

**Systematics, zoogeography, evolution and biodiversity of
Antarctic deep-sea Isopoda (Crustacea: Malacostraca)**

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Our knowledge can only be finite, while our ignorance must necessarily be infinite.

Karl Raimund Popper

**According to ICZN article 8.3 all names and nomenclatural acts
in this thesis are disclaimed for nomenclatural purposes.**

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Summary

The present thesis deals with the isopods obtained during the expeditions ANT XIX/3+4 (ANDEEP I+II) with RV “Polarstern” to the deep sea of the Southern Ocean.

It contains three major topics: Taxonomy, biodiversity and zoogeography, phylogeny.

In the taxonomy part two families are treated. Two new species of the family Ischnomesidae, *Stylomesus hexapodus* n. sp. and *Haplomesus corniculatus* n. sp., are described. Both species display neoteny, the retention of juvenile characters in adult specimens. This phenomenon was previously undescribed within the family, yet is common within several other isopod taxa.

The family Haploniscidae is treated in more detail. A description of the family and diagnoses for the four genera *Antennuloniscus* Menzies, 1916, *Mastigoniscus* Lincoln, 1985a, *Chauliodoniscus* Lincoln, 1985a and *Hydroniscus* Hansen, 1916 are given and the family and genera are discussed.

Three *Antennuloniscus* species are described from the ANDEEP material, the new species *A. latoperculus* n. sp. and the two species *A. armatus* Menzies, 1962 and *A. ornatus* Menzies, 1962.

Within the genus *Mastigoniscus* five species are described, *M. polygomphios* n. sp., *M. andeepi* n. sp., *M. pseudoelegans* n. sp., *M. sp. A* and *M. sp. B*. The latter two species remain unnamed, because they are known from juvenile specimens alone.

The genus *Haploniscus* Richardson, 1908 discussed and a species complex within this genus is described. The *Haploniscus cucullus* complex (named after one of its species) comprises the seven new species: *H. cassilatus* n. sp., *H. cucullus* n. sp., *H. weddellensis* n. sp., *H. procerus* n. sp., *H. kyrbasius* n. sp., *H. nudifrons* n. sp. and *H. microkorys* n. sp.

Additionally the intraspecific variation within the family is treated in detail with respect to sexual dimorphism, ontogeny and variation without relation to sex or age.

The biodiversity and zoogeography part deals with all isopods obtained by means of an epibenthic sledge during the ANDEEP expeditions. In total 5525 isopod specimens were sorted from the samples; they belonged to at least 312 species. Most abundant was the family Munnopsididae, followed by Haploniscidae, Ischnomesidae and Desmosomatidae. Only 2% of all isopod specimens belong to suborders other than the Asellota. The community and

diversity patterns were found to be patchy, but the importance of depth as environmental factor could be demonstrated.

Most species identified within the ANDEEP material were known from the Atlantic. Within the family Haploniscidae this is the first record of the genus *Mastigoniscus* in the Atlantic sector of the Southern Ocean. A worldwide distribution of most haploniscid genera can be supposed. Contrary the data from the *Haploniscus cucullus* complex indicate that the geographical range of species is small.

The phylogeny chapter deals with the family Haploniscidae; 48 species from five genera of the family were analyzed. The analysis was conducted with unweighted characters as well as with weighted characters. The resulting consensus trees of both analyses are similar.

The monophyly of *Antennuloniscus*, *Chauliodoniscus*, *Mastigoniscus* and *Hydroniscus* is supported, while *Haploniscus* proved to be polyphyletic, as was expected.

Antennuloniscus was found to be the most derived genus of the family, followed by *Chauliodoniscus* and *Mastigoniscus*. *Hydroniscus* was the most basal taxon. Several *Haploniscus* species are grouped in close proximity to *Antennuloniscus* or *Mastigoniscus*.

The consistency indices of the resulting trees and also most of the bootstrap values are low, and some of the important sister-group relationships are only weakly supported, leaving the relationships of the genera to each other somewhat uncertain. The resolution in some terminal clades of the tree also has to be considered as doubtful.

1 Introduction

1.1 The deep sea

The deep sea can be either defined by topographic criteria as beginning at the shelf break, which means at about 200 m depth, or by hydrographic criteria as those water masses below the permanent thermocline, which is a layer of rapid temperature decrease with depth. The depth of the permanent thermocline varies with latitude, at high latitudes it is nearly absent (Gage and Tyler, 1991).

The oceans cover two thirds of the earth's surface and 90% of the oceans are deep sea, i. e. below the shelf break. As investigation area it is difficult to access and expeditions devoted to the exploration of the deep sea require a huge amount of logistic as well financial capacities. Therefore the sampling activity in the deep sea is still deficient and so is our knowledge about this habitat.

The living conditions in the deep sea include almost complete darkness, high pressure, low temperatures and highly limited food availability. Sediments in the deep sea are mostly soft bottom sediments, often with a high proportion of biogenic material. Hard substrate is relatively rare. Due to the absence of light, species in the deep sea are often blind; some possess extremely sensitive eyes and a number of species show bioluminescence.

It is known that biomass and abundance of organisms decrease with depth and that both are low in the deep sea due to limited availability of food (Rex *et al.*, 1997). Therefore larger areas have to be sampled in the deep sea compared to shallow water to assess the diversity of this habitat.

While the deep sea was long regarded to be a habitat of low diversity, it was shown by Hessler and Sanders (1967) that it holds in fact a hitherto unexpected high diversity in benthic communities. To explain this high diversity in an apparently uniform environment, different factors were considered:

The high stability of this environment over long evolutionary periods, which allowed enhanced niche fragmentation (Sanders, 1968, Hessler and Sanders, 1967) on the one hand and habitat heterogeneity caused by biological activity, disturbance events on smaller and larger scale (Snelgrove and Smith, 2002), as well as patch food supply (Grassle, 1977) on the other hand. Gray (1997) showed that the conditions in the deep sea are not as stable as long suspected and that larger scale disturbances are caused by internal tides, hydrodynamic storms, down-slope cascading of cooled dense water, internal waves and eddies; although he found a negative correlation of macrobenthic diversity with increasing bottom current energy,

he stated that these large scale hydrodynamic disturbances might play a role for the high diversity of the deep-sea benthos. Snelgrove and Smith (2002) explained that modest disturbance may balance diversity in this low-energy environment, where a large food fall, for example, may have much longer lasting effects than in shallow water.

Diversity patterns were found to vary considerably at larger scales; Rex *et al.* (1997) described the variability of large-scale biodiversity patterns with respect to both bathymetry and latitude. Rex *et al.* (1997) found maximum species richness at mid-slope depth, while the species richness declined towards greater depth; nevertheless, this might be an artifact, caused by the decreasing abundance with depth (Gage and Tyler, 1992). While it is clear that in the southern hemisphere the diversity varies considerably between different deep sea areas, the database on latitudinal patterns is still weak (Rex *et al.* 1993). However, in the North Atlantic a decreasing diversity with latitude was found by several authors (e. g. Rex *et al.*, 1993).

1.2 The Southern Ocean

After the break-up of Gondwana and the separation of Antarctica and the Indian subcontinent approximately 130 Ma ago, Africa was the next continent that moved away from the Antarctic and both continents were separated about 90 Ma ago (Lawver *et al.*, 1992). The enhanced northward movement of Australia (45 Ma) resulted in the development of a deep water current around east Antarctica after the opening of a passage between the Tasman Rise and Antarctica (Lawver *et al.*, 1992), which led to a successive cooling and glaciation of the East Antarctic (Huber & Watkins, 1992). Finally the separation of South America and Antarctica and the opening of the Scotia Sea (about 30 Ma ago) resulted in the establishment of the circum-Antarctic current roughly 20 Ma ago (Lawver *et al.*, 1992) and further cooling of the Southern Ocean (Clarke and Crame, 1989, 1992).

The circum-Antarctic current is driven by the west winds and is the largest current system in the world oceans (Fahrbach, 1995). It isolates the shallow marine fauna of the Southern Ocean from other shelf areas (Clarke 1990). As a consequence the degree of endemism on the Southern ocean shelf is high (Clarke, 1996b; Clarke and Crame, 1989).

The Antarctic Bottom Water represents the deepest water masses in the oceans; it forms the circumpolar bottom water and spreads into all main world oceans (Gage and Tyler, 1992). As this might play an important role for the spreading of deep-sea organisms from the Southern Ocean into the deep sea of the world oceans, the deep-sea areas surrounding Antarctica and influenced by the Southern Ocean deep water production are particularly

interesting with respect to zoogeography. Besides the Ross Sea, and the Adelie Coast area, the Weddell Sea is one of the major sources of the Antarctic deep water production.

Extensive deep-sea areas are located around the Antarctic continent and its shelf. Sediments in these areas differ from deep sea sediments of lower latitudes in the higher proportion of siliceous biogenic material and material carried by icebergs, especially larger drop-stones, which provide hard substratum for sessile organisms amidst the soft bottom abyssal plains (Clarke, 1996a).

Due to the absence of a thermocline in the Southern Ocean, emergence and submergence may be enhanced, resulting in an increased faunal exchange between shelf and deep sea.

The Antarctic shelf holds a rich and diverse fauna (Clarke, 1996c). Arntz *et al.* (1997) demonstrated the predominance of crustaceans besides the relative important groups Polychaeta and Mollusca. While several groups of Crustacea, like Decapoda, Stomatopoda and Cirripedia, well represented in the world oceans, are rare or completely absent from Antarctic waters, the peracarid taxa Isopoda and Amphipoda are highly speciose and abundant in the Southern Ocean. The degree of endemism on the Antarctic shelf is high (87% for the Isopoda according to Brandt, 1991).

De Broyer and Jazdzewski (1996) and De Broyer *et al.* (2003) explained the high diversity of Antarctic benthic species and Antarctic Peracarida in particular with several factors: The long evolutionary history of this isolated environment; the habitat heterogeneity partly caused by iceberg drop stones; the low dispersal potential due to the fact that peracarids possess a brood pouch and lack free larvae; the limited mobility of bottom dwelling peracarids and finally the extinction of most Decapoda, especially brachyuran crabs, during the tertiary cooling of the Southern Ocean, which left ecological niches vacant for peracarid crustaceans.

The origin of the Southern Ocean shelf fauna is still enigmatic. Theories involve in situ evolution and invasion either via the Islands of the Scotia Arc or the deep sea (Clarke and Crame, 1989, Hessler and Thistle, 1975). Under this view, the deep sea areas of the Southern Ocean and its faunal composition are particularly interesting. While the shelf fauna of the Southern Ocean is at least partly well documented, the knowledge about the surrounding deep sea areas and the relationship between deep-sea and shelf fauna is still deficient.

1.3 Deep-sea Isopoda

Isopods represent an important group among the Crustacea in the deep-sea macrofauna (Gage and Tyler, 1991). Most of them belong to the suborder Asellota Latreille, 1803 and the

superfamily Janiroidea Sars, 1897 (Hessler *et al.*, 1979; Wilson and Hessler, 1987). Janiroidea show a great variety of body shapes; the family Munnopsididae contains swimming forms with a muscular pereon and flattened swimming legs; the family Ischnomesidae contains species with an elongated habitus; several groups like Acanthaspidiidae and Mesosignidae have developed extensive processes of the pereon and pleon, while others, e. g. the Haploniscidae, have a compact and smooth body shape. An important apomorphy of the Janiroidea is the modified endopod of pleopod 2, which has a closed sperm duct (Wägele, 1987). Wilson (1991) proposed that the modified mating system enabled the success of the Janiroidea in the deep sea, because it provides a longer time period for mating, not only the short phase during the molt, which is typical for other isopods. This might be an essential advantage in the deep sea, where abundances are low and mate finding might be difficult.

