopod II protopod* apex rounded; *stylet* thin with medial blade (tiny), extending beyond distal margin of protopod. *Uropods* length 0.40 length of pleotelson.

#### *Distribution*

Northwest Atlantic, off Virginia, south of Martha's Vineyard, south of Block Island, southeast of Georges Bank, 2155–3337 m.

#### *Remarks*

The pleotelson of *Heteromesus spinescens* Richardson was incompletely described by Richardson (1908). The holotype has a posterolateral pedestal spine on each side of pleotelson (inserted ventrally near the border of operculum). Three pairs of low tubercles on the dorsal surface of the pleotelson are arranged medially in two longitudinal rows. The uropods also have setae, not shown in Richardson's description.

Our database for *H. spinescens* was partially scored using the original description of Richardson (1908: 83–84), because the holotype was in such poor condition. Other material, mostly females and juveniles from the US National Museum of Natural History labelled as *H. spinescens* by Richardson, includes a mixture of at least four species

(including 1 *H. granulatus*). Among these, one male has 4 long spines on the head and is clearly from an undescribed species. *H. spinescens* differs from other species of *Heteromesus* by having the shortest pereonite 5 (length only 3.3 width) in the adult male.

***Heteromesus spinosus* (Beddard, 1886)**

(Fig. 30)

*Ischnosoma spinosum* Beddard 1886: 40–42, pl. VI, fig. 1–5.

*Heteromesus spinosus*.– Richardson 1908: 81.

*Material examined*

*Holotype*: female (4.3 mm), North Atlantic: off the Azores, 37°26'N, 25°13'W, 10 Jul 1873, R/V Challenger stn. 78, 1829 m (NHM 89.4.27.52).

*Remarks on type material*. A single whole preparatory female mounted in Canada balsam, smashed, long spines broken, but otherwise complete with the exception of one or two of the pereopods. The female specimen measures "approximately 6mm, with short immature ovigerous lamellae upon the first four thoracic segments" (remarks by Beddard 1886: 40).

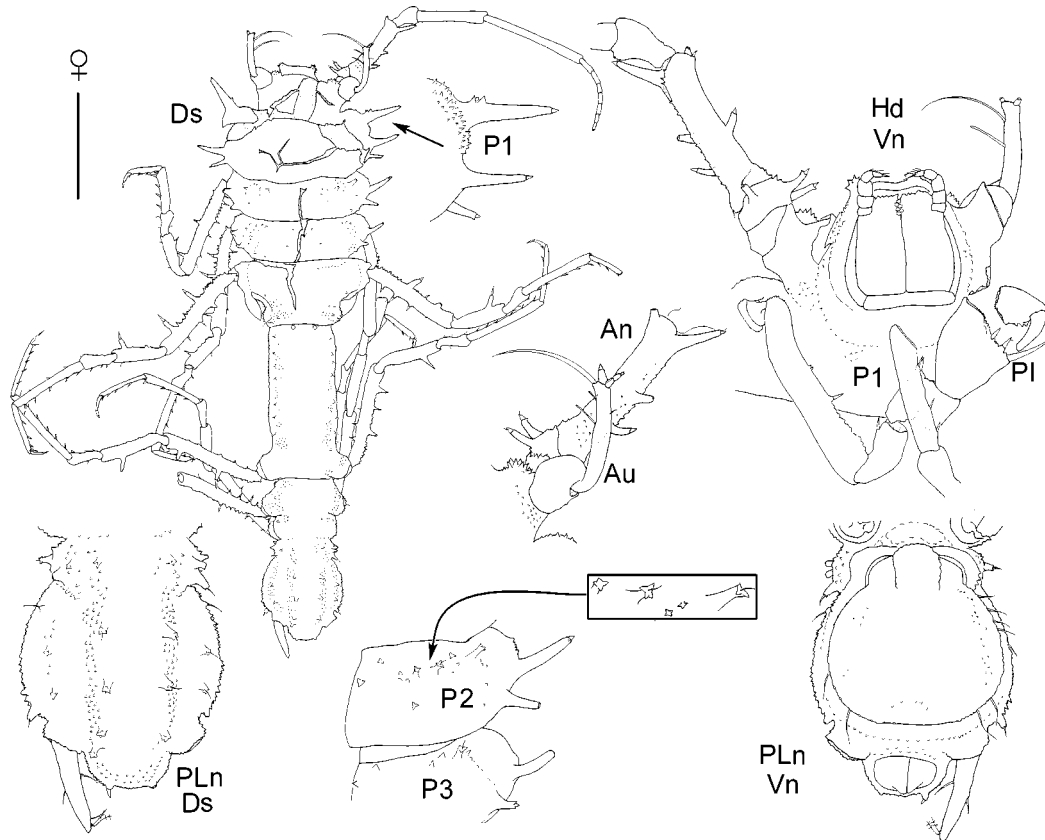
*Diagnosis (Female only)*

Pereonite 1 with 5 pairs of dorsal rook spines; pereonites 1–3 with long anterolateral and lateral pedestal spines; pereonites 6–7 with dorsal rook spines. Pereonite 5 length 2.3 width. Pleonite 1 region with lateral rook spines. Antennula with 5 articles altogether.

