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Revision of the genus *Haplomesus* (Isopoda : Asellota : Ischnomesidae) with erection of four new genera

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Abstract. This paper presents a revision of *Haplomesus* Richardson, 1908 (Ischnomesidae). Poor character definition, ineffective diagnosis of the genus and inadequate or poor descriptions and illustrations have resulted in difficulties in identification of species and generic membership. This study is based on type material and descriptions in the literature and encompasses 28 species. Four new genera are created, justified by a phylogenetic analysis of 37 ingroup taxa and two outgroup taxa. Three species of the ingroup were excluded owing to missing data. Four species are retained in *Haplomesus sensu stricto*, two species are removed to *Cornuamesus*, gen. nov., 11 species are removed to *Fortimesus*, gen. nov. and 12 species are removed to *Gracilimesus*, gen. nov. One species, *Haplomesus franklinae* Merrin & Poore, 2003 is removed from the group and placed in *Contrarimesus*, gen. nov. with another species, *Ischnomesus curtispinis* Brandt, 1992. The species level is conferred on *Haplomesus insignis orientalis* Birstein, 1960. *Haplomesus quadrispinosus sensu* Brandt (1992) is removed from *H. quadrispinosus* (Sars, 1879) and *Haplomesus* ?*gorbunovi sensu* Svavarsson (1984) is removed from *Gracilimesus gorbunovi* (Gurjanova, 1946).

Additional keywords: *Contrarimesus*, *Cornuamesus*, *Fortimesus*, *Gracilimesus*.

Introduction

The genus *Haplomesus* (Isopoda : Asellota : Ischnomesidae) consists of marine benthic asellote isopods found at bathyal and abyssal depths, with records from ~600 to 9000 m. The genus has a wide distribution, being found throughout the Atlantic and Pacific Oceans and having also been collected from the Antarctic and Arctic Oceans. The genus was established by Richardson in 1908 for *Ischnosoma quadrispinosus* Sars, 1879 because the generic name of *Ischnosoma* was preoccupied. To date, 28 species have been described exhibiting substantial morphological diversity, resulting in an imprecise generic diagnosis. For example, Merrin and Poore (2003) described *H. franklinae*, despite this species having a two-articled uropod. All other species of the genus possess one-articled uropods. Brökeland and Brandt (2004) described *Haplomesus corniculatus*, the first species of the genus without pereopod VII, a characteristic produced by progenesis (see Kavanagh *et al*. 2006). A further example of the diversity exhibited is the presence of long, thin anterolateral projections supporting the antennae in *Haplomesus biscayensis* Chardy, 1975 and *Haplomesus longiramus* Kavanagh & Sorbe, 2006. The remaining species in the genus have the antennae emerging directly from the head.

The aim of this study was to present a new classification for the species of *Haplomesus*, based on redescription and reillustration of type material and a phylogenetic analysis. The redescription of type material provides standard descriptions for all species of the genus, with new information on important characters added for many species. Full illustrations of new and previously existing characters supplement the descriptions. The purpose of the phylogenetic analysis was to ascertain if the wide range of diversity outlined above requires removing species to new genera and to examine the relationship of the *Haplomesus*-group with other genera in the family Ischnomesidae.

Materials and methods

Dissections and illustrations

Wherever possible, illustrations were made of type material. Pencil illustrations were prepared using a camera lucida on a Nikon microscope and then inked by tracing onto translucent vellum. Dissected parts were placed on glass slides in glycerin for temporary inspection and more permanent museum mounts were prepared using glycerin jelly.

Descriptions

Descriptions were generated using the taxonomic database system DELTA (Dallwitz 1980; Dallwitz *et al*. 2000) and diagnoses were constructed from the INTKEY output of DELTA. Measurements were made from drawings, using a stage micrometer for calibration. In general, character measurements are presented as ratios to normalise differences in body size, and where several specimens were available for measurement, ranges are displayed. Sizes of specimens were measured as the dorsal mid-length from the frontal margin of the head to the tip of the pleotelson, and we use the term subequal to mean 'within 5% of a measurement'. We use Roman numerals for pereopods and pleopods and arabic figures for other body parts, as in Kavanagh *et al*. (2006) and Cunha and Wilson (2006).

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Abbreviations

AM	Australian Museum (Sydney, Australia)
AMNH	American Museum of Natural History (New York, USA)
BM(NH)	British Museum of Natural History (now NHM, below)
MNHN	Museum National d'Histoire Naturelle (Paris, France)
NHM	Natural History Museum (British Museum, London, England)
MV	Museum Victoria (Melbourne, Australia)
SAM	South African Museum (Cape Town, South Africa)
ZMO	Zoological Museum (Oslo, Norway)
ZMUC	Zoological Museum of the University of Copenhagen (Copenhagen, Denmark)

Phylogenetic methods

The aim of the phylogenetic analysis was to discover whether the morphological diversity observed within *Haplomesus sensu lato* required the removal of species to new or existing genera. Nexus files for phylogenetic analysis were generated using the DELTA procedure 'tonex'. All phylogenetic analyses were performed using PAUP, version 5 (Swofford 2002). Taxa in the database include two outgroup taxa (*Ischnomesus bispinosus* Sars, 1868 and *I. antarcticus* Schultz, 1979) and 37 ingroup taxa. The two outgroup species were chosen to represent the diversity within the genus. Of the ingroup taxa, 27 are from the *Haplomesus*-group and ten are representatives from the genera *Heteromesus* Richardson, 1908, *Ischnomesus* Richardson, 1908 and *Stylomesus* Wolff, 1956. The inclusion of additional genera in the ingroup was deemed necessary because the ingroup relationships of the Ischnomesidae are not well characterised. The species included are: *Heteromesus granulatus* Richardson, 1908, *H. drachii* Chardy, 1974, *H. frigidus* Hansen, 1916, *H. schmidtii* Hansen, 1916, *H. similis* Richardson, 1911, *H. spinosus* (Beddard, 1886), *Stylomesus hexapodus* Brökeland & Brandt, 2004, *S. menziesi* Birstein, 1960 and *S. sarsi* Merrin & Poore, 2003. *Ischnomesus curtispinis* Brandt, 1992 was also included because examined type material was quite different in several respects from other species of *Ischnomesus* but similar to *Haplomesus franklinae*. Increasing the number of taxa from these genera was found to increase the resolution of the resulting cladograms.

Several species were excluded from the analysis. *Gracilimesus modestus*, comb. nov. and *G. modestatenuis*, comb. nov. were omitted because both of their corresponding type specimens are immature: the type of *G. modestus* (Hansen, 1916) is a juvenile female and the type of *G. modestatenuis* is a manca 3 male. The character scorings for these species are thus not comparable with adult specimens. *Fortimesus formosus*, comb. nov. was also excluded because the type specimen is a fragment with few characters present. These taxa were placed in their appropriate genus using the new diagnosis for each taxon.

Many characters were removed from the dataset following a preliminary analysis. An unweighted analysis resulted in clades that lacked stability under varying weights. Constant/uninformative characters were removed and the dataset was examined for characters with poor fit to the shortest unweighted cladograms. Characters with a retention index (*RI*) <0.1 were removed and the analysis was run again. Although the unweighted analysis resulted in the same clades as the preliminary unweighted analysis, the clades remained stable under two different objective weighting regimes, successive weighting and implied weights (Goloboff 1993). Each analysis used a stringent treespace search method ([hsearch addseq = random nchuck = 10 chuckscore = 1 nreps = 200 randomise = trees; hsearch start = current nchuck = 0 chuckscore = 0;]) for the unweighted analyses and successive weighted analysis. The parameters [nchuck = –500 nreps = 50] were used for implied weights analysis. Increasing the treespace allowed a wider search and maximised the chances of finding multiple islands of equally parsimonious trees (Maddison 1991; Goloboff 1999). Different concavity values (PAUP* command [pset GK = 1] to [pset GK = 7]) were used to vary the implied weights analysis. The trees from all analyses were combined into an overall strict consensus (Fig. 3*B*) and this was used to construct the final classification of genera. The data matrix (Table 1), character list and consensus diagrams in Fig. 3 are available at TreeBASE (http://treebase.org; study accession number S1903, matrix accession number M3496).

Character analysis

Sexual dimorphism

Within the Ischnomesidae, sexual dimorphism occurs in the number and pattern of projections observed on pereonites and the pleotelson. Males tend to have a greater number of, and more prominent, spines. The spination pattern of females may change as they mature, with older females losing spines (Svavarsson 1984). Females also have a wider pereonite 5. The sexual features differ between males and females as follows: female Asellota have pleopod I absent, with pleopod II forming an operculum over pleopods II–V (characters 59–60). Males have pleopods I and II modified for sperm transfer (characters 72–75). Pleopods III–V are similar for both sexes. Females have an exposed dorsal opening to the spermathecal ducts on pereonite 5, and ovigerous and mature females have oostegites that form the brood pouch on pereonites 1–4.

Continuous characters

For this analysis, continuous characters (see Kitching *et al*. 1998 for definition) are generally body measurements reported as ratios, for example, length versus width of pereonites. These were converted to multistate characters using simple gap coding (Mickevich and Johnson 1976); the mean and standard deviation were calculated for each character and the data were gap coded based on the standard deviation. Where data were separated by less than a standard deviation, this was considered uninformative and the characters were excluded from the analysis. These are referred to where appropriate in the text. The boundary for the character states was taken as the lowest point of the gap plus the standard deviation conservatively rounded up to one decimal place (e.g. value of 0.21 plus standard deviation of 0.12 = 0.33, limit = 0.4). In addition, some characters that did have gaps and were coded accordingly were subsequently proved uninformative and pruned from the analysis.

Table 1. Data matrix for the analysis of the *Haplomesus*-group

Species	Characters							
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	777777777 123456789
Heteromesus drachi	1222-112?-	----------	111??3111?	1-?3432321	4121?-1221	23?31211?1	--1---4221	-11112331
Heteromesus frigidus	1222-11?11	31111111-1	1111131111	1-12432211	433-213221	13?3121113	3213?A4112	?21112332
Heteromesus granulatus	1222-11??5	31111111-1	1111131111	1-12432311	433-213221	23?4121113	3213114???	???????21
Heteromesus schmidtii	1222-11?15	32555151-1	1111131111	1-12432211	433-223221	23?4122112	3213?2----	---------
Heteromesus similis	1222-112??	??????????	?????3?11?	???4????2?	????2?1221	23?31211?3	??1???4221	-211???31
Heteromesus spinosus	1222-11??4	2343431232	1124431115	2244432211	4211223221	43?4121112	3213?2----	---------
Haplomesus hanseni	2222131111	2111111221	1111121121	2215431121	321111?122	1221112331	4211112112	112211121
Haplomesus celticensis	2222131121	21111111-1	1111121121	2214431121	321211?122	12?1122331	4111112112	21?111121
Haplomesus angustus	22221311?-	---------1	1111211212	1144?11213	2121-?3221	2?1122331-	-1---3111-	1?1???21
Haplomesus corniculatus	22221111?-	----------	1111121121	2215431121	32111-?122	1211132331	--1---2111	-12212121
Haplomesus tropicalis	2222131121	31111111-1	1111121121	211?431121	?????1?122	12?112133?	4111114112	31?2???21
Haplomesus biscayensis	2222124??-	----------	1111121111	2115431-21	31112-?11?	?21123111?	--1---2222	31?213331
Haplomesus longiramus	2222114121	21111111-1	1411121111	2115431321	311211?111	2211121311	5113222222	211212332
Haplomesus brevispinis	2222111??5	325252523?	?111121122	1-35431222	3112???22?	??????????	221211----	---------
Haplomesus concinnus	2222111??-	----------	5525321124	1-35431221	2112?-?32?	?2112311??	--1---2522	12?211111
Haplomesus cornutus	2222121??-	----------	1111121122	1-35431522	31121-?12?	?221231121	--1---2221	-1?211111
Haplomesus consanguineus	22221111?1	32121211-1	1111121121	1-15431222	3111???32?	?2212311??	421111----	---------
Haplomesus gigas	2222121?11	31111111-1	1111121121	1-35431-22	3111?1?32?	?2112311??	3112114111	-11211111
Haplomesus gorbunovi	2222111??1	21111111-1	1111111121	2115431?21	221111??2?	??????????	??11?1----	---------
Haplomesus gorbunovi sensu Svavarsson	2222121111	2111111221	1111111121	2115431121	311111?222	1211132311	4111111112	111211121
Haplomesus insignis	22221211?-	----------	1111121121	2115431221	31111-?122	12111323?1	--1---1112	1112???31
Haplomesus orientalis	2222111??-	----------	1111121121	2115421121	31111-?12?	?21112232?	--1---2112	11?211121
Haplomesus ornatus	22221211?-	----------	1111132221	1-15431221	31112-?322	1211122111	--1---2121	-112???11
Haplomesus profundicolus	2222121??B	22B25221-2	5111121122	1-34431422	3112?1?32?	?2212311??	411111----	---------
Haplomesus bifurcatus	22221211?-	-----------	1111131321	1-1?431221	??1?1-?32?	?2?1122112	--1---2121	-11213111
Haplomesus quadrispinosus	22221211?1	21111111-1	1111131121	1-15431321	311121?322	1211122111	3?1111----	---------
Haplomesus quadrispinosus sensu Brandt	22221111?-	----------	1111132221	1-15431221	31112-?222	1211122321	--1---1121	-11213111
Haplomesus robustus	2222111??1	35155151-2	5111121121	1-15331221	3111?1?32?	?2212311??	421211????	??121111?
Haplomesus scabriusculus	2222111??1	-1111111-2	1121121121	1-35431222	3212?1?22?	?2?12311?1	221211----	---------
Haplomesus tenuispinis	22221111?1	2111111211	1111111121	2115431121	311111?122	?2111323?1	421311----	---------
Haplomesus thomsoni	2222111??-	----------	1525321121	1-3?????2?	?????-??22	1211131?12	--1----112	32?1???11
Haplomesus zuluensis	22221211?5	21555551-1	5111121121	1-1?431??1	311?21?22?	?211231111	??1111----	---------
Haplomesus franklinae	22222211?2	1111111231	1111121111	1-15431321	311121?222	1221132111	4223??2222	31?2111??
Ischnomesus antarcticus	1111-1111-	----------	111??1112?	1-?5421121	11121-?122	1312211111	--2---3112	221422231
Ischnomesus bispinosus	1111-11111	31111111-1	1111111121	1-15421221	211111112?	1322111211	2?23113111	-11223131
Ischnomesus curtispinis	22222111?1	21121511-1	1111121111	1-15431121	3212?1?322	?2211331?1	322312????	?????????
Stylomesus hexapodus	1122-231?1	31111111-1	1111111121	1-113313?1	4???21?222	13?2121133	412322----	---------
Stylomesus menziesi	1122-13?1-	----------	1111111121	1-15331221	32112-??2?	?3?11213?1	-2----111-	-1?213122
Stylomesus sarsi	1122-231??	??????????	1111121121	1-1?321221	????2??12?	?311121112	42232?4211	-12211132

Polymorphisms (12) = A, (25) = B.

Constant/uninformative characters

An *a priori* analysis of all characters used in descriptions was undertaken. From this, 48 characters were found to be constant and/or uninformative and were removed from the dataset. These characters are referred to in the discussion of characters. A further 32 characters were removed because they exhibited poor fit to the cladograms, with retention indices of <0.1 (31 characters had a retention index of 0 and 1 character had a retention index of 0.1). These characters are discussed separately following the discussion of included characters below.

Characters used in descriptions and analyses

Figure 1 illustrates the differences in morphology within the *Haplomesus*-group.

Body characters

Fusion of pereonites (*characters 1–3*). The degree of fusion of the posterior pereonites, the pleonites and the pleotelson (whether or not articulation is expressed between these segments) is the most important character complex for defining genera in the Ischnomesidae. A greater degree of articulation is presumed to be plesiomorphic. For example, in the genus *Ischnomesus* all of the pereonites are freely articulated and pleonite 1 also articulates freely with the pleotelson. Species in the genus where this is not the case (e.g. *Ischnomesus curtispinis*) are classified elsewhere (see below). The converse situation occurs in the *Haplomesus*-group and the genus *Heteromesus*, where posterior pereonites, pleonite 1 and the pleotelson are fused together. In the genera *Ischnomesus*, *Stylomesus* and *Heteromesus*, pereonite 5 is freely articulating with pereonite 6. The genus *Stylomesus* has an intermediate degree of fusion: pereonite 7, the pleonites and the pleotelson are fused together, whereas pereonites 5 and 6 are freely articulating with each other and with pereonite 7. Wolff (1962: 72–73), in his revision of the family, named several genera based on the combination of the fusion and the number of articles in the uropods. Some of these genera have subsequently been synonymised back into other taxa (Kussakin 1988). This variable degree of fusion of the posterior pereonites is also observed in other asellote families such as the Munnopsidae, Haploniscidae, Nannoniscidae and Dendrotionidae. The features of these families, however, are independent derivations from those in the Ischnomesidae and are unlikey to be homologus.

Body–pleonites fusion (*character 4*). Primitively, the class Malacostraca has six free pleonites and a telson. In Isopoda, the sixth pleonite is fused to the telson to form a pleotelson. In the Asellota, pleonites 4–5, and often pleonites 2 and 3, are fused to the pleotelson, which is an apomorphy for the suborder. Pleonites 1–2 and rarely 3, if distinct from pleotelson, are only small rings or cuticular bars visible ventrally. Sometimes the pleonite articulation will be absent and the pleotelson is a single, large segment, as is the case for species of the *Haplomesus*-group and the genus *Heteromesus*. Wolff (1962) discussed the number of pleonites in the Ischnomesidae (as implied by rounded regions of the pleotelson) and concluded that the number varies within genera of the family. For example, he stated that some species of the genus *Stylomesus*, such as *S. elegans* Menzies, 1962 and *S. inermis* Vanhoeffen, 1914, have two pleonites whereas other species, such as *S. simplex* Menzies, 1962 and *S. gracilis* Birstein, 1960, have three pleonites. He also recorded three pleonites for the species *Gracilimesus tenuispinis*, comb. nov., *G. modestus*, *Haplomesus quadrispinosus* and *Heteromesus frigidus*. We do not follow this analysis by Wolff because the rounded regions of the pleotelson do not strictly follow the plesiomorphic pattern of the pleonites. All species of Ischnomesidae have pleonites 2–6 and telson fused to form a pleotelson with, at most, one free pleonite. Most genera of the Ischnomesidae do not express the posterior articulation, and pleonite 1 is fused with the pleotelson in all genera except the genus *Ischnomesus*, where it is freely articulating, both anteriorly and posteriorly. We consider the free articulation of pleonite 1 to be the plesiomorphic condition for the family.

Haplomesus sensu lato segmental articulation (*character 5*). During the course of this analysis, an additional character state was discovered where, although the pereonites and pleotelson are completely fused together as in *Haplomesus*-group, faint suture lines are visible on the dorsal surface. This occurs in two species: *Contrarimesus curtispinis*, comb. nov. and *Contrarimesus franklinae*, comb. nov., and is analogous to the dorsal suture lines seen in the Haploniscidae, which are also inflexible. This state may be intermediate between the condition seen in *Stylomesus*/*Ischnomesus* and in *Haplomesus*.

Body pereonite 7 reduced (*character 6*). A phylogenetic trend exists throughout the Ischnomesidae towards reduction of pereonite 7 (Kavanagh *et al*. 2006). In the case of species that do not express pereopod VII (e.g. *Gracilimesus celticensis*, comb. nov. and *Gracilimesus hanseni*, comb. nov.) the last pereonite is reduced in width. (Fig. 1*E*). In other cases throughout the family, the last leg is reduced, and in some cases, pereonite 7 is also reduced correspondingly. This reduction is most widespread in the *Haplomesus*-group (e.g. *Fortimesus cornutus*, comb. nov.) and is also observed in the genus *Stylomesus* (e.g. *Stylomesus natalensis* Kensley, 1984). In species of *Ischnomesus* and *Heteromesus*, pereopod VII is always present and is the same length as pereopod VI; correspondingly, pereonite 7 is the same length as pereonite 6. We consider this to be the plesiomorphic condition.

Head anterolateral projections supporting antennae (*character 7*). Within the Ischnomesidae long, thin, anterolateral projections on the cephalon that support the antennae (Fig. 1) are a synapomorphy for the genus *Cornuamesus*, gen. nov. Anterolateral projections in the genus *Stylomesus* are robust and rounded, and are unlike the antennuated projections of *Cornuamesus*, gen. nov. Wolff (1962) stated that 'stalks' could also be found on *Gracilimesus orientalis*, comb. nov. (Birstein, 1960). Birstein's illustrations, however, show a broad cephalon rather than the presence of anterolateral projections. Some *Heteromesus* species have small squat projections supporting the antennae (Cunha and Wilson 2006), but the majority of genera and species in the Ischnomesidae have the antennae emerging directly from the head.

Head lobe on ventrolateral margin (*character 8*). Species of *Heteromesus* are observed to have a distinct lobe visible in lateral view (see Cunha and Wilson 2006). The lobes consist of broadly rounded ventral projections of the head surface that overlap the insertion of the mandibles. This lobe has not been observed in other genera of the family.

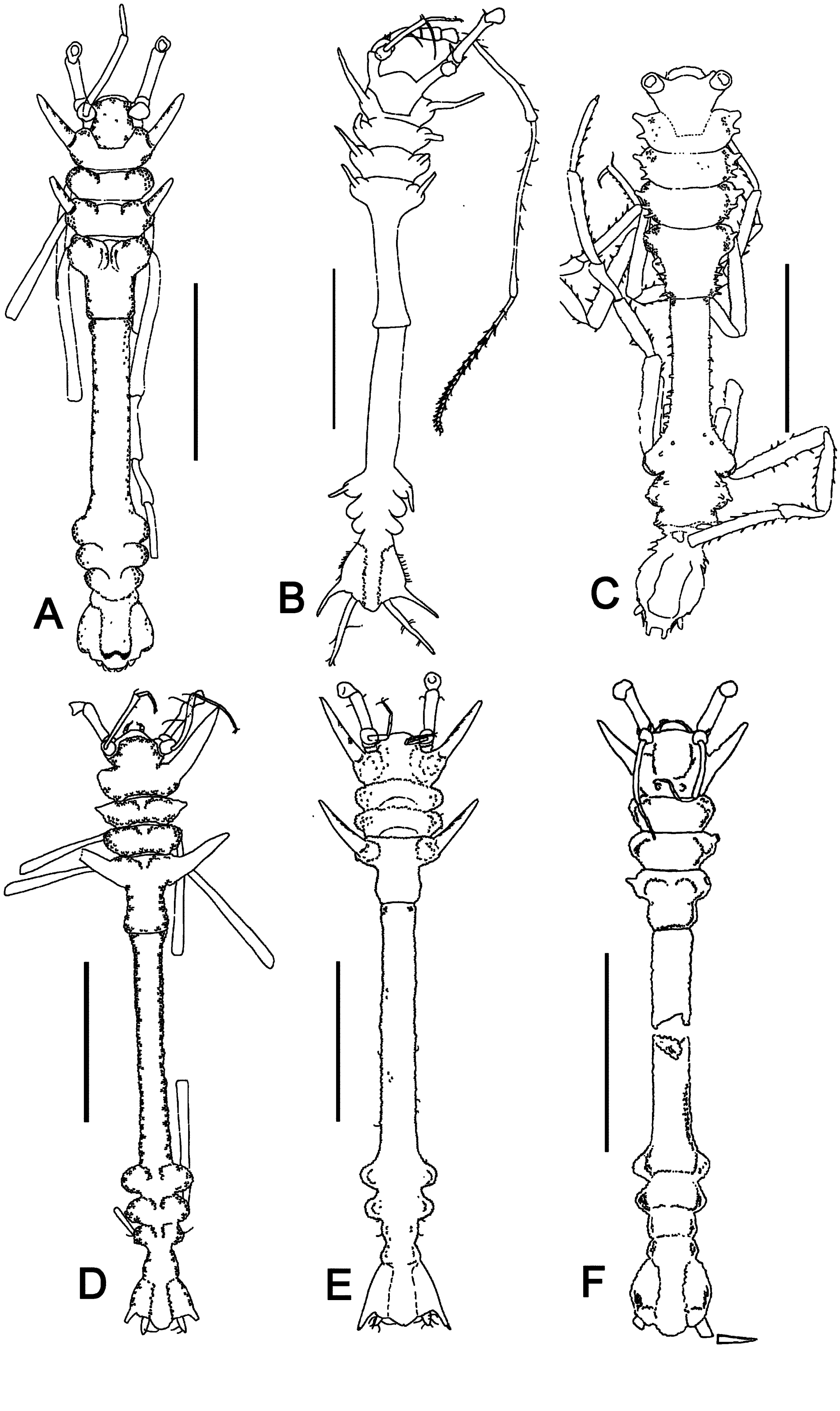

Fig. 1. Variation in overall body morphology of the *Haplomesus*-group. *A*, *Haplomesus ornatus*; *B*, *Cornuamesus longiramus*, comb. nov.; *C*, *Fortimesus thomsoni*, comb. nov.; *D*, *Gracilimesus insignis*, comb. nov.; *E*, *Gracilimesus hanseni*, comb. nov.; *F*, *Contrarimesus franklinae*, comb. nov. Scale bar = 1 mm.

Pereonites with spines or tubercles (*characters 9–24, 68–72*). Most ischnomesid species display spines on pereonites 1–4 (Fig. 1), and have fewer spines on the posterior pereonites. The spines are defined by their position on the body surface: median spines refer to spines in the centre of pereonites on the dorsal surface. Lateral spines refer to spines on the lateral margins of the pereonites that also may be either anteriorly or posteriorly located, and are thus referred to as anterolateral or posterolateral spines. Dorsal spines refer to any spines on the dorsal surface of the body that are not medially located. Spines are secondarily defined by type: simple spines consist of pointed spines without terminal simple setae; bifid spines refer to spines with two terminal points; pedestal spines refer to spines that are topped by a seta, either simple or robust, and, finally, rook spines refer to sub-cylindrical spines with several distally placed denticles, and usually a distally located simple seta (see Cunha and Wilson 2006). In addition to spines, species of Ischnomesidae may also have tubercles on the body surface. Tubercles differ from spines in that they are wider than long, and are rounded distally, resembling a nodule on the body surface. Tubercles are distinguishable from smaller granulation in the cuticle, which involves tiny projections that are more or less adjacent. Within the Ischnomesidae, simple spines located anterolaterally on the pereonites provide much of the variation between species. The size of the spines was determined by comparing them with the length or width of pereonite 1. Spines were considered 'extremely elongate' if they were longer than the width of pereonite 1; 'elongate' if they were longer than the length of pereonite 1; 'short' if they were shorter than the length of pereonite 1 and 'tiny' if they were much shorter than the length of pereonite 1. The anterolateral spines recorded display variation in their orientation; some spines are directed anteriorly, others may be anterolaterally or dorsally directed. Spines commonly vary in their orientation between and within species. A common spination pattern observed in species of the *Haplomesus*-group collected from the Atlantic Ocean consists of a pair of anterolateral spines on pereonite 1 and a second pair of spines on either pereonite 3 or pereonite 4.

The spination pattern on the anterior pereonites (pereonites 1–4) shows considerable variation both between males and females and can also vary with life history stages (see Svavarsson 1984). For example, juvenile specimens may not display all spines observed in adults (e.g. *Gracilimesus celticensis*, comb. nov.) and large adult females may lose spines observed in younger females (Svavarsson 1984). Characters that display intraspecific variability such as this tend to be more homoplastic (Archie 1985; Campbell & Frost 1993; Wiens 1995, 2001). Including homoplasious characters, however, is preferred over excluding them (Poe and Wiens 2000), with the positive benefit of total evidence (inclusion of all characters) outweighing the negative effect of the missing data on the analysis. Similarly, including taxa or characters with missing data is advocated in preference to excluding them (see Kearney 2002). Although Wiens (2001) argued that including such polymorphic characters increases phylogenetic accuracy, many analyses exclude these characters, for example, Scataglini *et al.* (2005). In the latter case, an analysis of a complex of the Coleoptera family Curculionidae, the authors excluded characters because, when included, the number of parsimonious trees increased significantly. They concluded that this character exhibited homoplasy and made it more difficult to find a single topology.

We include spines in the database because they are highly informative for identification of individual species, especially when complete data are available. Our analysis of the spination characters includes all of the missing data problems: one or another sex was not observed, either sex was damaged, or was incomplete (some species are known only from fragments) or immature. Spines can vary ontogenetically and bilaterally. Incomplete taxon sampling is another difficulty. As will be mentioned in a few places below, we know of unanalysed species in our collections, and almost certainly many species remain unsampled, given the projected diversity of the deep sea (e.g. extrapolations of Grassle and Maciolek 1992). All spination characters were included in the *a priori* analysis and only those that were constant/uninformative or had a retention index <0.1 were excluded in the final analysis. For the species in this analysis, no difference was found in the spination pattern of the posterior pereonites between sexes, so they were not coded separately. These spines are generally observed only in species of *Fortimesus*, gen. nov., with the exception of *Cornuamesus longiramus*, comb. nov., which displays posterolateral spines on pereonite 5. Species of the genus *Fortimesus*, gen. nov., most of which are recorded from the Pacific Ocean, display many tubercles and small simple spines on the dorsal and lateral margins of the pereonites and pleotelson. Several species of *Ischnomesus*, such as *I. armatus* Hansen, 1916 and *I. magnificus* Wolff, 1962, have spines on the posterior pereonites. In general, these spines are restricted to the lateral margins of the pereonites, with few dorsal tubercles or spines, with some notable exceptions including *I. birsteini* Wolff, 1962, *I. multispinis* Menzies, 1962 and *I. spaercki*. Similarly, some species of *Heteromesus* display lateral spines, and in the case of *H. drachii* and *H. wolffi* Chardy, 1974, dorsal tubercles. In the genus *Stylomesus*, few species apart from *S. hexaspinis* Birstein, 1963 display spines anywhere on the body.