The knowledge about the biology of the deep-sea species is limited; several studies have treated the gut contents of deep-sea isopods (e.g. Gudmundsson *et al.*, 2000; Svavarsson *et al.*) and revealed Foraminifera as important food source for some species; Wolff (1962) documented the postmarsupial development by means of specimens of different age; among others he studied four species of the family Haploniscidae. A study on the behavior of shallow water species of the janiroidean families Janiridae, Munnidae, Paramunnidae, Ischnomesidae, Desmosomatidae, Macrostylidae and Munnopsididae was published by Hessler and Strömberg (1989). The phylogeny of most groups is still unclear as well.

Both families dealt with in the taxonomy chapters of this thesis, Haploniscidae and Ischnomesidae, are frequently found in deep sea samples (e. g. Menzies, 1962, Wolff, 1962) and are known to be typical deep sea families (Hessler and Thistle, 1975).

Family Haploniscidae Hansen, 1916

Since the family Haploniscidae will be treated in more detail also in the phylogeny chapters, a short introduction in this family shall be given in the following.

The first species described from this family was *Haploniscus bicuspis* (Sars, 1877), which was originally placed in the genus *Nannoniscus* Sars, 1869, family Nannoniscidae Hansen, 1916. Richardson (1908) allocated it as type species into her newly established genus *Haploniscus*. The family was erected as “Haploniscini” by Hansen (1916) for the two genera *Haploniscus* Richardson, 1908 and *Hydrioniscus* Hansen, 1916; besides, several new species were described by Hansen, based on material from the Danish Ingolf Expedition in the North Atlantic. The third genus was established by Menzies (1962) for the type species *Haploniscus dimeroceras* Barnard, 1920 and new species from the *Vema* expeditions to the Atlantic, and

named *Antennuloniscus*. Menzies added 20 new species to the family from the *Vema* material. Menzies and Schultz (1968) described the monospecific genus *Aspidoniscus*, by means of a single juvenile specimen from the Southern Ocean. The second monospecific genus *Abyssoniscus* was added by Birstein, 1971. He described 12 species altogether from the Pacific (Birstein, 1963a, 1963b, 1968, 1969, 1971). Chardy (1974, 1975) contributed 7 species from the North Atlantic. Lincoln (1985a) described eight species from off New Zealand and seven species from the North Atlantic and established *Chauliodoniscus* and *Mastigoniscus*. *Mastigoniscus* was reviewed by Park (2000), who redefined the generic characters and added three new species to the genus. Recently another genus was erected by George (2004), *Chandraniscus*, whose taxonomic position will be discussed below. George also described several new species. Including these and the species described within this thesis the family now comprises 118 species.

The phylogenetic relations within the family are still doubtful. The only phylogenetic analysis of the Haploniscidae was done by Chardy (1977) based on morphological characters. His analysis of morphological similarities revealed the presence of four separated groups within *Haploniscus*, two of which were later described as the genera *Chauliodoniscus* and *Mastigoniscus* by Lincoln (1985a). This analysis by Chardy was mainly based on literature data. Due to the inadequate descriptions of most species Chardy's dataset was restricted to mostly habitus characters and therefore rather limited.

1.4 Aims and questions

This thesis deals with the isopods obtained during the ANDEEP I and II expeditions (ANT XIX/3+4) to the deep sea of the Southern Ocean. Several aims and questions are dealt with.

The identification and description of new isopod species from selected families is the first step and the basis for further research. Especially the taxonomy and morphology of the family Haploniscidae are treated within this thesis.

The biodiversity part deals with the following questions: What is the isopod composition of the Southern Ocean deep sea? How many isopod species can be found in the Antarctic deep sea? It also deals with patterns of biodiversity and distribution of deep sea isopods in the Southern Ocean

The phylogeny part deals with the family Haploniscidae again; the phylogenetic relationships within the family are investigated.

2 Material and Methods

2.1 Sampling

During the Expeditions ANT XIX/3+4 (ANDEEPI-II, ANtarctic benthic DEEP-sea biodiversity) with “RV Polarstern” in the Southern Ocean samples were obtained by means of an epibenthic sledge (construction by Nils Brenke, modified, but with the same sampler measurements as in Brandt and Barthel, 1995). The stations belonged to four different geographical areas. Stations 41, 42, 43, 46 and 129 were located close to the Shackleton Fracture Zone and around Elephant Island, stations 99, 105 and 114 were near the South Shetland Islands, stations 131-138 formed a transect down the continental slope east of the Antarctic Peninsula and across the western Weddell Sea and stations 139-142 were located around the South Sandwich Island.

The epibenthic sledge has two sampling boxes in the front part, both with an opening of 100 cm width and 33 cm height. The epibenthic sampler begins 27 cm above the seafloor, the suprabenthic sampler begins 100 cm above the seafloor. A plankton net of 0.5 mm mesh size is attached to each sampler. The samples accumulate in the cod ends, which are equipped with a one-way valve and have a mesh size of 0.3 mm. When the sledge touches the seafloor, a lever opens both samplers, while the sledge travels through the water column the boxes are closed to ensure that only benthic samples are obtained.

The sledge was hauled over the ground for 10 min at a mean velocity of 1 knot. The haul distances were calculated on the basis of the velocity of the ship and the winch during trawling and heaving until the sledge left the ground, based on the following formula:

$$\text{haul length } s = v_{ship} \times \Delta t_{trawling} + v_{winch} \times \Delta t_{heaving} + v'_{ship} \times \Delta t_{heaving}$$

v_{ship} = velocity of the ship during trawling

$\Delta t_{trawling}$ = trawling time (10 min)

v_{winch} = velocity of the winch during heaving

v'_{ship} = velocity of the ship during heaving (until the sledge leaves the ground)

$\Delta t_{heaving}$ = heaving time (from end of trawling until the sledge leaves the ground)

The haul length varied from 1314 to 6464 m (Table 1); for the comparative analysis the data were standardized to 1000 m hauls, respectively to an area of 1000 m² sampled by the sledge.

21 Stations in the Scotia Sea and the Weddell Sea were sampled. The depth range of these stations extends from 774 m to 6348 m in the South Sandwich Trench (Tab. 1; Fig. 2.1).

For the analysis and for station data of type locations supra and epibenthic sledge data were pooled.

All samples were fixed in 96% pre-cooled ethanol and kept at -20°C for at least 48 hours before sorting to ensure proper fixation for DNA extraction. Specimens were partly sorted on board or later in the laboratory in the Zoological Museum of the University of Hamburg.

The ANDEEP specimens dealt with in this study are from EBS samples alone.

Table 1: EBS stations of ANDEEP I (station 41-129) and II (stations 131-143).

station	date	depth (m)	latitude	longitude	haul length (m)
41-3	26.01.02	2370	59°22.24 S-59°22.57 S	60°04.06 W-60°04.05 W	4928
42-2	27.01.02	3689	59°40.30 S-59°40.32 S	57°35.42 W-57°35.64 W	4766
43-8	03.02.02	2893	60°27.13 S-60°27.19 S	56°05.12 W-56°04.81 W	4782
46-7	30.01.02	3894	60°38.33 S-60°38.06 S	53°57.38 W-53°57.51 W	5639
99-4	12.02.02	5191	61°06.40 S-61°06.40 S	59°16.57 W-59°17.61 W	5336
105-7	12.02.02	2308	61°24.16 S-61°24.25 S	58°51.56 W-58°51.56 W	2881
114-4	17.02.02	2921	61°43.54 S-61°43.51 S	60°44.21 W-60°44.43 W	4482
129-2	22.02.02	3640	59°52.21 S-59°52.20 S	59°58.75 W-59°58.63 W	4076
131-3	05.03.02	3053	65°19.83 S-65°19.99 S	51°31.61 W-51°31.23 W	3553
132-2	06.03.02	2086	65°17.75 S-65°17.62 S	53°22.81 W-53°22.86 W	2523
133-3	07.02.02	1121	65°20.17 S-65°20.08 S	54°14.30 W-54°14.34 W	1314
134-3	09.03.02	4069	65°19.20 S-65°19.05 S	48°03.77 W-48°02.92 W	4553
135-4	10.03.02	4678	65°00.05 S-65°59.97 S	43°03.02 W-43°00.82 W	2773
136-4	12.03.02	4747	64°01.54 S-64°01.51 S	39°06.88 W-39°06.88 W	5306
137-4	14.03.02	4976	63°44.98 S-63°44.74 S	33°47.75 W-33°48.23 W	4581
138-6	17.03.02	4542	62°58.08 S-62°57.99 S	27°54.10 W-27°54.28 W	4147
139-6	20.03.02	3950	58°14.10 S-58°14.15 S	24°21.20 W-24°21.21 W	6464
140-8	21.03.02	2970	58°15.98 S-58°16.28 S	24°53.73 W-24°54.09 W	4183
141-10	23.03.02	2312	58°25.07 S-58°24.63 S	25°00.78 W-25°00.74 W	3094
142-6	24.03.02	6348	58°50.78 S-58°50.44 S	23°57.75 W-23°57.59 W	4221
143-1	25.03.02	774	58°44.69 S-58°44.45 S	25°10.28 W-25°10.66 W	1441