*Description (Female characters only)*

*Body* length 4.3 mm; granular. *Head* length 0.55 width; dorsal cuticle fine spinous granulation. *Pereonite 1* width 0.25 total body length; with 1 median rook spine, 5 pairs of dorsal rook spines, 1 pair of anterolateral pedestal spines, 2 pairs of lateral pedestal spines. *Pereonite 2* with 1 median rook spine, 2–3 pairs of dorsal rook spines, 2 pairs of lateral pedestal spines. *Pereonite 3* with 1 median rook spine, 3 pairs of dorsal rook spines, 2 pairs of lateral pedestal spines. *Pereonite 4* length 0.50 width; with 1 pair of anterolateral simple spines and 2 paired posterolateral rook spines short to stout. *Pereonites 1–4* dorsal rook spines stout to long arranged in transverse rows, anterolateral pedestal spines long topped by short robust seta, decreasing in length from pereonite 1 to 3, length near pereonite 1 length, pereonite 4 anterolateral spine broad and short, length distinctly less than length of pereonite 1. *Pereonite 5* length 0.30 total body length; with lateral row of 7–8 short pedestal spines topped with simple seta. *Pereonites 6–7* only with 1 pair of short dorsal rook spines. *Pleonite 1* region of pleotelson with 1–2 pairs short to stout dorsal rook spines and 3 pairs of stout to long lateral rook spines. *Pleotelson* length 1.3 width; with 7–8 stout to long rook spines arranged in two longitudinal median rows and 2 additional

dorsal pairs on the lateral fields; posterolateral margin anterior to uropods with 1 pair of posterolateral pedestal spines, stout topped by simple seta; terminal margin with 1 pair of pedestal spines short topped by stout robust setae.



**FIGURE 30.** *Heteromesus spinosus* (Beddard, 1886). Holotype female, NHM 89.4.27.52: habitus dorsal; antennula; antenna; head ventral; details of pedestal spines on pereonite 1 and rook spines on pereonites 2–3; pleotelson dorsal and ventral. Scale bar 1.0mm.

*Antennula* article 2 length 0.55 head width, with 3 elongate stiff ventromedial setae, distal tip produced distally beyond insertion of next article, distal article inserting subapically; article 3 length similar to article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article, aesthetascs absent. *Antenna* article 2 with 2 medial and 1 ventral long pedestal spines; article 3 length 0.27 anterior body length, length 3.8 width, with 1 short distomedial pedestal spine, 1 elongate distolateral pedestal spine, 1 elongate ventromedial pedestal spine placed midlength and 2 long dorsal pedestal spines placed midlength and proximally on article; article 5 length 0.26 anterior body length; article 6 length 0.41 anterior body length.

*Labrum* knobs present, rounded, distally with sharp denticles.

*Pereopod bases* proximal shoulder with rook spines. *Pereopod I carpus* palm length

distinctly less than proximal region length, with 2 robust setae on palm distal to elongate seta; *propodus* ventral margin with 2 robust setae. *Pereopods II–VII bases* granulate, with stout to long pedestal spines topped by stout to long robust seta on dorsal and ventral margins of bases; *ischia* with 1 elongate pedestal spine on dorsal margin.

*Uropods* length 0.40 length of pleotelson.

#### *Distribution*

North Atlantic: off the Azores, 1829 m, volcanic mud.

#### *Remarks*

*Heteromesus spinosus* (Beddard) was scored partially using original description because some parts were deformed or obscured in the mounted holotype. This species was not listed in Kussakin (1988).

This species is similar to *H. ctenobasius*, but its most distinctive features are the long anterolateral and lateral pedestal spines on pereonites 1–3.

#### ***Heteromesus wolffi* Chardy, 1974**

*Heteromesus wolffi* Chardy 1974: 1543–1546, figs. 4–5; Kussakin 1988: 475–476, figs. 388–389.

#### *Material examined*

*Holotype*: male (6.2 mm), North Atlantic, Labrador Basin, 55°52.5'N 49°53.4'W, R/V Jean Charcot, Campagne Noratlante stn 10 prl E 04, 3465 m (MNHN IS-3361).

*Remarks on type material*. The holotype was dissected by Chardy. Some dissected parts were found loose in the vial.

#### *Diagnosis (Male only)*

Head with squat anterolateral projections supporting antennae, projection width exceeding length;. Pereonites 1–3 with median dorsal and anterolateral simple spines. Pereonite 5 length 8.6 width. Pleonite 1 region with dorsal tubercles. Pleotelson with dorsal tubercles; posterolateral margin anterior to uropods without spines or tubercles. Antennula with 4 articles altogether.

#### *Description (Male characters only)*

*Body* length 6.2 mm, granular. *Head* length 0.65 width; dorsal surface with pair of cephalic bullae, cuticular structure coarse tubercular granulation; lobe on ventrolateral margin absent in lateral view. *Pereonite 1* width 0.15 total body length; with median simple spine, 1 pair of anterolateral simple spines and 1 pair of lateral tubercles (indistinctly illustrated). *Pereonite 2* with median simple spine, 1 pair of lateral simple spines. *Pereonite 3* with median simple spine, 1 pair of lateral simple spines. *Pereonites*



1–3 long simple spines decreasing in length from pereonite 1 to 3, length near pereonite 1 length. *Pereonite 4* length 0.60 width. *Pereonite 5* length 0.40 total body length. *Pleonite 1* region of pleotelson with 1 pair of median tubercles and 2 pairs of dorsal tubercles. *Pleotelson* length 1.25 width; medially indented, bilobed posteriorly with 1 pair of dorsal tubercles on lateral fields above incision of lateral margin.