Pleonite 1 region of pleotelson with dorsal spines or tubercles (*character 25*). The pattern of spines on the posterior pereonites is outlined above, and a similar pattern is observed with regards to spination on the pleonites and pleotelson. The pleonite 1 region of the pleotelson was distinguishable by a distinct expansion extending ring-like around the pleon, just posterior to the margin of the last pereonite. Several species of *Fortimesus*, gen. nov. possess spines or tubercles on the pleonites and the pleotelson that are not observed in other genera of the *Haplomesus*-group.

Pleotelson dorsal surface axial ridge (*characters 26–28*). The division of the pleotelson into regions is an important character for species of the *Haplomesus*-group. All species of *Haplomesus sensu stricto* have a pleotelson with a prominent axial ridge that is strongly vaulted from the lateral fields of the pleotelson, and this is a unique apomorphy for this genus (Fig. 2*A–B*). The remainder of the species of the *Haplomesus*-group have a less prominent ridge that is either weakly separated from the lateral fields (e.g. *Fortimesus*, gen. nov., Fig. 2*D*) or not separated at all (e.g. some species of *Gracilimesus*, gen. nov.). Species of *Heteromesus*, *Ischnomesus* and *Stylomesus* also have the pleotelson vaulted to a greater or lesser degree. The unvaulted pleotelson is considered the plesiomorphic state. Lateral fields of the pleotelson, as distinguished from the axial ridge have been noted in the Nannoniscidae. In these species, whether or not this ridge is vaulted is unclear. In species of Ischnomesidae that have a distinct axial ridge, the ridge generally runs the length of the pleotelson. Within the genus *Haplomesus sensu stricto*, variation occurs in the length of the ridge, with several species exhibiting a truncated axial ridge, such as *Haplomesus ornatus* Menzies, 1962 (Fig. 2*B*). Most species of the *Haplomesus*-group have a smoothly arched axial ridge without any incisions. Variation occurs within the genus *Haplomesus sensu stricto* where *H. ornatus* has a bilobed axial ridge forming medial carinae and *H. bifurcatus* Menzies, 1962 has an incised axial ridge with a shallow narrow invagination (Fig. 2*A*–*B*). For the remainder of species of the family, the pleotelson axial ridge is smooth.

Uropod insertion on pleotelson (*character 29*). The position of the insertion of the uropods differs throughout the

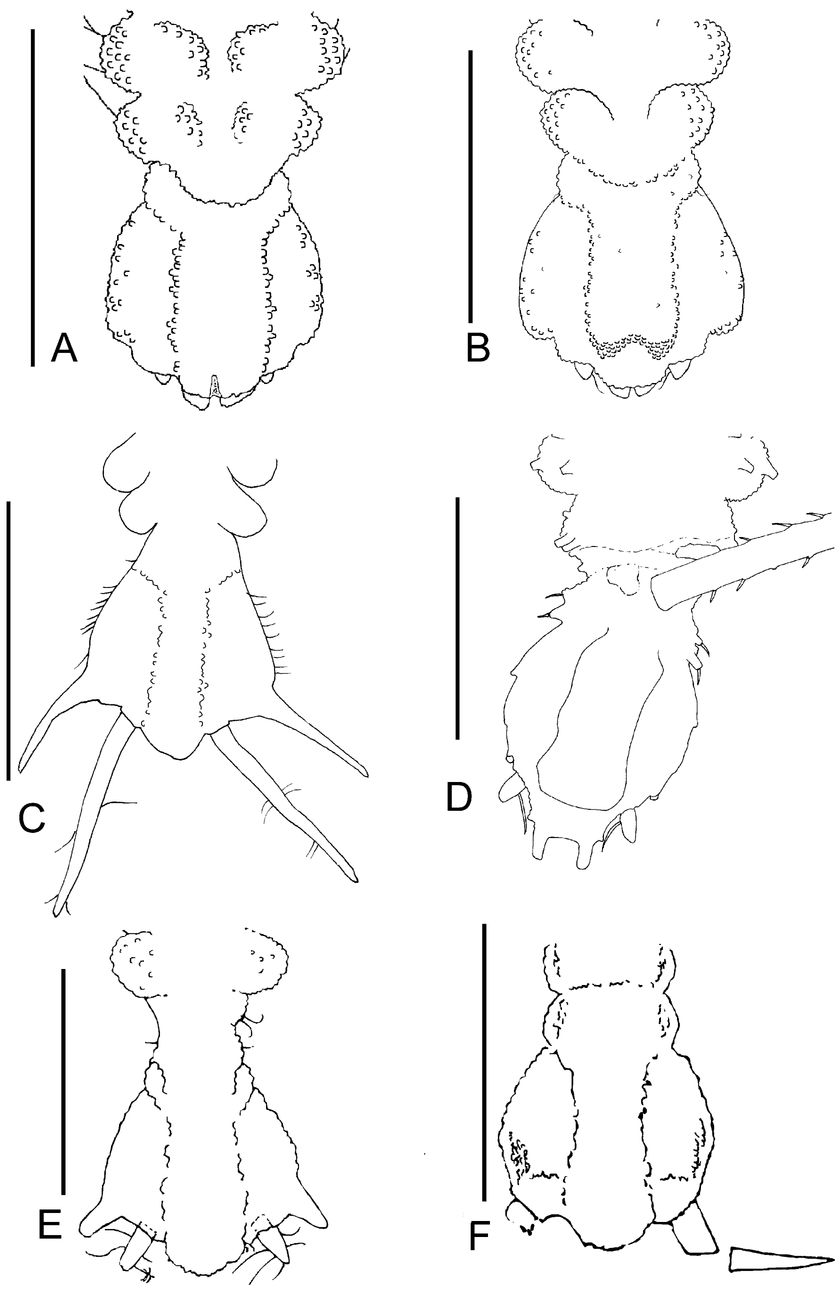

Fig. 2. Variation in the morphology of the pleotelson of the *Haplomesus*-group. *A*, *Haplomesus bifurcatus*; *B*, *Haplomesus ornatus*; *C*, *Cornuamesus longiramus*, comb. nov.; *D*, *Fortimesus thomsoni*, comb. nov.; *E*, *Gracilimesus hanseni*, comb. nov.; *F*, *Gracilimesus modestus*, comb. nov. Scale bar = 0.5 mm.

Asellota. In the basally-derived genera *Stenetrium* (Stenetriidae), *Janira* (Janiridae) and *Asellus* (Asellidae) uropods are biramous, possess a large protopod, and are inserted posteroventrally on either side of the anus. Although how the uropods insert has changed, their position in the Ischnomesidae has not diverged significantly from the primitive position observed in the Stenetriidae. In addition, variation occurs in the associated structures on the pleotelson, such as a variably produced posterior margin, along with the presence of posterolateral spines. Within the Ischnomesidae, the structure of the uropodal insertion may be of generic significance. Species of *Heteromesus*, *Cornuamesus*, gen. nov. and *Contrarimesus*, gen. nov. have a uropod point of insertion that is distinctly produced (Fig. 2*F*). The uropod emerges from a ring of cuticle projecting from the line of the posterolateral margin. In the genus *Ischnomesus*, some species such as *I. justi* Merrin & Poore, 2003 also have the produced posterolateral margin, whereas other species have the margin in the insertion of the uropod not distinctly produced, or uninflected. In *Haplomesus*-group species (e.g. *Gracilimesus celticensis* (Kavanagh *et al*., 2006)), the uropod sits in a distinct concavity.

Pleotelson with spines or tubercles (*character 30–33*). Dorsal and lateral spines are observed on the pleotelson of species in many asellote families such as Munnidae, Ilyarachnidae and Haplomunnidae. Within the Ischnomesidae, dorsal and lateral spines are observed on some species of Ischnomesus (e.g. *Ischnomesus spaercki* and *I. birsteini*) whereas many species of *Fortimesus*, gen. nov. have prominent tubercles and spines on the pleotelson. Some species of *Heteromesus* (e.g. *H. drachii*) have dorsal tubercles, but only *H. spinosus* has spines on the lateral margins of the pleotelson. No species of *Haplomesus sensu stricto*, *Gracilimesus*, gen. nov., *Contrarimesus*, gen. nov., *Cornuamesus*, gen. nov. or *Stylomesus* display dorsal or lateral spines or tubercles on the pleotelson.

Within the Ischnomesidae, the presence or absence of posterolateral spines is an important diagnostic character of genera. *Haplomesus sensu stricto*, *Ischnomesus*, *Contrarimesus*, gen. nov., *Stylomesus* and *Fortimesus*, gen. nov. do not have spines; *Heteromesus* has species both with and without spines and *Gracilimesus*, gen. nov. and *Cornuamesus*, gen. nov. display prominent posterolateral spines (Fig. 2*C*, *E*). Owing to the various spine forms in the Asellota, these spines are unlikely to be homologous. Finally, spines are also recorded on the terminal margin of the pleotelson, located between the uropods: several species of *Fortimesus*, gen. nov., (Fig. 2*D*), some species of *Heteromesus* (see Cunha and Wilson 2006) and *Ischnomesus birsteini* Wolff, 1962. Several characters pertaining to the body were excluded from the analysis. Body length for both male and female specimens was excluded because this was based on one specimen only in each case, the holotype or paratype. In several cases, type specimens were immature and not necessarily representative of the species. In addition, the size of adult specimens of the same species can vary by ~1 mm, for example, specimens of *Haplomesus quadrispinosus* as examined by Svavarsson (1984). Constant characters that are excluded are: general body shape, fusion of pereonite 1 and cephalon, width of pereonites 5–7, and projection of body tergites. The presence/absence of spines/tubercles on the head was found to be uninformative.

Features of the limbs

Antennula (*characters 34–44*). The antennulae of almost all Isopoda are uniramous, in contrast to many other Malacostraca that possess biramous antennulae (Brusca and Wilson 1991). Within the Isopoda, exceptions (e.g. the Flabellifera *sensu lato*, the Phreatoicidea and the Tainisopidae) possess a vestigial flagellum or antennular scales. We refer to the total number of articles present in the antennula, and avoid the use of the term 'flagellum' owing to confusion in previous species descriptions about which segments are included. In the Ischnomesidae, although articles 3 and 4 are not flagellar, they are sometimes referred to as such owing to their distinction from articles 1 and 2, and their similarity to 'flagellar' articles. The number of articles in the antennula varies throughout the Asellota, and is useful to distinguish between species rather than genera or families in many instances.

The ischnomesid antennula differs from that of other asellotans in several respects. In all species of Ischnomesidae, article 1 is squat and globular, article 2 is elongate and articles 3–5/6/7/8 (if present) are short. Wolff (1962) found the number of articles in flagella of the genus *Ischnomesus* to be 4–8, *Stylomesus* 3–4, *Haplomesus* 4 and *Heteromesus* 2–3 small articles, where 'flagellum' was used to describe all articles distal to article 2. Species of the genus *Heteromesus* are most easily recognised by their tiny or rudimentary antennular articles distal to article 2. Since Wolff's diagnosis, species of the *Haplomesus*-group have been recorded with three distal articles. Thus, species have antennulae consisting of five or six articles. Furthermore, in the genus *Stylomesus*, *S. hexapodus* has an antennula with only two articles. Therefore, with the exception of the genus *Heteromesus*, the number of articles in the antennula is not a reliable character for distinguishing genera but may be useful for distinguishing species. This feature is further confounded by the frequent miscounting of the tiny distal articles by previous authors, as discovered for species of *Heteromesus* (Cunha and Wilson 2006). Re-inspection of types, as we have done here, seems to be necessary for many of the described species. Reduction in the number of distal articles is considered apomorphic within the Ischnomesidae.

In most species of *Heteromesus* and the *Haplomesus*-group, the second article of the antennula is at least 3× as long as article 1. The only exception is *Fortimesus robustus*, comb. nov. (Birstein, 1960), where article 2 is approximately twice as long as article 1. In most species of *Ischnomesus* and *Stylomesus* article 2 is shorter than observed in the *Haplomesus*-group, approximately twice as long as article 1. The elongate article may be the apomorphic state owing to its reduced length in other Asellota, as discussed above. This character has been gap-coded based on the length of article 2 relative to article 1 for all species of *Heteromesus* (Cunha and Wilson 2006), the *Haplomesus*-group, several outgroups from the genera *Ischnomesus* and *Stylomesus*, and the primitive state observed in the Asellota (article 2 subequal to article 1). The observed result was distinct discrete states for this character, which reflected the genera of the family in most cases, as discussed above.

The cumulative length of the distal articles of the antennula of Ischnomesidae is not always greater than the length of article 2, unlike the situation generally observed in the Asellota. In general, the distal articles are subequal to or longer than article 2 in the genus *Ischnomesus*. In the genus *Stylomesus* and in the *Haplomesus*-group, the distal articles are shorter than in article 2, and in species of *Heteromesus* the distal articles are minute compared with article 2. Article 2 being longer than the distal articles is apomorphic within the Ischnomesidae, and is closely related to the number of articles in the antennula (character 34). The relative lengths of articles 3 and 4 may be a generic character within the Ischnomesidae. In species of *Ischnomesus* and the *Haplomesus*-group, antennula article 3 is generally longer than article 4. Species of *Heteromesus* and *Stylomesus* have articles 3 and 4 of similar length, and can be quite short. In several species of *Stylomesus* (e.g. *S. hexapodus* and *S. natalensis*) only two articles are present, thus this character was inapplicable. In the genus *Heteromesus*, some species have a squat article 3 that is wider than long, but for most species of Ischnomesidae, and other Asellota, article 3 is much longer than wide. The presence of a squat article 3 is an apomorphy for the genus *Heteromesus*. Within the Ischnomesidae, the genus *Heteromesus* has the terminal article shorter than the penultimate; in the *Haplomesus*-group, *Ischnomesus*, and *Stylomesus*, both character states occur. Where the terminal article is longer than the penultimate article, it possibly consists of two articles with loss of articulation, which would be apomorphic.

In addition to differences in the number and relative lengths of the various antennula articles, the family Ischnomesidae has other structures of the antennula that differentiate the appendage from those of other Asellota. First, the insertion of article 2 onto article 1 differs in the Ischnomesidae. In most non-ischnomesids, and in the genus *Ischnomesus*, article 1 inserts anteriorly on article 2. In species of *Heteromesus* and the *Haplomesus*-group, article 2 inserts dorsally on article 1, with the exception of *Gracilimesus orientalis* (Birstein, 1960), comb. nov., and we consider this to be apomorphic. In the genus *Stylomesus*, article 2 may insert either dorsally (e.g. *S. hexapodus*) or anterodorsally (e.g. *S. sarsi*). Species of the *Haplomesus*-group, *Stylomesus* and *Ischnomesus* as in most other families of Asellota, have an article 2 that is straight, and not curved at proximal insertion. In contrast, species of the genus *Heteromesus* have a strong curve visible at the point of proximal insertion to article 1, and this is a unique synapomorphy for the genus.

Most species of Ischnomesidae have long setae present on article 2 of the antennula that are not consistently observed in other Asellota. These long setae are nearly as long as article 2, typically cross the midline and are stiff and curving. Other setae on the second article are much shorter, such as the row of setae in *Fortimesus gigas*, comb. nov. Although the setae are not a diagnostic character at the generic level, and may be broken during sampling or poorly illustrated, they may be useful for discerning between species. Several species of *Heteromesus* have the distal tip of article 2 of the antennula produced so that that distal article inserts subapically. All species of the *Haplomesus*-group have the distal article inserting apically. Most species of Ischnomesidae have only ventromedial setae on antennula article 2. As mentioned above, some species of *Fortimesus*, gen. nov. have a row of robust setae on article 2 that is not observed elsewhere in the family, or in the Asellota as a whole, for example, *Fortimesus gigas*, comb. nov. and *F. brevispinis*, comb. nov. This follows the general trend of species of *Fortimesus*, gen. nov. displaying more ornamentation on the body than other genera of the family. Uninformative characters for the antennula include: the length of article 2 versus the width of the head for both male and female specimens; presence/absence of aesthetascs on the antennula.

Antenna (*characters 45–46*, *73*). The antennae of most isopods have five robust basal articles and a flagellum with non-musculated tapering articles. The Asellota, including the Ischnomesidae, have a six-articled basal part, with three protopodal articles; in these, a scale sometimes occurs on the third article. In the Ischnomesidae, antenna article 3 is usually at least 3× as long as wide, much longer than articles 1 and 2 combined, and at least twice article 4 length, and also lacks the scale. The cuticle of antenna article 3 in the Ischnomesidae may be either smooth or granulate; this character is diagnostic of species rather than genera. The cuticle, however, may have become decalcified over time and the original state may be difficult to discern. In many instances, the state of the cuticle is not included in a description. Only one character could be gap-coded: length versus width of article 3 in female specimens. The mean of this measurement was 4.9 with a standard deviation of 3. One gap was observed in the data between 10 (*Fortimesus profundicolus*, comb. nov.) and 13.8 (*Fortimesus gigas*, comb. nov.), resulting in two character states of antenna article 3 length versus width in females less than or greater than 13. However, this character proved to be uninformative in the analysis and was subsequently omitted.

Various types of spines are observed on articles 2 and 3 of the antennae of Ischnomesidae but do not provide any generic characters. Spines on antenna article 3 are useful for distinguishing species. The type species of *Haplomesus sensu stricto*, *Haplomesus quadrispinosus*, has a group of distomedial spines on article 3 (Fig. 4*C*), a feature not observed in any other species of the *Haplomesus*-group, and thus this provides an important diagnostic character for this species. This character, however, proved uninformative for the analysis. The presence/absence of ventromedial spines on article 3 proved informative in females.

The asellotan antennal flagellum exhibits sexual dimorphism, depending on the group. The normal condition is a flagellum that tapers distally, with the individual articles generally longer than wide, with few setae and no aesthetascs. In many deep-sea taxa, generally where the antennula is small or tiny, the antenna of fully adult (or terminal) males becomes inflated basally to different degrees, so that the proximal segments become wider and then narrower, and, at least basally, are often wider than long. This condition is often combined with many flagellar setae that are somewhat like aesthetascs, but on close inspection are setae (e.g. fig. 3*C* in Kavanagh *et al*. 2006). Unfortunately, owing to the brittle nature of the Ischnomesidae, the antennae are rarely intact in specimens, resulting in missing data for some characters. Initial measurements for the length of the male flagellum as a ratio of length of the whole antenna suggest that this might be a useful character for these species in the future. The mean of the species recorded was 0.39 with a standard deviation of 0.14. A gap was observed in the data between 0.36 (*Fortimesus cornutus*, comb. nov.) and 0.65 (*Cornuamesus longiramus*, comb. nov.) Thus, a limit could have been set at 0.5. In light of the large amount of missing data, along with differences in life history stages, this character was omitted as being potentially misleading.

Uninformative characters for the antenna include article 3 length versus width; article 3 length versus length of anterior pereonites (pereonites 1–4); article 5 length versus length of anterior pereonites and article 6 length versus length of anterior pereonites. Length versus width of article 3; ventromedial and/or lateral spines on antenna article 2; distal spines on antenna article 3; the number of articles of the antenna flagellum for both males and females; the length of the flagellum versus the length of the entire antenna for males and females.

Mouthparts

Labrum knobs (*character 47*). Several species of *Heteromesus* have distinct knobs on the labrum. Unfortunately, the labrum is rarely recorded for species of Ischnomesidae, with no descriptions for species of the *Haplomesus*-group.

Mouthparts (*characters 48–49*). The maxilliped of isopods consists of four distinct regions: a proximal article (coxa), the basis with an enlarged, distal, anteriorly directed endite, an epipod of varying size and shape, lateral to the coxa, and a palp of five articles. The basis endite of the maxilliped is well developed in the Ischnomesidae, much broader than observed in other asellote taxa. In the Ischnomesidae, the maxilliped palp contains five articles. Within the Ischnomesidae, article one is short, with few (if any) setae. Articles 2 and 3 are subequal in length with several setae on the lateral margins. Articles 4 and 5 are narrower than articles 2 and 3, with four distal setae on article 5. Variation does occur in the width of articles 2 and 3. In the genera *Heteromesus* and some species of *Stylomesus*, these articles are subequal to each other and to article 1. In *Haplomesus sensu stricto* and species of *Ischnomesus* articles 2 and 3 are expanded wider than article 1 and may differ in width themselves. The presence of expanded articles in the presumedly least derived genus, *Ischnomesus*, as well as in the basally-derived families Janiridae and Munnidae, indicates that this is the plesiomorphic condition.

Most species of Ischnomesidae have the maxilliped epipod that lacks spines. Only two possess spines on the epipod of the maxilliped: *Cornuamesus biscayensis*, comb. nov. and *Cornuamesus longiramus*, comb. nov.

Several features of the mouthparts were not included in the analysis. The lateral lobe of the maxillula has several robust setae on the distal margin, generally numbering 10–12. This character was not used in the analysis as the precise number of setae is not well recorded for most species. In cases where the maxillula was illustrated, the number of setae was not distinguishable. Characters pertaining to the length and width of the maxilliped palp versus the endite were found to be constant, and therefore, uninformative for the Ischnomesidae.

Pereopods

Pereopod bases (*characters 50–51*). Species of the *Haplomesus*-group have a distinct thin neck between the pereopodal articulation of the basis and coxa and the shaft of the basis, with the basis neck and shaft forming an approximate right angle. Species of *Heteromesus* also have this character, but with an added spinose shoulder (Cunha and Wilson 2006). The spines can be either simple, rook or bifid spines. A spinose shoulder is also recorded for *Cornuamesus longiramus*, comb. nov. The distinct 'neck' probably occurs in the majority of species of Ischnomesidae but has not been illustrated well; many illustrations of isopods do not show the pereopods *in situ*, or even show lateral or ventral views of the body. Therefore, the importance of this character, and its probable status as an apomorphy of the Ischnomesidae, is unclear at this time.

Pereopod I shape (*character 52*). Species of Ischnomesidae have pereopod I either strongly or weakly carposubchelate; that is, with the major articulation between the propodus+dactylus and the carpus, so that the proximal palm is on the carpus. The plesiomorphic state within the Isopoda is propodosubchelate, with the major articulation between the dactylus and propodus. Pereopod I is said to be strongly carposubchelate where it is distinctly shorter than the posterior pereopods, with a well developed major hinge between the carpus and propodus resulting in the propodus and dactylus reflexing against an elongate carpus. In addition, many Ischnomesidae have some flexure between the dactylus and propodus. Strongly carposubchelate pereopods are found in the genera *Heteromesus* and *Ischnomesus*. Weakly carposubchelate pereopods differ from those that are strongly carposubchelate because the carpus is largely tubular, weakly setose and the ventral margin is not expanded. In such limbs, the propodus-dactylus flexure is similar to that for the carpus-propodus articulation. This is the state that is observed in the *Haplomesus*-group and the genus *Stylomesus*.

Pereopod I merus (*character 53*). Species of Ischnomesidae may possess one or two robust setae on the dorsal surface of the merus. The character varies within genera, and thus is useful for distinguishing between species only.

Pereopod I carpus (*characters 54–57*). Most Isopoda have a carpus that is short, broad and nearly triangular, and does not take part in the grasping function, which instead is carried out by the dactylus and propodus. In more derived families of the superfamily Janiroidea such as the Ischnomesidae and the Desmosomatidae, the first pereopod more closely resembles the more posterior pereopods, with an elongate carpus that fully opposes the propodus, and this is regarded as an apomorphic state within the Asellota (Wilson 1987). Species of the *Haplomesus*-group and the genus *Stylomesus* have a carpus that is subequal in width along its length, that is, without a ventral palm. Species of *Ischnomesus* have a carpus that is expanded proximally, although some species, such as *Ischnomesus bruuni*, have a carpus that is subequal in width and some species of *Heteromesus* have a carpus that is expanded medially to varying degrees.

Setae on the carpus are involved in grasping actions. Setae tend to occur in two distinctly different sizes in many Ischnomesidae, with elongate robust setae defining the proximal margin of the palm, and shorter robust setae being proximally or distally located. The palm is the ventral margin of the carpus that opposes the propodus (in asellotan propodo-carposubchelate taxa). In this family, the palm is the margin that is distal to the large elongate robust seta on the ventral margin. In several cases, two major setae are present, one slightly longer than the other (e.g. *Cornuamesus biscayensis*, comb. nov., and *Fortimesus cornutus*, comb. nov.), whereas in *Ischnomesus justi* only fine setae are present.

As well as elongate setae delimiting the palm, Isopoda may have setae proximal or distal to this. Most Ischnomesidae have only one robust seta proximal to the palm. Exceptions include

Ischnomesus antarcticus and *Gracilimesus hanseni*, comb. nov., which both have two proximal setae. Other species (e.g. *Cornuamesus biscayensis*, comb. nov. and many species of *Fortimesus*, gen. nov.) have no setae proximal to the palm region. Most species of Ischnomesidae have setae distal to the palm region. *Contrarimesus curtispinis* and *Gracilimesus modestatenuis* have no setae present, but both these described specimens are immature, which may account for the lack of setae.

Pereopod I propodus setae (*character 58*). In the Ischnomesidae, the propodus is subequal to the remaining segments of the pereopod, elongate and does not form a palm; instead it is fully opposed to the carpus. Robust setae on the propodus ventral margin may aid in its grasping function. Most species of Ischnomesidae have setae on the propodus; exceptions include *Ischnomesus bispinosus* Sars, 1868 and *Gracilimesus modestatenuis*, although in the case of the latter, this may be a result of its immature state as outlined above.

Pereopod VII presence (*character 59*). As outlined in character 7 (pereonite 7 reduced), the presence of pereopod VII is an important characteristic within the Ischnomesidae, as is the length of pereopod VII relative to anterior pereopods. One species of the genus *Stylomesus* and several species of *Gracilimesus*, gen. nov. lack pereopod VII. In species of *Ischnomesus*, pereopod VII is generally equal in length to the anterior pereopods, and this is considered to be the plesiomorphic condition. Some species of the *Haplomesus*-group, for example, *Gracilimesus orientalis*, comb. nov. and *Fortimesus cornutus*, comb. nov. have pereopod VII shorter than pereopod VI. In the Ischnomesidae, the lack of pereopod VII is brought about by progenesis, a type of heterochrony that exhibits an early cessation in development of a structure or structures. See Kavanagh *et al*. (2006) for further discussion.

Pereopod II–VII bases (*character 60*). Most species of the *Haplomesus*-group have the cuticle of the bases of pereopods II–VII smooth and without spines. *Haplomesus bifurcatus*, comb. nov. is the only species with granulate bases. Not all species have the cuticle of the pereopods described or illustrated and as mentioned for other characters of the cuticle, they may have become decalcified over time. In the genus *Heteromesus*, most species have the bases granulated, and several (e.g. *Heteromesus spinescens* and *Heteromesus similis*) possess sharp denticles or teeth. Species of *Ischnomesus* generally possess a smooth cuticle, and all character states are present in the genus *Stylomesus*.

Several characters pertaining to the pereopods were not included in the analysis. The precise number of spines and robust setae on the merus, carpus and propodus of pereopod I were not included, as they could be easily damaged during sampling or examination of specimens. Instead, the characters were coded as either having one, none or several setae or spines present. The following characters are uninformative: the number of dactylar claws; the presence/absence of pereopodal 'neck' between the basis and coxa; the position of setae on pereopod I merus; presence/absence of pectinate setae on pereopod I carpus ventral margin.

Pleopods

Male pleopod I (*character 74*). In the Ischnomesidae, most males have pleopod I with the lateral margins indented midway, with the exception of *Cornuamesus longiramus*, comb. nov. that has straight lateral margins. The male pleopod I may be furnished with distal, lateral or dorsal setae. The presence or absence of setae on the distal margin of pleopod I is a useful trait to distinguish between species of Ischnomesidae (e.g. *Gracilimesus celticensis*, comb. nov. and *Gracilimesus hanseni*, comb. nov.) but is not useful at the generic level. In the genus *Heteromesus*, only one specimen is recorded with distal setae, *H. dentatus*, but pleopod I is not recorded for all species.