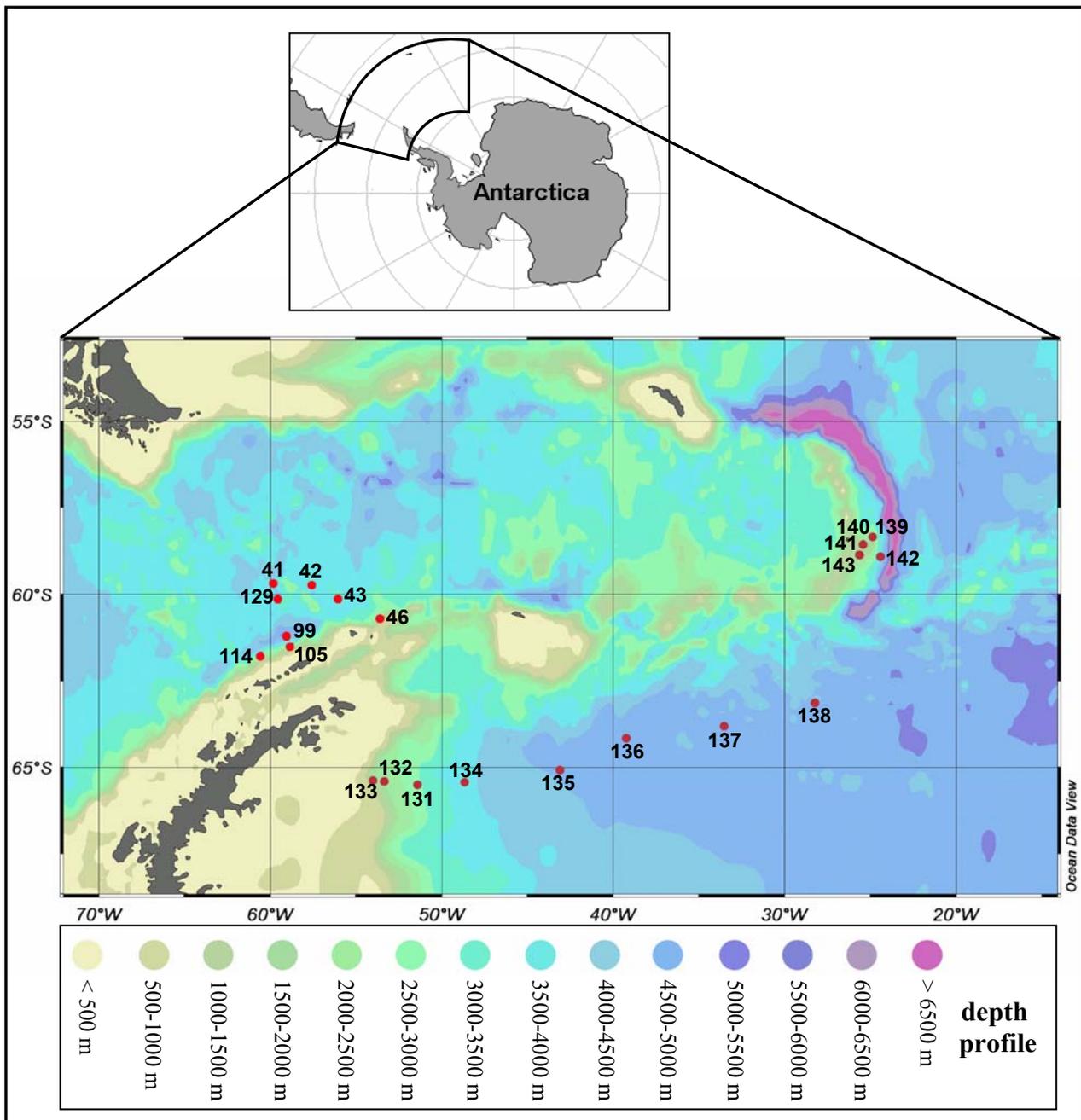


Figure 1: Map of the expedition area, with ANDEEP I and II stations

2.2 Taxonomy

Isopod specimens were sorted and identified to species level. Since species names are only known for a small fraction of the material, species were provisionally numbered and characterized until complete description.

Species were identified using a Leica MZ 75 dissecting microscope and illustrated using a Leitz Dialux compound microscope, equipped with a camera lucida. Total body length was

measured in lateral view from the anterior edge of the head to the posterior medial tip of the pleotelson. Length of the pleotelson was measured medially from the anterior margin to posterior margin; the anterior margin was defined as the line between the anterior angles of the pleotelson, because this segment is usually fused with pereonite 7. The length of the head is measured without rostral process. Generally length-width ratios refer to the greatest length and width of the limb or segment. The differentiation in peduncular and flagellar articles of the antennae follows Lincoln (1985a) and Wägele (1983).

2.3 Biodiversity analysis

The distribution data were analyzed using the program PRIMER (version 5.2.8, © 2001 PRIMER-E Ltd.; Clarke 1993). Classification and ordination procedures were used to delineate groups of stations with similar faunal composition. The resemblance of isopod composition between stations was measured by the quantitative Bray-Curtis similarity index (Bray and Curtis 1957) of fourth-root transformed abundance data. The stations were ordered in a two-dimensional plane such that they reflect the faunistic similarities by non-metric multidimensional scaling (MDS). This explorative approach involved no statistical testing for the significance of station groupings. The “bioENV” module of PRIMER (Clarke and Ainsworth, 1993) was used to calculate the influence of different environmental variables on the isopod composition for samples from the ANDEEP II stations, for which sediment data were available, using the Spearman rank correlation method and normalized Euclidean distance as a similarity measure. The following variables were tested: depth (m), CTD temperature, CTD salinity, number of Tanaidacea, number of Amphipoda, number of Cumacea, number of Mysidacea, proportion of sand, proportion of silt, proportion of clay, steepness, latitude S, longitude E.

To confirm whether the number of samples was sufficient to obtain the almost full number of species inhabiting the sampled area, a species area plot was prepared.

2.4 Phylogenetic methods

The phylogenetic analysis was based on a character matrix established with the program DELTA (DEscription Language for Taxonomy, DELTA Editor, 1.04, © CSIRO 1998-2000, Dallwitz, 1980; Dallwitz *et al.*).

The analysis was conducted with the help of the program PAUP* (β -test version 4.0b10 for Windows, Swofford 1998) after converting the DELTA matrix into a nexus file.

The matrix contained 53 taxa and 99 characters (see Table in the appendix); 87 characters were parsimony informative, the remaining 12 characters distinguish the ingroup and outgroup or some outgroup taxa and the other taxa.

A heuristic search was conducted with randomized addition of taxa (addseq=random) using tree bisection-reconnection (TBR) as swapping algorithm. 1000 replicates were performed with no more than ten trees saved during branch swapping in each replicate (nchuck = 10 chuckscore = 1 nreps = 1000 randomize = trees). During a second search with branch swapping of the resulting trees, all minimum length trees were saved (hsearch start = current nchuck = 0 chuckscore = 0). Both accelerated transformation (ACCTRAN) as well as delayed transformation (DELTRAN) was tested as character state optimization criteria.

In the first analysis all characters had equal weight; for a second analysis different weights were assigned to the characters *a priori*. For this purpose the probability of homology for each character was estimated. A bootstrap analysis with 100 replicates was performed for both outcoming topologies.

Strict and 50% majority-rule consensus trees were calculated and drawn with the program TreeView (version 1.6.6, © Roderic D. M. Page, 2001, Page, 1996). The character history for the consensus trees was visualized with the help of the Mesquite software package (version 1.03, © 2004 by Wayne P. Maddison and David R. Maddison, Maddison and Maddison, 2004), by linking the nexus file with the consensus trees calculated by PAUP*.

3 Results

3.1 Taxonomy

Of the 15 asellote isopod families found during ANDEEP I and II the families Ischnomesidae and Haploniscidae are treated in the taxonomy part of this thesis.

3.1.1 Family Ischnomesidae Hansen, 1916

A recent diagnosis of the family was given by Merrin and Poore (2003).

3.1.1.1 Genus *Stylomesus* Wolff, 1956

Type species: *Rhabdomesus inermis* Vanhöffen, 1914

Diagnosis

The diagnosis for *Stylomesus* by Merrin and Poore (2003) is followed with one exception concerning antenna 1, which has usually six articles, but sometimes only two like in the present species.

3.1.1.1.1 *Stylomesus hexapodus* n. sp.

Figs 3.1-3.5

Material

Holotype: ovigerous female, 3.9 mm; station 133-3, 65°20.17'-20.08'S 54°14.30'-14.34' W, 1121m depth; ZMH K40635.

Paratypes: same locality as holotype: two ovigerous females, 3.6 mm and one fragment; eight females, 3.2 mm – 4.2 mm; nine juveniles, 1.8 mm – 3.0 mm; ZMH K40636-40637.

Etymology

The name refers to the species' six pairs of pereopods, derived from the Greek *hexa* meaning six and *podos* meaning foot.

Diagnosis

Anterolateral margins of pereonite 1 with small acute projection, of pereonites 2 and 3 rounded; pereonite 4 about as long as wide, pereonite 5 about 1.3 times as long as wide, 0.2 times as long as body; pereonite 7 and pleonite 1 well distinguishable but fused with pleotelson. Pleotelson about as long as wide, with medial elevation dorsally, lateral margins strongly convex, terminal margin produced, rounded. Second article of antenna 2 with distal conical projection ventrally. Carpus of pereopod 1 with 3 sensory spine-like setae and 1 stout enlarged simple seta, propodus with 2 ventral sensory spine-like setae. Pereopod 7 absent in adult females. Uropods with 2 articles, 0.6 times as long as pleotelson.

Description of brooding female

Body (Fig. 3.1, 3.2) 4.4 times longer than wide; relative length ratio of head, pereonites, pleonite 1 and pleotelson: 1.0 : 0.4 : 0.9 : 0.9 : 1.4 : 2.0 : 0.7 : 0.6 : 0.6 : 1.0. Head trapezoidal, 2.2 times as broad as long, with antennae inserting on large dorsolateral projections. Pereonite 1 slightly narrower than head, anterolateral margins with small acute projection, lateral margins of pereonites 2 and 3 rounded; pereonite 4 about as long as wide, narrowing in the posterior third, broadest part 1.6 times as broad as narrowest part; pereonite 5 about 1.3 times as long as wide, 0.2 times as long as body, broadening gradually in the distal part, broadest part about 1.35 times as broad as narrowest part; pereonites 5 and 6 ventrally fused with each other and with pereonite 7; pereonite 7 and pleonite 1 well distinguishable but completely fused with pleotelson. Pleotelson about as long as wide, with elevation mediodorsally, lateral margins convex, terminal margin produced, rounded, bearing the anus, distance between branchial chamber and anal valves 0.2 times as long as pleotelson. Marsupium extending from pereonite 1 to posterior margin of pereonite 5. Body surface covered with small tubercles (see detail, Fig.3.1. C).

Antenna 1 (Fig. 3.2) about 0.13 as long as body, with two articles; article 1 globular, 1.6 times as long as wide; article 2 twice as long as article 1, with 1 basal and several distal broom setae, 3 lateral long simple setae, and 1 stout apical sensory seta of about the same length as article.

Antenna 2 (Fig. 3.2) about 0.7 times as long as body; peduncle 1.7 times as long as flagellum, peduncular article 1 triangular, short and narrow (only illustrated in Figs 3.1 and 3.2B), article 2 slightly longer than article 1, with stout sensory seta on distoventral conical projection; article 3 about 0.15 times as long as whole antenna, with several simple setae; article 4 about 0.3 times as long as article 3, with 1 broom and 1 simple seta; article 5 about as long as article 3, more slender, with 2 broom and 2 simple setae; article 6 about 1.5 times as long as

article 5, with several simple setae. Articles 3-6 dorsally and ventrally covered with numerous small cuticular teeth. Flagellum with 16 articles, article 1 about twice as long as following articles, each article with 1-5 simple distal setae.

Mandibles (fig 3.3) with toothed outer margin. Incisor with 5 blunt teeth, spine row of 4 serrated spine-like setae and 2-3 simple setae; *lacinia mobilis* of left mandible with 5 blunt teeth, right mandible with a stout serrated spine instead. Molar with smooth grinding surface and 6-7 setulated subapical setae, distal part of molar with several short rows of small bristles, left molar with 3 lateral setulated setae, right molar with 1 lateral simple seta.

Maxilla 1 (Fig. 3.3) outer lobe with 11 large serrated spine-like apical setae; medial margin with several rows of simple setae, lateral margin with rows of fine bristles. Inner lobe with many slender apical setae and a subapical spine-like seta, lateral margin with numerous fine bristles.

Maxilla 2 (Fig. 3.3) basis with numerous rows of short setae; outer and median lobes each with 4 apical setulated spine-like setae and several rows of fine setae on lateral margin; outer lobe with several simple apical setae; inner lobe more than twice as broad as median or outer lobes, distal margin bearing 3 stout serrated setae distomedially, 7 setulated setae, some simple setae and numerous fine bristles; medial margin with 2 setulated prominent setae, 1 simple stout simple seta and several slender setae; surface of with several rows of setae.

Maxillipeds (Fig. 3.2,) with 3 retinacula and several cuticular teeth on medial margin. Palp articles with 1-6 simple setae each, article 3 with additional fine bristles medially, articles 1-3 of almost equal width, about 0.3 times as broad as endite. Endite 1.9 times as long as broad, vaulted medial margin with numerous simple setae dorsally; apical margin with 3 fan setae, 1 short, blunt simple spine-like seta and some simple setae. Epipod sickle-shaped, as long as endite (Fig. 3.2).