*Antennula* article 2 length 0.9 head width, with 3 elongate stiff ventromedial setae (possibly 4); article 3 length similar to article 4, article 3 short and tubular, length near width, aesthetascs absent. *Antenna* article 3 length 0.64 anterior body length, 6.5 width, with distomedial spine (indistinctly illustrated).

*Labrum* knobs low. *Maxillula* medial lobe without robust dentate setae. *Maxilla* with 2 long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe.

*Pereopod I carpus* palm length near proximal region length, with 4 robust setae on palm distal to elongate seta; *propodus* ventral margin with 2 robust setae.

*Pleopod I* distal tip with lateral horns. *Pleopod II protopod* apex narrow, tapering; *stylet* tapering and pointed, not heavily calcified, not extending to distal margin of protopod. *Uropods* length 0.50 length of pleotelson.

#### *Distribution*

North Atlantic: Labrador Basin (55°52.5'N, 49°53.4'W), south of Reykjanes Ridge (54°21.6'N, 27°06.0'W) and south of the Azores (36°48.5'N, 49°53.4'W), 3178–3663m.

#### *Remarks*

*H. wolffi* differs from other *Heteromesus* species in having the most elongated pereonite 5, long median dorsal and anterolateral simple spines on pereonites 1–3 and by its peculiar shape of the head and pleotelson. In particular, the antennae are born on squat projections that are shorter than the robust projections seen in *Stylomesus*. The long spines and the shape of head and pleotelson resemble some *Haplomesus* species, although the generic differences serve to separate these species. The holotype male of *Heteromesus wolffi* Chardy was scored according to Chardy (1974: 1543–1546, figs. 4–5) that also provided the following additional information on sexual dimorphism: “pereonite 5 [in female] proportionally wider and shorter; spine-like tubercles on cephalon developed into spines” (in the description of the male holotype Chardy placed the pair of “spine-like” tubercles laterally on pereonite 1).

## **Discussion**

### **Sexual dimorphism and morphological features**

*Heteromesus* females always have a generally more compact body than the male, mainly

owing to the proportionally shorter and broader pereonite 5. Some limited variability also occurs in the number, size and arrangement of tubercles and spines on the pereonites, pleotelson and antennae but *H. frigidus* presents radically different males and females.

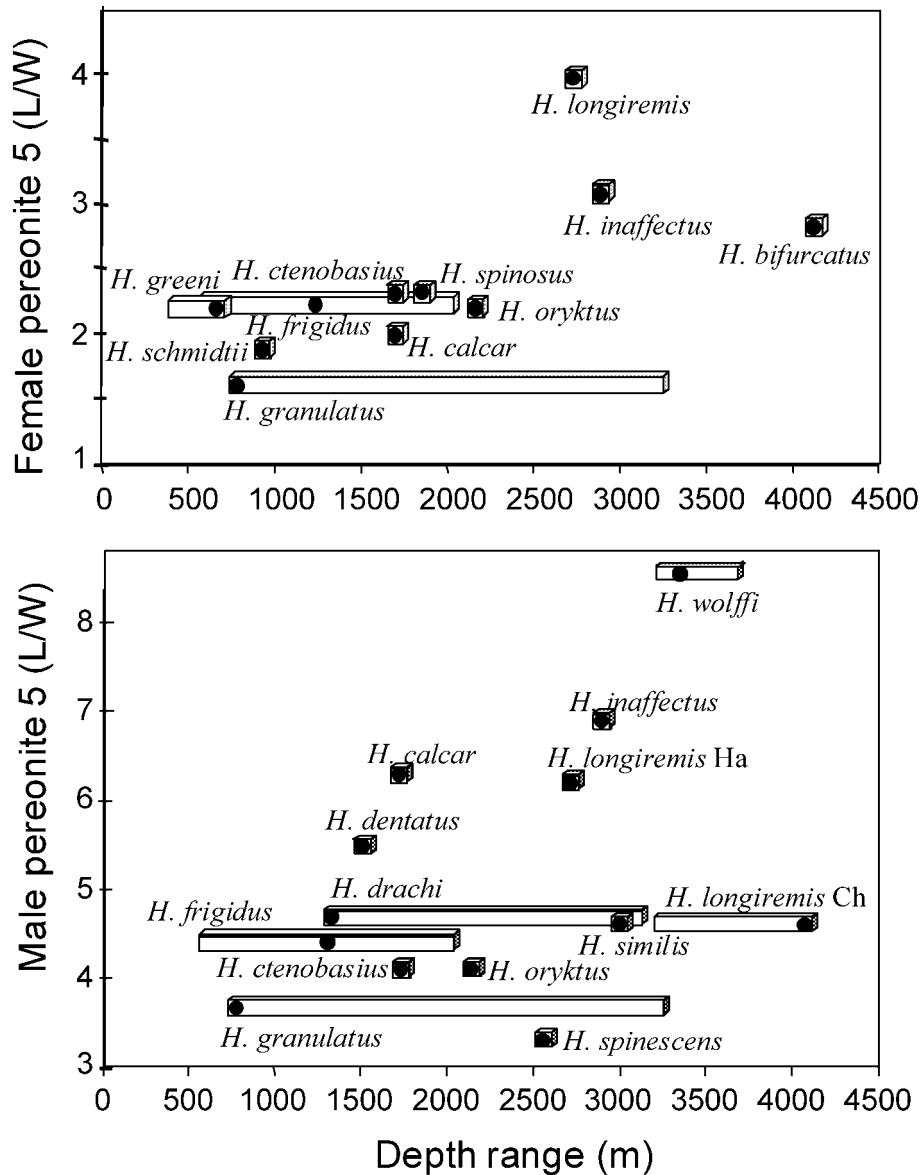
In some species, namely *H. calcar* **sp. nov.** and *H. inaffectus* **sp. nov.**, we found intersex individuals. These specimens have the general appearance of a large female (they are amongst the larger or are the largest specimens in the sample) and they have both the specific sexual features of the female (dorsal opening to spermathecal ducts) and male (pleopods I and II).