Male pleopod II (*characters 75–77*). Within the Asellota, the second pleopods of the male are involved in sperm transfer in conjunction with the first pleopods (Wilson 1991). The pleopodal exopod is a small, non-lamellar structure, and the endopod is modified as a 'stylet' for sperm transfer. Within the Ischnomesidae, the stylet varies within most genera; for example, in the genus *Ischnomesus*, some species have a short stylet that does not reach the distal margin of the protopod (e.g. *Ischnomesus bidens* Menzies, 1962) whereas in other species (e.g. *Ischnomesus wolffi* Menzies, 1962) the stylet is extremely elongate, approximately twice as long as the length of the protopod. Variation also occurs in the genera *Stylomesus*, *Heteromesus*, *Haplomesus sensu stricto*, *Gracilimesus*, gen. nov. and *Fortimesus*, gen. nov.; thus this character is diagnostic at the species level for these genera. In species of *Cornuamesus*, gen. nov., the stylet reaches beyond the distal margin of the endopod. Only two species are described for this genus thus far, and the character may prove to be inconsistent as more species are described.

The shape of the stylet also exhibits variation between and within families. Wilson (1981, 1987) examined the ontogeny of the stylet in the superfamily Janiroidea, and found that in juvenile males, the distal tip of the stylet is a club-shaped process, which then develops into a distally sharp tip. This suggests that the tapering and pointed stylet is the apomorphic state. In the Ischnomesidae, both rounded stylet tips (e.g. *I. latimanus*) and pointed tips (e.g. *I. chardyi*) are recorded for the genus *Ischnomesus*. In the genus *Heteromesus*, the tip of the stylet ranges from tapering and pointed, to thick and blunt, to thin with a medial blade, whereas species of *Cornuamesus*, gen. nov. have a thick and blunt tip on the male pleopod II stylet. For the remainder of the genera of the *Haplomesus*-group, and the genus *Stylomesus*, the tip is pointed.

In the Ischnomesidae, all species of *Heteromesus*, the *Haplomesus*-group and *Stylomesus* have setae on both the lateral and distal margins of the pleopod II protopod. Many species of *Ischnomesus* have setae on the distal margin only, with *I. justi* recorded as having no setae on either margin.

Female pleopod II (*characters 61–62*). Female Asellota lack the first pair of pleopods, with pleopod II forming an operculum over pleopods III–V. The operculum exhibits a large amount of diversity in the Ischnomesidae. For example, in many species of *Ischnomesus* (e.g. *Ischnomesus birsteini* Wolff, 1962) the operculum is a flap-like shape, much longer than wider, with straight proximal and distal edges. The shape of the female operculum is a diagnostic character for genera of the *Haplomesus*-group. In *Haplomesus sensu stricto*, the operculum has a narrow proximal neck and is almost circular posteriorly; this is also the implicit state for this character in species of *Heteromesus*. *Cornuamesus longiramus*, comb. nov.

has a similar shaped operculum but it is weakly concave distally, a characteristic also observed in some species of *Ischnomesus*. Other genera have a different shape, for eample, *Gracilimesus*, gen. nov. has a distinctive shape of narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex, and this is also observed in some species of *Stylomesus* (e.g. *S. sarsi*). In some species of *Stylomesus* (e.g. *S. gracilis* Birstein, 1960) the distal margin of the operculum has a distinctive medial shallow incision.

Many species of Asellota have setae on the distal and lateral margins of the pleopod II female operculum. Where females are recorded, all species of *Heteromesus* have plumose setae in these positions. For the remaining genera of Ischnomesidae, the presence or absence of setae differs between species, and is not useful at the genus level.

The following characters were excluded from the analysis as uninformative: lateral margins of pleopod I straight or indented; length of pleopod I more/less than twice proximal width; pleopod I presence/absence of lateral horns; pleopod I presence/absence of lateral setae; pleopod II stylet cuticle calcified versus not heavily calcified; presence/absence of setae on pleopod III; presence/absence of an exopod on pleopod IV, and the presence/absence of pleopod V are uninformative characters.

Uropods (characters 63–65; 78–79)

The number of rami and articles in the uropod varies throughout the Asellota. All species of *Heteromesus* and the *Haplomesus*-group have uniramous single-articled uropods. *Contrarimesus franklinae*, which has a two-articled uropod, was placed in *Haplomesus* and is now removed to *Contrarimesus*, gen. nov. Species of *Ischnomesus* and *Stylomesus* also have a two-articled uropod, and we consider this to be the plesiomorphic state for the Ischnomesidae.

Within the Ischnomesidae, the length of the uropoda varies considerably between genera. In the genera *Ischnomesus* and *Stylomesus*, species have an elongate two-articled uropod, whereas species of *Heteromesus* and *Cornuamesus*, gen. nov. have an elongate one-articled uropod, all of which extend past the tip of the pleotelson. Species of the genus *Haplomesus sensu stricto* have minute uropoda posteriorly directed; species of *Fortimesus*, gen. nov. also have short uropods, posteriorly directed, although they are generally longer than those observed in *Haplomesus sensu stricto*. Despite the short length, the uropods may extend past the tip of the pleotelson in both of these genera. Finally, species of *Gracilimesus*, gen. nov. have more elongate uropods, directed posterolaterally. Many species of this genus have the uropods just reaching the tip of the pleotelson and this is a result of a posterolateral, rather than a posterior, orientation of the uropods in many cases, and pleotelson with produced posterior margin. The length of the uropods was recorded separately for males and females.

As outlined above, the length of the uropods relative to the tip of the pleotelson does not necessarily reflect their actual length. The length versus the basal width of the uropods was calculated for males and females. In this instance, outgroups with two-articled uropods (*Stylomesus*, *Contrarimesus* and *Ischnomesus*) were not included in the analysis. The mean length versus width of uropods for females was 2.38 with a standard deviation of 1.54. One gap was recorded in the data between 3.2 (*Heteromesus granulatus*) and 7.6 (*Cornuamesus longiramus*, comb. nov.). The length relative to the entire pleotelson length is informative for some species. The mean for the length of the uropods versus the pleotelson was 0.15 for females, with a standard deviation of 0.13. One gap that exceeded the standard deviation was recorded between 0.19 (*Gracilimesus tropicalis*, comb. nov.) and 0.61 (*Cornuamesus longiramus*, comb. nov.). Character 66 is uropods in female less than 0.4× the length of pleotelson (1) greater than or equal to 0.4× the length of pleotelson (2). For male specimens, the mean was 0.21 with a standard deviation of 0.19. One gap that exceeded the standard deviation was recorded between 0.27 (*Gracilimesus insignis*, comb. nov.) and 0.88 (*Cornuamesus longiramus*, comb. nov.).

Excluded characters

As mentioned above, the following 32 characters were removed from the analysis as they had a retention index of <0.1, thus showing extremely poor fit to the cladogram.

Body characters

Body covering (*cuticle*). The cuticle of all species of Ischnomesidae is highly calcified and brittle, which results in damage to the specimens during collection. For some *Haplomesus* type specimens, the cuticle has become decalcified over time and we rely on the literature for information on the original condition. In many cases, there is no reference to the cuticle in the literature. In addition, the degree of granulation of the cuticle may be observed to be 'sharper' directly after a moult, becoming more subtle between moults. Although the cuticle of all species of *Heteromesus* and most of the species of the *Haplomesus*-group is granulated to various degrees, the granulation of the cuticle displays sufficient intrageneric variation to result in poor fit to the cladogram.

Body setation. Most setae characters show considerable intrageneric variation. Although they can nevertheless prove technically informative for the analysis, information on body setation exhibited a retention index of zero on the unweighted cladogram.

Head dorsal surface cephalic bullae. The presence of cephalic bullae (as defined by Cunha and Wilson 2006) is observed on one species only of the *Haplomesus*-group—*Fortimesus consanguineus*, comb. nov (Mezhov, 1980)—and thus is not useful for defining genera.

Spination characters. The spine characters observed on species of Ischnomesidae are essential for species identification as they vary considerably between species. However, as discussed above, they also exhibit considerable homoplasy. Characters with a retention index of zero include the presence/absence of anterolateral spines in female pereonites 2 and 3 and male pereonite 1; the length of the anterolateral spines in male pereonites 2 and 3; presence/absence of median dorsal spines in female pereonite 4; presence/absence of paired dorsal spines in male pereonites 1, 3 and 4 and the presence/absence of lateral spines in male pereonites 1–3.

The spination characters for pereonites 5–7 are not coded separately as they do not differ between species in this analysis.

Nevertheless, they exhibit a significant amount of homoplasy and the following characters had a retention index of zero: presence/absence of dorsal spines on pereonite 7 and pleonite 1 and the presence/absence of lateral spines on the pleotelson.

Features of the limbs

Antenna and antennula. Characters removed from the dataset include the number of ventromedial setae on antennula article 2 and the presence/absence of lateral and ventromedial spines on antenna article 2.

Mouthparts

Maxillula and maxilla medial lobe. The number of pectinate setae on both the maxillula and maxilla medial lobe shows considerable intrageneric variation.

Maxilliped endite. The number of receptaculi on the maxilliped is highly variable. Although the number of receptaculi may be used as a diagnostic character for some genera (e.g. all species of *Heteromesus* have three receptaculi present) all other genera exhibit variation.

Pereopod. The number of distal setae on the pereopod I carpus ventral margin and the presence/absence of spines on pereopods II–VII bases had a retention index of zero on the unweighted cladogram. The number of robust setae on the pereopod I propodus ventral margin had a retention index of 0.1.

Pleopods and uropods. The presence/absence of a fringe of fine setae on pleopod III exopod and the presence/absence of lateral setae on pleopod I male had a poor fit to the cladogram owing to their high level of variability. The shape of pleopod II protopod apex also had a retention index of zero and is useful for distinguishing between species only.

Cladistic analysis and classification

An unweighted analysis of the data (Table 1, TreeBASE study accession number S1903, matrix accession number M3496; http://treebase.org) of 39 species and 79 characters found 48 trees (Fig. 3*A*), length 307 (homoplasy index = 0.57, retention index (*RI*) = 0.63, consistency index (*CI*) = 0.44, rescaled consistency index = 0.28). As discussed above, an *a priori* analysis of the data including 111 characters exhibited considerable homoplasy caused by minor features such as spines on the pereopods or setae. Characters that had *RI* = 0.1 or less in the unweighted analysis were removed. Characters with *RI* = 0 (29 altogether) and one character with *RI* = 0.1 were removed (see character discussion above). The small size of the character set along with homoplasy from minor characters resulted in most clades having a Bremer support of 2 or less and failing to be retained in a jackknife (33% characters deleted analysis).

All new genera were retained in a combined consensus produced from all analyses with a strict consensus retaining all the genera (Fig. 3*B*). The successive weighted analysis resulted in nine trees and the implied weights analysis with the range of concavity values (K) from 1–7, found 21 trees with all genera retained in both analyses. In addition, genera were retained in the same position in the tree for all analyses. The analysis shows that the wide range of morphological diversity within the group requires the creation of new genera to classify the species in monophyletic groups. The *Haplomesus*-group, therefore, is divided into five genera: *Haplomesus sensu stricto*; *Cornuamesus*, gen. nov.; *Contrarimesus*, gen. nov.; *Fortimesus*, gen. nov. and *Gracilimesus*, gen. nov. The apomorphies for each genus are presented in Table 2. *Contrarimesus franklinae* and *Contrarimesus curtispinis* are more closely related to species of *Heteromesus* than to the *Haplomesus*-group, and they are clearly separate from the remainder of species in the group. Thus we retain these two species in a new clade *Contrarimesus*, gen. nov. Manually placing *Contrarimesus* in the *Haplomesus*-group incurred a minimum parsimony debt of 3 steps. *Cornuamesus*, gen. nov. is also closely related to the genus *Heteromesus*. This is a result of both genera having elongate uropods and a pleotelson that is produced at the point of insertion of the uropods. The apomorphies for each genus of the *Haplomesus*-group are listed in Table 2.

Taxonomy

Haplomesus quadrispinosus; *H. bifurcatus* Menzies, 1962; *H. insignis* Hansen, 1916; *H. modestus* Hansen, 1916; *H. modestatenuis* Menzies & George, 1972; *H. ornatus* and *H. tenuispinis* Hansen, 1916 are reillustrated from the type material. *Haplomesus angustus* Hansen, 1916 and *H. tropicalis* Menzies, 1962 have been reillustrated previously (Kavanagh *et al*. 2006). Additional specimens of *H. franklinae* are illustrated, as well as the paratype of *Ischnomesus curtispinis* as this has similarities to *H. franklinae* and the two species form a new clade: *Contrarimesus*, gen. nov. Four additional new genera are proposed based on phylogenetic analysis: *Cornuamesus*, gen. nov.; *Fortimesus*, gen. nov.; *Gracilimesus*, gen. nov. and *Contrarimesus*, gen. nov., with four species retained in *Haplomesus sensu stricto*. The five genera are collectively referred to as the *Haplomesus*-group throughout the text. Taxa are listed in alphabetical order, except the type genus *Haplomesus sensu stricto* is presented first, as is the type species of each new genus.

Implicit characters

The descriptions make use of 'implicit characters', which are characters that are common in the taxa described in this paper. If a species does not have a feature described explicitly, then it will have the state mentioned in the implicit characters. Any characters that are listed in the diagnosis of each genus are not repeated in the species descriptions. Where possible, the description of the female specimen is presented first, and only characters that differ are presented for the male. Unless indicated otherwise, the following attributes are implicit throughout the descriptions, except where the characters concerned are inapplicable.

Female

Body cuticle granulate; with only scattered setae; pereon thin, pereonites 5–7 and pleotelson lacking intersomite articulations, pereonites 4 and 5 elongate, subcylindrical, produced backwards and forwards respectively, pereonite 5 longest; pereonites 5–7 narrowing posteriorly, pereonite 7 length not reduced, similar to pereonite 6; tergites not projecting. Head dorsal surface without bulges or protuberances, without spines or tubercles. Pereonites 1–7 without spines or tubercles. Pleonite 1 region of pleotelson without spines or tubercles. Pleotelson posterolateral margin adjacent to uropods convex;

without spines or tubercles; posterolateral margin anterior to uropods without spines or tubercles; terminal margin without spines or tubercles.

Antennula and antenna. Antennae emerging directly from head, not on projections. Antennula article 1 squat and globular, without spines; article 2 length >3 article 1 length, straight, not curved at proximal insertion, inserting on article 1 dorsally, projecting anteriorly, with long ventromedial setae; terminated with aesthetascs. Antenna article 2 without lateral or ventromedial spines; article 3 length at least twice article 4 length, article 3 cuticle granulate, without spines.

Mouthparts. Mandible palp absent. Maxilliped palp shorter than basis, narrower than endite, articles 2 and 3 width subequal, articles 4–5 narrower than articles 1–3, epipod setae absent.

Pereopods. Pereopod bases with conspicuous neck connecting shaft to coxal articulation, without dorsal projection on proximal part of shaft. Pereopod I weakly carposubchelate;

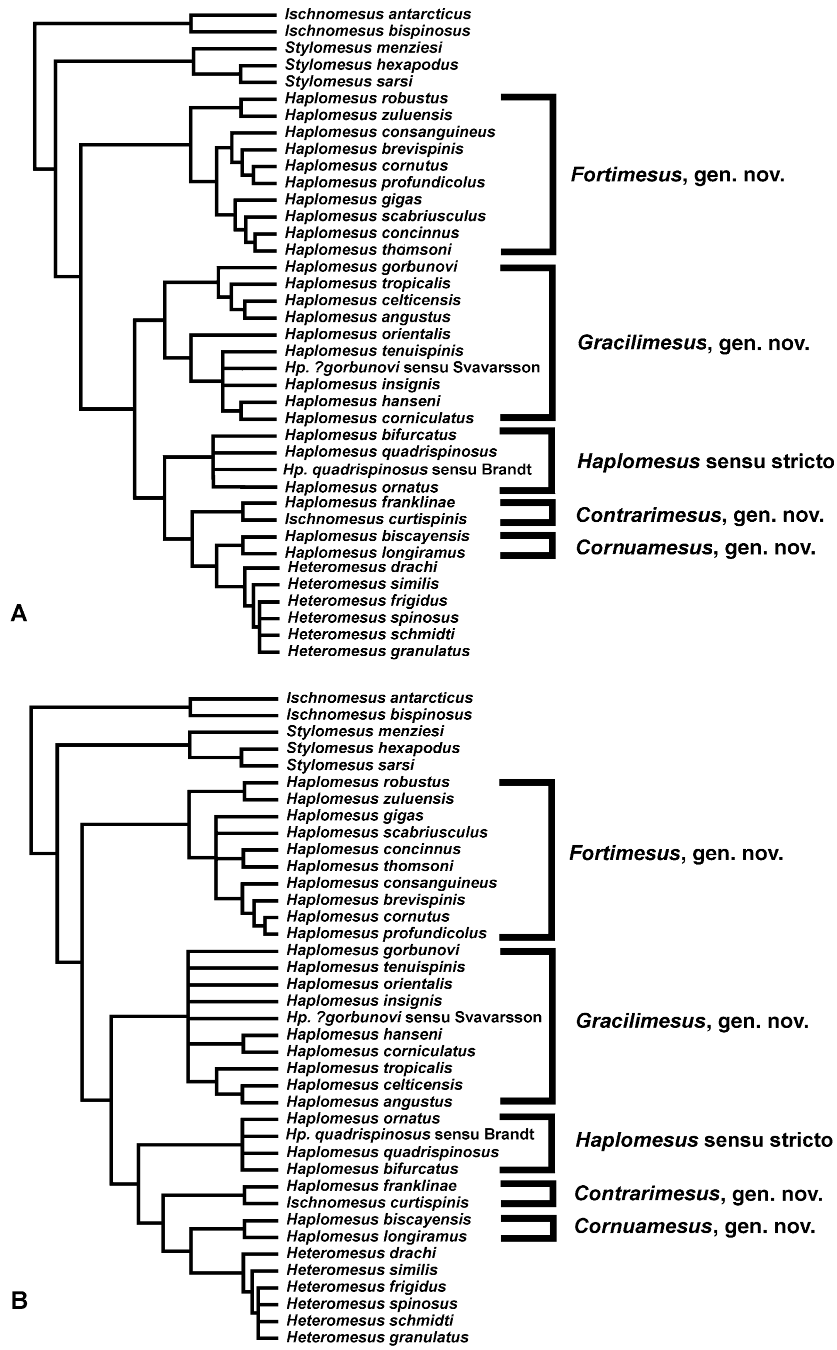

Fig. 3. Strict consensus trees from the phylogenetic analyses with new genera outlined. *A*, Unweighted analysis; *B*, combined consensus analysis.

carpus palm without pectinate setae, carpus ventral margin without distinctly wider part, with 1 elongate robust seta; with one dactylar claw. Pereopod VII present, as long as pereopod VI. Pereopods II–VII bases smooth, with no spines; ischia without spines.

Pleopods and uropods. Pleopod II operculum with narrow proximal neck, almost circular posteriorly, with plumose setae on lateral and distal margins. Pleopod III exopod length more than half endopod length, thin, pointed, with one distal plumose seta; endopod quadrate, with three distal plumose setae. Pleopod IV without exopod; pleopod V absent. Uropod paucisetose, uniramous, inserting terminally and lateral to anus.

Male

Antenna. Antenna flagellum tubular, longer than wide, decreasing in width distally.

Pleopods and uropods. Pleopod I length more than twice proximal width, lateral margins indented midway along length, without simple setae on distal or lateral margins. Pleopod II protopod with setae on lateral and distal margin, tapering and pointed, not heavily calcified.

Family **ISCHNOMESIDAE** Hansen

Ischnomesini Hansen, 1916: 54. – Wolff, 1956: 86.

Ischnomesidae Gurjanova, 1932: 40. – Menzies, 1962: 111; Wolff, 1962: 71–73; Birstein 1971: 198–199; Menzies & George, 1972: 971; Chardy, 1974: 1537; Kussakin, 1988: 418.

Diagnosis

See Kavanagh *et al*. (2006).

Key to genera previously classified as *Haplomesus*

1. Uropod with one article 2
   Uropod with two articles . . . . . *Contrarimesus*, gen. nov.
2. Pleotelson axial ridge strongly vaulted, separated from lateral fields by distinct indented lines . . . . *Haplomesus sensu stricto*
   Pleotelson axial ridge weakly vaulted, separated from lateral fields only by shallow elongate concavities. . 2
3. Pleotelson posterolateral margin anterior to uropods without posterolateral spines or tubercles. . . . . *Fortimesus*, gen. nov.
   Pleotelson posterolateral margin anterior to uropods with posterolateral spines or tubercles 3
4. Pereonite 4 at least 1.5× as long as wide; head with long, thin anterolateral projections supporting antennae . . . . *Cornuamesus*, gen. nov.
   Pereonite 4 as long as wide, head without anterolateral projections supporting antennae . . . . *Gracilimesus*, gen. nov.

Genus ***Haplomesus*** Richardson

Haplomesus Richardson, 1908: 81. – Hansen, 1916: 59; Gurjanova, 1932: 42; Birstein, 1960: 6; 1963: 59; 1971: 209; Menzies, 1962: 117; Wolff, 1962: 86: Menzies & George, 1972: 973; Kussakin, 1988: 445; Kavanagh et al. 2006: 5–7.

Not *Haplomesus*; Merrin & Poore, 2003: 286.

Type species: *Ischnosoma quadrispinosus* Sars, 1879.

Species included: *H. bifurcatus* Menzies, 1962; *H. ornatus* Menzies, 1962; *H. quadrispinosus* (Sars, 1879); *H.* cf. *quadrispinosus sensu* Brandt, 1992.

Diagnosis

Pleotelson dorsal surface axial ridge strongly vaulted, separated from lateral fields by distinct indented line; without posterolateral spines; indented into margin at uropod insertion. Antennula with 5–6 articles, distal flagellar articles much longer than wide. Pereopods with distinct neck between the pereopodal articulation of the basis and coxa, and the shaft of the basis, with the basis neck and shaft forming an approximate

Table 2. Apomorphies for the genera of the *Haplomesus*-group

Genus	Apomorphy	Character state text	Exceptions
Haplomesus sensu stricto	24: 3	Pleotelson axial ridge strongly vaulted, separated from lateral margins by distinct indented lines	*H. quadrispinosus* (Sars) (no males described)
	74: 2	Pleopod II male stylet extending to distal margin of endopod	
Contrarimesus	5: 2	Segmental articulation present, rudimentary, non-functional	
	59: 4	Pleopod II operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex	
Cornuamesus	7: 4	Head with long, thin anterolateral projections supporting antennae	
	29: 2	Pleotelson posterolateral margin with spines or tubercles	
	47: 1	Maxilliped epipod with spines	
Fortimesus	38: 2	Antennula article 2 with lateral row of robust setae	*F. robustus*, *F. zuluensis* and *F. concinnus*
	53: 2	Pereopod I carpus with two elongate robust setae	*F. concinnus*
	55: 1	Pereopod I carpus ventral margin with several distally placedrobust setae on palm	
Gracilimesus	29: 2	Pleotelson posterolateral margin with spines or tubercles	
	46: 1	Antennula article 2 with up to two elongate stiff ventromedial setae	
	56: 3	Pereopod I propodus ventral margin with one robust seta	*G. insignis*
	59: 4	Pleopod II operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex	
	76: 2	Uropods in male extending near posterior margin of pleotelson	*G. insignis*

right angle. Pereopod I carpus ventral margin without palm or distinctly expanded part. Pleopod I distal tip with lateral horns. Pleopod II female operculum with narrow proximal neck, almost circular posteriorly. Uropods short, single segmented, distally tapering.

Distribution

The genus *Haplomesus* is found throughout the Atlantic Ocean and species have also been recorded from the Antarctic Ocean. However, species themselves appear to have limited distributions, and are confined to small regions.

Remarks

Species within the genus *Haplomesus* have a distinctive round pleotelson, lack posterolateral spines and have a heavily indented pleotelson dorsal surface. Variation is observed in the shape of the pleotelson axial ridge (Fig. 2): the ridge may run the full length of the pleotelson, as observed in *H. bifurcatus*, or it may be truncated at approximately two-thirds the length of the pleotelson, as observed in *H. ornatus*. The distal end of the pleotelson may be medially smooth as in *H. quadrispinosus*, it may be bilobed, forming medial carinae as observed in *H. ornatus*, or it may be medially incised with narrow invagination as observed in *H. bifurcatus*. The robust body, the cuticle of which is densely covered with sharp spines, also distinguishes these species from others in the family.

Key to species of *Haplomesus sensu stricto*

1. Pleotelson axial ridge not bilobed, rounded posteriorly; antenna article 3 with distomedial spines . . . . *Haplomesus quadrispinosus* (Sars)
   Pleotelson axial ridge bilobed or indented posteriorly; without distomedial spines on antenna article 3 2
2. Pleotelson axial ridge not truncated, indented medially; spines on pereonite 3 arising anterodorsally . . . . *H. bifurcatus* Menzies, 1962
   Pleotelson axial ridge truncated; spines on pereonite 3 arising anterolaterally 3
3. Pleotelson axial ridge medially bilobed, forming dorsal medial carinae . . . . *H. ornatus* Menzies, 1962
   Pleotelson axial ridge indented with shallow, narrow invagination. . . . . *H.* cf. *quadrispinosus sensu* Brandt, 1992

Haplomesus quadrispinosus (Sars)

(Fig. 4)

Ischnosoma quadrispinosum G. O. Sars, 1879: 432. – 1886: 126, pl. II, figs 26–29.

Haplomesus quadrispinosus; Richardson, 1908: 81; Birstein, 1960: 15; Menzies, 1962: 119, fig. 20*F–H*; Wolff, 1962: 86, 216, 221, 262, 290, fig. 143; Gurjanova, 1964: 258; Birstein, 1963: 62.

Not *Haplomesus quadrispinosus*; Hansen, 1916: 59–61, pl. V, fig. 1A–P; Brandt, 1992: 184, fig. 1–4; Svavarsson, 1984: 29–30, figs 3–4.

Material examined

Holotype. Adult ♀, by monotypy (examined). Norway: Norwegian Sea. ZMO F1701

Remarks on type material

Although Sars did not designate a type, he stated that he collected only one specimen upon which his description and illustrations are based. Brandt (1992: 184) reported that specimen ZMO F1701 is broken, separating the head and anterior pereonites from the posterior segment. The posterior segment unfortunately was not in the vial, and must be considered lost. The remaining anterior segment has been further damaged. The antennula, antennae, and pereopods, which Sars illustrated, have been broken off. The holotype is a preparatory female with developing oostegites on pereonites 1–4. Hansen (1916: 61) stated that Sars drew the posterior half of the specimen distinctly broader than it was in his specimen.

Diagnosis

Antennula with six articles; antenna article 3 with distinct group of distomedial spines; pereonite 4 wider than long in female; pleotelson dorsal surface axial ridge not truncated, length of pleotelson, medially smooth; uropods extending near posterior margin of pleotelson.

Description of female (male unknown)

Body length 4.2 mm; granular. Head length 0.69 width; lobe on ventrolateral margin absent in lateral view; dorsal cuticle covered in spiky granulations. Pereonite 1 width 0.19 total body length, with one pair of anterolateral simple spines, short, length near pereonite 1 length. Pereonite 3 with one pair of anterolateral simple spines, tiny, length distinctly less than length of pereonite 1. Pereonite 4 length 0.7 width. Pereonite 5 length 2.33 width; 0.33 total body length. Pleotelson length 1.29 width.

Antennula and antenna

Antennula article 2 length in female 0.82 head width, with four elongate, stiff, ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna article 3 length 0.27 anterior body length, 5 width; with distomedial group of 3–4 spines with rounded tips.

Mouthparts

Maxilliped palp article 3 wider than article 2.

Pereopods

Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus one shorter robust seta proximal to elongate seta, with one robust seta on palm distal to elongate seta. Pereopod I propodus ventral margin with four robust setae, increasing in length distally.

Uropods

Length 1.3 basal width, 0.08 length of pleotelson.

Distribution

North-west Pacific, 4000–4150 m (Birstein 1960, 1963; Gurjanova 1933, 1964); Davis Strait, Norwegian Sea (Sars 1879); Arctic Ocean, 510 and 698 m (Gorbunov 1946).

Remarks

From examining specimens labelled as '*Haplomesus quadrispinosus*' in Hansen's collections (ZMUC), differences between the species illustrated by Sars and those collected by Hansen indicate that they are a different species, albeit closely related. Hansen's specimens have truncated, bilobed pleotelsons as observed in *H. ornatus* and *H. bifurcatus*. Brandt (1992) and Svavarsson (1984) also recorded *H. quadrispinosus* specimens with bilobed pleotelsons. Neither Hansen or Svavarsson, however, examined the holotype directly. Thus, whether they are the same species or not cannot be confirmed, so we exclude these specimens from this analysis.