Pereopods (Figs 3.4 and 3.5): With small cuticular teeth on dorsal and ventral margin of basis, ischium, merus and on ventral margin of carpus. Pereopod 1 basis 4.6 times as long as broad, ischium 2.6 times as long as broad; merus about as long as broad, with distal sensory spine-like seta, 1 large simple spine-like seta and a single seta; carpus about 2.0 times as long as wide, slightly tapering distally, ventral margin with 3 spine-like sensory setae, 1 long spine-like seta and several small scales distally; propodus about 1.8 times as long as wide, 0.8 times as long as carpus, with 2 spine-like sensory setae ventrally and 4 simple long setae dorsally, dactylus with 4 lateral and 3 ventral setae near unguis insertion.

Pereopods 2-6 basis and ischium with different numbers of setae; merus of pereopods 2 and 3 with 2 dorsal and 2 ventral setae, of pereopods 4 and 6 with 2 dorsal and 1 ventral seta; carpus of pereopods 2-6 with 3 ventral sensory spines and 2-5 dorsal setae, subapical ventral simple

seta on carpus of pereopods 2 and 3; apical carpus of pereopods 2-6 with row of small spines, a subapical plumose seta dorsally on carpus of pereopod 2; propodus with comb-like rows of scales on ventral margin, pereopods 2 and 6 with 3 ventral sensory spines, of pereopods 3 and 4 with 4 ventral sensory spines of different lengths; propodus of pereopods 2-6 with 2-5 dorsal simple setae and 1 dorsal subapical plumose seta; dactyli of all pereopods with 4 lateral setae and 3 setae inserting near base of unguis.

Pereopod 7 absent.

Pleopods (Figs 3.4, 3.5): Plp 2 subcircular, 0.8 times as long as pleotelson, ventral surface with small quadrangular elevation near anterior margin; lateral and posterior margins with several simple setae. Plp 3 endopod, almost rectangular, 1.4 times as long as broad, with 3 distal plumose setae; exopod almost as long and 0.3 times as wide as endopod, with apical plumose seta and a fringe of fine bristles on medial margin. Plp 4 uniramous, 1.8 times as long as wide, without setation. Plp 5 absent.

Uropod (Figs 3.1, 3.2) two-articulated, 0.6 times as long as pleotelson, inserting posterolaterally, exceeding terminal margin of pleotelson, protopod about 1.5 times longer than ramus, exceeding terminal margin of pleotelson.

Remarks

The lack of pereopod 7 in brooding females distinguishes this species from the other known species of the genus. In contrast to most species of *Stylomesus* only *S. pacificus* Birstein, 1961, *S. inermis* (Vanhöffen, 1914) and the new species are relatively compact with short and broad pereonites 4 and 5.

S. pacificus also differs from the new species in the shape of the pleotelson which is more slender than in the new species and in the number of articles of antenna 1 which has six articles in *S. pacificus*. *S. inermis* closely resembles the new species with regard to antenna 1 and the habitus, however the lateral margins of the pleotelson are less convex and pereonite 5 is slightly longer in *S. inermis*.

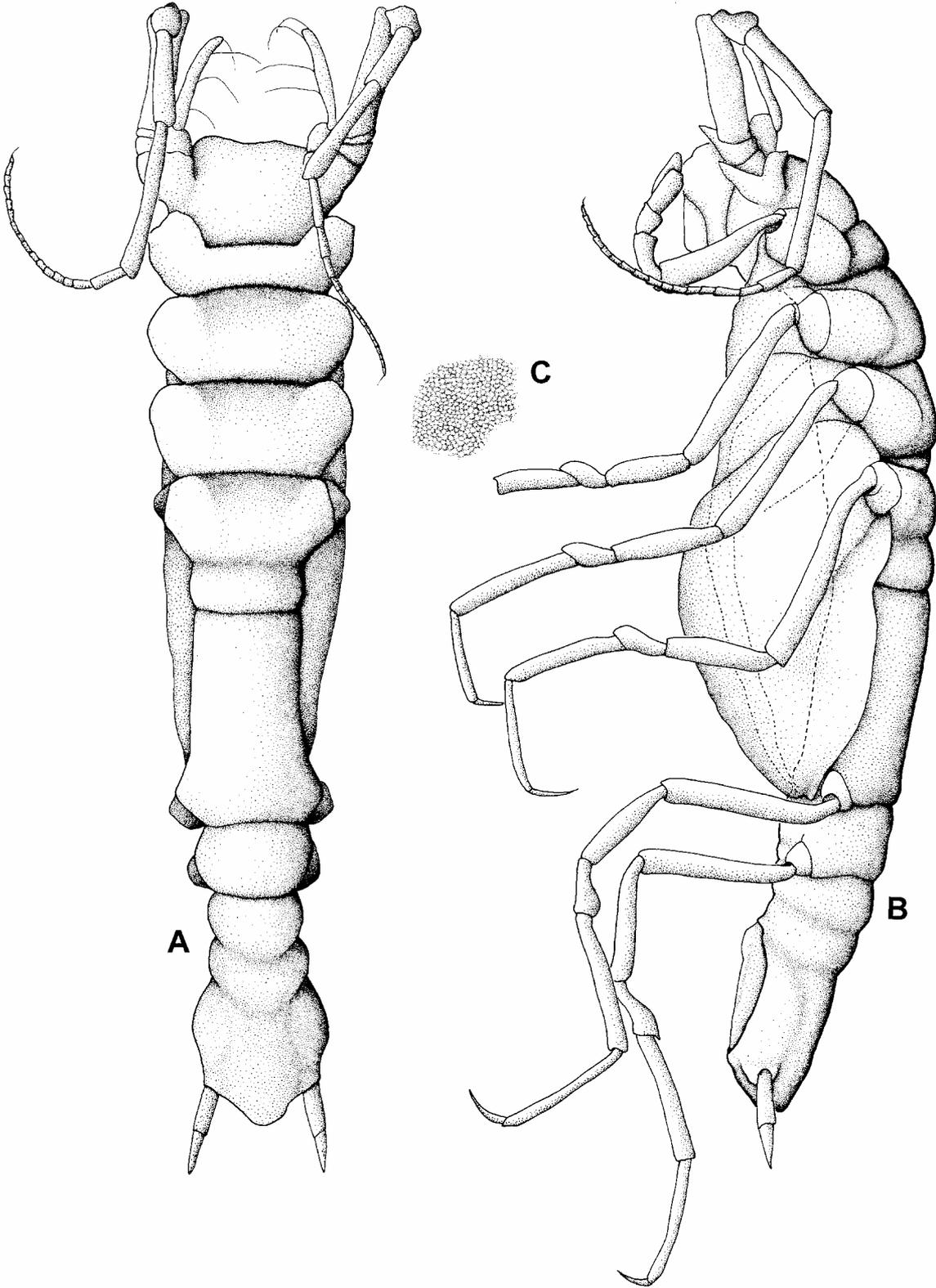


Figure 3.1: *Stylomesus hexapodus* n. sp. Brökeland & Brandt, 2004, holotype, female, 3.6 mm: A entire, dorsal view; B entire, lateral view, C detail of body surface structure.

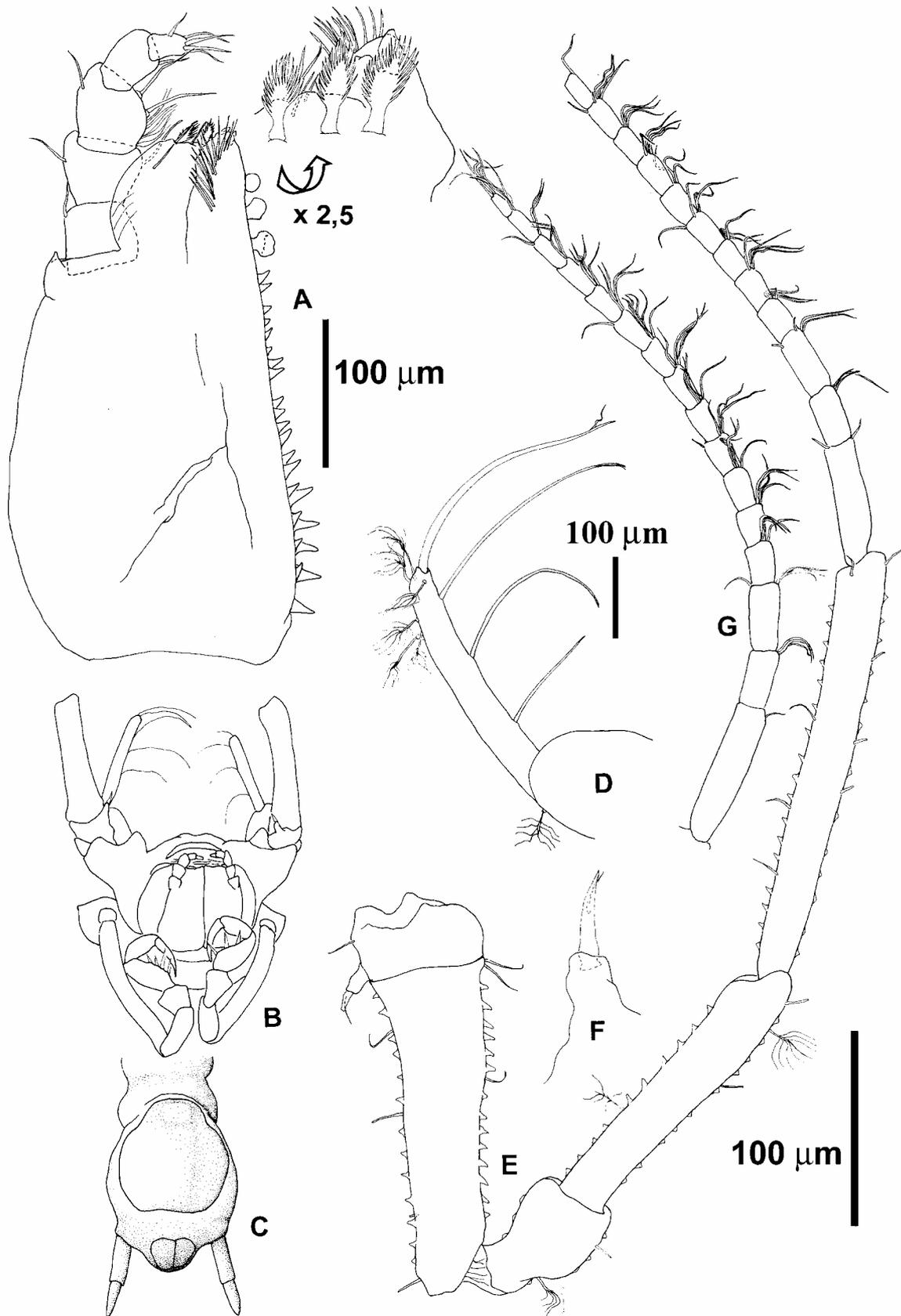


Figure 3.2: *Stylomesus hexapodus* n. sp., paratype, female, 3.6 mm: A right maxilliped (dorsal view) with detail (ventral view); B anterior body, ventral view; C posterior body, ventral view; D antenna 1; E antenna 2 (first article lost during dissection); F antenna 2, spine of article 2; G antenna 2, flagellum.