Intraspecific variation in morphology is accentuated by the usual slight but evident asymmetry in the size, arrangement and sometimes even the number of tubercles and spines on pereonites, pleotelson and antennae, and in the size and shape of other features such as the labrum knobs and uropods.

The coxa-basis articulation is a peculiar morphological feature of *Heteromesus* (also found in other genera of the Ischnomesidae). The proximal part of the basis is hemispherical with a central extension (the neck) connecting the shaft in a perpendicular position. The shaft has a proximal shoulder often armed with simple, bifid or rook spines. This articulation allows a wide range of rotation of all pereopods.

One of the most distinctive features of Ischnomesidae is the elongate pereonite 5. Within the genus *Heteromesus*, a wide range of variation is found in the length-width ratio of pereonite 5. In the females of some species, *H. granulatus* (L/W=1.6) and *H. schmidtii* (L/W=1.9), this value falls short of the range given in the family diagnosis ("at least twice as long as wide", Merrin & Poore 2003: 1). An interesting trend in the presently known species of *Heteromesus* is the apparent elongation of pereonite 5 with increasing depth (Fig. 31). Both in males and females, deeper species have generally a higher pereonite 5 length-width ratio and shallower species have more compact bodies with a proportionally shorter and broader pereonite 5.

Another interesting morphological pattern is observed in relation to the development of spines. Pedestal spines, topped by a robust seta that generally have a sensilla subdistally, are common in the antennae of most species (placed distomedially, distolaterally or on the proximal length of article 3, and sometimes also on article 2) but the development of such spines on the bases (and ischium) of pereopods is restricted to four species all found in the Triple Junction region around the Azores. This exceptional development of the pedestal spines might be related to a need to sense thermal or chemical environmental changes. Indeed, *H. spinosus* was collected from volcanic mud and *H. calcar* and *H. ctenobasius*, live close to the hydrothermal vents. Possibly these species use the setae with sensilla sitting on the top of elongated pedestals as probes of the environment. The mature females are more exuberantly decorated (e.g., *H. ctenobasius* and *H. spinosus* have lateral rows of spines on P5), a condition that could be related to the brood protection (avoiding toxic environments). We admit, however, that this proposal is speculative.



**FIGURE 31.** Relationship between the pereonite 5 length:width ratio and depth. The ratio is taken from only the type locality (●), but the entire known depth range of the species is shown. Top – females; bottom – males.

### Ecology

Isopods are among the most abundant and diverse taxa in the deep-sea (Hessler & Sanders 1967; Hessler *et al.* 1979; Wilson 1998; Raupach *et al.* 2004). The Asellota have undergone an extensive radiation that resulted in the evolution of diverse and often bizarre

morphologies (Hessler & Thistle 1975). Common behaviour of deep-sea isopods includes grooming, especially keeping the flagellum of antennae clean, respiratory movement, ability to burrow and general mobility (Hessler & Strömberg 1989). Ischnomesids are excellent walkers, the length and orientation of their pereopods (II–VI) enables them to move rapidly on jumbled surfaces as well as across smooth seabed and they also can use the anterior pereopods (PI) to make permanent burrows; they are known to bury or half-bury themselves in "vertical" holes and they are capable of substantial ventral flexure despite their elongate body that is nonetheless adequate for a domicolous existence (Hessler & Strömberg 1989). The peculiar coxa-basis articulation of *Heteromesus* allows the isopod to change from the normal walking position of the posterior pereopods to a forward position; the pereopods are tightly "stored" ventrally along the body allowing the isopod to occupy narrow spaces.