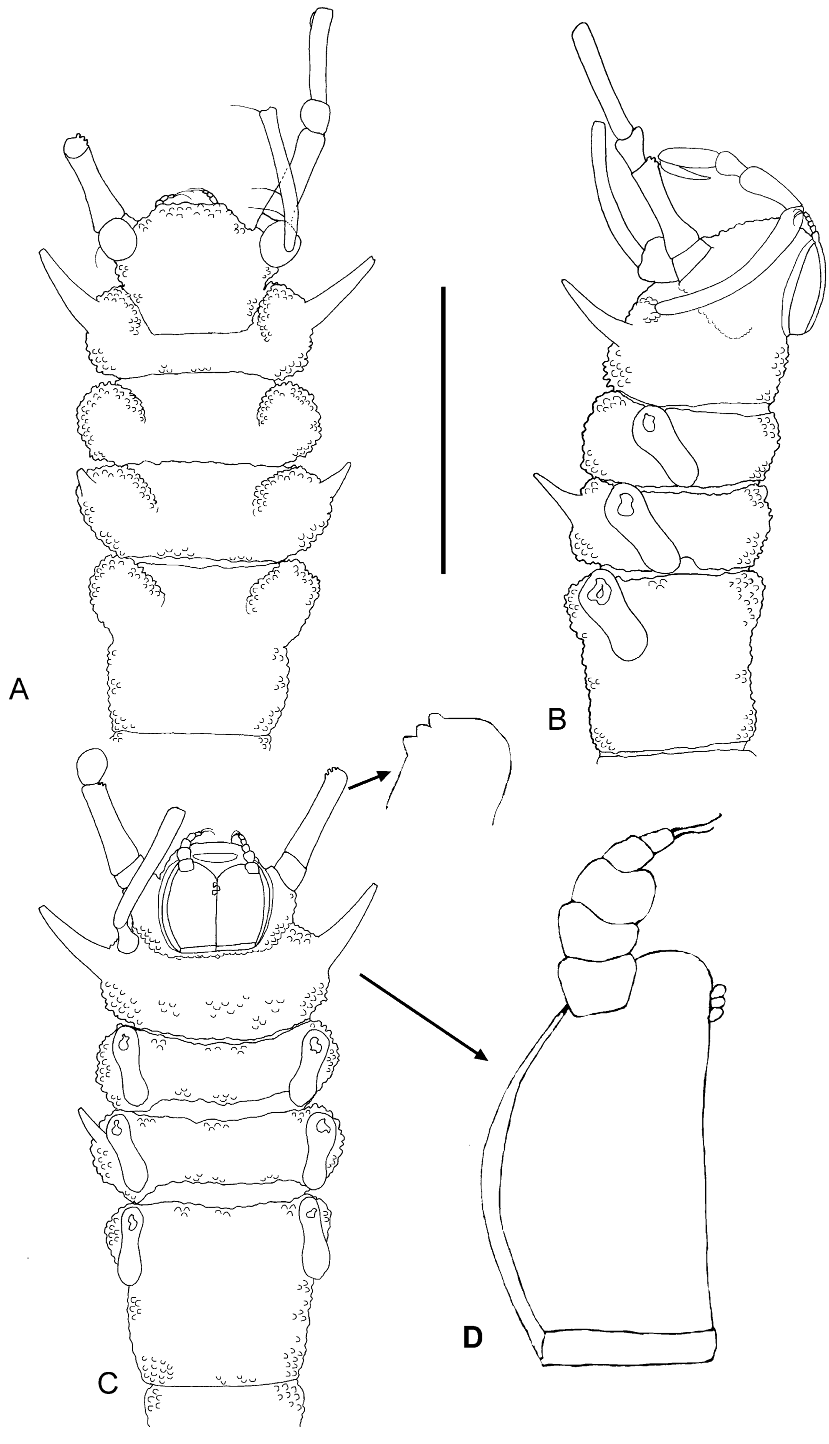

Fig. 4. *Haplomesus quadrispinosus* (holotype female ZMO F1701). *A*, Body dorsal view; *B*, body ventral view; *C*, body lateral view. Scale bar = 0.5 mm.

The species described by Brandt (1992) as *Haplomesus quadrispinosus* is excluded from this taxon. *Haplomesus quadrispinosus* Sars is distinct from *H*. cf. *quadrispinosus sensu* Brandt, 1992 by having a pleotelson dorsal surface axial ridge that runs the length of the pleotelson, and that is smooth distally (i.e. not incised). In addition, the spines on pereonite 1 of *H. quadrispinosus* Sars are shorter (1.1 versus 1.6× length of head and pereonite 1 in male) and possess a rounded tip. It also differs from *H*. cf. *quadrispinosus sensu* Brandt and other closely related species, *H. ornatus* and *H. bifurcatus*, by the presence of distomedial spines on article 3 of the antennae (Fig. 4*C*). (See remarks under *H. ornatus* and *H. bifurcatus* for further discussion.)

Haplomesus bifurcatus Menzies

(Fig. 5)

Haplomesus bifurcatus Menzies, 1962: 121, fig. 21*C–I*.

Material examined

Holotype. ♂ (examined), Argentina: South Atlantic L.G.O. Biotrawl no. 12, *Vema*-12–1, 6 April 1957, 38°58.5′S, 41°45′W, 5024 m, northern part of Argentine rise south-east of Rio Grande, AMNH 12010.

Remarks on type material

The holotype is in good condition, with antennae flagella tips missing and only three pereopods intact. The spines on pereonite 3 are more dorsally located (Fig. 5*A*) than originally illustrated (Menzies 1962: 121, Fig. 21H).

Diagnosis

Pleotelson axial ridge not truncated, length of pleotelson, medially with narrow invagination; spines on pereonite 3 arising dorsally; pereonite 4 as long as wide in male, female unknown; antennula with six articles; antenna article 3 without distinct group of distomedial spines; uropods minute; pleopod I male with dorsal and distal setae; pleopod II protopod narrow, tapering.

Description of male (female unknown)

Body length 5 mm, cuticle granular. Head length 0.82 width; lobe on ventrolateral margin absent in lateral view; cuticle granulated. Pereonite 1 width 0.16 total body length. Pereonites 1 and 3 with one pair of anterolateral simple spines, elongate, length near width of pereonite 1, spines on pereonite 1 somewhat longer. Pereonite 4 in male length equals width. Pereonite 5 length 2.28 width; 0.35 total body length. Pleotelson length 1.04 width.

Antennula and antenna

Antennula article 1 without setae; article 2 length 0.73 head width, with 3 elongate stiff ventromedial setae; article 3 elongate and tubular, much longer than wide. Antenna article 3 length 0.16 anterior body length, 3.1 width, cuticle smooth; article 5 length 0.3 anterior body length; article 6 length 0.36 anterior body length.

Mouthparts

Maxilliped palp article 3 wider than article 2.

Pereopods

Pereopod I carpus with one shorter robust seta proximal to elongate seta, with one robust seta on palm distal to elongate seta. Pereopod I propodus ventral margin with two robust setae, in centre of margin. Pereopods II–VII bases granulate.

Pleopods and uropods

Pleopod II stylet extending to distal margin of protopod. Uropods not extending near posterior margin of pleotelson. Uropods length 0.65 basal width, 0.03 length of pleotelson.

Distribution

South Atlantic, known only from type locality.

Remarks

This species can be distinguished from other species in the genus by the spines on pereonite 3, which are much more dorsally located than in any other species. It can be further distinguished from *H. quadrispinosus* Sars by the lack of distomedial spines on the third article of the antenna and by the narrow medial incision of the pleotelson dorsal surface axial ridge. *H. bifurcatus* can also be distinguished from *H. ornatus* and *H*. cf. *quadrispinosus sensu* Brandt by the pleotelson dorsal surface axial ridge, which runs the length of the pleotelson in *H. bifurcatus*, and is truncated in *H. ornatus* and *H*. cf. *quadrispinosus sensu* Brandt.

Haplomesus ornatus Menzies

(Figs 6–7)

Haplomesus ornatus Menzies, 1962: 121, fig. 21*A–B*.

Material examined

Holotype. ♂, (examined), South Atlantic: L.G.O. Biotrawl no. 18, *Vema*-12–6, 7 May 1957, 23°00′S, 08°11′E, 4047 m, crest of Walvis Ridge Front Range west of Walvis Bay, South-West Africa, AMNH 12023.

Paratypes. ♂, (examined), **South Atlantic**: same data as for holotype. ♂, (examined), **South Atlantic**: L.G.O. Biotrawl no. 52, *Vema*-14–29, 30 March 1958, 41°03′S, 07°49′E, 4960 m; and paratype male AMNH 12179 L.G.O. Biotrawl no. 214, *Vema*-15–130, 2 April 1959, 42°00′S, 45°01.5′W, 5293 m, AMNH 12024

Remarks on type material

Menzies (1962: 121) stated that only two specimens are known from the type locality: one male that he designated 'holotype' and one fragment. Vial (AMNH 12023) has a male and a fragment from the type locality labelled as 'non-type' on the outside label, 'paratypes' on the inside label, and finally a hand-written note that refers to the material as 'types'. From original illustrations and the details of the type locality, these specimens are the holotype and the fragment that Menzies mentioned. By implication of the handwritten note, the fragment could be considered a paratype. A second vial (AMNH 12024) contains a male specimen of *H. ornatus* labelled 'paratype' from a second locality, which Menzies mentions but doesn't designate as a paratype. An undated note in the vial by M. Jones states that it was made a 'temporary holotype'. This note may have arisen from the confusion with the type material as discussed above and should be disregarded. A third vial (AMNH 12179) contains two fragments labelled 'paratypes', from a third locality that Menzies listed but

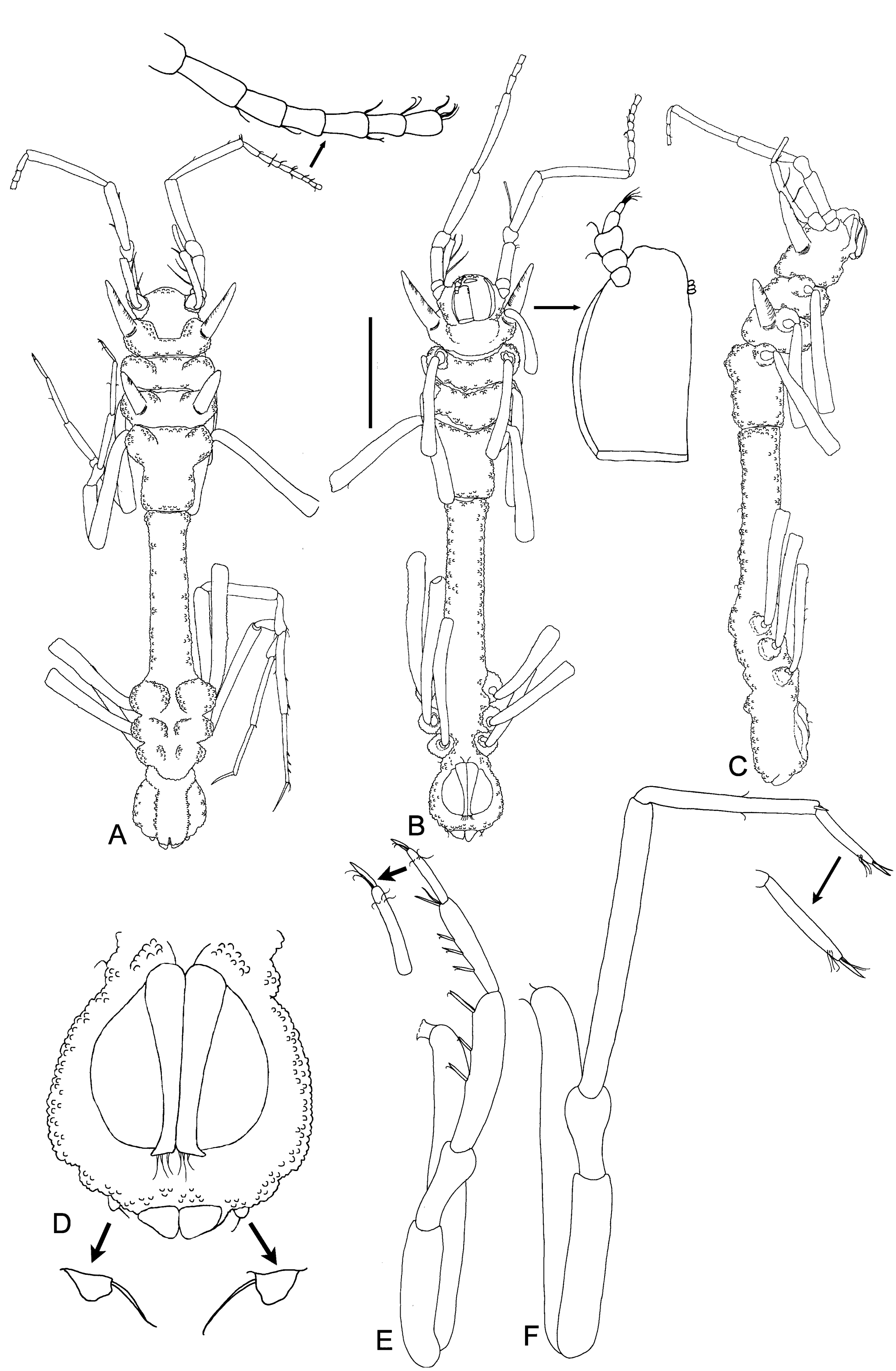

Fig. 5. *Haplomesus bifurcatus* (holotype male, AMNH 12010). *A*, Body dorsal view; *B*, body ventral view; *C*, body lateral view; *D*, pleotelson ventral view; *E*, pereopod IV; *F*, pereopod V. Scale bar = 0.5 mm.

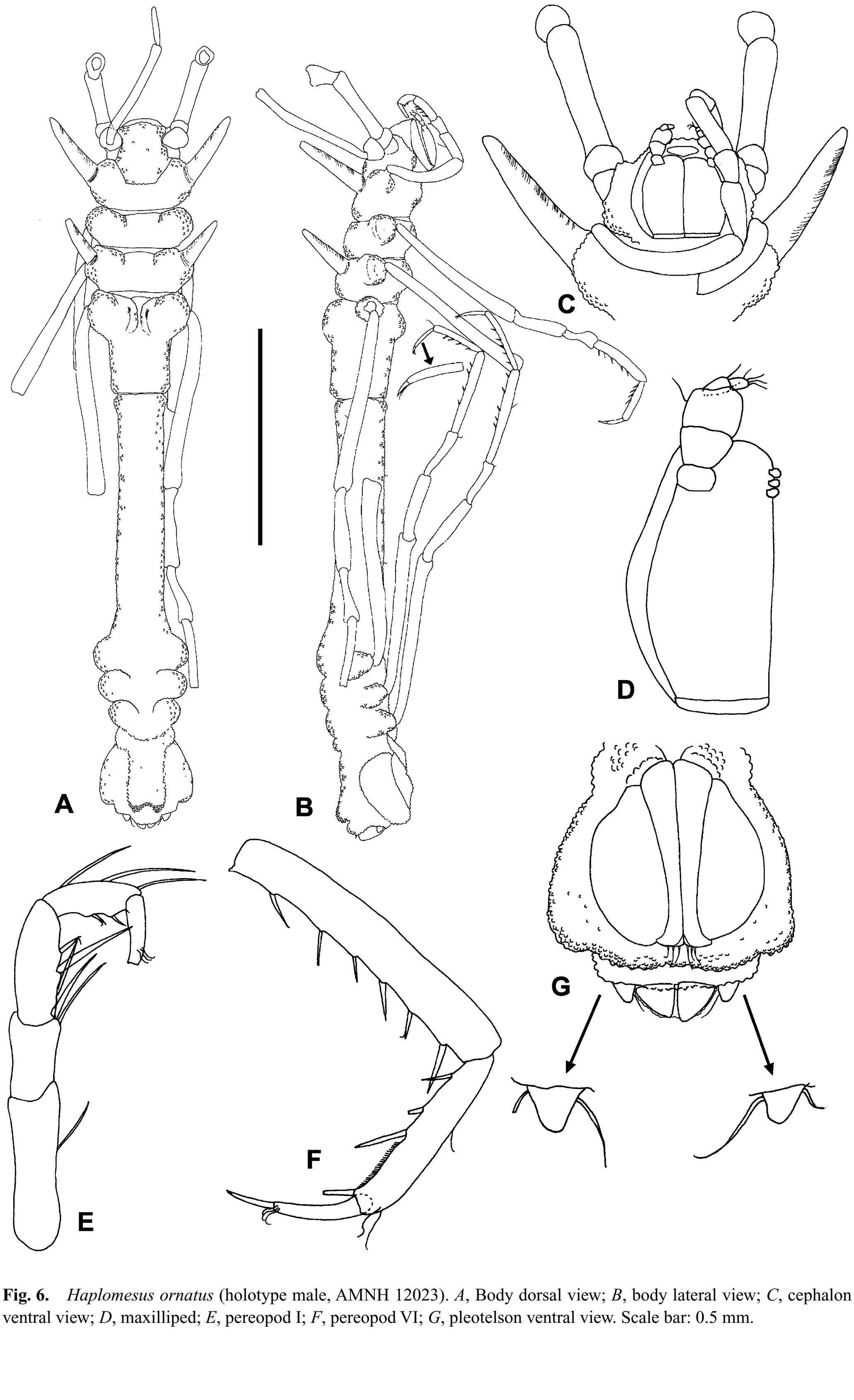

Fig. 6. *Haplomesus ornatus* (holotype male, AMNH 12023). *A*, Body dorsal view; *B*, body lateral view; *C*, cephalon ventral view; *D*, maxilliped; *E*, pereopod I; *F*, pereopod VI; *G*, pleotelson ventral view. Scale bar: 0.5 mm.

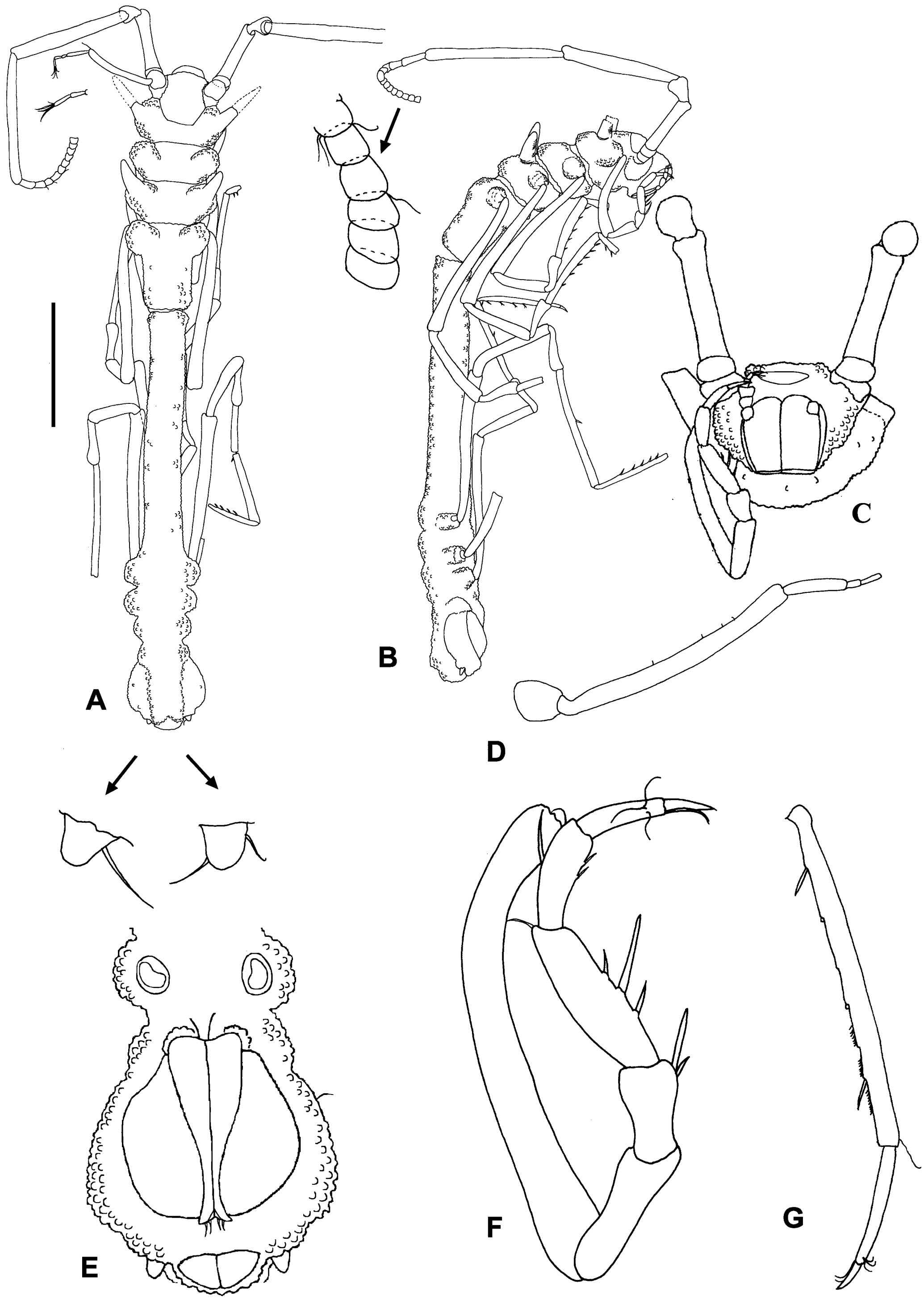

Fig. 7. *Haplomesus ornatus* (paratype male AMNH 12024). *A*, Body dorsal view; *B*, body lateral view; *C*, cephalon ventral view; *D*, antennula; *E*, pleotelson ventral view; *F*, pereopod I; *G*, pereopod VII. Scale bar = 0.5 mm.

again did not designate paratypes. All of this material is in good condition. The spines on pereonite 1 are more anteriorly directed than indicated by Menzies (1962; fig. 21*A*).

Diagnosis

Pleotelson axial ridge truncated, approximately two-thirds length of pleotelson, bilobed distally forming two medial carinae; antenna article 3 without distinct group of distomedial spines; pereopods II–VII propodus with distal row of short robust setae (Fig. 6*E*); pleopod I male with distal setae.

Description of male (female unknown)

Body length 6.8 mm, cuticle granular. Head length equals width; cuticle granulated; lobe on ventrolateral margin absent in lateral view. Pereonite 5 fused with pereonite 6. Pereonite 1 with one pair of anterolateral simple spines, elongate, length near width of pereonite 1, acute and laterally directed. Pereonite 3 with one pair of anterolateral simple spines, short, length near pereonite 1 length, acute. Pereonite 4 length equals width. Pereonite 5 length 2.85 width; 0.14 total body length. Pleotelson length 1.08 width.

Antennula and antenna

Antennula with six articles altogether; article 1 without setae; article 2 length 1.16 head width, with three elongate stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article four, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna article 3 length 0.23 anterior body length, 5.17 width; article 5 length 0.47 anterior body length; article 6 length 0.56 anterior body length.

Mouthparts

Maxilliped palp article 3 wider than article 2.

Pereopods

Pereopod I strongly carposubchelate, differs from pereopod II. Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus ventral margin without palm or distinctly wider part, with one shorter robust seta proximal to elongate seta, with one robust seta on palm distal to elongate seta. Pereopod I propodus ventral margin with two robust setae.

Pleopods and uropods

Uropods not extending near posterior margin of pleotelson, length 0.8 basal width, 0.03 length of pleotelson.

Distribution

South Atlantic.

Remarks

Haplomesus ornatus is closely related to *H. bifurcatus*, *H. quadrispinosus* Sars and *H.* cf. *quadrispinosus sensu* Brandt (see remarks above under *H. bifurcatus*). It is easily distinguished, however, from the first two species above by the truncated axial ridge on the dorsal surface of the pleotelson. *Haplomesus ornatus* can be further distinguished from *H. quadrispinosus* Sars by lack of distomedial spines on antenna article 3 and orientation of the spines on pereonite 3. The spines on pereonite 3 of *H. ornatus* are anteriorly directed whereas in *H. quadrispinosus* Sars, they are directed laterally. Both the pleotelson of *H. ornatus* and *H.* cf. *quadrispinosus sensu* Brandt are truncated and medially incised. The incision on the axial ridge of *H. ornatus*, however, has a short, wide margin that divides the axial ridge into two medial carinae whereas the incision on the axial ridge of *H.* cf. *quadrispinosus sensu* Brandt is a long, narrow invagination. The axial ridge is also somewhat longer in *H.* cf. *quadrispinosus sensu* Brandt. The spines on pereonite 1 of *H. ornatus* are short (0.8× length of head and pereonite 1), rounded at the tip and more laterally directed than those observed in *H.* cf. *quadrispinosus sensu* Brandt, which, as well as being more anteriorly directed, are also acutely pointed at the tip and much longer (1.6× length of head and pereonite 1).

Haplomesus cf. ***quadrispinosus*** *sensu* Brandt

Haplomesus quadrispinosus (Sars): Brandt, 1992: 184, fig. 1–4.

Material examined

One adult ♂, **Antarctica:** East of the Gunnerus ridge, Antarctica, station 1821–5, 67°03.9′S, 37°28.7′E, 4028 m.

Diagnosis

Pleotelson axial ridge truncated, approximately two-thirds length of pleotelson, distally with narrow invagination; pereopods II–VII with numerous simple setae; pleopod I male with simple dorsal and distal setae.

Description of male (female unknown)

Body length 6.5 mm, cuticle granular. Head length 0.44 width; lobe on ventrolateral margin absent in lateral view. Pereonite 1 width 0.15 total body length, with one pair of anterolateral simple spines, extremely elongate, length distinctly greater than width of pereonites. Pereonite 3 with one pair of anterolateral simple spines, short, length near pereonite 1 length. Pereonite 4 in male length equals width. Pereonite 5 length 3.28 width; 0.43 total body length. Pleotelson length 1.11 width.

Antennula and antenna

Antennula with six articles altogether; article 1 with no robust setae, with one penicillate seta; article 2 length equals head width, with three elongate, stiff, ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna length 2.35 anterior body length; article 3 length 0.29 anterior body length, length 5.83 width; article 5 length 0.47 anterior body length; article 6 length 0.62 anterior body length; flagellum length 0.31 total antennal length, flagella with 18–21 articles.

Mouthparts

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

Pereopods

Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus with one shorter robust seta proximal to elongate seta, with one robust seta on palm distal to elongate seta. Pereopod I propodus ventral margin with one robust seta, in median position. Pereopod VII present, shorter than pereopod VI in adults.

Pleopods and uropods

Pleopod II protopod apex rounded, stylet extending to distal margin of protopod. Pleopod III exopod with plumose setae, with fringe of fine setae. Uropods not extending near posterior margin of pleotelson, length 1.25 basal width, length 0.08 length of pleotelson.

Distribution

Southern Ocean, east of Gunnerus Ridge, Antarctica, 4028 m.

Remarks

This species, described by Brandt (1992) as *Haplomesus quadrispinosus* Sars, is not that species. The type of *Haplomesus quadrispinosus* lacks the distinctive indentation in the axial ridge of the pleotelson seen in this species. This feature is also shared with the South Atlantic species *H. ornatus* and *H. bifurcatus* that were described by Menzies (1962). In both *H. ornatus* and *H*. cf. *quadrispinosus sensu* Brandt, 1992, however, the pleotelson dorsal surface axial ridge is truncated, whereas in *H. bifurcatus*, the axial ridge runs the length of the pleotelson. The shape of the incision is also quite different in *H. ornatus* and *H. bifurcatus* (see discussions above). *Haplomesus* cf. *quadrispinosus sensu* Brandt also lacks the distinct distomedial spines observed on article 3 of the antennae of the holotype of *H. quadrispinosus* Sars. Because no specimens are available and the original specimen from the redescription was dissected completely, we cannot provide a new name for this species owing to the absence of usable type material.

Genus ***Cornuamesus***, gen. nov.

Type species: *Haplomesus longiramus* Kavanagh & Sorbe, 2006.
Species included: *Haplomesus biscayensis* Chardy, 1975, comb. nov.; *H. longiramus* Kavanagh & Sorbe, 2006, comb. nov.

Diagnosis

Pereonites 5–7, pleonite 1 and pleotelson lacking intersomite articulations. Pereonites 5–7 narrowing posteriorly. Pereonite 4 elongate, produced posteriorly, at least 1.5× as long as wide. Cephalon with long thin anterolateral projections supporting antennae, projection width distinctly less than length. Pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields only by shallow elongate concavities, with distinct posterolateral spines. Antennula article 2 inserting on article 1 dorsally, straight, not curved at insertion. Pereopod I carpus ventral margin without palm or distinctly wider part. Pleopod II stylet distal tip rounded. Uropods uniramous, single segmented, distally tapering.

Distribution

Both of the species listed above were collected in the Bay of Biscay. Several undescribed species of this genus, however, have been collected throughout the Atlantic (see Kavanagh and Sorbe 2006).

Remarks

The genus *Cornuamesus*, gen. nov. is distinct within the Ischnomesidae owing to the anterolateral thin projections that support the antennae, and the elongate pereonite 4. In most species of Ischnomesidae, pereonite 4 is approximately as long as wide. Some species of the nonmonophyletic genus *Ischnomesus* (e.g, *Ischnomesus tasmanensis* Merrin & Poore, 2003) also have elongate pereonites 4, although their relationships are currently unknown. Several additional undescribed species of this genus have been encountered in deep-sea isopod collections.

Etymology

The genus name comes from the Latin '*cornu*' meaning horns or antlers, referring to the anterolateral projections supporting the antennae.

Key to species of *Cornuamesus*, gen. nov.

Pereonite 5 of male with one pair of dorsolateral spines, uropods extremely elongate, at least 6× as long as wide in both sexes . . . . *Cornuamesus longiramus* (Kavanagh & Sorbe)
Pereonite 5 of male without dorsolateral spines, uropods of male ~4× as long as wide, distal margin of male pleotelson linear . . . . *Cornuamesus biscayensis* (Chardy)

Cornuamesus biscayensis (Chardy), comb. nov.