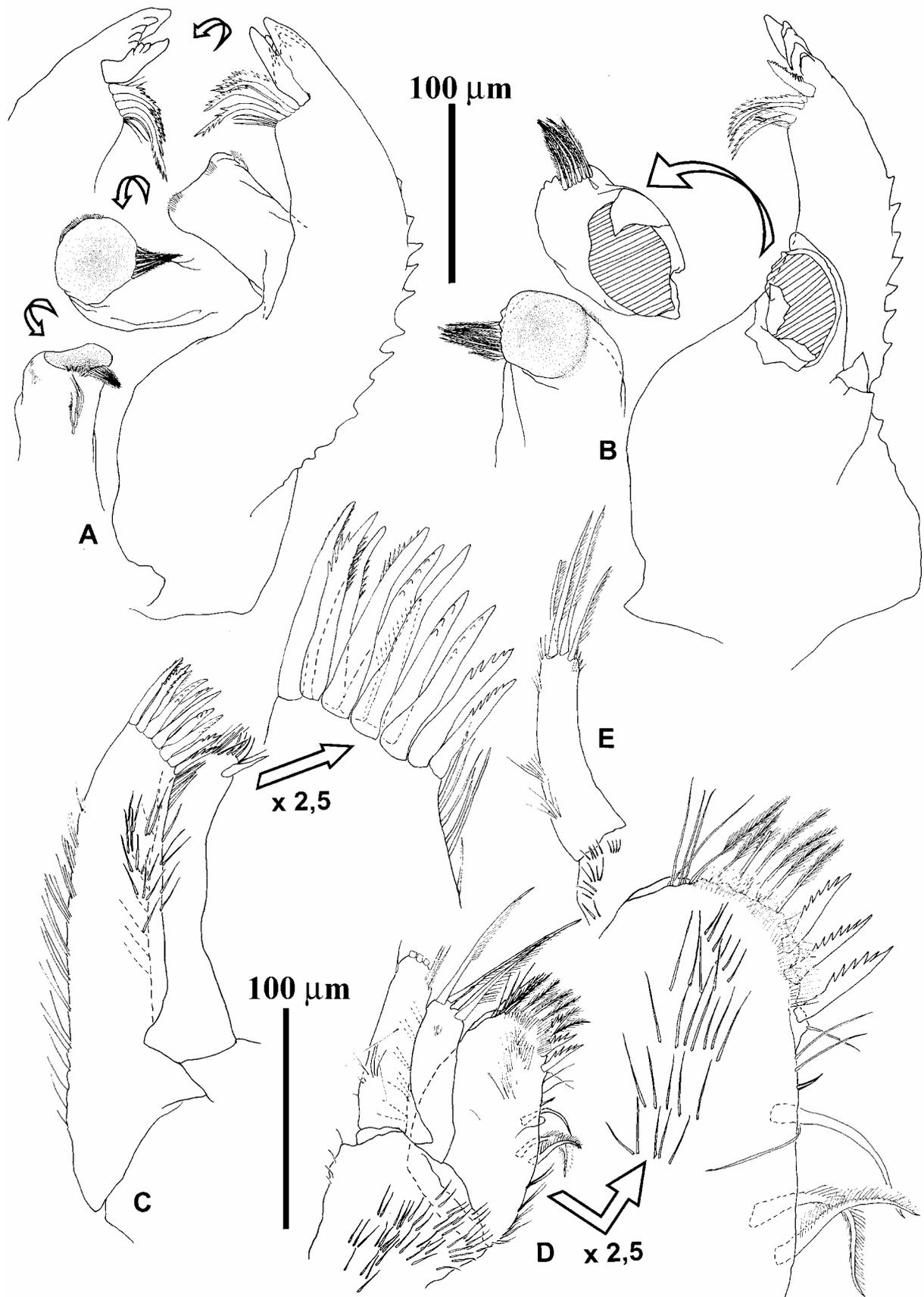


Figure 3.3: *Stylomesus hexapodus* n. sp., paratype, female, 3.6 mm: A left mandible (with details of incisor and molar process); B right mandible (with detail of molar process); C maxilla 1; D maxilla 2; E maxilla 2, outer endite

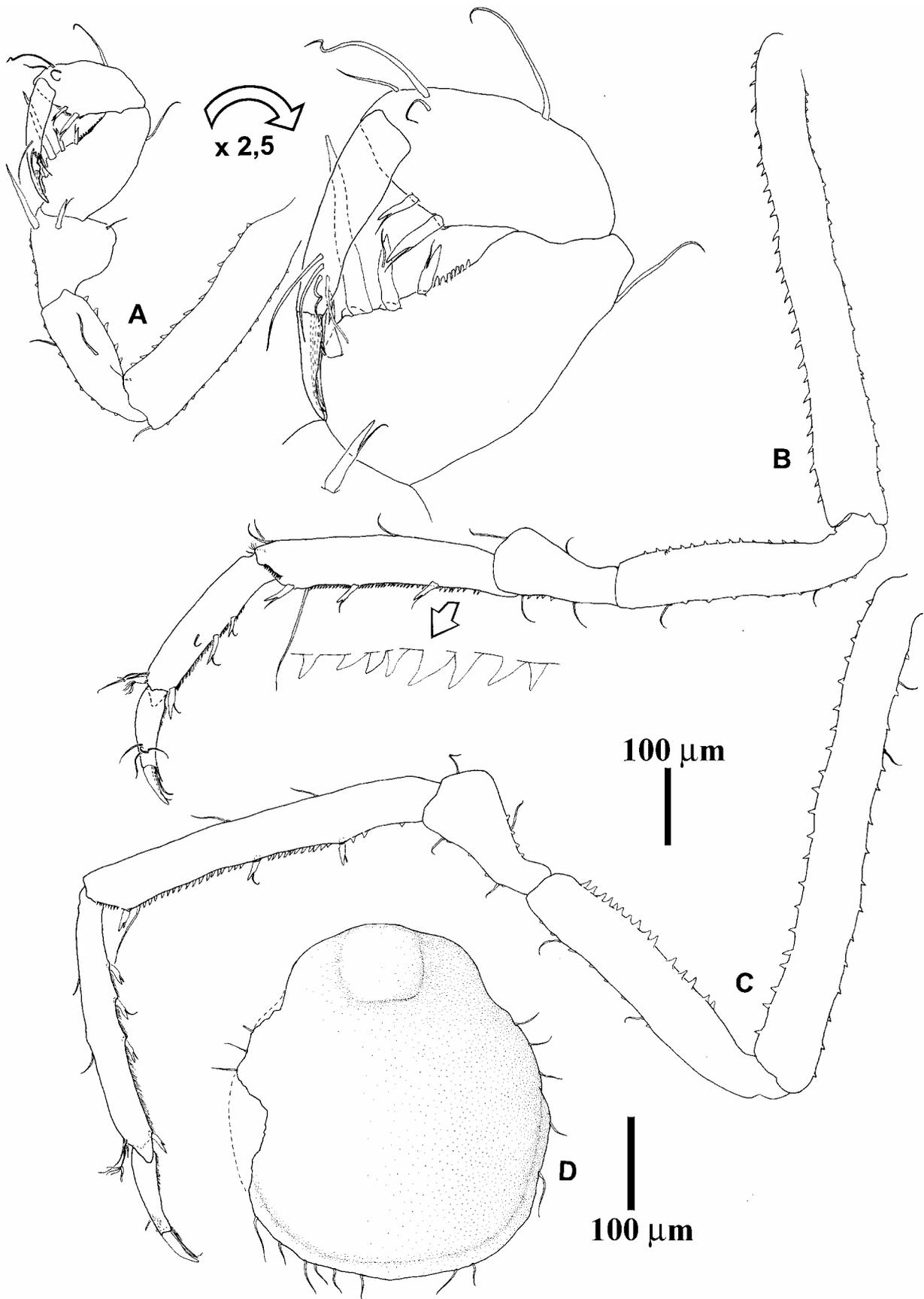


Figure 3.4: *Stylomesus hexapodus* n. sp., paratype, female, 3.6 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pleopod 2.

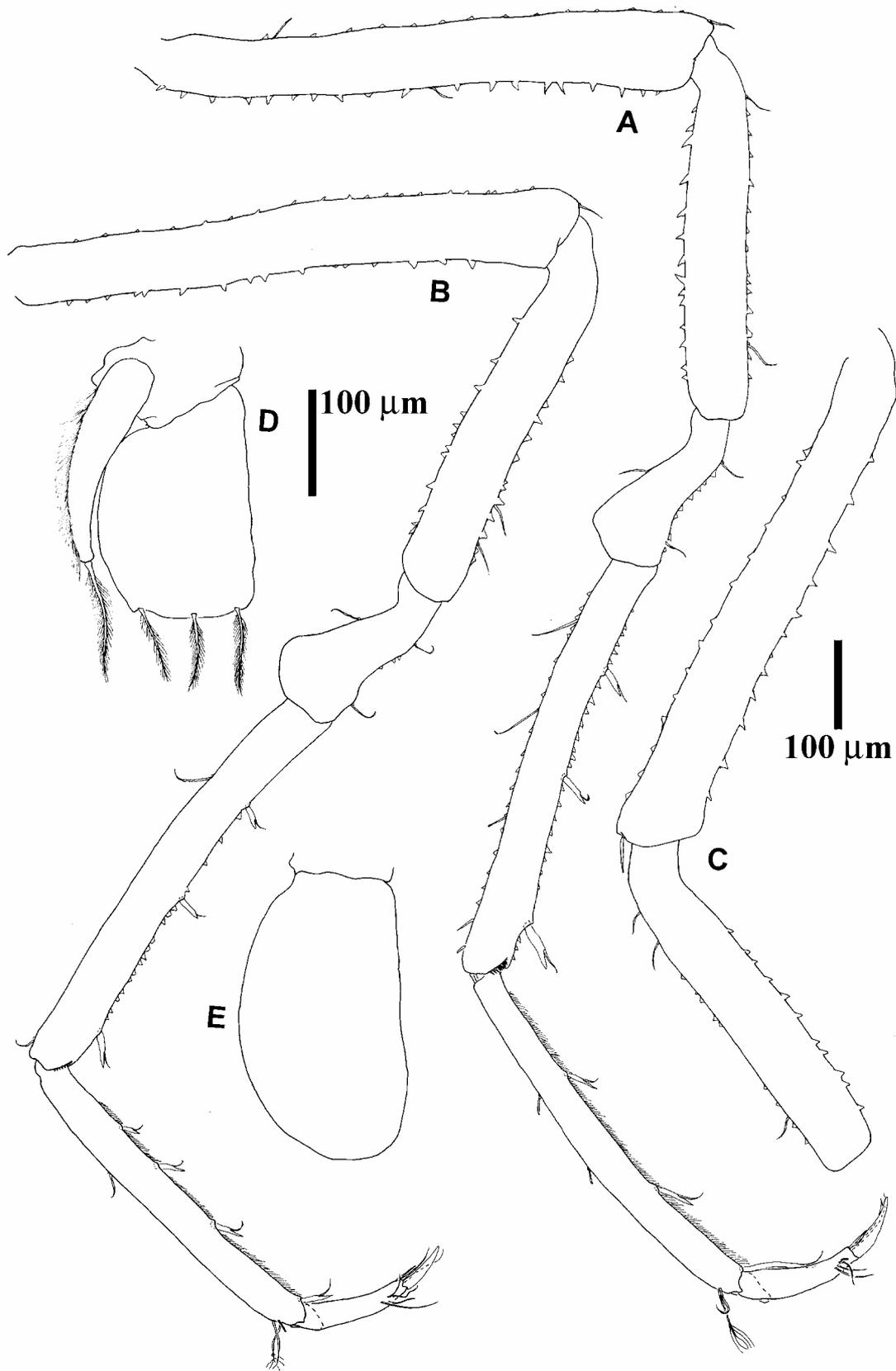


Figure 3.5: *Stylomesus hexapodus* n. sp., paratype, female, 3.6 mm: A pereopod 6; B pereopod 4; C pereopod 5, basis and ischium; D pleopod 3; E pleopod 4.