Thistle and Wilson (1987) classified Ischnomesidae as infaunal but the mobility of these isopods also enables them to explore a variety of epibenthic habitats. The epibiont community of *H. frigidus* with high prevalence of ciliates, heavy peritrich infestation and high number of suctorian species appears to be shaped by the behaviour of the isopod hosts and their habitat utilization, living in shallow pits or having limited burrowing activity (Ólafsdóttir & Svavarsson 2002). According to Svavarsson and Davídsdóttir (1994), the presence of epibiont Foraminifera, which occur only on epibenthic species, suggests that *H. frigidus* lives on the sediments or may even cling to larger objects such as sponges or agglutinating foraminifer tubes that commonly extend above the bottom at bathyal and abyssal depths.

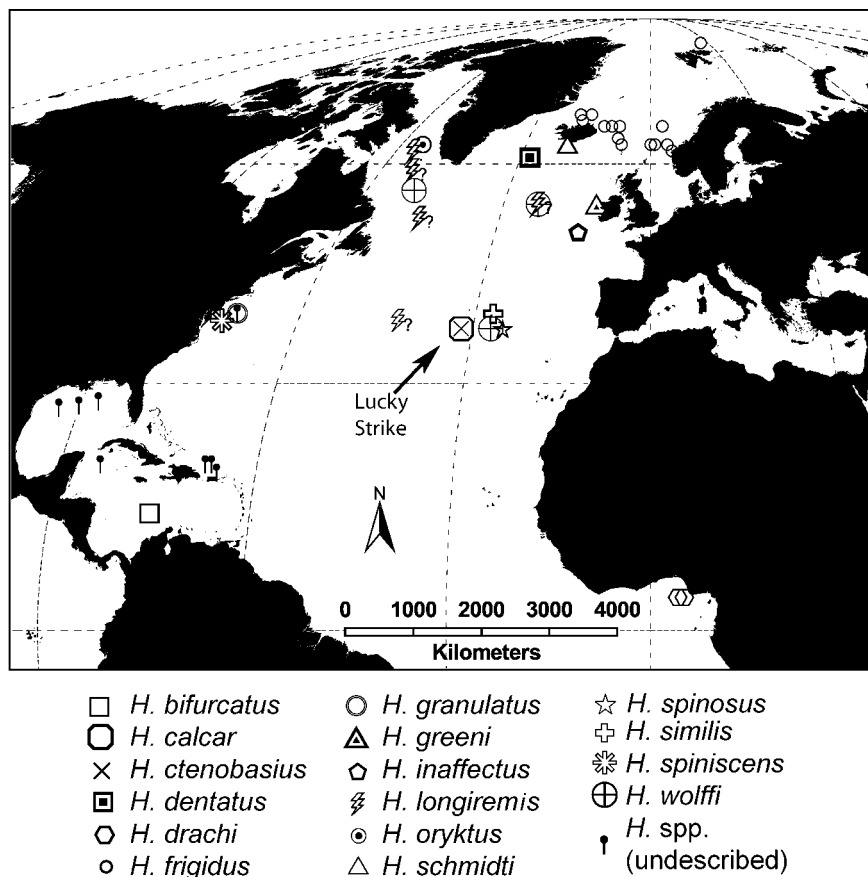
In fact, ischnomesids' ability to burrow and to use cavities and crevices (Hessler & Strömberg 1989) is confirmed by our own observations of *H. oryktus* **sp. nov.** that was found inside burrows in mudstones and by other observations on undescribed *Heteromesus* species using various biogenic structures. *Heteromesus* species were recorded living inside large agglutinated tubes made by ammodiscacean foraminifers, *Bathysiphon rusticus*, (Gooday 1984) and within hollow turtlegrass, *Thalassia testudinum*, rhizomes (Wolff 1979); the animals were believed to be using the plant material as a shelter rather than as a food source.

Although many *Heteromesus* records coincide with geologically active areas (such as the Caribbean Arc and Mid-Atlantic Ridge), the available ecological information is scarce and except for *H. calcar* **sp. nov.** and *H. ctenobasius* **sp. nov.**, no evidence of association with peculiar habitats is available. These two latter species were collected inside the Lucky Strike hydrothermal vent field in areas of diffuse mild venting characterized by the presence of mussel beds (*Bathymodiolus azoricus*) and associated assemblage (the polychaetes *Branchipolynoe seepensis*, and *Amathys lutzi*, limpets and other gastropods) and in a more external ring where the filter feeding organisms settle (faunal zonation according to the scheme given by Colaço *et al.* 2002). Nevertheless, we cannot infer that these isopods are vent endemics because in relatively shallow (<2000 m) hydrothermal

vent fields, such as Lucky Strike, phase separation of the vent fluid provides a less toxic environment and allows background species to enter (Van Dover 1995). One of the first described species, *H. spinosus* was collected from volcanic mud near the Azores (Beddard 1886) at the same depths as the two new species from Lucky Strike.

### Biogeography

The 16 described species of *Heteromesus*, as well as many undescribed species known to us, are restricted primarily to the North Atlantic and Arctic Seas (Fig. 32), although a few unpublished records are from off Africa. Most species occur on the North American and North European margins and along the Mid-Atlantic Ridge (especially in the Triple Junction region around the Azores islands), at depths ranging 300 to 3000 m. Except for *H. longiremis* sensu Chardy, which spans across the western North Atlantic abyssal Plain, deeper records of the genus occur within a relatively short distance from the continental margins. The deepest records of the genus, 7935 m and 8330 m are given by Wolff (1979) for two undescribed species found in the Puerto Rico Trench.