Haplomesus biscayenis Chardy, 1975: 692–696, figs 3–4.

Material examined

Holotype. Adult ♂ by original designation (illustration examined), France: Bay of Biscay, Biogas station 6 DS 52, 44°05′N, 4°61′W, 1877 m, type material lost.

Remarks on type material

Chardy stated that the holotype is deposited in the Museum Natural d'Histoire National, Paris. This Museum, however, had no record of this species, so the whereabouts of the holotype remains uncertain. According to Chardy (1975: 692) the holotype was an adult male with both antennae broken off. Only pereopod I was illustrated. Chardy also ascribed to this species two undocumented female specimens from a second station near the type locality.

Diagnosis

Pereonite 4 much longer than wide in male, length 1.9 width; antennula article 2 without long ventromedial setae; pereopod I carpus with two elongate robust setae; maxilliped epipod with spines; maxilla with one medial pectinate seta; pleopod I male lateral margins indented, with distal setae; uropods subequal in length to posterolateral spines; posterior margin of pleotelson linear.

Description of male (female unknown)

Body length 4.3 mm, cuticle granular. Head length 0.59 width. Pereonite 1 width 0.15 total body length. Pereonite 1 with one pair of anterolateral simple spines, acute and elongate. Pereonite 2 with one pair of anterolateral simple spines, tiny. Pereonite 3 with one pair of anterolateral simple spines, short. Pereonite 4 in male length 1.9 width, with one pair of anterolateral simple spines, tiny. Pereonite 5 length 3 width; 0.34 total body length. Pleotelson length 1.34 width; posterolateral margin anterior to uropods with simple spines, triangular in shape, extending past pleotelson and uropods; posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula with six articles altogether; article 2 length 0.8 head width, without long ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna article 3 length 0.23 anterior body length, 4.7 width.

Mouthparts

Maxillula with 11 robust setae on lateral lobe; medial lobe with one robust medially-projecting dentate seta. Maxilla with one long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe. Maxilliped palp article 2 wider than 3; epipod spines present.

Pereopods

Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus with no robust setae proximal to elongate seta, with four robust setae on palm distal to elongate seta. Pereopod I propodus ventral margin with two robust setae and one elongate simple seta, all setae placed distally.

Pleopods and uropods

Pleopod I distal tip with lateral horns. Pleopod II protopod apex rounded, stylet extending beyond distal margin of protopod, thick and blunt. Uropods extending beyond end of pleotelson. Uropods length 4 basal width, 0.15 length of pleotelson.

Distribution

Bay of Biscay, type locality and station 6 DS 51, 44°44′N, 4°17′W, 2039 m.

Remarks

Both *Cornuamesus biscayensis*, comb. nov. and *C. longiramus*, comb. nov. possess thin, elongate, anterolateral projections that support the antennae (Fig. 1*B*), an elongate pereonite 4 and spines on the epipod of the maxilliped. Males of both species have pleopod II with an elongate stylet with a rounded tip. In the remainder of genera in the family, the stylet tends to be shorter than the posterior border of the pleopod II endopod, and the tip is tapering and pointed. Several differences between the two species, however, make them distinguishable. The males of *C. longiramus*, comb. nov. possess laterally directed spines on pereonite 5, and both males and females possess elongate uropods, much longer than the pleotelson posterolateral spines (Fig. 2*C*). The uropods of *C. biscayensis*, comb. nov. are approximately equal in length to the pleotelson posterolateral spines, and the males do not possess spines on pereonite 5. The female of *C. biscayensis*, comb. nov. is unknown. The maxilliped palp of *C. longiramus*, comb. nov. possesses unique pedestal spines, not observed elsewhere in the genus.

Genus ***Fortimesus***, gen.nov.

Type species: *Haplomesus thomsoni* Beddard, 1886. This species is designated as type here because it was the only type specimens available to be examined directly.

Species included: *H. concinnus* Birstein, 1960; *H. consanguineus* Mezhov, 1980; *H. cornutus* Birstein, 1971; *H. formosus* Mezhov, 1981; *H. gigas* Birstein, 1960; *H. profundicolus* Birstein, 1971; *H. robustus* Birstein, 1960; *H. scabriusculus* Birstein, 1960; *H. thomsoni* Beddard, 1886; *H. zuluensis* Kensley, 1984.

Diagnosis

Body surface tuberculate, with numerous lateral and dorsal tubercles. Pereonites 5–7, pleonite 1 and pleotelson lacking intersomite articulations; narrowing posteriorly. Pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields only by shallow elongate concavities. Pleotelson dorsal surface axial ridge medially smoothly arched; pleotelson without posterolateral spines. Antennula with 5–6 articles, distal flagellar articles much longer than wide. Uropods one-articled, distally tapering.

Distribution

With the exception of *Fortimesus zuluensis*, species of this genus were reported from the north Pacific, and most have only been recorded from the type localities. This probably reflects low sampling effort in the Pacific compared with the Atlantic, and in recent years, in the Southern Ocean where most asellotan collecting activities has been concentrated.

Remarks

Species of *Fortimesus*, gen. nov. lack posterolateral spines on the pleotelson, distinguishing them from species of *Gracilimesus*, gen. nov. and *Cornuamesus*, gen. nov. Species may be similar to those in *Haplomesus sensu stricto*, but differ in several respects. The pleotelson dorsal surface axial ridge of *Fortimesus*, gen. nov. species is separated from the lateral fields only by shallow elongate concavities whereas in species of *Haplomesus sensu stricto* it is separated by distinct indented lines. The female operculum of *Haplomesus sensu stricto* is rounded posteriorly, whereas in *Fortimesus* species, it is weakly convex posteriorly, or, in the case of *F. brevispinis*, comb. nov. broadly triangular. The number and size of lateral spines of species of *Fortimesus*, gen. nov. varies considerably, with species displaying many tubercles and spines on both lateral and dorsal surfaces. They may also possess a pair of distal spines on the pleotelson (see also some species of *Heteromesus*). Species of *Haplomesus sensu stricto* always possess one pair of anterolateral spines on pereonite 1 and an additional pair on pereonites 3. They do not possess any tubercles or spines elsewhere on the body as observed in *Fortimesus*, gen. nov.

Etymology

The genus name comes from the latin word '*fortis*' meaning robust or strong, referring to the robust body form of the species in the genus.

Key to the species of *Fortimesus*, gen. nov.

1. Pleotelson terminal margin with no spines or tubercles 2
   Pleotelson terminal margin with simple spines 4
2. Body pereonite 7 length not reduced, similar to pereonite 6; maxillula medial lobe with one robust medially-projecting dentate seta; pereopod I merus dorsal margin with distinctly robust setae; maxilliped palp article 3 wider than article 2 3
   Body pereonite 7 length reduced, less than pereonite 6; maxillula medial lobe with two robust medially-projecting dentate seta; pereopod I merus dorsal margin without distinctly robust setae; maxilliped palp articles 2 and 3 width subequal . . . . *F. zuluensis* Kensley
3. Pleotelson with no lateral spines or tubercles; pereonite 5 with no spines or tubercles; antennula article 2 length greater than 3.0 article 1 length; antennula article 2 lateral margin with row of robust setae. . . . . *F. consanguineus* (Mezhov)
   Pleotelson with simple lateral spines; pereonite 5 with anterodorsal tubercles; antennula article 2 length ~2.0 article 1 length; antennula article 2 lateral margin without row of robust setae . . . . *F. robustus* (Birstein)
4. Pereonite six with no lateral spines or tubercles 5
   Pereonite six with pedestal spines . . . . *F. concinnus* (Birstein)
   Pereonite six with simple spines . . . *F. formosus* (Mezhov)
   Pereonite six with tubercles . . . . . *F. thomsoni* (Beddard)
5. Body pereonite 7 length not reduced, similar to pereonite 6. 6
   Body pereonite 7 length reduced, less than pereonite 6 . . 7
6. Pereonite 4 in female with no anterolateral spines; pereonite 1 in female with no paired dorsal spines or tubercles; pereonite 1 in female with no anterolateral spines; pereonite 1 in female with no lateral spines or tubercles . . . . *F. scabriusculus* (Birstein)
   Pereonite 4 in female with 1 pair of anterolateral simple spines; pereonite 1 in female with dorsal spines; pereonite 1 in female with one pair of anterolateral simple spines; pereonite 1 in female with lateral . . . . spines . . . . *F. brevispinis* (Birstein)
7. Pleotelson with no lateral spines or tubercles . . . . *F. gigas* (Birstein)
   Pleotelson with simple lateral spines. . . . . *F. profundicolus* (Birstein)
   Pleotelson with lateral tubercles . . *F. cornutus* (Birstein)

Fortimesus thomsoni (Beddard), comb. nov.

(Fig. 8)

Ischnosoma thomsoni Beddard, 1886: 168–172, fig. 1.
Heteromesus thomsoni Richardson, 1908: 81. – Menzies, 1962: 122.
Haplomesus thomsoni Birstein, 1960: 6. – Wolff, 1962: 86, 87, 265, fig. 39; 1971: 209, 210; Kussakin, 1988: 467–468, fig. 383; Merrin & Poore, 2002: 82–84; ICZN, 2004: 82–84.
Not *Haplomesus thomsoni*; Birstein, 1963*b*: 60, fig. 27.

Material examined

Holotype. Adult ♂ by monotypy. North-west Pacific: station 246, 36°10′N, 178°0′E, 2050 fathoms (3749 m); bottom temperature, 35.1°F, bottom globigerina ooze, NHM.

Remarks on type material

Although Beddard did not designate a type, he stated that only one specimen was collected and this was used for the description and illustrations. The holotype is damaged and permanently mounted on a slide, dorsal side up. The thickness of the slide and mounting material prevented a detailed examination of the ventral surface. The specimen differed considerably from Beddard's (1886) original illustration. The spination pattern was not as symmetrical as indicated by Beddard, and the pereonite shapes and proportions also differed.

Diagnosis

Pereonites with numerous lateral and dorsal tubercles; pereonite 5 with lateral row of pedestal setae. Pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by distinct lines, without posterolateral spines, with one pair of terminal spines subequal in length to uropods; pleotelson with lateral pedestal spines; pereopods II–VII pereopod bases with dorsal and ventral spines in a random pattern; male pleopod I without distal setae.

Description of male

Body granular, length 6 mm. Head length 1.18 width, cuticle granulated. Pereonite 1 width 0.16 total body length, with two pairs of lateral tubercles. Pereonites 2–3 with three pairs of lateral tubercles. Pereonite 4 length 0.8 width; with one pair of anterolateral simple spines, tiny, length distinctly less than pereonite 1 length, four posterolateral tubercles on the left side, five posterolateral tubercles on the right side. Pereonite 5 length 1.94 width; 0.33 total body length. Pereonite 6 with one pair of lateral spines, plus three pairs of dorsolateral spines. Pereonite 7 with three pairs of dorsolateral tubercles. Pleotelson length 1.45 width; posterolateral margin anterior to uropods with tubercles; posterolateral margin at uropod insertion indented into margin; terminal margin with one pair of distal spines, subequal in length to the uropods.

Mouthparts

Maxillula medial lobe with one robust medially-projecting dentate seta. Maxilla with two long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe.

Pereopods

Basis proximal shoulder with simple spines only. Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus without robust setae proximal to elongate seta, with two robust setae on palm distal to elongate seta. Pereopods II–VII bases granulate.

Pleopods and uropods

Pleopod I distal tip with lateral horns. Uropods not extending near posterior margin of pleotelson, length 2.4 basal width, length 0.11 length of pleotelson.

Distribution

North-west Pacific (Beddard 1886; ?Birstein 1971) 3749(–6710?) m.

Remarks

The species concept of *Fortimesus thomsoni*, comb. nov. has been complicated by varying generic placements, including designation as the type of *Heteromesus* Richardson, 1908 by Menzies (1962). This classification designation has been set aside by ICZN (2004) on the application and argument of Merrin and Poore (2002). Birstein (1963) recorded two males of *F. thomsoni* from the north-west Pacific at a depth of 3860 m. Birstein's illustrations reveal differences between the two specimens: the head is 2.5× as wide as long, much broader than Beddard's specimen, which is 1.3× as wide as long. Pereonites 1–4 were illustrated as narrowing posteriorly in Birstein's specimens, whereas in Beddard's specimen pereonites 1–4 were equal in width. A different spination pattern was seen in Birstein's illustration of pereonites 1–4, which had a dorsal tuberculation pattern that was not present on Beddard's specimen. Birstein explained these differences as inaccuracies in Beddard's descriptions and illustrations. Although Beddard's descriptions are inaccurate, Birstein's illustrations still do not match the type specimen, so we do not consider them to be the same species. Birstein (1971) recorded *F. thomsoni* specimens from 43°59′N, 149°39′E, 6435–6710 m. Birstein, however, did not describe these specimens so we cannot be sure if these specimens are, in fact, *F. thomsoni* or if they resemble the specimens collected by Birstein in 1963.

Fortimesus concinnus (Birstein), comb. nov.

Haplomesus concinnus Birstein, 1971: 211–213, fig. 21.

Material examined

Holotype. Adult ♂ by monotypy (illustration examined), north-west Pacific: 44°17′N, 149°34′E, 4840 m. Location of type material unknown.

Remarks on type material

The holotype has both antennae broken off. Only pereopod I was illustrated.

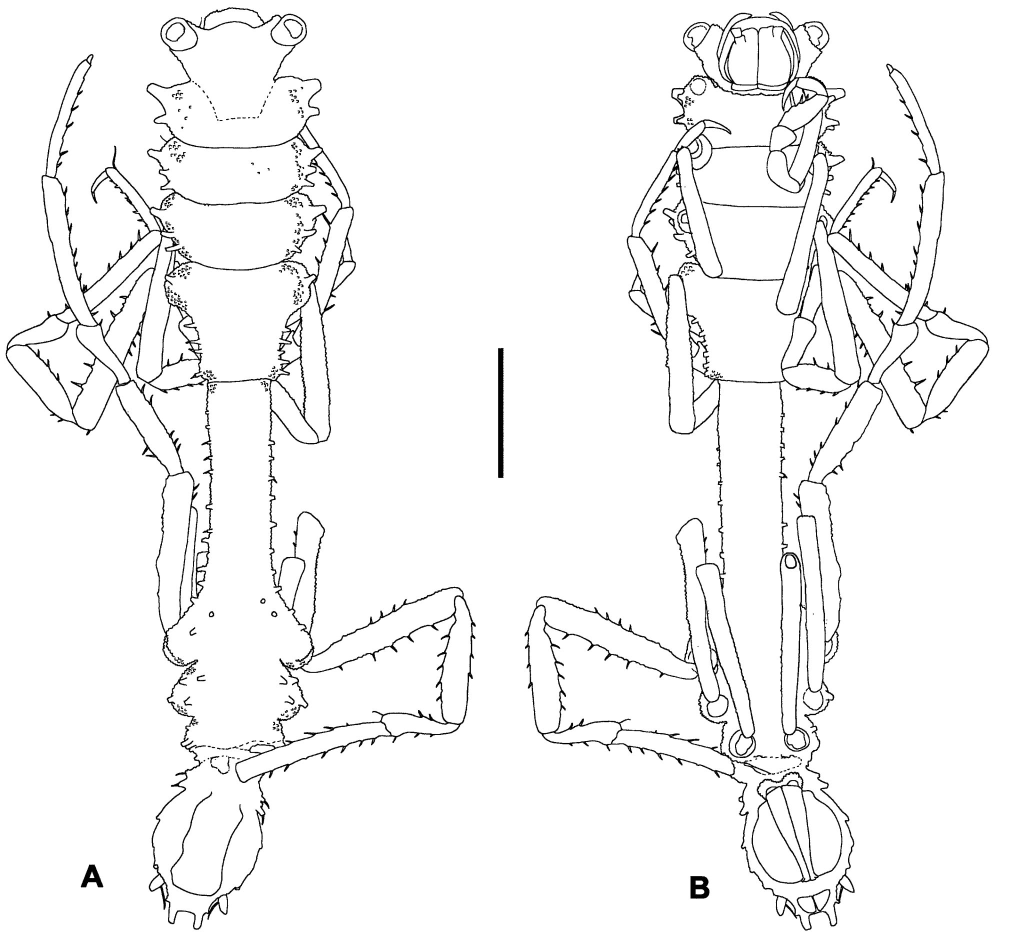

Fig. 8. *Fortimesus thomsoni*, comb. nov. (holotype male NHM). *A*, Body, dorsal view; *B*, body ventral view. Scale bar = 1 mm.

Diagnosis

Pereonites 1, 3 and 4 in male with elongate anterolateral spines; pereonite 2 with tiny anterolateral spines; pereonites 4–7 with dorsal tubercles, pereonite 5 with two rows of dorsal tubercles; pereonites 6 and 7 with one pair of lateral setae; pereonite 6 with one pair of lateral pedestal spines; pleotelson with lateral and terminal spines; pleopod I male with distal setae.

Description of male (female unknown)

Body length 7.7 mm, cuticle granular. Head length 1.25 width. Pereonite 1 width 0.11 total body length. Pereonite 4 in male length 0.7 width, with one pair of dorsal tubercles, three pairs of posterolateral tubercles and one pair of setae. Pereonite 5 length 3.8 width; 0.41 total body length; with 14 pairs of lateral pedestal spines, 14 pairs of anterodorsal tubercles and one pair of posterodorsal tubercles. Pleonite 1 region of pleotelson with one pair of dorsal tubercles and one pair of lateral pedestal spines. Pleotelson length 1.2 width; posterolateral margin at uropod insertion indented into margin; with one pair of dorsal spines and one pair of dorsal tubercles; terminal margin with pair of simple spines, longer than uropods.

Antennula and antenna

Antennula with six articles altogether; article 1 without setae; article 2 length 0.7 head width, with three elongate stiff ventromedial setae; distal articles altogether subequal to article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article longer than penultimate article; aesthetascs absent. Antenna article 3 length 0.43 anterior body length, 10 width.

Mouthparts

Maxillula with 10 robust setae on lateral lobe; medial lobe with one robust medially-projecting dentate seta. Maxilla with two long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe. Maxilliped palp article 3 wider than article 2.

Pereopods

Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus with 1 shorter robust seta proximal to elongate seta, with three robust setae on palm distal to elongate seta. Pereopod I propodus ventral margin with two robust setae and one simple elongate seta.

Pleopods and uropods

Pleopod II protopod apex rounded, stylet not extending to distal margin of protopod. Pleopod III exopod with plumose setae and fringe of fine setae. Uropods not extending near posterior margin of pleotelson, length 2 basal width, 0.17 length of pleotelson.

Distribution

Type locality (see above); also taken by Birstein two other stations: station 5620, 44°48′N, 156°33′E 5005–5045 m; station 5634, 44°07′N, 149°34′E, 6090–6135 m.

Remarks

Fortimesus concinnus, comb. nov. possesses distinctive anterolateral spines on pereonites 1, 3 and 4, typical of the spines observed on species from the Atlantic such as *Gracilimesus insignis*, comb. nov. and *H. bifurcatus*. The pleotelson is similar to species from the Pacific such as *F. cornutus* and *F. profundicolus*. The pleotelson is ovate, with lateral and distal spines, with dorsal tubercles, and without posterolateral spines. *Fortimesus concinnus*, comb. nov. also possesses many dorsal tubercles on pereonites 4–7 (See Birstein 1971: 211–213, fig. 21). Overall, this species is most similar to *F. cornutus*, but with noticeable differences in spine size, orientation and overall spination pattern.

Fortimesus cornutus (Birstein), comb. nov.

Haplomesus cornutus Birstein, 1960: 12–14, figs 8–9. – Birstein, 1963: 62; Kussakin, 1988: 463–465, fig. 380, 381.

Material examined

Holotype. Adult ♂ by monotypy, (illustration examined), north-west Pacific: station 3457, 41°17′N, 145°5.02′E, 6471–6571 m. Location of type material unknown.

Remarks on type material

The holotype is an adult male with all appendages intact and illustrated.

Diagnosis

Pereonites 1–3 with anterolateral spines, elongate on pereonite 1 and directed anteriorly, short on pereonites 2–3 and directed anterolaterally; pereonite 7 with pair of dorsal tubercles; pleotelson with lateral spines; pereopod II–VII basis, ischium and merus with numerous robust setae on dorsal and ventral surfaces, carpus and propodus with setae on ventral surfaces only; pereopod I carpus ventral margin with two major elongate setae; pleopod I male with distal setae.

Description of male (female unknown)

Body length 9.8 mm, hirsute, with numerous setae, cuticle granular. Head length 1.5 width. Pereonite 1 width 0.16 total body length. Pereonite 5 length 2.9 width; 0.4 total body length. Pleotelson length 1.1 width; posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula with six articles altogether; article 1 with eight robust setae; article 2 length 1.75 head width, with four elongate, stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article longer than penultimate article; aesthetascs absent. Antenna length 2.26 anterior body length; article 3 length 0.43 anterior body length, length 8.3 width, cuticle smooth; article 5 length 0.55 anterior body length; article 6 length 0.55 anterior body length; flagellum length 0.36 total antennal length, with 19 articles.

Mouthparts

Maxilla with two long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe. Maxilliped palp article 2 wider than 3.

Pereopods

Pereopod I carpus with no robust setae proximal to elongate setae, with two robust setae on palm distal to elongate setae. Pereopod I propodus ventral margin with two robust setae. Pereopod VII present, shorter than pereopod VI in adults.

Pleopods and uropods

Pleopod II protopod apex rounded, stylet not extending to distal margin of protopod. Pleopod III exopod with plumose setae, without fringe of fine setae. Uropods not extending near posterior margin of pleotelson, length 1.5 basal width, 0.125 length of pleotelson.

Distribution

North-west Pacific.

Remarks

Fortimesus cornutus, comb. nov. is similar to *F. concinnus*, comb. nov. in that it possesses large anterolateral processes on the anterior pereonites along with an ovate pleotelson lacking posterolateral spines (see remarks under *F. concinnus*, comb. nov.).

Fortimesus consanguineus (Mezhov), comb. nov.

Haplomesus consanguineus Mezhov, 1980: 820–822, fig. 1.

Material examined

Holotype. Adult ♀ by monotypy, (illustration examined), north-west Pacific, station 6153-A, 34°25′N, 142°06′E, 8800–8830 m. Location of type material unknown.

Remarks on type material

The holotype has both antennae and one antennula have been broken off. No intact pereopods were illustrated. The body appears to be in good condition.

Diagnosis

Head dorsal surface with cephalic bullae; pereonites 1–3 with several lateral and anterolateral small spines; entire body covered with smaller tubercles; pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by indistinct lines, without any spines; antennula article 2 with lateral row of robust setae; pereopod I carpus ventral margin with two elongate robust setae.

Description of female (male unknown)

Body length 14.4 mm, cuticle granular. Head length 0.8 width; lobe on ventrolateral margin absent in lateral view; dorsal cuticle coarsely granulated. Pereonite 1 width 0.18 total body length, with one pair of anterolateral simple spines, tiny, length distinctly less than length of pereonite 1, with two pairs of lateral simple spines. Pereonite 2 with three pairs of lateral simple spines. Pereonite 3 with two pairs of lateral simple spines. Pereonite 4 length 0.8 width. Pereonite 5 length 1.72 width, 0.28 total body length. Pleotelson length 1.06 width; posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula with six articles altogether; article 2 length in female 0.78 head width, with three elongate, stiff, ventromedial setae, lateral margin with row of 11 robust setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent.

Mouthparts

Maxillula with 12 robust setae on lateral lobe; medial lobe with one robust medially-projecting dentate seta. Maxilliped palp article 3 wider than article 2.

Pereopods

Pereopod I merus dorsal margin with one distinctly robust seta, placed distally. Pereopod I carpus with two elongate robust setae, with no robust setae proximal to elongate setae, with four robust setae on palm distal to elongate setae. Pereopod I propodus ventral margin with two robust setae, one medially and one distally located, and with one elongate distal seta.

Pleopods and uropods

Pleopod II operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex. Uropods extending near posterior margin of pleotelson; length 0.11 length of pleotelson.

Distribution

North-west Pacific.

Remarks

Fortimesus consanguineus, comb. nov. is most similar to *F. thomsoni* owing to the numerous small lateral spines present on the anterior pereonites. However, as well as being more than twice the length of *F. thomsoni*, it also possesses cephalic bullae on the head, a characteristic that is not observed in any other species of the *Haplomesus*-group. The large body size observed here also occurs in *F. gigas*, comb. nov., but the pattern of spines and tubercles are quite different on *F. gigas*, comb. nov., as well as the overall body shape.

Fortimesus formosus (Mezhov), comb. nov.

Haplomesus formosus Mezhov, 1981: 72–73, fig. 4.

Material examined

Holotype. Adult ♂ by monotypy, (illustration examined), north Pacific, near Map-Maker Seamounts, station 6015: 26°51′N, 165°32′E, 5850 m. Location of type material unknown.

Remarks on type material

The holotype has the head and pereonite 1 and 2 are missing. Pereonite 3 is damaged. No intact pereopods were illustrated. Length of pereonites 3–7: 4.5 mm. Estimated entire body length 5.5 mm.

Diagnosis

Pereonite 5 with one pair of large posterolateral spines; pereonites 6–7 and pleonite 1 with one pair each of small dorsal spines; pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by weak indentations; distal margin with one pair of small simple spines; pleopod I male with simple setae on distal margin.

Description

Body cuticle granular. Pereonite 4 in male length equals width, with one pair of anterolateral simple spines, short, length near pereonite 1 length. Pereonite 5 length 4.8 width. Pleotelson length 1.27 width; with one pair of small, anteriorly located tubercles; with two pairs of simple spines, one located anteriorly, and one medially.

Pleopods and uropods

Pleopod II protopod apex rounded, stylet extending to distal margin of protopod. Uropods extending beyond end of pleotelson, length 3 basal width, 0.21 length of pleotelson.

Distribution

North Pacific.

Remarks

This species is unlike other species of the genus owing to the posterolateral spines on pereonite 5, the small lateral spines on pereonite 6, and the dorsal spines on pereonites 6, 7 and pleonite 1. Mezhov's illustration shows a damaged specimen (Mezhov 1981: 71, Fig. 4) that may have spines on pereonite 3, too. The shape of the pleotelson, its lateral and distal spines and the absence of posterolateral spines on the pleotelson align it with other Pacific species such as *Fortimesus concinnus*, comb. nov. and *F. profundicolus*, comb. nov. *Fortimesus formosus* was excluded from the phylogenetic analysis owing to the large amount of missing data as discussed above. It was placed into the genus *Fortimesus* using the characters discussed above.

Fortimesus gigas (Birstein), comb. nov.

Haplomesus gigas Birstein, 1960: 6–7, fig. 3–4. – Wolff, 1962: 84, 87, 235, 269, 275; Birstein, 1963: 59, tbl. 1, 3; 1971: 209; Mezhov, 1980: 822; Kussakin, 1988: 460–463, fig. 378–379.

Material examined

Syntypes. Adult ♂, adult ♀, (illustrations examined), north-west Pacific: 46°31′N, 54°22′E, 8330–8430 m. Location of type material unknown.

Remarks on type material

The type series consists of an adult ♂ from which one antenna has been broken off and an adult ♀, also with one antenna broken off. Only pereopod I is illustrated.

Diagnosis

Antennula article 2 with lateral row of short simple setae, male and female with one pair of anterolateral spines on pereonite 1, directed anteriorly; pleotelson with terminal spines; pereopod I carpus ventral margin with two elongate robust setae; maxilliped endite with five receptaculi; male pleopod I with distal and lateral setae; female pleopod II operculum without plumose setae.

Description of female

Body length 14.5 mm, cuticle granular. Head in female length equals width, dorsal cuticle coarsely granular. Pereonite 1 width 0.16 total body length, with one pair of anterolateral simple spines, tiny. Pereonite 4 length 0.9 width. Pereonite 5 length 1.52 width, 0.25 total body length. Pleotelson length 1.3 width; posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula with six articles altogether; article 1 without setae; article 2 without long ventromedial setae, lateral margin with row of 20 robust setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna length 1.75 anterior body length; article 3 length 0.35 anterior body length, length 13.75 width; article 5 length 0.31 anterior body length; article 6 length 0.37 anterior body length; flagellum with 15 articles, length 0.36 total antenna length.

Mouthparts

Maxillula with ten robust setae on lateral lobe; medial lobe with one robust medially-projecting dentate seta. Maxilla with two long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe. Maxilliped palp article 3 wider than article 2.

Pereopods

Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus ventral margin with no robust setae proximal to elongate seta, with seven robust setae on palm distal to elongate seta, robust setae decreasing in length distally; propodus ventral margin with four robust setae, one longer simple seta placed distally.

Pleopods and uropods

Pleopod III exopod length more than half endopod length, with plumose setae and fringe of fine setae. Uropods minute, not extending near posterior margin of pleotelson; length 0.07 length of pleotelson.

Description of male

Body length 13.5 mm. Head length 0.88 width, cuticle granular. Pereonite 1 width 0.16 total body length. Pereonite 4 in male length 0.8 width. Pereonite 5 length 1.97 width; 0.29 total body length. Pleotelson length 1.1 width.