3.1.1.2 Genus *Haplomesus* Richardson, 1908

Type species: *Ischnosoma quadrispinosum* Sars, 1879

Diagnosis

A recent diagnosis of the genus was given by Merrin and Poore (2003).

3.1.1.2.1 *Haplomesus corniculatus* n. sp.

Figs 3.6-3.10

Material

Holotype: male, 4.2 mm, station 42-2, 59°40.30'-40.32'S 57°35.42'-35.64'W, 3689 m depth; ZMH K40638.

Paratypes: same locality as holotype: one male, 4.2 mm, ZMH K40639; one male, destroyed for DNA-extraction. Station 43-8, 60°27.13'-27.19'S 56°05.12'-04.81'W, 3962 m depth: two males, 4.3 mm and 4.4 mm; ZMH K40640. Station 46-7, 60°38.33'-38.06'S 53°57.38'-57.51'W, 3894 m: one male, 3.9 mm; ZMH 40641.

Etymology

The Latin name refers to the anterolateral processes of pereonite 1, *corniculatus* meaning horned.

Diagnosis

Pereonite 1 with large anterolateral projections, forming an angle of about 45° with body axis, exceeding frontal margin of head; lateral margins of pereonites 2 and 3 rounded; pereonite 4 without processes, 1.1 times as long as wide, pereonite 5 about 4 times as long as wide, 0.5 times as long as body; pereonite 7 and pleonite 1 well distinguishable but fused with pleotelson. Pleotelson 1.25 times as wide as long, with median elevation dorsally, lateral margins slightly convex, forming two laterocaudally directed processes anteriorly of uropod insertion, terminal margin produced, rounded. Carpus of pereopod 1 with 2 ventral spine-like sensory setae, propodus with 1 ventral spine-like sensory seta; pereopod 7 completely reduced. Uropods small, 0.2 times as long as pleotelson, with 1 article.

Description of male

Body (Fig. 3.6) about 7 times as long as wide (measured at pereonite 1 without anterolateral processes), relative length ratio of head, pereonites, pleonite 1 and pleotelson: 1.0 : 0.3 : 0.35 : 0.4 : 1.2 : 4.7 : 0.4 : 0.4 : 0.25 : 1.0.

Head trapezoidal, 1.25 times as long as wide, antennae inserting on short lateral processes.

Pereonite 1 widest, with large anterolateral processes, processes 2.4 times as long as pereonite, forming an angle of about 45° with the longitudinal body axis, extending beyond second article of antenna 2, tapering distally. Lateral margins of pereonites 2 and 3 rounded; pereonite 4 1.1 times as long as wide, narrowing abruptly in the posterior half, broadest part 1.3 times as broad as narrowest part; pereonite 5 about 4 times as long as wide, 0.5 times as long as body, broadening in the distal seventh, broadest part about 2.2 times as broad as narrowest part; pereonites 5 and 6 ventrally fused together and with pereonite 7; pereonite 7 and pleonite 1 well distinguishable but completely fused with pleotelson. Pleotelson 1.25 times as wide as long, with median elevation dorsally, lateral margins slightly convex, forming two laterocaudally directed processes anteriorly of uropod insertion, terminal margin produced, rounded, bearing the anus, distance between branchial chamber and anal valves 0.1 times as long as pleotelson. Body surface covered with small cuticular spinules (Fig. 3.6 C).

Antenna 1 (Fig. 3.7) about 0.17 times as long as body, with six articles; article 1 globular, article 2 slender, about 3 times as long as article 1, with 2 broom setae and 1 distal sensory seta of almost the same length as article; distal articles short, 0.25 times as long as article 2 and slender, article 5 with 2 broom setae, terminal article with 5 apical simple setae.

Antenna 2 (Fig. 3.7) about 0.8 times as long as body, peduncle about 2 times as long as flagellum; peduncular articles 1 and 2 short; article 3 1.7 times as long as articles 1 and 2 together, with several indistinct cuticular teeth on ventral and dorsal margins, article 4 0.75 times as long as article 3; articles 5 and 6 elongated, with several small setae; article 5 almost 0.25 as long as whole antenna, article 6 slightly longer and narrower; flagellum with 20 articles, each article dense tuft of slender distal setae.

Mandible incisor (Fig. 3.7) with 5 blunt teeth, spine row with 4 serrated spine-like setae on left and five serrated spine-like setae on right mandible; *lacinia mobilis* of left mandible with 5 blunt teeth; molar process of both mandibles with 4 small teeth on apical surface, 5 serrated setae, and row of fine bristles.

Maxilla 1 (Fig. 3.8) outer lobe with 12 serrated spine-like distal setae; surface with combs of setae, lateral and medial margin with rows of fine bristles; inner lobe with spine-like serrated

seta, spine-like simple seta and many slender simple setae on distal margin, lateral and medial margin bearing numerous setae.

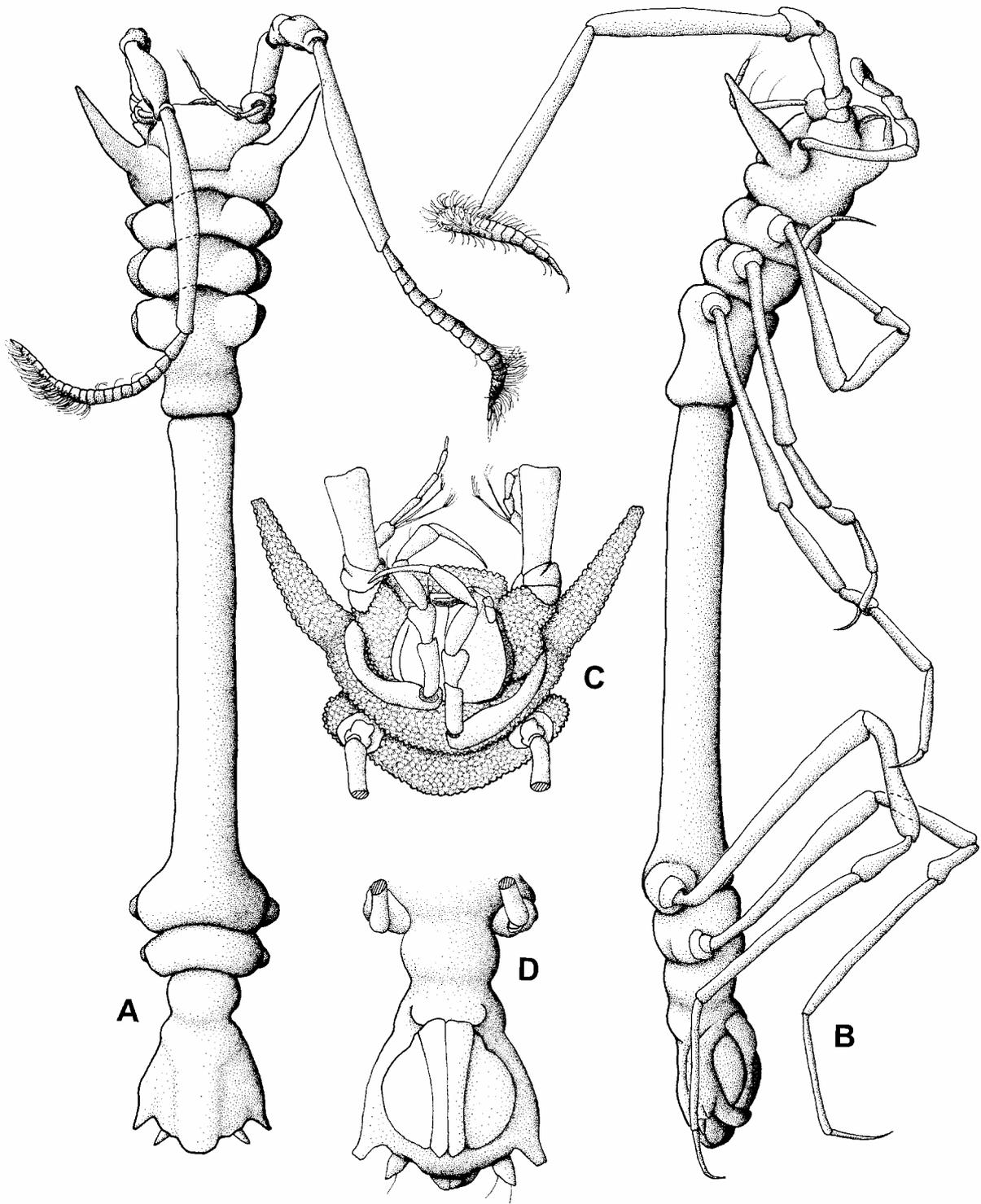


Figure 3.6: *Haplomesus corniculatus* n. sp., holotype, male, 4.2 mm: A entire, dorsal view; B entire, lateral view; C anterior body, ventral view; D posterior body, ventral view.

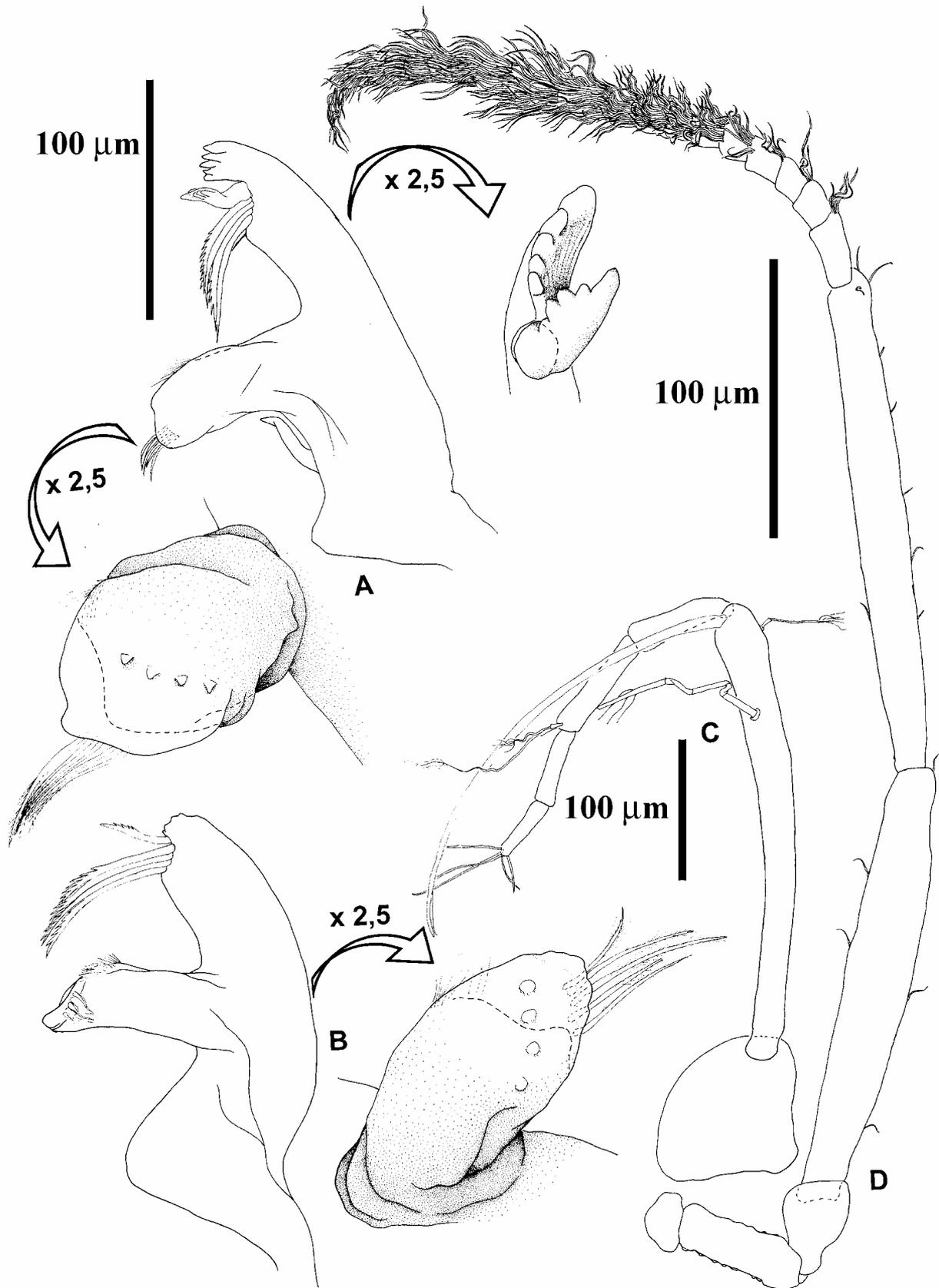


Figure 3.7: *Haplomesus corniculatus* n. sp., paratype, male, 4,2 mm: A left mandible (with detail of molar process); B right mandible (with detail of molar process); C antenna 1; D antenna 2 (first article lost during dissection).