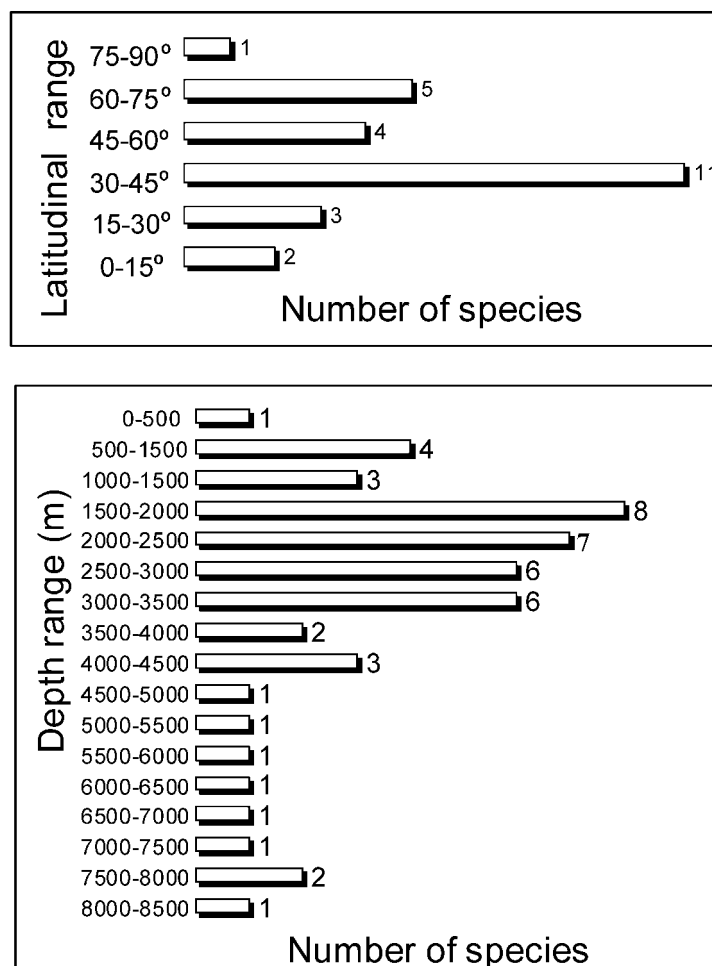
**FIGURE 32.** Distribution of *Heteromesus* species in the North Atlantic. Lines of 30° latitude and longitude, dashed lines.

Most described *Heteromesus* species are rarely recorded and are known from a single or a few finds only. *H. frigidus*, the only species of the genus recorded in the Norwegian and North Polar Seas, is an exception because it has often been recorded in several localities. The southern limit of its distribution is the Greenland-Iceland-Faeroe Ridge that has the saddle depths at a maximum of 850 m in the Faeroe channel and that acts as a barrier restricting the migration of deep-sea species (Svavarsson *et al.* 1993). In equatorial waters, only one described species, *H. drachi*, is known from two locations from the West African margin. Interestingly, several undescribed species are known from near St. Peter and St. Paul Rocks in the Equatorial Atlantic, and 4 undescribed species are known from off Angola and Walvis Bay – the southern-most localities for this genus. Several undescribed species and *H. bifurcatus* are known from the Caribbean region and Gulf of Mexico (15–20°N), and 4 described species (including *H. oryktus* **sp. nov.**) are only known from the Northern seas of Iceland and west Greenland (60–63°N) and two more around Ireland (50–54°N). A diversity peak of the described species occurs at 35–40°N with 4 species only known from near the Azores (including *H. calcar* **sp. nov.** and *H. ctenobasius* **sp. nov.**), two described and several undescribed species off Virginia, adding to *H. longiremis* *sensu* Chardy and *H. wolffi* whose distribution spans 36–58°N in the Atlantic Abyssal plain.

Figure 33 shows depth and latitudinal diversity patterns of the described species of *Heteromesus*, based on the present limited knowledge of species distributions with presumed depth boundaries at coastal and hadal depths and presumed latitudinal boundaries at 0° and 90°N. Species richness is obtained from the count of species with overlapping distributions at a given depth or latitude range. The nearly unimodal patterns of diversity, with peaks at intermediate depths (1500–3500 m) and latitudes (30–45°N) may be partially explained by boundary constraints, the mid-domain effect (Colwell *et al.* 2004). Stochastic placement of species ranges between presumed upper and lower boundaries will produce a unimodal pattern of diversity, suggesting that boundaries may affect the general shape of diversity-depth or diversity-latitude patterns while other important features of the patterns are decidedly non-random (Levin *et al.* 2001 and references therein).

During the 1960s and 1970s, an abundant collection of deep-sea fauna was gathered during WHOI cruises in the Atlantic (Hessler & Sanders 1967; Wilson 1998; Gage *et al.* 2004). The majority of this isopod collection remains undescribed taxonomically but the data on these unpublished records of *Heteromesus* spp. sets the southern limit of its distribution at around 23°S in the Eastern South Atlantic off Africa (Walvis Bay). Unlike localities in the North Atlantic, the most southern localities each have only one unique but related species of *Heteromesus* at each site; North Atlantic sites have up to 7 species of this genus. This distribution allows us to predict a much more diverse composition of the genus. The future study of this collection will contribute to our knowledge on the distribution of *Heteromesus* in areas covered by the Cork, Gay-Head Bermuda and

Equatorial transects and will certainly reinforce the number of species at equatorial and temperate regions and at depth ranges between 1500 and 5000 m.