Antennula and antenna

Antennula article 2 length 1.23 head width. Antenna length 2.03 anterior body length; article 3 length 0.38 anterior body length, length 11.5 width; article 5 length 0.31 anterior body length; article 6 length 0.28 anterior body length; flagellum length 0.35 total antennal length, with 16–17 articles.

Pleopods and uropods

Pleopod II protopod apex rounded, stylet not extending to distal margin of protopod. Uropods length 0.07 length of pleotelson.

Distribution

North-west Pacific (Birstein 1960, 1971; Mezhov 1980) 6675–8430 m.

Remarks

The large size of *Fortimesus gigas*, comb. nov. sets it apart from other species of the genus. *F. consanguineus*, comb. nov. also displays a large body size, but the presence of cephalic bullae as well as the numerous lateral spines of this species, make *F consanguineus*, comb. nov. distinctive. The maxilliped endite of *F. gigas*, comb. nov. possesses five receptaculi. This is unusual as most species possess only three, apart from *F profundicolus*, comb. nov. and *F. scabriusculus*, comb. nov. that possess four receptaculi.

Fortimesus profundicolus (Birstein), comb. nov.

Haplomesus profundicola Birstein, 1971: 215–217, fig. 23. – Kussakin, 1988: 470–471, fig. 385.

Material examined

Holotype. Adult ♀ by monotypy, (illustration examined), north-west Pacific: 46°00′N, 153°27′E, 7265–7295 m. Location of type material unknown.

Remarks on type material

Both antennae have been broken off from the holotype. Only pereopod I is illustrated.

Diagnosis

Antennula with five articles, article 2 with lateral row of dorsal robust setae; pereonite 1 with anterolateral spines, directed anteriorly; pereonites 1–4 with numerous lateral, and several dorsal tubercles; pereonite 5 with two rows of dorsal tubercles; pleotelson with lateral and terminal spines, without posterolateral spines; pereopod I carpus ventral margin with two elongate robust setae; pereopod I basis with row of dorsal spines; maxilliped epipod with setae; pleopod II operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex, without plumose setae.

Description of female (male unknown)

Body length 10.1 mm, cuticle granular. Head length equals width. Pereonite 1 width 0.16 total body length, with five pairs of dorsal tubercles, anterolateral simple spines, short, and curved medially with three pairs of lateral simple spines. Pereonite 2 with three pairs of dorsal tubercles, seven pairs of lateral simple spines. Pereonite 3 with three pairs of dorsal tubercles, three pairs of lateral tubercles. Pereonite 4 length 0.6 width, with two pairs of dorsal tubercles, five pairs of lateral simple spines. Pereonite 5 length 2.6 width, 0.3 total body length; with 14 anterodorsal tubercles positioned towards the lateral margins. Pleotelson length 1.2 width; posterolateral margin at uropod insertion indented into margin; with five pairs of dorsal tubercles positioned along the axial ridge; with two pairs of lateral simple spines, and one pair of terminal short spines.

Antennula and antenna

Antennula article 1 without setae; article 2 length 1.6 head width, with five elongate stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article longer than penultimate article; aesthetascs absent. Antenna article 3 length 0.34 anterior body length, length 10 width.

Mouthparts

Maxillula with nine robust setae on lateral lobe; medial lobe with one robust medially-projecting dentate seta. Maxilla with two long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe. Maxilliped endite with four receptaculi. Maxilliped palp article 3 wider than article 2.

Pereopods

Pereopod I merus dorsal margin with one distinctly robust setae, placed distally. Pereopod I carpus with no robust setae proximal to elongate seta, with three robust setae on palm distal to elongate seta. Pereopod I propodus ventral margin with two robust setae.

Pleopods and uropods

Pleopod III exopod with plumose setae and with fringe of fine setae. Uropods extending near posterior margin of pleotelson, length 3.1 basal width, 0.14 length of pleotelson.

Distribution

North-west Pacific.

Remarks

Fortimesus profundicolus, comb. nov. is closely allied to other pacific species such as *F. scabriusculus*, comb. nov. and *F. robustus*, comb. nov. by the overall body shape, numerous lateral and dorsal projections, the shape of the pleotelson and the presence of lateral setae on antennula article 2. However, the anterolateral spines on pereonite 1 are significantly larger than those observed on most *Fortimesus* species from the Pacific (with the exception of *F. cornutus*, comb. nov. and *F. orientalis*, comb. nov.; see discussion above). The presence of setae on the epipod of the maxilliped also distinguishes this species from all other species of the genus. *F. profundicolus*, comb. nov. possesses four receptaculi on the maxilliped endite, instead of the usual three. Only *F. scabriusculus*, comb. nov. and *F. gigas*, comb. nov. possess four and five receptaculi respectively.

Fortimesus robustus (Birstein), comb. nov.

Fortimesus robustus Birstein, 1960: 9–11, fig. 6. – Wolff, 1962: 84, 87, 265; Birstein, 1963: 60; 1971: 213; Kussakin, 1988: 456–459, fig. 376.

Material examined

Syntypes. Adult ♀, adult ♂, (illustrations examined), north-west Pacific: 39°02.9′N, 151°50.6′E, 5817–5807 m. Location of type material unknown.

Remarks on type material

The type series contains an adult ♀, with one antenna broken off at article 3. Only pereopod I is illustrated. The pleopods of an adult ♂ are illustrated.

Diagnosis

Antennula article 2 with short setae on lateral surfaces; pereonite 1 female with minute anterolateral spines directed anteriorly; pereonite 4 wider than long; pereonite 5 short, length 1.3 width, with two dorsolateral rows of minute tubercles; pleotelson with small lateral spines; pereopod I carpus ventral margin with two elongate robust setae; pereopod I with robust setae on dorsal and ventral surface of basis; pleopod I male with distal setae; pleopod II female operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex.

Description of female

Body length in female 7.5 mm. cuticle granular. Head length 1.37 width. Pereonite 1 width 0.21 total body length, anterolateral simple spines, tiny, with one pair of lateral tubercles. Pereonite 2 with one pair of lateral tubercles. Pereonite 3 with two pairs of dorsal tubercles. Pereonite 4 length 0.63 width, with five pairs of dorsal tubercles, four pairs of posterolateral pedestal spines. Pereonite 5 length 1.31 width; 0.22 total body length, with seven pairs of tubercles arranged in longitudinal row at lateral margin, four pairs of tubercles arranged medially. Pleotelson length 1.18 width; posterolateral margin at uropod insertion indented into margin; with two pairs of lateral spines.

Antennula and antenna

Antennula with six articles altogether; antennula article 2 length ~2.0 article 1 length, length 1.05 head width, with three elongate, stiff, ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna length 1.2 anterior body length; article 3 length 0.2 anterior body length, article 3 length 5.8 width; article 5 length 0.22 anterior body length; article 6 length 0.46 anterior body length; flagellum length 0.35 total antennal length.

Mouthparts

Maxillula with eight robust setae on lateral lobe; medial lobe with one robust medially-projecting dentate seta. Maxilliped palp article 3 wider than article 2.

Pereopods

Pereopod I merus dorsal margin with one distinctly robust seta, placed distally. Pereopod I carpus ventral margin with two elongate robust setae, with no robust setae proximal to elongate setae, with five robust setae on palm distal to elongate setae. Pereopod I propodus ventral margin with two robust setae, with one distal simple seta.

Pleopods and uropods

Pleopod III exopod with plumose setae, with fringe of fine setae. Uropods not extending near posterior margin of pleotelson, length 1.5 basal width, 0.11 length of pleotelson.

Description of male

Body length 7.8 mm.

Pleopods and uropods

Pleopod II protopod apex rounded, stylet not extending to distal margin of protopod.

Distribution

Type locality (see above); collected by Birstein at an additional station in 1960: station 3575, 37°54.5′N, 141°43.9′W, 5450 m, one female specimen; collected by Birstein in 1971, station 5617, 45°32′N, 153°46′E, 6674–6710 m; station 5620, 44°48′N, 156°33′E, 5005–5045 m.

Remarks

Fortimesus robustus, comb. nov. is closely allied to other species from the Pacific such as *F. scabriusculus*, comb. nov. and *F. profundicolus*, comb. nov. (see remarks under *F. profundicolus*, comb. nov. above). However, the overall robustness of the body shape as well as the short and wide pereonite 5 (1.31× as long as wide) makes *H. robustus*, comb. nov. distinctive.

Fortimesus scabriusculus (Birstein), comb. nov.

Haplomesus scabriusculus Birstein, 1960: 7–9, fig. 5. – Wolff, 1962: 85–87, 265; Birstein, 1963: 60; 1971: 213; Kussakin, 1988: 468–470, fig. 384.

Material examined

Holotype. Adult ♀ by monotypy, (illustration examined), north-west Pacific: station 3575, 37°54.5′N, 141°43.9′E 5450 m. Location of type material unknown.

Remarks on type material

The holotype has both antennae broken off at article 4. Two intact pereopods, pereopods I and pereopod IV, are illustrated. The specimen appears to be in good condition.

Diagnosis

Antennula article 2 with lateral row of robust setae; body covered with sharp denticles; pereonite 1 with median simple spine; pereonite 5 with lateral row of pedestal setae; pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by weak indentations, with lateral spines, with dorsal tubercles, without posterolateral spines, with one pair of terminal spines; pereopod I carpus ventral margin with two elongate robust setae; pleopod II operculum flap-like, much longer than wide.

Description of female (male unknown)

Body length 8 mm, cuticle granular. Head length 0.93 width. Pereonite 1 width 0.18 total body length. Pereonite 4 length 1.1 width; entire body covered with simple spines, all short (basal width approximating length). Pereonite 5 length 1.6 width; 0.23 total body length. Pleotelson length 1.15 width; posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula with six articles altogether; article 1 without setae; article 2 length greater than 3.0 article 1 length, length 2.17 head width, with three elongate stiff ventromedial setae, lateral margin with row of 10 robust setae; distal articles altogether small, shorter than article 2; article 3 length similar to article 4, elongate and tubular, much longer than wide; terminal article longer than penultimate article; aesthetascs absent. Antenna article 3 length 0.35 anterior body length, length 8.33 width.

Mouthparts

Maxillula with eight robust setae on lateral lobe; medial lobe with one robust medially-projecting dentate seta. Maxilla with one long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe. Maxilliped endite with four receptaculi.

Pereopods

Pereopod I carpus with no robust setae proximal to elongate setae, with five robust setae on palm distal to elongate setae. Pereopod I propodus ventral margin with two robust setae, positioned medially and distally, with one distal elongate simple seta.

Pleopods and uropods

Pleopod III exopod with plumose setae, with fringe of fine setae. Uropods minute, not extending near posterior margin of pleotelson, length 2 basal width, 0.1 length of pleotelson.

Distribution

Type locality (see above); collected by Birstein (1971), station 5624, 45°26′N, 154°12′E, 5200 m.

Remarks

Fortimesus scabriusculus, comb. nov. is closely allied to other species from the Pacific such as *F. robustus*, comb. nov. and *F. profundicolus*, comb. nov. (see remarks under *F. profundicolus*, comb. nov. above). It is distinguished from these species by the increasing width of pereonites 1–3, with pereonite 4 approximately the same width as pereonite 1.

Fortimesus zuluensis (Kensley), comb. nov.

Haplomesus zuluensis Kensley, 1984: 291–293, fig. 41.

Material examined

Holotype. Adult ♀ by original designation, (illustrations examined), South Atlantic Ocean: 27°09′S, 32°58′E, 800–810 m, SAM-A17858.

Remarks on type material

The holotype is an ovigerous female, with both antennae broken off. Only pereopods I and VII are illustrated.

Diagnosis

Female pereonite 1 with one pair of anterolateral spines; pereonites 1–5 with dorsal tubercles; pereonites 2 and 3 with lateral tubercles; pereonite 4 with median dorsal tubercle; pereopod I carpus ventral margin with two elongate robust setae; maxilla with one pectinate seta on medial lobe.

Description of female (male unknown)

Body length 4.9 mm, cuticle granular. Head length 0.86 width; lobe on ventrolateral margin absent in lateral view; dorsal cuticle very finely granulate. Pereonite 1 width 0.17 total body length, anterolateral simple spines, short, with one pair of lateral tubercles. Pereonites 2 and 3 with one pair of dorsal tubercles. Pereonite 4 length equals width, with four pairs of dorsal tubercles. Pereonite 5 length 2.38 width, 0.32 total body length, with seven pairs of median tubercles. Pleotelson length 1.3 width; posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; aesthetascs absent. Antenna article 3 length 0.11 anterior body length, length 3 width; article 5 length 0.31 anterior body length; article 6 length 0.37 anterior body length.

Mouthparts

Maxillula with 11 robust setae on lateral lobe; medial lobe with two robust medially-projecting dentate seta. Maxilla with one long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe.

Pereopods

Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus with no robust setae proximal to elongate seta, with two robust setae on palm distal to elongate seta; propodus ventral margin with two robust setae, placed distally, with one elongate distal seta.

Pleopods and uropods

Uropods extending near posterior margin of pleotelson, length 1.25 basal width, 0.05 length of pleotelson.

Distribution

South Atlantic.

Remarks

Kensley stated that *F. zuluensis*, comb. nov. displayed some similarity to *H. quadrispinosus* Sars, but that the spines on pereonite 1 are much smaller. *F. zuluensis*, comb. nov. also lacks spines on pereonite 3 and has dorsal tubercles, which *H. quadrispinosus* does not. The dorsal surface of the pleotelson of *F. zuluensis*, comb. nov. does resemble *H. quadrispinosus* (Kensley 1984: 291–293, Fig. 41), but as Kensley did not illustrate the ventral surface it is unclear how similar *F. zuluensis* is to the *Haplomesus sensu stricto*. The presence of dorsal and lateral tubercles on the body and pleotelson, along with the weakly vaulted pleotelson places this species in *Fortimesus*, gen. nov.

Genus ***Gracilimesus***, gen. nov.

Type species: *Haplomesus celticensis* Kavanagh, Wilson & Power, 2006.

Species included: *H. angustus* Hansen, 1916; *H. celticensis* Kavanagh, Wilson & Power, 2006; *H. corniculatus* Brökeland & Brandt, 2004; *H. formosus* Mezhov, 1981; *H. gorbunovi* Gurjanova, 1946; *H.* cf. *gorbunovi sensu* Svavarsson, 1988; *H. hanseni* Kavanagh, Wilson & Power, 2006; *H. insignis* Hansen, 1916; *H. modestatenuis* Menzies & George, 1972; *H. modestus* Hansen, 1916; *H. orientalis* Birstein, 1960; *H. tenuispinis* Hansen, 1916; *H. tropicalis* Menzies, 1962.

Diagnosis

Pereonites 5–7, pleonite 1 and pleotelson lacking intersomite articulations. Pereonites 5–7 narrowing posteriorly. Pleotelson axial ridge smooth arched, not separated from lateral fields, or weakly vaulted, separated from lateral fields only by shallow elongate concavities, medially smoothly arched. Pleotelson with distinct posterolateral spines. Antennula with 5–6 articles, distal flagellar articles much longer than wide. Pereopods with distinct neck between the pereopodal articulation of the basis and coxa and the shaft of the basis, with the basis neck and shaft forming an approximate right angle. Pleopod II female operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex. Uropods with one article, distally tapering.

Descriptions

See Kavanagh *et al*. (2006) for descriptions of *Gracilimesus celticensis*, comb. nov.; *G. hanseni*, comb. nov.; *G. angustus*, comb. nov. and *G. tropicalis*, comb. nov.

See Brökeland and Brandt (2004) for description and illustrations of *G. corniculatus*, comb. nov.

Distribution

Species of the genus *Gracilimesus*, gen. nov. are found throughout the Atlantic Ocean. Species have also been recorded from the Pacific and Antarctic Oceans. However, as with species of *Haplomesus sensu stricto*, species themselves have limited distributions and are confined to small regions. Several undescribed species of this genus have been collected from locations throughout the Atlantic (see Kavanagh *et al*. 2006; Fig. 1).

Remarks

Species of the genus *Gracilimesus* are distinctive owing to an elongate pereonite 5, with a length to width ratio of, on average, 3.1 in females and 4.4 in males. This is higher than the mean ratios observed in other genera. In the genus *Haplomesus sensu stricto*, the mean ratio is 2.4 in females and 3.2 in males; in *Cornuamesus*, gen. nov. the ratio is 2 in females and 2.7 in males. Finally, in the genus *Fortimesus*, gen. nov. the ratios are lower again, 1.86 in females and 2.49 in males. Pereonite 5 also constitutes a higher ratio of the total body length in *Gracilimesus*, gen. nov. 0.39 and 0.49 in females and males respectively. For species of the genus *Haplomesus sensu stricto* the ratio is 0.33 in females and 0.36 in males; in *Cornuamesus*, gen. nov. the ratio is 0.28 in females and 0.31 in males; finally in *Fortimesus*, gen. nov. the ratios are 0.27 and 0.34 in females and males respectively; this feature contributes further to the elongate body shape of *Gracilimesus*, gen. nov. species.

In addition to this character, species are recognised by the presence of distinct posterolateral spines that distinguishes species from those of *Haplomesus sensu stricto* and *Fortimesus*, gen. nov. Although the type specimens of *Gracilimesus modestus* and *G. tenuispinis* do not possess these spines, this is a result of the fact that they are immature specimens (see remarks section under each species). The weakly convex posterior margin of the female operculum also distinguishes this genus from *Haplomesus sensu stricto*, species of which have a round posterior margin on the operculum as described above. Several species of *Gracilimesus* do not possess pereopod VII, a feature produced by progenesis (see Kavanagh *et al*. 2006 for full discussion). This is not a unique generic feature, as it is also observed in a species of *Stylomesus* (Brökeland and Brandt, 2004).

Etymology

The genus name comes from the Latin word '*gracilis*' meaning thin, referring to the elongate body form of the species belonging to this genus.

Key to species of *Gracilimesus*, gen. nov.

1. Body pereonite 7 length not reduced, similar to pereonite 6 2
   Body pereonite 7 length reduced, less than pereonite 6 . . 7
   Body pereonite 7 absent 8
2. Pleotelson dorsal surface axial ridge smooth arched, not separated from lateral fields 3
   Pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields only by shallow elongate concavities 6
3. Pleotelson pleonite 1 region with no dorsal spines or tubercles 4
   Pleotelson pleonite 1 region with dorsal spines . . . . *G. modestatenuis* (Menzies & George)
4. Pereonite 4 in female with no anterolateral spines; pereonite 5 in female length up to 2.5 width; body smooth; uropods in female extending near posterior margin of pleotelson . . . . *G. gorbunovi* (Gurjanova)
   Pereonite 4 in female with one pair of anterolateral simple spines; pereonite 5 in female length 2.51 width or more; body granular; uropods in female extending beyond posterior margin of pleotelson 5
5. Pereonite 4 in female elongate anterolateral spines, length near width of pereonite 1; pereonite 2 in female with no lateral spines or tubercles; pereonite 2 in female with no anterolateral spines; pereonite 3 in female with no anterolateral spines . . . . *G. tenuispinis* (Hansen)
   Pereonite 4 in female with tiny anterolateral spines, length distinctly less than length of pereonite 1; pereonite 2 in female with paired lateral simple spines; pereonite 2 in female with one pair of anterolateral simple spines; pereonite 3 in female with one pair of anterolateral simple spines . . . *G. modestus* (Hansen)
6. Pereonite 4 with no anterolateral spines; pleopod II stylet extending beyond distal margin of protopod; antennula article 2 inserting on article 1 dorsally; pereopod VII absent in adults . . . . *G. corniculatus* (Brökeland & Brandt)
   Pereonite 4 with one pair of anterolateral simple spines; pleopod II stylet not extending to distal margin of protopod; antennula article 2 inserting on article 1 anterodorsally; pereopod VII present, shorter than pereopod VI in adults . . . . *G. orientalis* (Birstein)
7. Uropods extending near posterior margin of pleotelson; antennula article 2 with up to two elongate stiff ventromedial setae; pleotelson dorsal surface axial ridge smooth arched, not separated from lateral fields; pere-

onite 2 with no lateral spines or tubercles. . . . . *G. ?gorbunovi sensu* Svavarsson

Uropods extending beyond end of pleotelson; antennula article 2 with 3 elongate stiff ventromedial setae; pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields only by shallow elongate concavities; pereonite 2 with paired lateral simple spines . . . . *G. insignis* (Hansen)

8. Pereonite 4 with no anterolateral spines; maxilliped palp article 3 wider than article 2 . . . *G. angustus* (Hansen)

Pereonite 4 with one pair of anterolateral simple spines; maxilliped palp article 2 wider than article 3 9

9. Pereonite 4 with elongate anterolateral spines, length near width of pereonite 1 . . . . *G. hanseni* (Kavanagh Wilson & Power)

Pereonite 4 with short anterolateral spines, length near pereonite 1 length . . . . *G. celticensis* (Kavanagh Wilson & Power)

Pereonite 4 with tiny anterolateral spines, length distinctly less than pereonite 1 length . . . . *G. tropicalis* (Menzies)

Gracilimesus gorbunovi (Gurjanova), comb. nov.

Haplomesus gorbunovi Gurjanova, 1946: 273, fig. 2. – Gurjanova, 1964: 259; Kussakin, 1988: 453, figs 372–374.
Helomesus gorbunovi; Wolff, 1962: 84, 259.
Stylomesus gorbunovi; Birstein, 1971: 199.

Material examined

Holotype. Adult ♀ by monotypy, (illustration examined), Arctic Ocean: station 60, 82°09′N, 83°08′E, 698 m. Location of type material unknown.

Remarks on type material

The holotype has both antennae broken off. Confusion surrounds the number of articles of the uropoda (see discussion under remarks below).

Diagnosis

Female with thin anterolateral spines on pereonite 1 and minute lateral spine on pereonite 2, male unknown; pereonite 4 as long as wide; pleotelson dorsal surface axial ridge smooth, not separated from lateral fields, posterolateral spines shorter than uropods.

Description of female (male unknown)

Body length 4.5 mm. Head length 0.93 width. Pereonite 1 width 0.16 total body length; anterolateral simple spines short. Pereonite 4 length 0.9 width. Pereonite 5 length 0.28 width; 0.38 total body length. Pleotelson length 1.78 width; posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula with six articles altogether; article 2 length in female 1.2 head width; distal articles altogether subequal to article 2; article 3 length similar to article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna article 3 length 0.18 anterior body length, length 5 width.

Pleopods and uropods

Uropods extending near posterior margin of pleotelson; length 0.11 length of pleotelson.

Distribution

Arctic Ocean.

Remarks

See discussion below under *G.* cf. *gorbunovi* (*sensu* Svavarsson). The two-articled uropoda described by Gurjanova would place this species in a different genus. However, this description of the uropod is dubious, and without access to the type material, this species should remain in the genus *Gracilimesus*, gen. nov.

Gracilimesus cf. ***gorbunovi*** (*sensu* Svavarsson)

Haplomesus ?gorbunovi Svavarsson, 1984: 31, fig. 5–6.

Material examined

Adult ♂ and ♀, (illustrations examined), **Norway**: Norwegian sea, 64°16.9′N, 00°11.7′W, 2630 m; bottom temp –0.9°C.

Diagnosis

Male and female with anterolateral spines on pereonites 1 and 4; in female spines short and curved, in males elongate and straight; pleotelson dorsal surface axial ridge smooth, not separated from lateral fields; pleopod I male with distal setae.

Description of female

Body length 4.2 mm. Head length 0.94 width; lobe on ventrolateral margin absent in lateral view; dorsal cuticle smooth. Pereonite 1 width 0.16 total body length anterolateral simple spines, short. Pereonite 4 length 0.91 width, anterolateral simple spines, short. Pereonite 5 length 3.2 width, 0.34 total body length. Pleotelson length 1.3 width; posterolateral margin at uropod insertion indented into margin; posterolateral spines about half length of uropods, posteriorly directed; pleopod II operculum without plumose setae.

Antennula and antenna

Antennula with six articles altogether; article 1 without setae; article 2 length 0.63 head width, straight, not curved at proximal insertion, with two elongate stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna length 1.48 anterior body length; article 3 length 0.13 anterior body length, length 3.89 width, cuticle smooth; article 5 length 0.22 anterior body length; article 6 length 0.29 anterior body length; flagellum with eight articles, flagellum length 0.31 total antenna length.

Pereopods

Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus with no robust setae proximal to elongate seta, with one robust seta on palm distal to elongate seta; propodus ventral margin with one robust seta, placed medially.

Pleopods and uropods

Uropods extending near posterior margin of pleotelson; length 0.14 length of pleotelson.

Description of male

Body length 4.4 mm. Head length 0.88 width. Pereonite 1 width 0.14 total body length; anterolateral simple spines extremely elongate, length distinctly greater than width of pereonites. Pereonite 4 length 1.3 width; anterolateral simple spines elongate, length near width of pereonite 1. Pereonite 5 length 4.86 width, 0.43 total body length. Pleotelson length 1.08 width.

Antennula and antenna

Antennula article 2 length 0.86 head width. Antenna length 2.36 anterior body length; article 3 length 0.22 anterior body length, length 3.67 width; article 5 length 0.53 anterior body length; article 6 length 0.72 anterior body length; flagellum length 0.3 total antennal length, flagellum with 19 articles.

Pleopods and uropods

Pleopod II protopod apex rounded, stylet not extending to distal margin of protopod. Uropods extending near posterior margin of pleotelson, length 0.1 length of pleotelson.

Distribution

Norwegian Sea, north Polar Sea.

Remarks

Svavarsson's (1984) specimens differ from Gurjanova's (1946) in the spination pattern and the number of articles of the uropods. The difference in spination pattern is attributed to a difference in maturity and size. Gurjanova's specimen is a larger, older female, which Svavarsson stated has lost the spine on pereonite 4 that is observed in Svavarsson's specimens. The description of a two-articled uropod by Gurjanova is, according to Svavarsson, simply a mistake. The male of Svavarsson's specimen more closely resembles *G. insignis*, comb. nov. by the large spines on pereonites 1 and 4, although they are directed more anteriorly than in *G. insignis*, comb. nov. and also by the large posterolateral processes on the pleotelson. The uropods, however, are much shorter than in *G. insignis*, comb. nov., not reaching beyond the posterior tip of the pleotelson. The specimens Gurjanova and Svavarsson examined are not the same species: They were collected from different oceans, and although the sampling history is limited, species are generally restricted to ocean basins (cf. Just and Wilson 2004). Therefore, we consider this specimen a new species. As we did not examine these specimens, we do not provide a new name for this distinct species.

Gracilimesus insignis (Hansen), comb. nov.

(Fig. 9)

Haplomesus insignis Hansen, 1916: 63, pl. V, fig. 3*a*–*d*. – Gurjanova, 1932: 43, fig. XV, 50; 1933: 410; Menzies, 1962: 121, fig. 20N–P; Wolff, 1962: 72, 86, 217, 262, 275, 290, 301; Kussakin, 1988: 451–452, fig. 371.

Material examined

Holotype. Adult ♂, (examined), by original designation, Denmark: Davis Strait, station 36, 61°50′N 56°21′W 1435 fathoms (2702 m), temp 1.5°C, 1 specimen, ZMUC CRU-6846.

Remarks on type material

The holotype is an adult male, which is in good condition. One of the spines on pereonite 1 and half a spine from pereonite 3 have been broken off since the original description. Pereonites 2 and 3 are a different shape than indicated in Hansens illustration; the lateral margins are more convex than linear.

Diagnosis

Antennula with six articles, article 3 elongate, 10× as long as wide; pereonite 4 as long as wide; pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by weak indentations; uropods subequal to pleotelson posterolateral spines; spines on pereonites 1 and 4 extremely robust, elongate; pereonite 2 with one pair of minute lateral spines; pleopod I male with distal setae.

Description of male (female unknown)

Body length 4.5 mm; cuticle granular. Head length 1.27 width; lobe on ventrolateral margin absent in lateral view; cuticle granulated. Pereonite 1 width 0.13 total body length, with one pair of anterolateral simple spines, extremely elongate, anteriorly directed. Pereonite 4 in male length 1.1 width; with one pair of anterolateral simple spines, elongate, more laterally directed than observed on pereonite 1. Pereonite 5 length 3.8 width; 0.44 total body length. Pleotelson length 1.28 width; posterolateral margin anterior to uropods with simple spines; posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula with six articles altogether; article 1 without setae; article 2 length 0.76 head width, with three elongate stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna length 1.93 anterior body length; article 3 length 4.75 width, cuticle smooth; article 5 length 0.52 anterior body length; article 6 length 0.53 anterior body length; flagellum length 0.28 total antennal length, flagellum with 19 articles.

Mouthparts

Maxilliped palp article 2 wider than 3.

Pereopods

Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus ventral margin with no robust setae proximal to elongate seta, with one robust seta on palm distal to elongate seta. Pereopod I propodus ventral margin with one robust seta, placed distally.

Pleopods and uropods

Uropods extending beyond end of pleotelson, length 0.27 length of pleotelson.