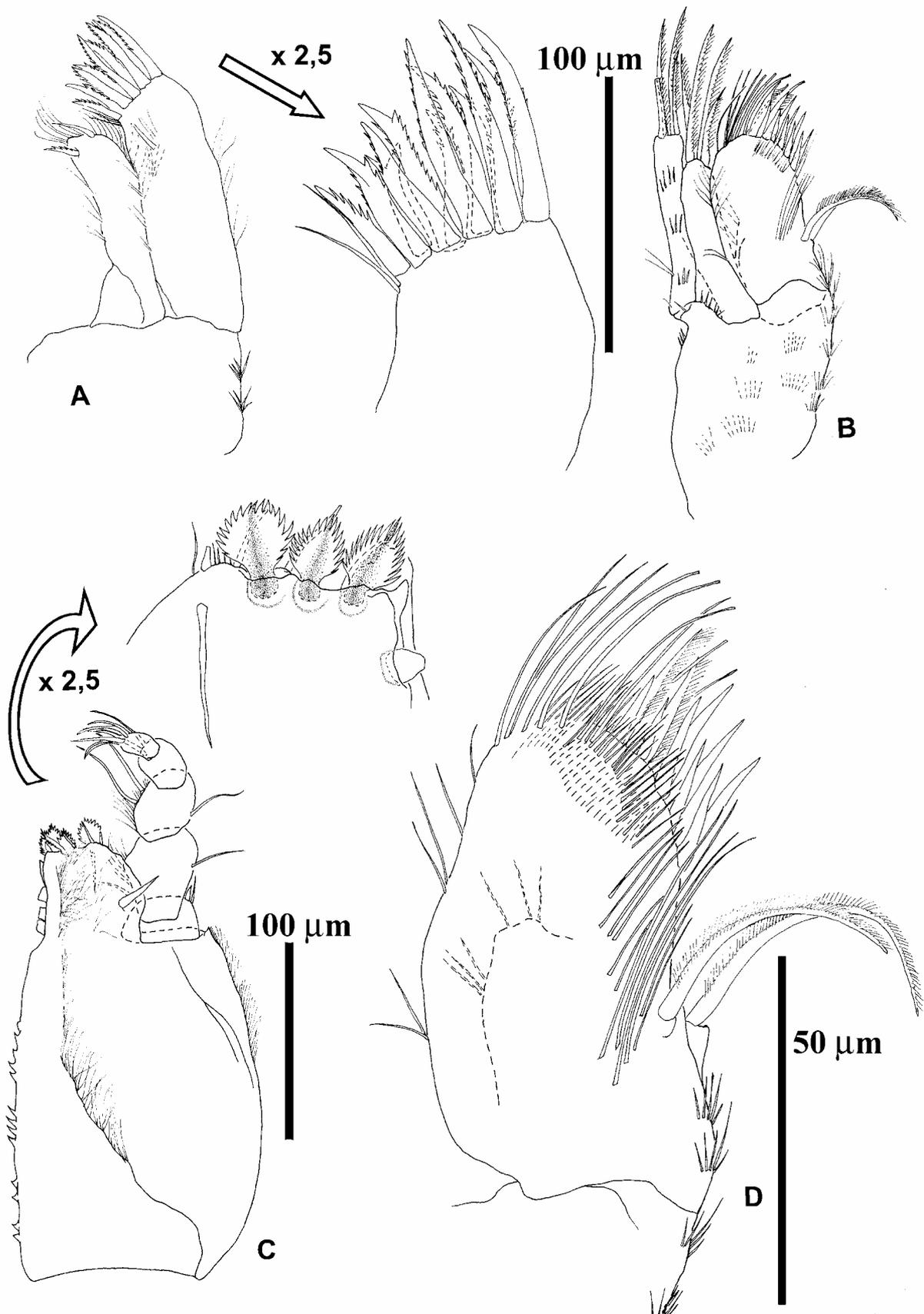


Figure 3.8: *Haplomesus corniculatus* n. sp., paratype, male, 4.2 mm: A maxilla 1; B maxilla 2; C right maxilliped (dorsal view) with detail of left maxilliped (ventral view); D maxilla 2, inner endite.

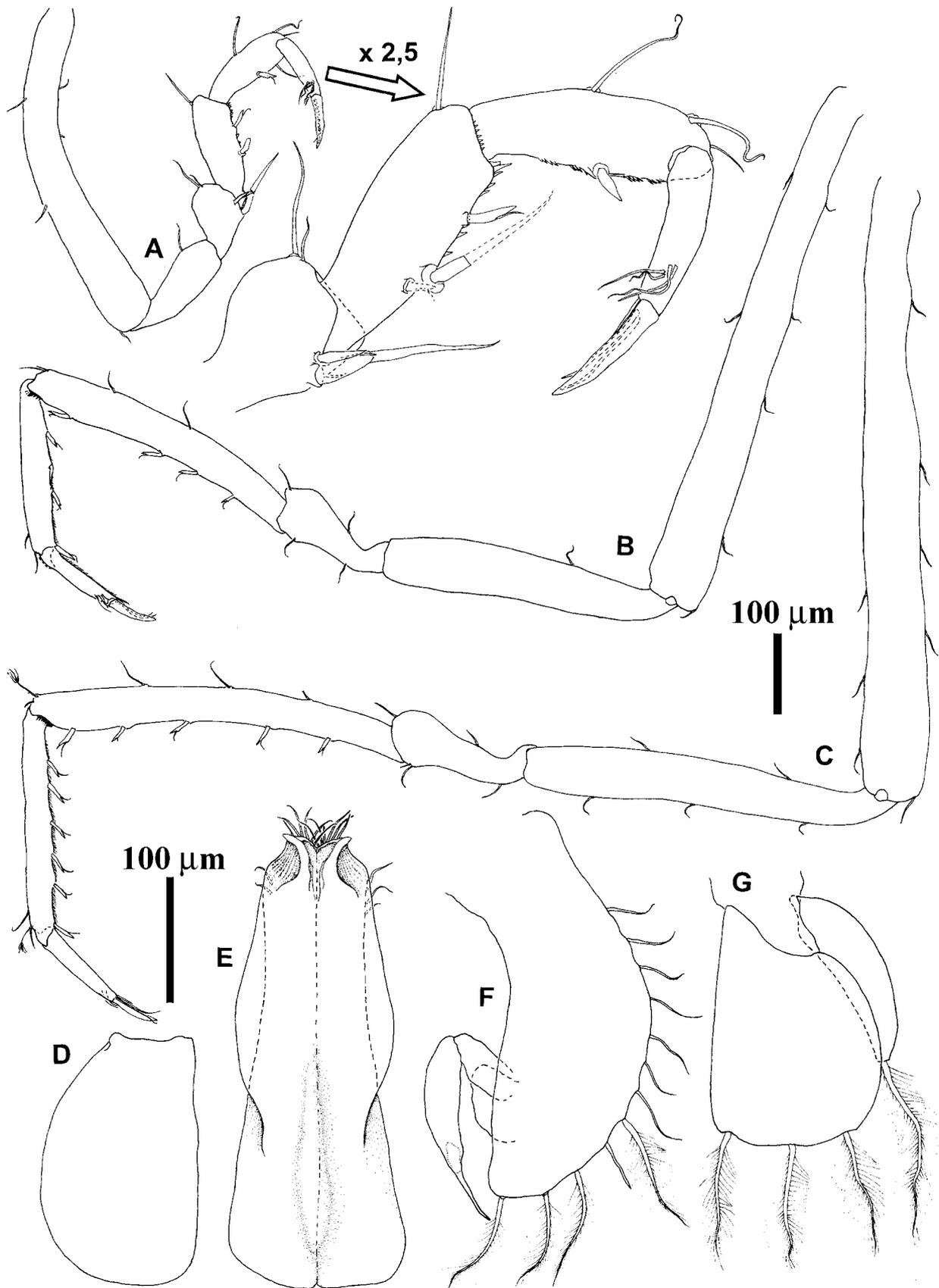


Figure 3.9: *Haplomesus corniculatus* n. sp., paratype, male, 4.2 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pleopod 4; E pleopod 1; F pleopod 2; G pleopod 3.