**FIGURE 33.** Distributional ranges of *Heteromesus* species in the North Atlantic (according to data shown in Table 1). Top, latitudinal ranges, in groupings of 15° North. Bottom, depth ranges, in groupings of 500 metres.

### Acknowledgements

The first author greatly acknowledges the invitation to participate in TTR10, and TTR13 cruises (Training Through Research Programme, IOC-UNESCO) by Hipólito Monteiro (LNETI — Geologic and Mining Institute of Portugal) and Michael Ivanov (Moscow State University). Some illustrations were inked by Joana Oliveira and Suzanne Bullock. Sue Lindsay (Australian Museum) was the SEM operator. This work was supported by Fundação para a Ciência e Tecnologia (Grant SFRH/BSAB/364/2003) and by Fundação

Calouste Gulbenkian (Ref. 418145, 2003). Howard Sanders, Frederick Grassle, Robert Hessler, George Hampson (Woods Hole Oceanographic Institution) collected the type material of *H. inaffectus*, on funding from the US National Science Foundation.

**TABLE 1.** Localities of species of *Heteromesus*. Samples with different beginning and ending positions are given as midpoints.

NAME	Locality	Depth	Latitude	Longitude	RV (Program)	Remarks
<i>H. bifurcatus</i>	Caribbean	4077	14°05.0'N	75°25.0'W	Vema	Menzies 1962 *
<i>H. calcar</i>	Lucky Strike	1685	37°17.4'N	32°16.6'W	Prof. Logachev (TTR10)	<b>sp. nov.</b> * volcanic rocks
<i>H. calcar</i>	Lucky Strike	1712	37°17.5'N	32°16.9'W	Prof. Logachev (TTR10)	<b>sp. nov.</b> sulphide chymneys
<i>H. calcar</i>	Lucky Strike	1675	37°17.4'N	32°16.6'W	Prof. Logachev (TTR10)	<b>sp. nov.</b> sulphide rubble
<i>H. ctenobasius</i>	Lucky Strike	1685	37°17.4'N	32°16.6'W	Prof. Logachev (TTR10)	<b>sp. nov.</b> * volcanic rocks
<i>H. ctenobasius</i>	Lucky Strike	1704	37°17.3'N	32°16.5'W	Prof. Logachev (TTR10)	<b>sp. nov.</b> volcanic rocks
<i>H. ctenobasius</i>	Lucky Strike	1720	37°17.5'N	32°16.9'W	Prof. Logachev (TTR10)	<b>sp. nov.</b> sulphides
<i>H. dentatus</i>	Iceland	1461	60°37.0'N	27°52.0'W	Ingolf	Hansen 1916 *
<i>H. drachi</i>	Ivory coast	1261	04°21.2'N	04°35.2'E	Jean Charcot (Walda)	Chardy 1974 *
<i>H. drachi</i>	Ivory coast	3109	04°04.1'N	03°42.0'E	Jean Charcot (Walda)	Chardy 1974
<i>H. frigidus</i>	Norwegian Sea	1284	63°36.0'N	07°30.0'W	Ingolf	Hansen 1916 (syntypes)
<i>H. frigidus</i>	Norwegian Sea	1242	63°22.0'N	06°58.0'W	Ingolf	Hansen 1916 (syntypes)
<i>H. frigidus</i>	Norwegian Sea	982	66°23.0'N	12°05.0'W	Ingolf	Hansen 1916 (syntypes)
<i>H. frigidus</i>	Norwegian Sea	1371	66°23.0'N	10°26.0'W	Ingolf	Hansen 1916 (syntypes)
<i>H. frigidus</i>	Norwegian Sea	1393	65°34.0'N	07°31.0'W	Ingolf	Hansen 1916 (syntypes)
<i>H. frigidus</i>	Norwegian Sea	905	67°40.0'N	15°40.0'W	Ingolf	Hansen 1916 (syntypes)
<i>H. frigidus</i>	Norwegian Sea	830–860	62°10.0'N	04°49.0'E	Håkon Mosby	Svavarsson 1984
<i>H. frigidus</i>	Norwegian Sea	1260	63°17.1'N	04°24.8'E	Håkon Mosby	Svavarsson 1984
<i>H. frigidus</i>	Norwegian Sea	2019–2024	65°39.5'N	02°38.0'E	Håkon Mosby	Svavarsson 1984
<i>H. frigidus</i>	Norwegian Sea	1279–1288	63°25.4'N	04°05.4'E	Håkon Mosby	Svavarsson 1984
<i>H. frigidus</i>	Norwegian Sea	1484–1494	63°11.9'N	00°41.6'E	Håkon Mosby	Svavarsson 1984

to be continued



TABLE 1 (continued).