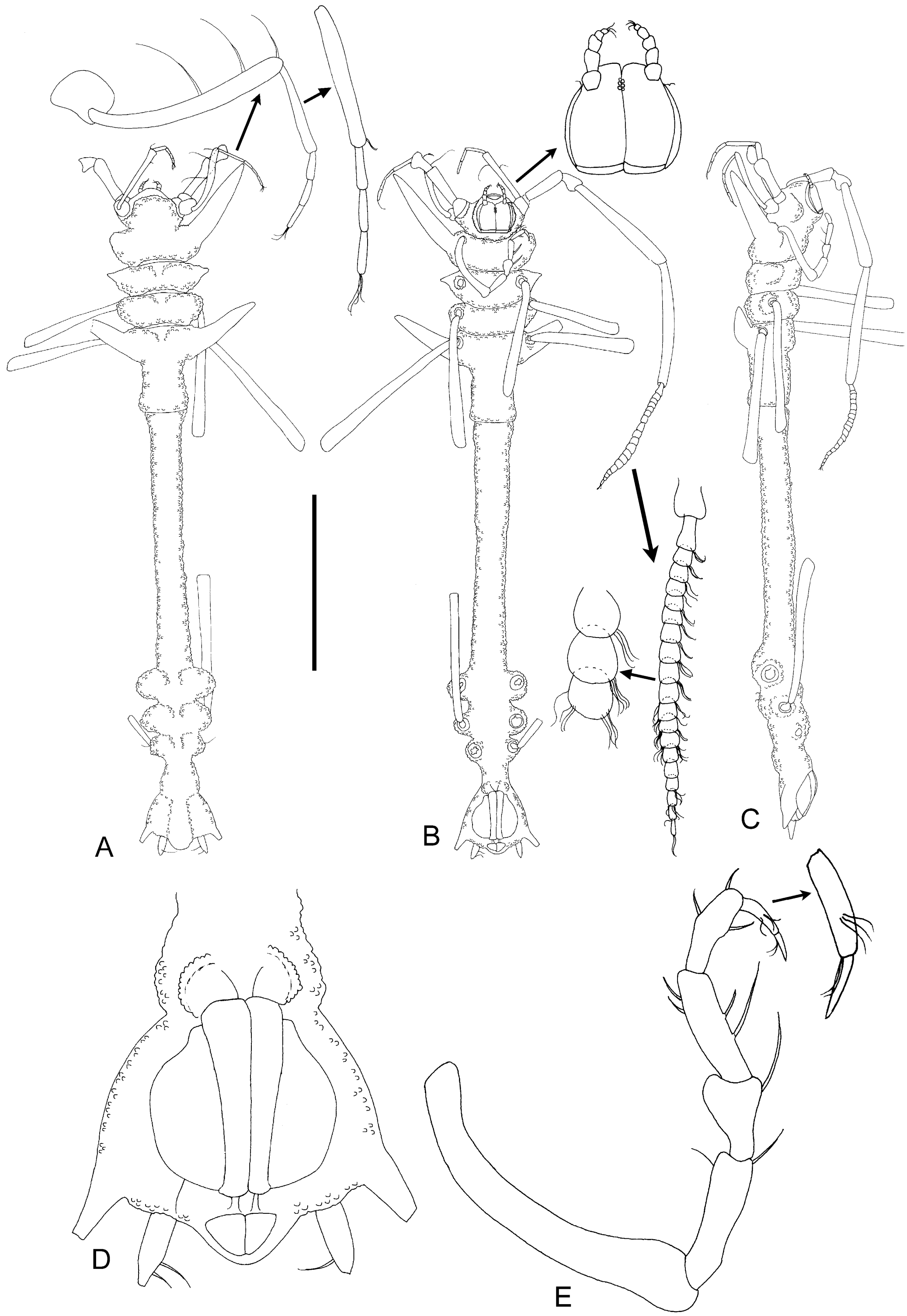

Fig. 9. *Gracilimesus insignis*, comb. nov. (holotype male ZMUC CRU-6846). *A*, Body dorsal view; *B*, body ventral view; *C*, body lateral view; *D*, pleotelson ventral view; *E*, pereopod I. Scale bar = 1 mm.

Distribution

Davis Strait (type locality); north-west Atlantic (Menzies 1962; L.G.O. Biotrawl no. 234 *Vema*-15–150, 11 Jun 1959, 20°21.3′N, 66°24′W, 5477–5494 m); Arctic Ocean (Gorbunov 1946).

Remarks

Gracilimesus insignis, comb. nov. has distinctive robust, large spines on pereonites 1 and 4 that are subequal in length. In addition, the antennular third article is more elongate than is the normally observed value: 3.5× longer than article 4 (Fig. 9*A*), compared with, for example, 1.2 in *G. hanseni*, comb. nov. male paratype and 1.3 in *G. tenuispinis* holotype.

Gracilimesus modestatenuis (Menzies & George), comb. nov.

(Fig. 10)

Haplomesus modestatenuis Menzies & George, 1972: 9, 73, fig. 49*C*–*F*.

Material examined

Holotype. Manca 3 ♂, (examined), by original designation, Peru-Chile: from Peru-Chile trench. Anton Bruun station 179, 4th November 1965, 08°54′S, 81°41′W 4823–4925 m, collected using Menzies trawl, USMN 120994.

Remarks on type material

The holotype is not an intersex specimen as designated by Menzies and George (1972). Rather, it is a manca 3 male (distinctive 'bump' in lateral view shows development of first pleopod). The specimen has become decalcified and slightly damaged compared with the original illustration and the dorsal spines on pleonite 1 are only visible in lateral view (see remarks).

Diagnosis

Pereonites 1–4 male with anterolateral spines; pleotelson dorsal surface axial ridge smooth, not separated from lateral fields; posterolateral spines present; pleonite 1 with pair of small dorsal spines, posteriorly directed.

Description of male (female unknown)

Body cuticle granular. Head lobe on ventrolateral margin absent in lateral view. Pereonite 1–4 anterolateral simple spines, short; pereonites 1–3 with 2 pairs of lateral tubercles. Pleonite 1 region of pleotelson with two small spines (similar to those found on *G. tenuispinis*) set close to midline in dorsal view, directed at an angle from the body. Pleotelson posterolateral margin at uropod insertion indented into margin; posterolateral margin anterior to uropods with posterolateral simple spines, very small, spiniform.

Antennula and antenna

Antennula with six articles altogether; article 1 without setae; article 2 with two elongate stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna flagellum with 10 articles.

Pereopods

Pereopod I merus dorsal margin two distinctly robust setae. Pereopod I carpus ventral margin with no robust setae proximal to elongate seta, with no robust setae on palm distal to elongate setae. Pereopod I propodus ventral margin with no robust setae, placed on median part of margin, with one distal simple seta.

Pleopods and uropods

Uropods extending beyond end of pleotelson.

Distribution

South Atlantic.

Remarks

As stated above, the holotype is a manca male. An adult male may have larger spines on pereonites 1–4 and larger posterolateral processes of the pleotelson in addition to the fully developed pleopods. Body measurement ratios are not reported because those of the manca will be different from adult males, and may be misleading. *Gracilimesus modestatenuis* possesses a pair of spines on the dorsal surface of pleonite 1, a feature also seen in *G. tenuispinis*. The spines of *G. tenuispinis*, however, are further apart and smaller than those of *G. modestatenuis*. The spines of *G modestatenuis* are set at a lateral angle to the body-axis, whereas the spines of *G. tenuispinis* are directed mainly backwards. As suggested by the name, *G. modestatenuis* also resembles *G. modestus* owing to the same spination pattern. However, as both are immature specimens and differ from adults, it is difficult to determine any real similarities.

Gracilimesus modestatenuis was excluded from the phylogenetic analysis because it is an immature specimen, and because missing data dominated its scores. This species was assigned to *Gracilimesus*, gen. nov. *a posteriori* using the following characters: pleotelson dorsal surface axial ridge not separated from lateral fields, smoothly arched, presence of posterolateral spines, lack of dorsal spines or tubercles on pereonites or pleotelson, lack of lateral spines on pleotelson and elongate body form.

Gracilimesus modestus (Hansen), comb. nov.

(Fig. 11)

Haplomesus modestus Hansen, 1916: 65–66 pl. V, fig. 5*a*–*b*; Gurjanova, 1932: 44; 1933, 410; Wolff, 1962: 72, 86, 87, 88, 217, 265, fig. 40, pl. III, B-C; Kussakin, 1988: 449–450, fig. 369.

Material examined

Holotype. Juvenile ♀, (examined), by original designation, Denmark: Davis Strait, station 24, 63°06′N 56°00′W 1199 fathoms (2258 m), 2.4°C, 1 specimen, ZMUC CRU-7359.

Remarks on type material

The holotype consists of a headless and mutilated immature female. The specimen has become damaged since Hansen's (1916) original illustration and, as a result, the spines on the right side of the anterior pereonites are no longer visible. Because the specimen was decalcified, no information on the cuticle could be obtained.

Diagnosis

Pereonite 2 with one pair of lateral spines in female, male unknown; pleotelson dorsal surface axial ridge smooth, not separated from lateral fields, with small posterolateral spines.

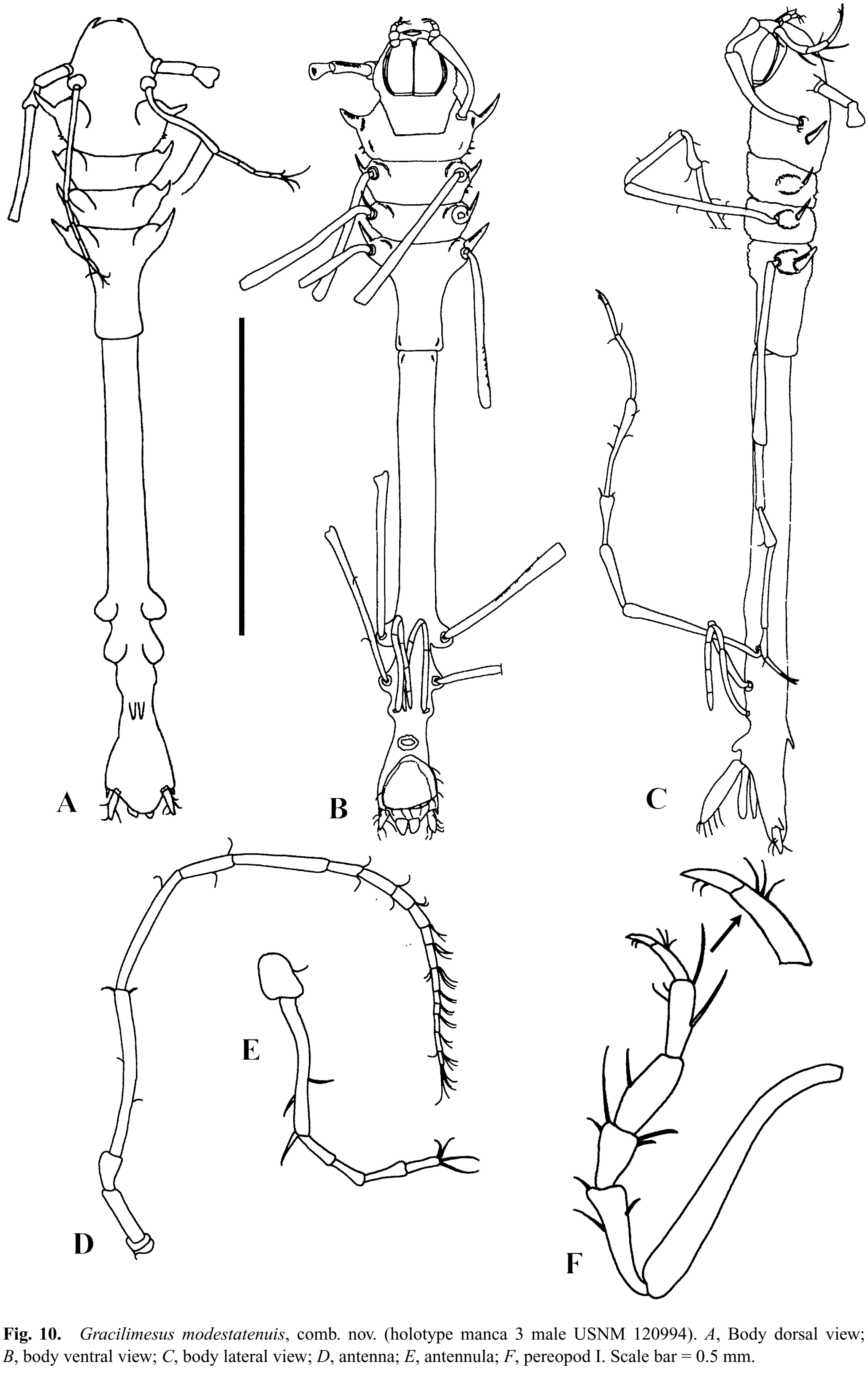

Fig. 10. *Gracilimesus modestatenuis*, comb. nov. (holotype manca 3 male USNM 120994). *A*, Body dorsal view; *B*, body ventral view; *C*, body lateral view; *D*, antenna; *E*, antennula; *F*, pereopod I. Scale bar = 0.5 mm.

Description of female (male unknown)

Body cuticle granular. Pereonites 2–4 anterolateral simple spines, tiny; with one pair of lateral spines. Pereonite 4 length 0.9 width. Pereonite 5 length 3.13 width. Pleotelson length 1.65 width; posterolateral margin at uropod insertion indented into margin; posterolateral margin anterior to uropods with weakly produced posterolateral processes owing to immaturity of specimen.

Pleopods and uropods

Uropods extending beyond posterior margin of pleotelson; length 0.13 length of pleotelson.

Distribution

North-east Atlantic.

Remarks

The holotype of *G. modestus* is a juvenile female. A fully grown adult female will look different to this specimen: the spines on the pereonites will be larger when fully developed, as will the posterolateral processes of the pleotelson. The spines on the male of this species are likely to be much larger than in the female and the spination pattern may be different. The presence of small, lateral spines on pereonite 2 (Hansen 1916: 65–66, fig. 5*a*) are only observed in one other species: *G. insignis*, comb. nov.

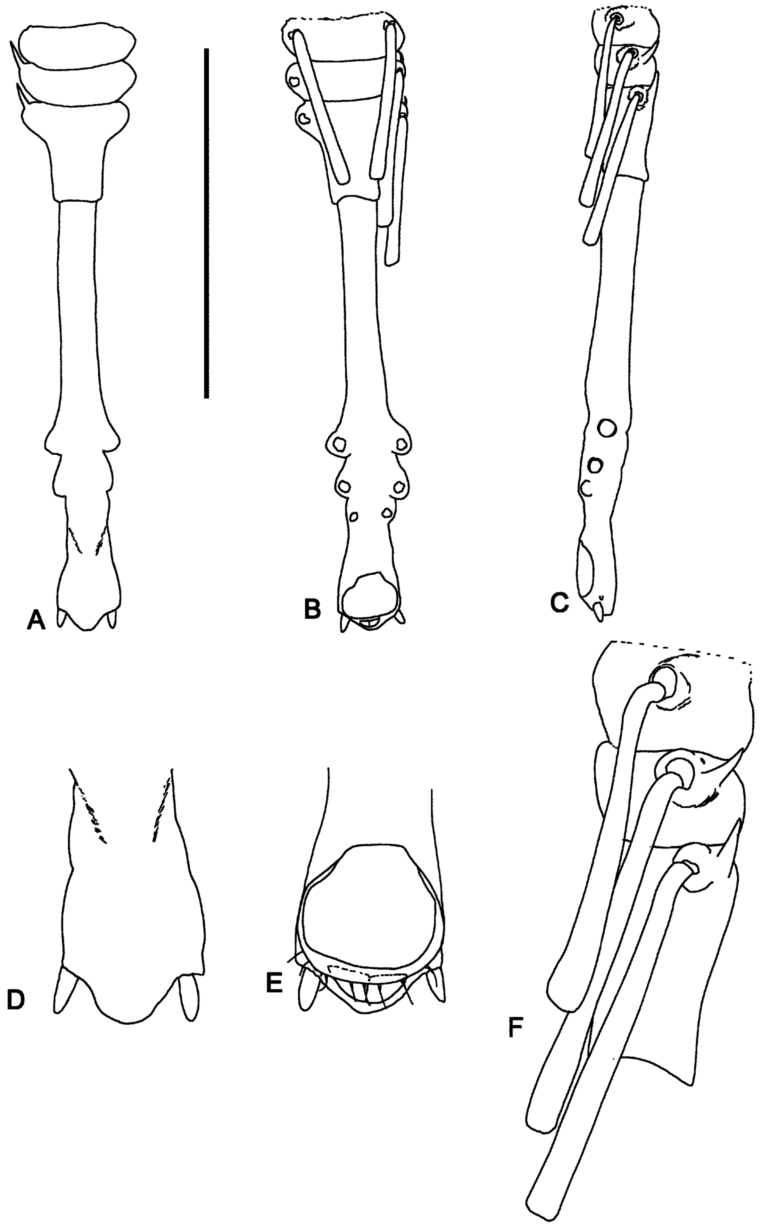

Fig. 11. *Gracilimesus modestus*, comb. nov. (holotype female ZMUC CRU-7359). *A*, Body dorsal view; *B*, body ventral view; *C*, body lateral view; *D*, pleotelson dorsal view; *E*, pleotelson ventral view; *F*, pereonites 2–4 lateral view. Scale bar = 1 mm.

As with *G. modestatenuis*, *G. modestus* was excluded from the phylogenetic analysis owing to it being an immature specimen and the large amount of missing data caused by the head and first pereonite being missing. The species was then placed in the genus *Gracilimesus*, gen. nov. *a posteriori* based on the following characters: pleotelson dorsal surface axial ridge smoothly arched, not separated from lateral fields, presence of pleotelson posterolateral spines, lack of dorsal spines or tubercles on pereonites or pleotelson, lack of lateral spines or tubercles on pleotelson.

Gracilimesus orientalis (Birstein), comb. nov.

Haplomesus insignis orientalis Birstein, 1960: 14–15, fig. 10; 1963*b*: 83.

Material examined

Holotype. Adult ♂, (illustration examined), by monotypy 5.1 mm, north-west Pacific Ocean: off the Kurile Islands, *Vityaz* station 3250, 4150–4000 m, 24 October 1955, 28°53.5′N, 137°21.1′E, Sigsbee Trawl. Location of type unknown.

Remarks on type material

The holotype is an adult male from which both antennae have been broken at article 4. Several intact pereopods are illustrated. Paratypes consist of three fragmentary specimens.

Diagnosis

Male pereonites 1 and 4 with elongate anterolateral spines; pereonite 7 with pair of dorsal setae; pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by weak indentations, with elongate posterolateral spines; male pleopod I with distal and lateral setae.

Description of male (female unknown)

Body length 5.1 mm. Head length 0.78 width. Pereonite 1 width 0.13 total body length, anterolateral spines directed anteriorly. Pereonite 4 in male length 1.1 width, anterolateral spines directed anterolaterally. Pereonite 5 length 4.45 width; 0.51 total body length. Pleotelson length 0.89 width; posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula with six articles altogether; article 1 without setae; article 2 length 0.85 head width, with two elongate stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna article 3 length 0.32 anterior body length, length 7 width, cuticle smooth.

Mouthparts

Maxilliped palp article 2 wider than 3.

Pereopods

Pereopod I carpus ventral margin with one shorter robust seta proximal to elongate seta, with one robust seta on palm distal to elongate seta. Pereopod I propodus ventral margin with one robust seta, placed distally, with 1 smaller distal simple seta. Pereopod VII present, shorter than pereopod VI in adults.

Pleopods and uropods

Pleopod II protopod apex rounded, with setae on lateral and distal margin, stylet not extending to distal margin of protopod. Uropods extending near posterior margin of pleotelson, length 2 basal width, length 0.23 length of pleotelson.

Distribution

North-west Pacific.

Remarks

No evidence for the subspecific status *Gracilimesus insignis orientalis*, comb. nov. was presented in Birstein (1960), so we therefore raise this taxon to species status. Naming of subspecies is rife in asellotan literature but in all such cases, the subspecies category is justified only by a short list of features that differ, regarded by the original author as 'minor'. Such justification is insufficient because the taxa involved remain diagnosably different, despite the original author's opinion of those features. Without clear genetic or morphological evidence of introgression, hybrid zones or similar data, the subspecies category is unjustified. *Gracilimesus orientalis*, comb. nov is one such case.

Gracilimesus orientalis, comb. nov. differs from *G. insignis*, comb. nov. by the following features: the spines on pereonite 1 of *G. orientalis*, comb. nov. are much smaller (approx. half) than those observed on *G. insignis*, comb. nov. The spines on pereonite 3 are approximately the same length in both species but they are much more robust in *G. insignis*, comb. nov. Antennula article 3 is 1.3× the length of article 4 in *G. orientalis*, comb. nov.; in *G. insignis*, comb. nov. article 3 is much longer, with a ratio to article 4 of 3.6; the posterolateral processes of the pleotelson are much longer in *G. orientalis*, approximately twice the length of the uropoda; the uropoda and posterolateral processes are subequal in *G. insignis*, comb. nov. Additionally, pereonite 7 of *G. orientalis* has two dorsal setae, a character not observed in *G. insignis*, comb. nov.

Gracilimesus tenuispinis (Hansen), comb. nov.

(Figs 12, 13)

Haplomesus tenuispinis Hansen, 1916: 64–65, pl. V, fig. 4a–f. – Gurjanova, 1932: 43–44, fig. XV, 52; 1933: 410; Gorbunov, 1946: 76; Menzies, 1962: 119–120, fig. 20I–J; Wolff, 1962: 72, 86, 272, 275, 288; Gurjanova, 1964: 259; Kussakin, 1988: 450–451, fig. 370.

Material examined

Holotype. Adult ♀, by original designation, Norway: Davis Strait, station 24, 63°06′N, 56°00′W, 1199 fathoms (2258 m), 2.4°C, 1 specimen, ZMUC CRU-8366.

Paratype. Adult ♀, **Norway:** Davis Strait, station 22, 58°10′N, 48°25′W, 1845 fathoms (3474 m), 1.4°C, 1 specimen without head, ZMUC CRU 9225

Remarks on type material

Hansen (1916) described two damaged female specimens, neither being designated holotype. Hansen, however, stated that in the event of the specimens being deemed separate species, the name *Haplomesus tenuispinis* be applied to the fragment consisting of the head and anterior pereonites (Hansen 1916: 65).

This is an indication that this specimen should be considered the holotype, as now labelled by the ZMUC. The second specimen consists of pereonites 3–7 and the pleotelson, and is labelled paratype. No reason was found to consider the two specimens different species. Both the holotype and paratype have become decalcified and as a result, the dorsal spines on pleonite 2 of the paratype are difficult to distinguish.

Diagnosis

Pereonites 1 and 4 in female with anterolateral spines, spines on pereonite 1 directed anterolaterally, spines on pereonite 4 directed anteriorly, male unknown; pleotelson dorsal surface axial ridge smooth, not separated from lateral fields, posterolateral spines present, tiny; pleonite 1 with one pair of posteriorly directed spines.

Description of female (male unknown)

Body cuticle granular. Head length 0.9 width, lobe on ventrolateral margin absent in lateral view. Pereonite anterolateral simple spines, short. Pereonite 4 length equals width, anterolateral spines, elongate. Pereonite 5 length 3.9 width. Pleotelson length 1.8 width; posterolateral margin at uropod insertion indented into margin, with one pair of spines on pleonite 2, directed posteriorly; posterolateral margin anterior to uropods with posterolateral spines weakly produced, much shorter than uropods.

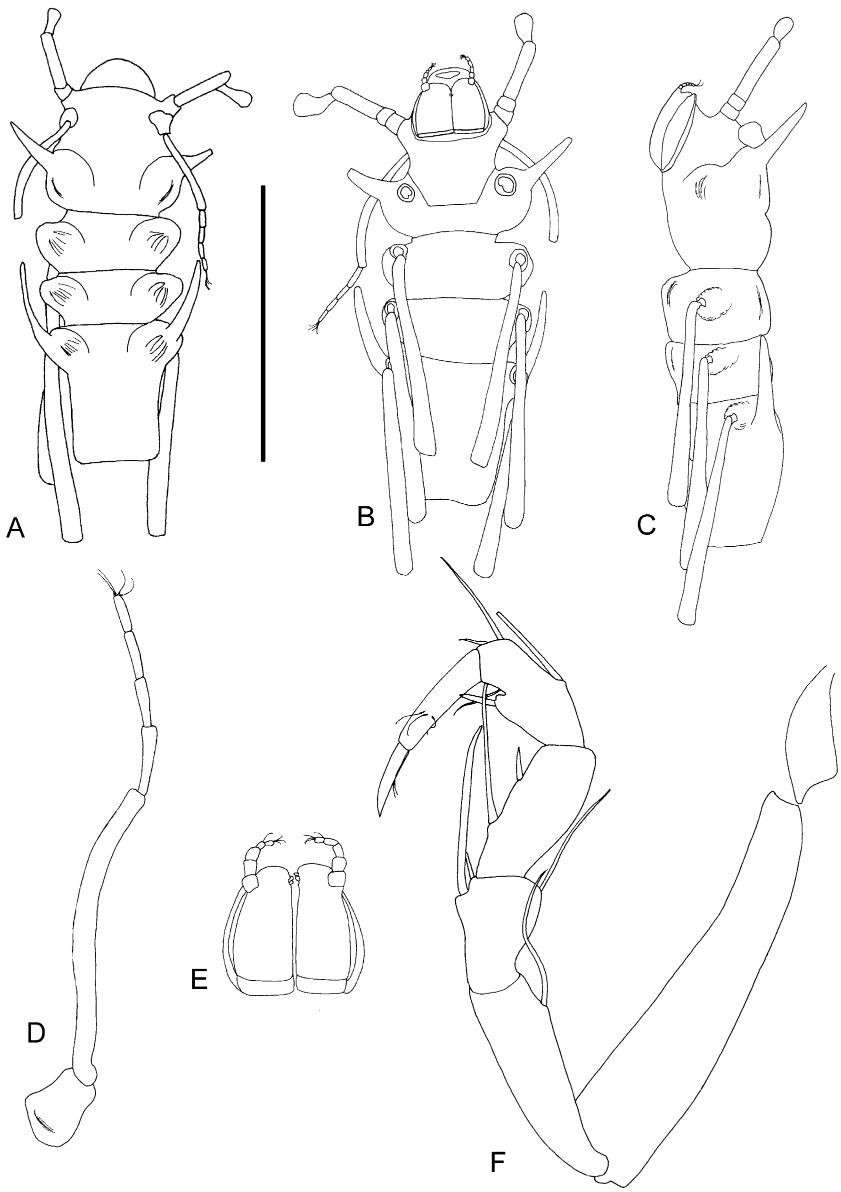

Fig. 12. *Gracilimesus tenuispinis*, comb. nov. (holotype female CRU-8366). *A*, Body dorsal view; *B*, body ventral view; *C*, body lateral view; *D*, antennula; *E*, maxilliped; *F*, pereopod I. Scale bar = 1 mm.

Antennula and antenna

Antennula with six articles altogether; article 1 with one penicillate seta; article 2 length 0.9 head width, with two elongate stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide; terminal article shorter than penultimate article; aesthetascs absent. Antenna article 3 length 0.15 anterior body length, length 4.6 width, cuticle smooth.

Mouthparts

Maxilliped endite with 2 receptaculi, palp article 2 wider than 3.

Pereopods

Pereopod I merus dorsal margin without distinctly robust setae. Pereopod I carpus with no robust setae proximal to elongate seta, with one robust seta on palm distal to elongate seta. Pereopod I propodus ventral margin with one robust seta, elongate, placed in centre of margin.

Pleopods and uropods

Uropods extending beyond posterior margin of pleotelson, length 2.6 basal width, length 0.16 length of pleotelson.

Distribution

Davis Strait (type locality); south of Davis Strait (paratype locality); Arctic Ocean, 698 m (Gorbunov 1946).

Remarks

Gracilimesus tenuispinis possesses dorsal spines on pleonite 1, as also seen on *G. modestatenuis* (see discussion under *G. modestatenuis* above). The spines on pereonite 4 of the

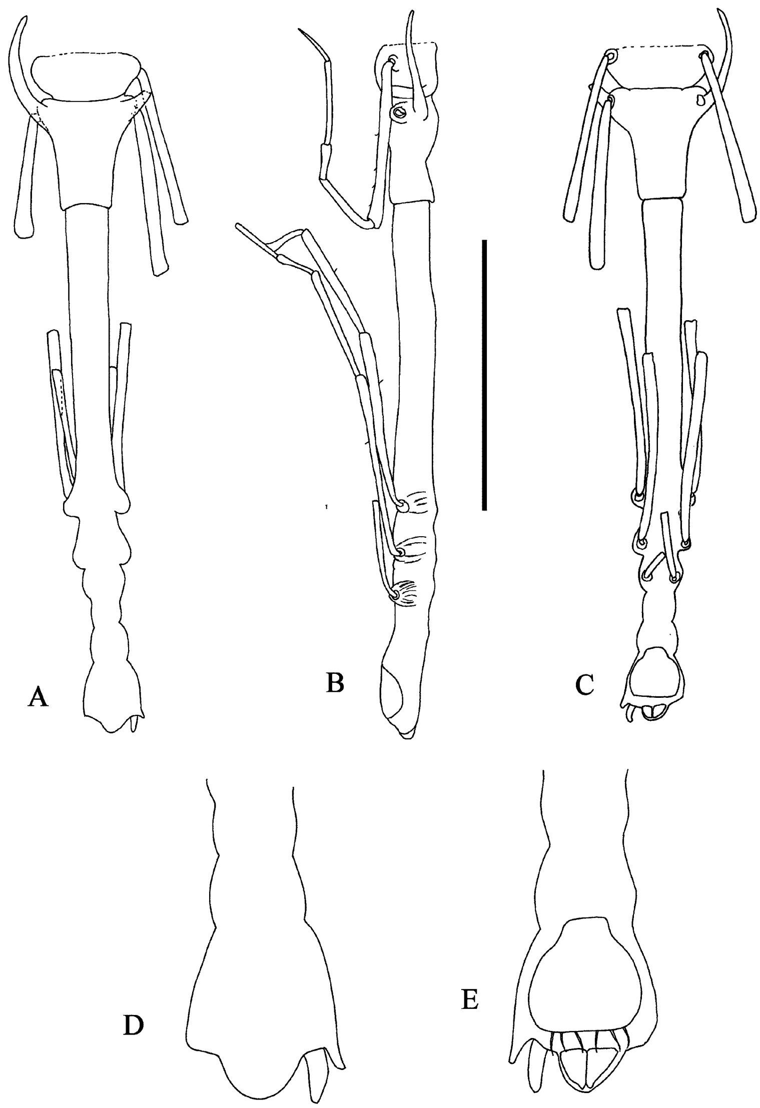

Fig. 13. *Gracilimesus tenuispinis*, comb. nov. (paratype female CRU-8366). *A*, Body dorsal view; *B*, body ventral view; *C*, body lateral view; *D*, pleotelson dorsal; *E*, pleotelson ventral. Scale bar = 1 mm.

species are distinctive, first by the elongate narrow shape, and second in that they are directed completely anteriorly and are in line with the main body-axis.

Genus ***Contrarimesus***, gen. nov.

Type species: *Haplomesus franklinae* Merrin & Poore, 2003.

Species included: *Haplomesus franklinae* Merrin & Poore, 2003; *Ischnomesus curtispinis* Brandt, 1992.

Diagnosis

Head lobe on ventrolateral margin absent in lateral view. Pereonites 5–7 articulation rudimentary, non-functional. Pereonites 5–7 narrowing posteriorly. Pleotelson dorsal surface axial ridge weakly vaulted, separated from lateral fields by shallow elongate concavities; posterolateral margin anterior to uropods without spines; posterolateral margin produced at uropod insertion. Antennula with six articles, distal flagellar articles much longer than wide. Pereopods with distinct neck between the pereopodal articulation of the basis and coxa and the shaft of the basis, with the basis neck and shaft forming an approximate right angle. Pereopod I merus dorsal margin with distal robust seta. Pereopod I carpus ventral margin without palm or distinctly wider part. Pleopod II female operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex. Uropods with two-articles, protopod distinct.

Distribution

Southern hemisphere: Tasman Sea off south-east Australia and the Southern Ocean, in the Eastern Sector off Queen Maud Land, Antarctica.

Remarks

Contrarimesus species differs from other members of the *Haplomesus*-group in that the uropoda consist of two articles instead of one. An examination of the type material of *Contrarimesus curtispinis* and *Contrarimesus franklini* showed that these two species are closely allied morphologically. Both have pereonites 5–7 and pleotelson fused but with faint sutures on the dorsal surface, along with a two-articled uropod. They also have a similar spination pattern and body shape. As discussed in the section on phylogenetic analysis (above), these species were placed separately from all other species, both of the *Haplomesus*-group and other genera. Although they could be considered basally derived to the *Haplomesus*-group, they are nevertheless distinct from all species therein. The discovery of further species similar to *C. franklinae* and *C. curtispinis* may resolve the relationship between them and the remainder species of the *Haplomesus*-group.

Etymology

From the Latin word '*contrārius*' meaning conflicting. This refers to the combination of characters from different genera: two-articled uropod and fused posterior pereonites and pleotelson that have resulted in these species previously being placed in incorrect genera.

Contrarimesus franklinae (Merrin & Poore), comb. nov. (Figs 14–15)

Haplomesus franklinae Merrin & Poore, 2003: 286–289, fig. 1–6.

Material examined

Holotype. Adult ♀, (illustration examined), Australia: Victoria, south of Point Hicks 38°25′S, 149°00′E, 1500 m, compacted clay, MV J20300.

Paratype. Adult ♂ (illustration examined), **Australia:** same details as holotype, MV J20303.

Other material examined. Adult ♂ (♂1 examined; non-terminal adult ♂ (♂2 examined); adult ♀ (examined), **Australia:** South of Point Hicks (38°29.33′S, 149°19.98′E), 1840–1750 m, sandy mud, MV J40688.

Remarks on type material

The holotype (MV J20300; 6 slides) was not examined. The male paratype (MV J20303) has been dissected and the remaining parts were decalcified and squashed; the dissected parts were not usable.

Diagnosis

Body hirsute, with numerous setae; pereonite 1 with paired median dorsal simple spines; pleotelson axial ridge truncated, approximately one-third length of pleotelson; pereopod I weakly carposubchelate, slightly different from pereopod II; pereopod I carpus with one shorter robust seta proximal to elongate seta, with one robust seta on palm distal to elongate seta; antennula terminal article shorter than penultimate article; antennula with aesthetascs; male pleopod I with distal and lateral setae; female pleopod II operculum with plumose setae.

Description of female

Body length 6 mm, cuticle granular; hirsute, with numerous setae; pereonite 5 fused with pereonite 6, articulation present and rudimentary, non-functional; pereonite 7 length reduced, less than pereonite 6. Head length 0.79 width; dorsal cuticle granulated, brittle and calcified. Pereonite 1 width 0.16 total body length; with one pair of anterolateral simple spines, elongate, length near width of pereonite 1. Pereonite 2–3 with one pair of anterolateral simple spines, short, length near pereonite 1 length. Pereonite 4 length 0.7 width, with one pair of anterolateral simple spines, tiny, length distinctly less than length of pereonite 1. Pereonite 5 length 4.4 width; 0.37 total body length. Pleotelson length 1.47 width.

Antennula and antenna

Antennula with six articles altogether; article 1 with one penicillate seta; article 2 length 0.86 head width, inserting on article 1 dorsally, straight, not curved at proximal insertion, with four elongate stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 longer than article 4, elongate and tubular, much longer than wide. Antenna article 3 length 0.21 anterior body length, length 3.3 width, with randomly-placed simple spines on ventral surface.

Mouthparts

Maxillula with 12 robust setae on lateral lobe; medial lobe with one robust medially-projecting dentate seta. Maxilla with two long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe.

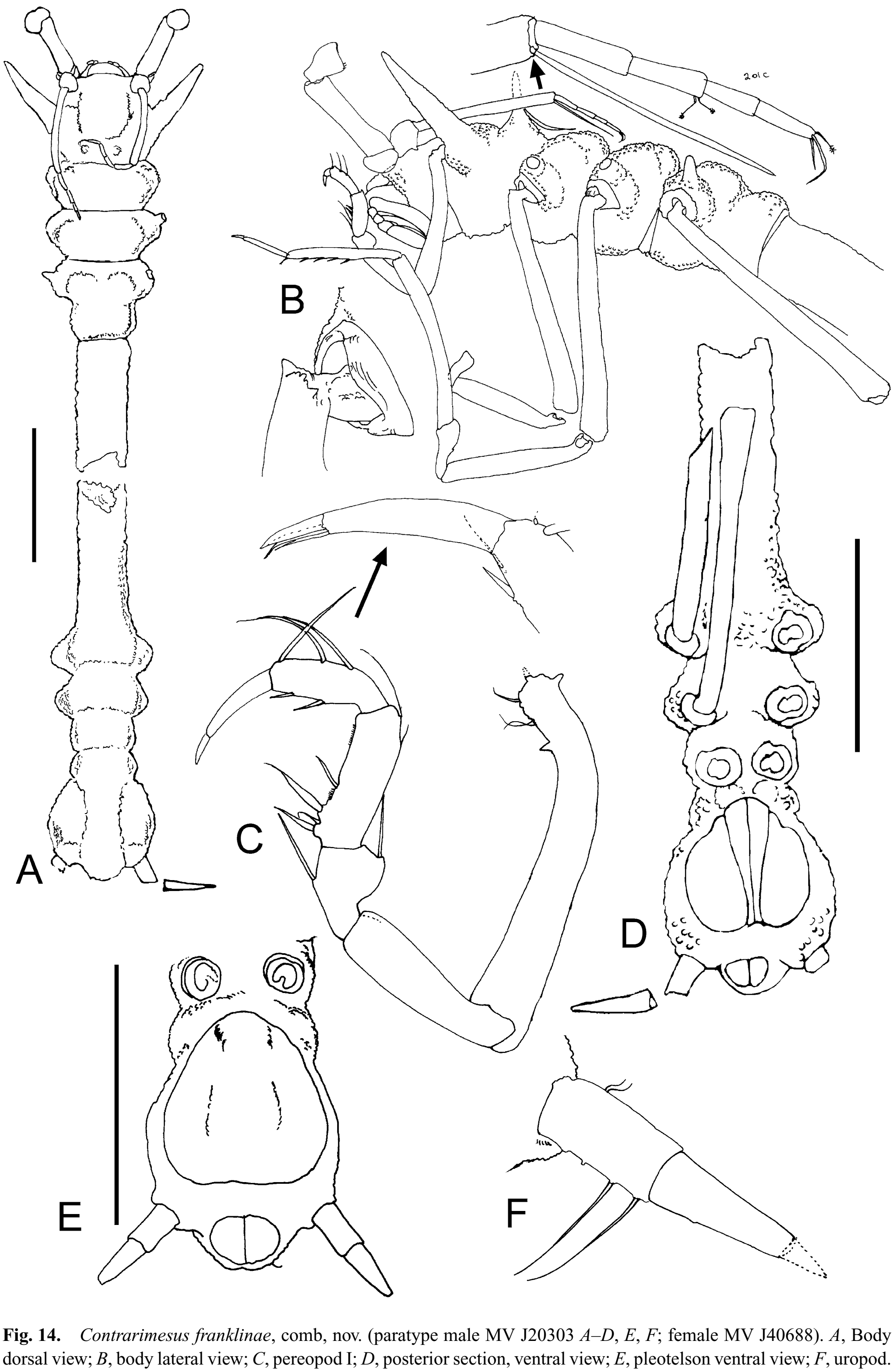

Fig. 14. *Contrarimesus franklinae*, comb, nov. (paratype male MV J20303 *A–D*, *E*, *F*; female MV J40688). *A*, Body dorsal view; *B*, body lateral view; *C*, pereopod I; *D*, posterior section, ventral view; *E*, pleotelson ventral view; *F*, uropod. Scale bars = 1.0 mm.

Pereopods

Pereopod I propodus ventral margin with two robust setae, one distal elongate simple seta. Pereopods II–VII bases with random pattern of simple spines on dorsal and ventral margin.

Pleopods and uropods

Pleopod II operculum with narrow proximal neck, laterally convex, broadening posteriorly to rounded angles, posterior margin weakly convex. Pleopod III exopod with plumose setae, with fringe of fine setae.

Description of male

Body length 6.0 mm. Head length 0.82 width; cuticular structure granular. Pereonite 1 width 0.14 total body length. Pereonite 4 in male length 1.3 width. Pereonite 5 length 3.3 width; 0.49 total body length. Pleotelson length 1.25 width.

Antennula and antenna

Antennula article 2 length 1.13 head width. Antenna article 3 length 0.25 anterior body length, 3.8 width.

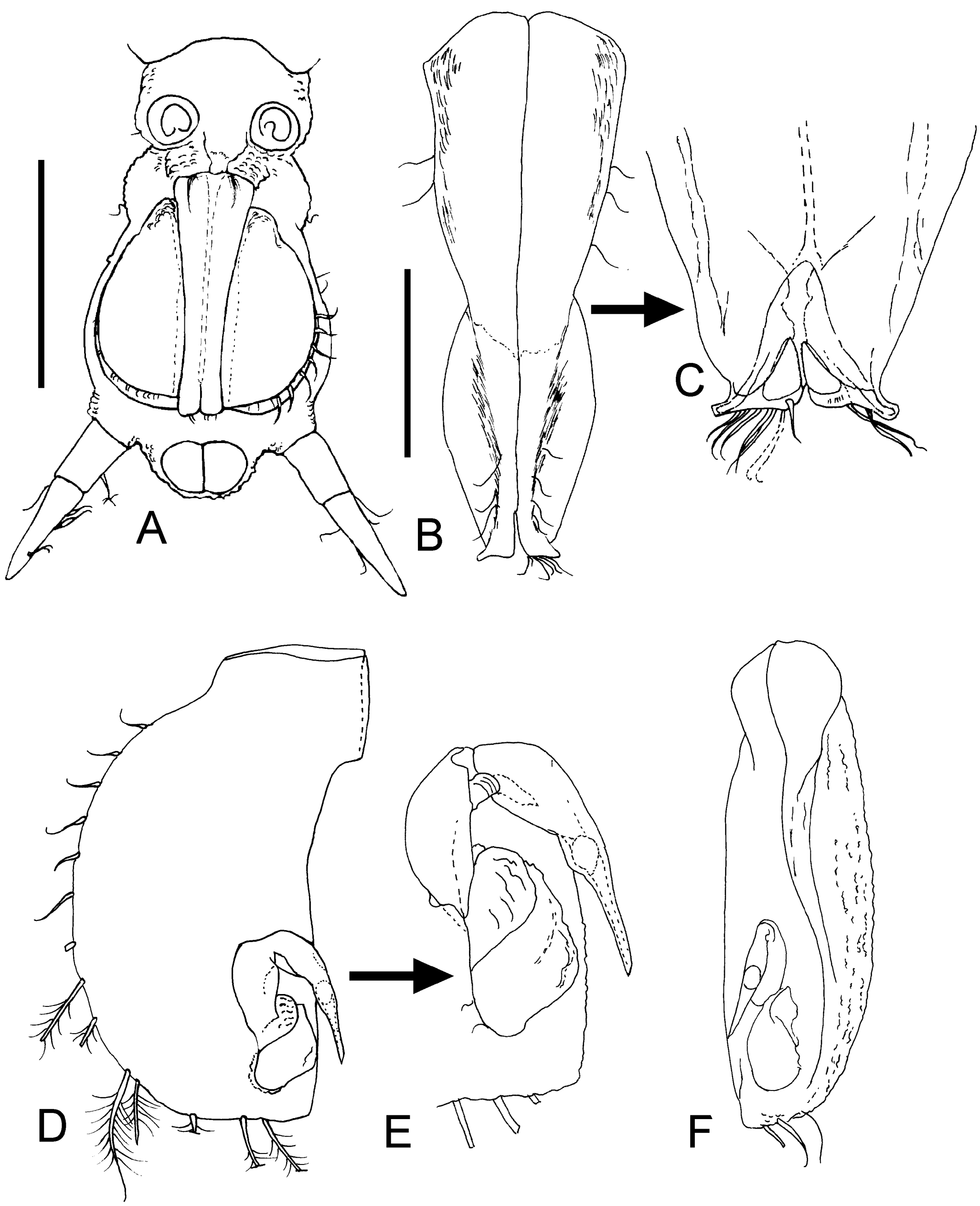

Fig. 15. *Contrarimesus franklinae*, comb, nov. (male pleopods male 2 MV J40688). *A*, Pleotelson ventral; *B*, pleopod I, ventral view; *C*, pleopod I, dorsal view; *D*, pleopod II; *E*, pleopod II stylet; *F*, pleopod II medial view. Scale bar *A* = 0.5 mm, *B*–*F*, 0.1 mm.

Pleopods and uropods

Pleopod I with simple setae on distal margins, with simple setae on lateral margins. Pleopod II protopod rounded, stylet not extending to distal margin of protopod.

Distribution

South-east Australia, 990–1840 m.

Remarks

Contrarimesus franklinae can be distinguished from *C. curtispinis* by several characters. The spination pattern of the anterior pereonites differs between the two species: *C. franklinae* has paired median dorsal spines on pereonite 1 and anterolateral spines on pereonites 1–4. It also possesses numerous setae on the body surface. *Contrarimesus curtispinis* has anterolateral spines on pereonite 1 only, lateral spines on pereonites 2–3 and only scattered setae on the body surface.

Contrarimesus curtispinis (Brandt), comb. nov.

(Fig. 16)

Ischnomesus curtispinis Brandt, 1992: 193–197, figs 5–7.

Material examined

Holotype. Manca (examined), by original designation. Antarctica, sample ANT VIII/, station 1805–5, 66°11.5′S 35°18.7′E, 4149 m, collected using a box-corer, NHM 1990: 46: 1.

Paratypes. 2 mancas (examined), **Antarctica:** same details as Holotype, BM(NH) 1990: 47: 2.

Remarks on type material

The holotype is a manca, without any trace of pereopod VII. It has been dissected and the head, pereonite 1, pereonites 6–7 and pleotelson have been removed. The pleotelson itself has not been illustrated, nor has the slide of the pleopods or the pleotelson been deposited. The pleotelson of an adult female was also collected, from a second locality (station 1822–1, 66°55.1'S 34°18.1'E, 1981 m, collected using box-core) and the pleopods were described from this. Two additional manca specimens from the type locality were designated paratypes. One of the manca paratypes is clearly a different species and belongs to the genus *Cornuamesus*, gen. nov., determined by the presence of long, thin anterolateral projections supporting the antennae and elongate single-articled uropods.

Diagnosis

Body with scattered setae only; pereonite 2 with lateral spines; pereonites 3 and 4 with lateral tubercles; antennula without aesthetascs; antennula article 2 with one ventromedial seta, inserting on article 1 anterodorsally; antennula terminal article longer than penultimate article; Pereopod I carpus with no robust setae proximal to elongate seta, with no robust setae on palm distal to elongate seta; mandible with one receptaculi; pleopod II operculum with plumose setae.

Description of manca

Body cuticle granular; pereonite 5 fused with pereonite 6, articulation present and rudimentary, non-functional. Head length 0.9 width. Pereonite 1 width 0.15 total body length, with one pair of anterolateral simple spines, short, length near pereonite 1 length. Pereonite 4 0.7 width. Pereonite 5 in female length 3 width; 0.4 total body length. Pleotelson posterolateral margin at uropod insertion indented into margin.

Antennula and antenna

Antennula with six articles altogether; article 1 with one penicillate seta; article 2 length ~2.0 article 1 length, length 0.77 head width, inserting on article 1 anterodorsally, with one elongate stiff ventromedial setae; distal articles altogether small, shorter than article 2; article 3 elongate and tubular, much longer than wide; aesthetascs absent. Antenna article 3 length less than twice article 4 length, 0.15 anterior body length, length 3.6 width; flagellum with nine articles.

Mouthparts

Maxillula with 12 robust setae on lateral lobe; medial lobe with one robust medially-projecting dentate seta. Maxilla with two long (approximately as long as lateral lobes) medially-projecting pectinate seta on medial lobe. Maxilliped palp at widest point width narrower than endite, article 3 wider than article 2.

Pereopods

Pereopod I propodus ventral margin with two robust setae.

Pleopods and uropods

Pleopod III exopod with plumose setae, with fringe of fine setae. Uropods with two articles, protopod distinct; extending beyond posterior margin of pleotelson; length 4 basal width; length 0.42 length of pleotelson.

Distribution

Southern Ocean off Queen Maud Land, Antarctica, East of the Gunnerus Ridge. Known only from the type locality.

Remarks

The observations regarding the fusion of pereonites 5–7 and the pleotelson have been made from the paratype that does belong to this species. We are confident that it is the same species as the holotype. The fusion of the pereonites means that this species does not belong to the genus *Ischnomesus*.

Remarks on the genus *Mixomesus* Wolff

The genus *Mixomesus* currently has only one described species, *M. pellucidus* Wolff, 1962. The type is in poor condition, so new specimens and species are needed to ascertain the status of genus. Therefore, we have excluded this genus from the analysis. The main characters for the species are described.

The body cuticle of *M. pellucidus* is granulated. Pereonites 5–7 were described as ‘probably’ freely articulated. As in *Cornuamesus*, gen. nov., pereonite 4 is more elongate than normally observed, a condition also found in some species of *Ischnomesus*. No spines are present on the body or the pleotelson. The pleotelson axial ridge is weakly vaulted, and Wolff (1962) recorded the specimen as having no uropods present. Although Wolff noted a tiny groove on the ventral surface of the pleotelson that might be the point of insertion, he was certain that the uropods were not present. The antennula of *M. pellucidus* has

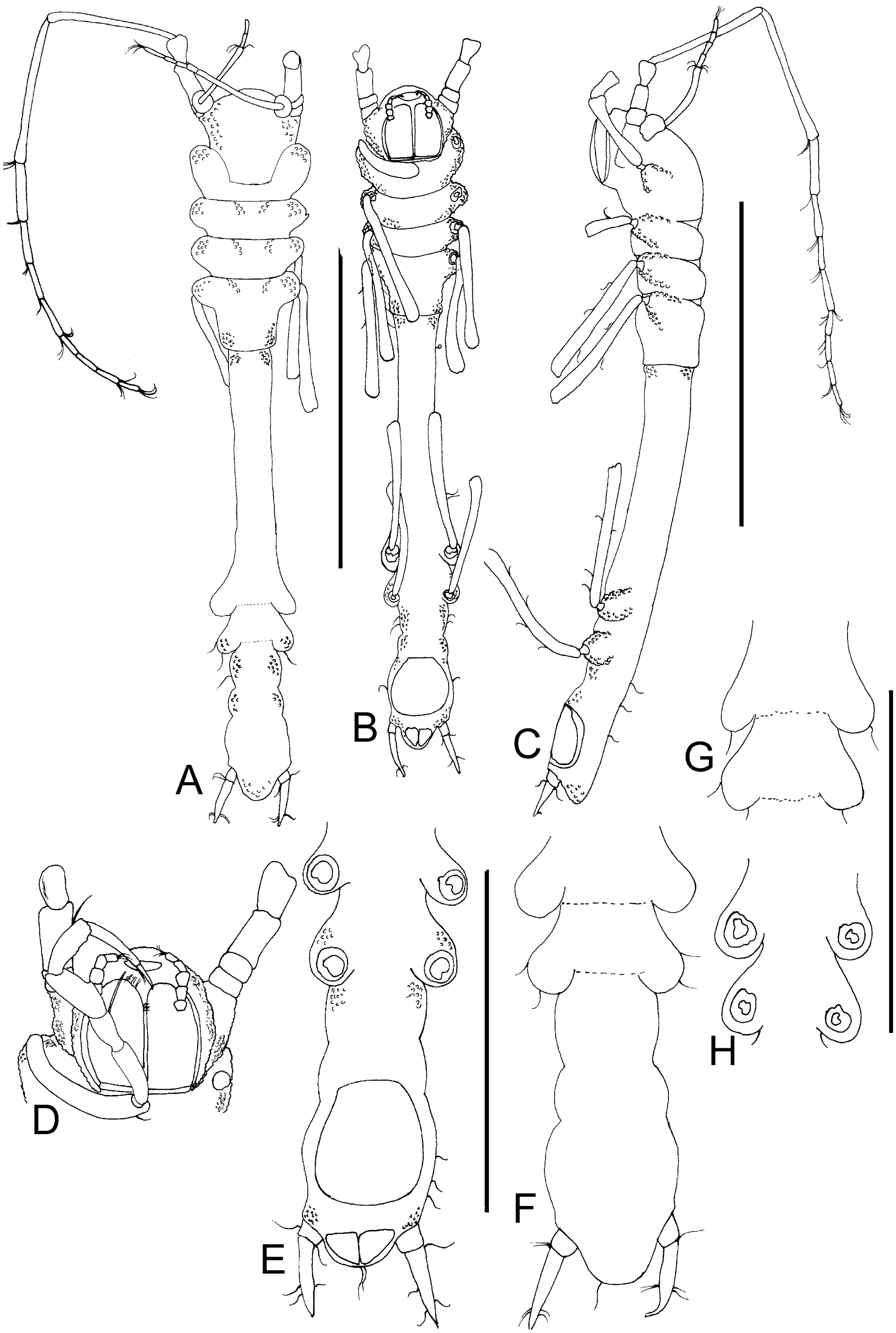

Fig. 16. *Contrarimesus curtispinis*, comb. nov. (manca paratype BM (NH): 1990: 46 1 *A–F*; manca holotype BM (NH): 1990: 47: 2 *G–H*). *A*, Body dorsal; *B*, body ventral; *C*, body lateral; *D*, head ventral; *E*, pleotelson dorsal; *F*, pleotelson ventral; *G*, p5–6 dorsal; *H*, p5–6 ventral. Scale bars = 1 mm.

seven articles, consisting of a squat first article as for the remainder of the family. In place of the usual long second article, however, Wolff illustrated four articles of equal length, which he considered part of the 'peduncle,' followed by two short articles that constituted the flagellum. Antennula article 2, as described, is only slightly longer than article 1, the distal articles are longer than article 2, articles 3 and 4 are of similar length and the terminal article is longer than the penultimate article. We interpret these four articles as pseudoarticulation caused by damage to article two. If the basal section of the antennula did constitute five articles, this would be an apomorphy for the genus. Thus, the elongate antennula article 2 inserts dorsally on article 1, and is straight, not curved at proximal insertion. Ventromedial setae are not present on article 2, and distomedial and distolateral spines are not present on article 3 of the antenna. The maxilliped of *M. pellucidus* has two receptaculi, with articles 2 and 3 expanded wider than article 1. Pleopod III exopod is more than half the endopod length, with several short setae on the exopod. As no male specimens of the species have been collected, the male pleopods are unknown. In addition, uropods, pereopods and female operculum are unknown for *Mixomesus pellucidus*.

Recently, we have seen a new undescribed species of this genus from the Arafura Sea (between Indonesia and Australia), and can confirm that *Mixomesus* does have a uropod, although tiny, thin and biarticulate. The tiny uropod explains why open insertions for the lost uropods were not observed on Wolff's (1962: 89) specimen. Other features of the genus include incompletely articulated pereonites 5–7 and pleon; the posterior somites are largely inarticulate but with grooves similar to *Contrarimesus* species. Males of *Mixomesus* are more robust and have pereonites with lateral elongate stiff setae sitting on heavy calcified bases. This genus does not belong to *Haplomesus sensu lato* (research in progress).

Distribution and diversity

Most described species of the *Haplomesus*-group are rarely recorded and are known from a single find only. Significant regions of the world ocean have not been sampled, particularly in the southern hemisphere, so the distributions of genera are likely to change with increased sampling effort. All genera of the *Haplomesus*-group have wide distributions, recorded from at least two oceans. *Haplomesus sensu stricto* is recorded throughout the Atlantic and one species, *Haplomesus* cf. *quadrispinosus sensu* Brandt is recorded from the Southern Ocean in the Antarctic. Species of *Fortimesus*, gen. nov. are recorded from the north-west Pacific Ocean, with one exception, *Fortimesus zuluensis*, comb. nov., which is recorded from South Africa. Owing to its presumed absence in the Atlantic Ocean, one might predict that new localities for this genus may be found in the Indian Ocean. Species of *Gracilimesus*, gen. nov. are recorded mostly from the Atlantic Ocean, with some species found in the Arctic Ocean. Both species of *Contrarimesus*, gen. nov. are recorded from the southern hemisphere, from the South Pacific and Antarctic Oceans. Finally, although the two described species of *Cornuamesus*, gen. nov. are recorded from the Bay of Biscay, undescribed species exist throughout the Atlantic Ocean (see Kavanagh and Sorbe 2006). Species of *Fortimesus*, gen. nov. are recorded from deeper waters than other genera. The depth range for species of the genus is 800–8830 m. Most species, however, are recorded below 3500 m with one exception: *Fortimesus zuluensis*, comb. nov. is recorded from 800–810 m. The remaining four genera have similar depth ranges, with an upper limit of ~500 m and a lower limit of ~5000 m, although the lower limit is subject to sampling bias. An exception is *Cornuamesus*, gen. nov., which has a lower limit of 1877 m. However, as only two species are described, this is a provisional range.

The region with the highest diversity is the north-east Atlantic Ocean, with three of the four genera of the *Haplomesus*-group recorded from here. This observation, however, is a reflection of sampling bias. Most of asellote research has been carried out in the north-east Atlantic, resulting in more detailed regional knowledge of diversity (e.g. Sars 1869; Hansen 1916; Chardy 1974, 1975). Significant differences in the morphology of species in the Pacific compared with the Atlantic Ocean are apparent in our data. Species recorded from the Pacific Ocean are more spinose and tuberculate than species from the Atlantic Ocean, and several exhibit a large body size (e.g. *Fortimesus gigas*, comb. nov. and *Fortimesus consanguineus*, comb. nov.).

To conclude, the *Haplomesus*-group can be characterised as comprising deep-water species, collected across most of the world's oceans, with further sampling likely to yield new species with novel morphologies in less well sampled regions.

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