NAME	Locality	Depth	Latitude	Longitude	RV (Program)	Remarks
<i>H. frigidus</i>	Norwegian Sea	1494–1501	63°12.1'N	00°41.6'E	Håkon Mosby	Svavarsson 1984
<i>H. frigidus</i>	Norwegian Sea	1001–1003	62°48.0'N	00°02.6'E	Håkon Mosby	Svavarsson 1984
<i>H. frigidus</i>	Norwegian Sea	800	62°33.2'N	00°58.9'E	Håkon Mosby	Svavarsson 1984
<i>H. frigidus</i>	Norwegian Sea	800–804	62.33.6'N	00°58.9'E	Håkon Mosby	Svavarsson 1984
<i>H. frigidus</i>	North Polar Sea	698				Gurjanova 1964
<i>H. frigidus</i>	North Polar Sea	970–1020	81°31.3'N	26°08.0'E	Ymer	Svavarsson 1984
<i>H. frigidus</i>	Iceland	539	67°13.3'N	17°48.9'W	(BIOICE)	Ólafsdottir & Svavarrson 2002
<i>H. frigidus</i>	Iceland	1141	68°00.1'N	19°25.3'W	(BIOICE)	Ólafsdottir & Svavarrson 2002
<i>H. granulatus</i>	off Virginia	713			Albatross	Richardson 1908 *
<i>H. greeni</i>	off West Ireland	698			Helga	Tattersall 1905 *
<i>H. inaffectus</i>	off Ireland	2890–2868	50°12.3'N	13°35.8'W	CHAIN (cruise 106)	<b>sp. nov.</b> *
<i>H. longiremis</i>	Davis Strait	2624	61°50.0'N	56°21.0'W	Ingolf	Hansen 1916 *
<i>H. longiremis</i> <sup>c</sup>	Atlantic Abyssal Plain	3178	54°21.6'N	23°00.2'W	Jean Charcot (Noratlante)	Chardy 1974
<i>H. longiremis</i> <sup>c</sup>	Atlantic Abyssal Plain	4100	52°10.4'N	45°32.3'W	Jean Charcot (Noratlante)	Chardy 1974
<i>H. longiremis</i> <sup>c</sup>	Atlantic Abyssal Plain	3610	58°47.7'N	52°56.5'W	Jean Charcot (Noratlante)	Chardy 1974
<i>H. longiremis</i> <sup>c</sup>	Atlantic Abyssal Plain	3181	38°28.2'N	43°03.0'W	Jean Charcot (Noratlante)	Chardy 1974
<i>H. oryktus</i>	off West Greenland	2140	63°14.1'N	55°26.0'W	Prof. Logachev (TTR13)	<b>sp. nov.</b> * in mudstones
<i>H. schmidtii</i>	Iceland	929	62°57.0'N	19°58.0'W	Thor	Hansen 1916 *
<i>H. similis</i>	Azores	2995	38°38.0'N	27°26.0'W	Talisman	Richardson 1911 * in white mud
<i>H. spinescens</i>	off Virginia	2551			Albatross	Richardson 1908 *
<i>H. spinosus</i>	Azores	1829	37°26.0'N	25°13.0'W	Challenger	Beddard 1886 * volcanic mud
<i>H. wolffi</i>	Labrador Basin	3465	55°52.5'N	49°53.4'W	Jean Charcot (Noratlante)	Chardy 1974 *
<i>H. wolffi</i>	S of Reykjanes Ridge	3178	54°21.6'N	23°00.2'W	Jean Charcot (Noratlante)	Chardy 1974
<i>H. wolffi</i>	Azores	3663	36°48.5'N	27°06.0'W	Jean Charcot (Noratlante)	Chardy 1974

to be continued

TABLE 1 (continued).

NAME	Locality	Depth	Latitude	Longitude	RV (Program)	Remarks
<i>H. spA</i> (undescribed)	Puerto Rico Trench	7430	19°24.0'N	66°11.0'W	Akademik Kurchatov (cruise14)	Wolff 1979 inside turtlegrass
<i>H. spA</i> (undescribed)	Puerto Rico Trench	8330	19°38.0'N	67°46.0'W	Akademik Kurchatov (cruise14)	Wolff 1979 inside turtlegrass
<i>H. spA</i> (undescribed)	Northern Caribbean	4417	19°48.0'N	83°30.0'W	Akademik Kurchatov (cruise 14)	Wolff 1979 inside turtlegrass
<i>H. spB</i> (undescribed)	Puerto Rico Trench	7938	19°45.0'N	67°00.0'W	Akademik Kurchatov (cruise 14)	Wolff 1979 inside turtlegrass
<i>H. spp</i>	off Virginia	3338			Albatross	Richardson 1908
<i>H. spp</i>	off Virginia	2789			Albatross	Richardson 1908
<i>H. spp</i>	S of Block Island	2154			Albatross	Richardson 1908
<i>H. spp</i>	off George's Bank	2359			Albatross	Richardson 1908
<i>H. spp</i>	SE of George's Bank	2480			Albatross	Richardson 1908
<i>H. spp</i>	Porcupine Seabight / S of Canary Islands	997–4414			Discovery / Challenger	Gooday 1984 inside rhizopod tests

<sup>c</sup> *H. longiremis* sensu Chardy.

\* Type locality.

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