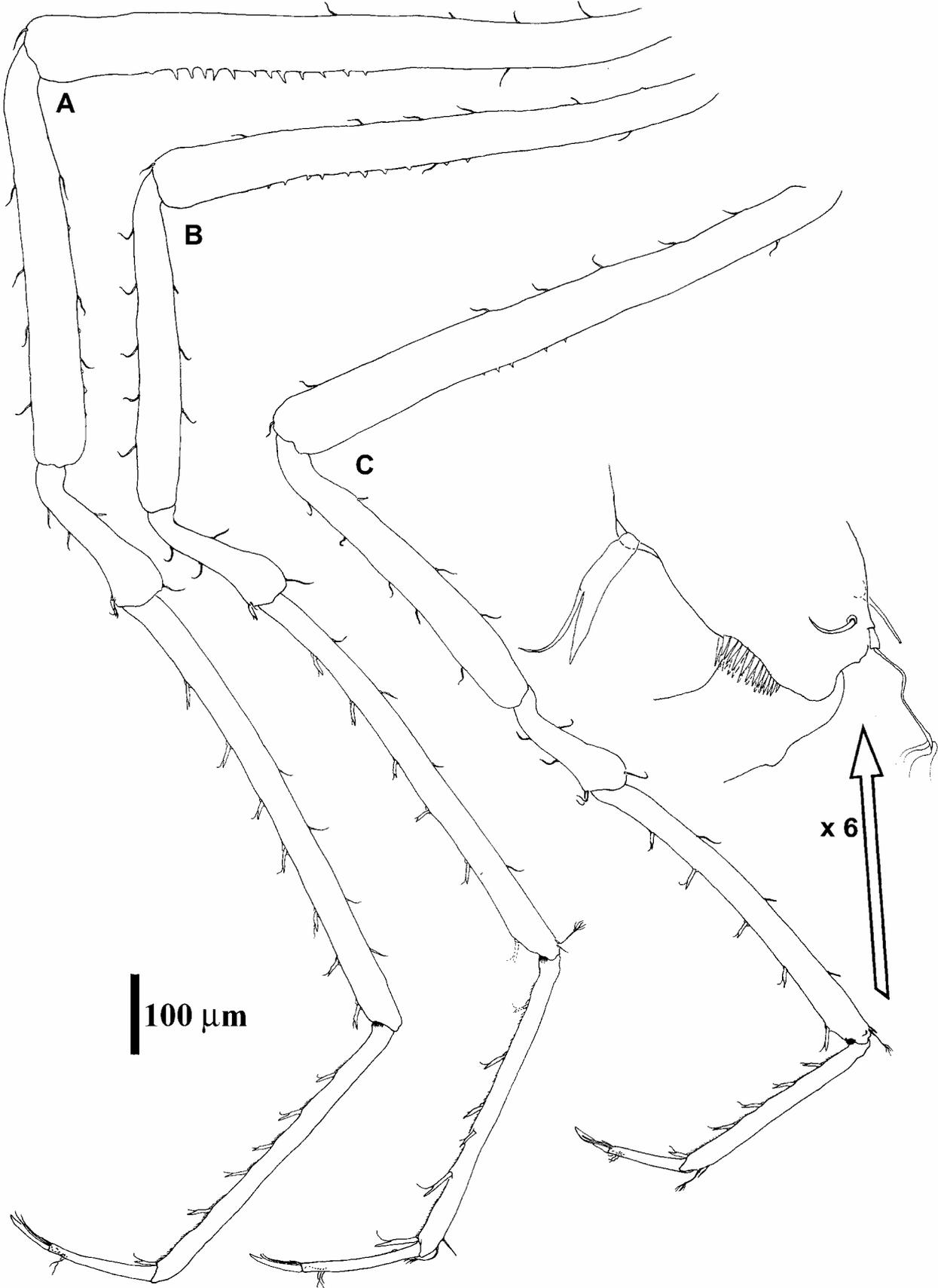


Figure 3.10: *Haplomesus corniculatus* n. sp., paratype, male, 4.2 mm: A pereopod 5; B pereopod 6; C pereopod 4.

Maxilla 2 (Fig. 3.8) outer lobe with 3 stout apical setulated setae and combs of setae on surface and lateral margin; median lobe bearing 4 apical setulated setae; inner lobe more than twice as wide as outer or median lobe, distal margin with 8 simple spine-like setae and 2 setulated spine-like setae; apical and lateral margin and surface with numerous simple setae, medial margin with 2 setulated large spine-like setae, combs of setae proximally; basipod with several combs of short setae.

Maxilliped (Fig. 3.8) medial margin with 3 retinaculi in the distal part and several cuticular teeth posterior of these; palp article 1 with 2 setae and a small spine-like seta, article 2-5 each with 1-4 setae, articles 1 and 2 with some fine bristles. Endite vaulted medial margin with numerous setae; apical margin with 3 fan setae, 1 setulated seta and several simple setae; dorsal surface of endite near palp insertion with simple spine-like seta, lateral margin with fringe of fine bristles. Epipod sickle-shaped, as long as endite (Figs 3.6).

Pereopods (Figs 3.9, 3.10): Pereopod 1 basis about 7 times as long as wide; ischium about 2.5 times as long as wide; merus about as long as wide, with distoventral sensory spine-like seta, 1 large simple spine-like seta and 2 simple dorsal setae; carpus about 2.2 times as long as wide, ventral margin with 2 spine-like sensory setae, 1 large spine-like simple seta and several small cuticular teeth, apical margin with several small spine-like scales; propodus 2.7 times as long as wide, with 1 spine-like sensory seta ventrally and 3 simple setae dorsally, dactylus with 4 lateral and 3 ventral setae near unguis insertion. Basis of pereopods 2-6 with several dorsal and ventral simple setae; basis of pereopods 4-6 with several ventral cuticular teeth; ischium with different numbers of dorsal and ventral setae (sometimes broken off); merus of pereopods 5 and 6 with 1 distal sensory spine; merus with 2 dorsal and 2 ventral setae; ventral margin of carpus with 4 sensory spines on pereopod 2, 5 sensory spines on pereopod 3 and 4, 6 on pereopod 5 and 7 on pereopod 6; dorsal margin of carpus with 2-5 setae; subapical carpus of pereopods 3-5 bearing a plumose seta (probably broken off on pereopods 2 and 6); apical carpus with 2 comb-like spine rows; propodus of all pereopods with ventral row of small setae; propodus of pereopod 2 with 3, of pereopod 3 and 6 with 6, of pereopod 4 with 5 and of pereopod 5 with 7 sensory spines; propodus dorsally with 1 or 2 simple and 1 plumose seta (broken off on pereopod 5); dactylus with 4 lateral setae and 3 setae inserting near base of unguis. Pereopod 7 absent.

Pleopods (Fig. 3.9): Plp 1 2.6 times as long as wide; apical margin with 12 setae, distolateral margins with 3 setae each, lateral margin forming a rim for reception of pleopod 2 median margin. Plp 2 protopod 2.8 times as long as wide, with 4 distolateral plumose setae and 8 lateral simple setae; endopod extending slightly beyond terminal margin of protopod, stylet 0.5 times as long as protopod, sperm duct opening closer to distal end; exopod a simple lobe posteriorly of

endopod. Plp 3 endopod, 1.3 times as long as wide, with 3 distal plumose setae; exopod 1.3 times as long and 0.3 times as wide as endopod, with apical plumose seta. Plp 4 uniramous, 1.7 times as long as wide, without setation. Plp 5 absent.

Uropods (Fig. 3.6) single-articulated, short, 1.7 times as long as wide, 0.2 times as long as pleotelson, not reaching terminal margin of pleotelson, inserting between posterolateral processes and terminal margin of pleotelson.

Remarks

Several species of *Haplomesus* possess processes on pereonite 1 but only in *H.* (Gurjanova, 1946) their size, shape and the angle formed with the longitudinal body axis is similar as in the new species. All three species possess a second pair of processes which is located on pereonite 3 in *H. quadrispinosus* and on pereonite 4 in the other two species. Besides the pleotelson of *H. quadrispinosus* has strongly convex margins and only minute posterolateral processes while the pleotelsonic processes of *H. gorbunovi* are directed caudally and not laterocaudally as in the new species. A few species of *Haplomesus* are described with only six pairs of pereonites as discussed below.

3.1.2 Family Haploniscidae Hansen, 1916

Composition: *Haploniscus* Richardson 1908, *Hydrioniscus* Hansen, 1916, *Aspidoniscus* Menzies and Schultz, 1968, *Abyssoniscus* Birstein, 1971, *Antennuloniscus* Menzies, 1962, *Chauliodoniscus* Lincoln, 1985a and *Mastigoniscus* Lincoln, 1985a.

Diagnosis

Janiroidea with oval or subrectangular body, dorsally vaulted; lateral margins of pereonites expanded, covering insertion of pereopods from dorsal. Eyes absent. Pereonites 1-4 free. Pereonite 7 fused with pleotelson in all species but *Abyssoniscus ovalis* Birstein, 1971. Pleotelson with posterolateral processes close to terminal margin. Antenna 1 with 3 peduncular articles, article 3 small, resembling flagellar articles. Antenna 2 with six peduncular articles, article 3 with dorsal tooth in all but the *Hydrioniscus* species. Mandible with cylindrical, truncate molar process, incisor with 5 blunt teeth, palp article 3 with row of serrated spine-like setae, distal seta longest. Maxilla 2 inner lobe with 2 serrated spine-like setae. Maxilliped endite distally as broad as proximally, apical margin with deep notch, with 1 larger and 2 smaller fan setae, 1 serrated and 1 mostly smooth spine-like seta; epipod broad, triangular. Pereopods ambulatory, increasing in length from 1-7; carpus with apical comb-like scale row at least on P1; ventral comb-like scale rows distinct on carpus and propodus, distal part of carpus and propodus with broom seta dorsally; ventral claw reduced, forming a small scale near dorsal claw. Pleopod 3 exopod single-articulated small, short, lateral margin rounded with dense fringe of bristles and several simple setae; endopod with 3 plumose setae, outer seta longest. Pleopod 4 exopod single articulated, slender, with fringe of setae on lateral margin and long plumose seta apically. Pleopod 5 uniramous, without setation.

Uropods uniramous, short, inserting in deep fold between pleotelsonic processes and uropods.

Description

Body oval or almost rectangular, dorsally vaulted; tergites laterally expanded, covering the insertion of the pereopods from dorsal. Head mostly wider than long, but sometimes almost as long as wide, frontal margin straight, concave, due to extension of lateral margins or convex, often with rostral process of varying size and shape, from small and knoblike to elongated and acute or almost quadrate; eyes absent. Pereonites 1-4 free in all species, pereonites 4 or 5 longest; anterior and posterior margins of pereonites 2-4, posterior margin of pereonite 1 and anterior margin of pereonite 5 of many species serrated in intersegmental gaps, with numerous setae; lateral margins of pereonites rounded or almost straight and angles of some pereonites,

especially posterior angle of pereonite 4 and anterior angle of pereonite 5, with small acute prolongation; all pereonites with several setae, especially at lateral margins. Pereonite 7 fused to pleotelson middorsally in all species, pereonites 5 and 6 fused middorsally to each other and pereonite 7 in most species, but suture lines often visible; lateral fusion highest in species of *Hydroniscus*; pereonite 7 sometimes reduced considerably, but pereopod 7 always present in adult specimens.

Pleotelson tapering distally, with two posterolateral processes of varying length close to terminal margin in almost all species (Fig. 3.11), sometimes hardly visible dorsally. Terminal margin mostly convex, but in species with large posterolateral processes straight or even slightly concave. Dorsal surface of several species with two sharp longitudinal keels or two rounded longitudinal ridges, often also with two large tubercles. Ventral surface of some species with bulge around branchial chamber tapering towards anus (Fig. 3.11). Anus separated from branchial chamber by strong ventral ridge, anal valves semicircular when closed. Cuticle with numerous small tubercles, small depressions or smooth; heavily calcified.

Antenna 1 with three peduncular articles; article 1 usually broad with several broom setae, simple setae and numerous parallel cuticular ledges along lateral surface, often with fine bristles; article 2 in most species longer and more slender than article 1 with several broom setae and simple setae; article 3 short, resembles flagellar articles, usually with 1 simple seta. Flagellum with 3 to 6 articles, only *Hydroniscus vitjazi* Birstein 1963a, with 14 flagellar articles, article 1 always smaller than following articles, with small broom seta; following articles mostly with aesthetascs distally, terminal article often with 2 lateral and 2 distal aesthetascs and 2 or 3 simple setae as well as a small broom seta.

Antenna 2 usually distinctly larger than antenna 1, with 6 peduncular articles. Article 1 well developed in most species, reduced in *Antennuloniscus* Menzies, 1962 (Fig. 4.4); articles 1 and 2 short, with some simple setae; article 3 about as long as wide or distinctly longer, in all but the *Hydroniscus* species with a dorsal tooth of different length; tooth mostly with 1-3 simple setae, sometimes with jagged margins or apically bifid; article with dorsal groove distally from tooth, most strongly expressed in *Antennuloniscus*. Article 4 short, distally broader than basally; articles 3 and 4 with several simple setae; article 5 longer than article 4, with some broom setae and several simple setae, article 6 often longer than articles 1-5, with some broom setae and several, sometimes numerous simple setae, in some species with apical tooth; peduncular articles often ornamented, with the overall cuticle structure of the body or articles 4-6 with numerous small scales. Flagellum with at least 6, but often distinctly more (12-16, but up to 37

(Lincoln, 1985a)), articles of decreasing width; all articles with several, in males sometimes up to 20 or 30, simple setae.

Mandible distinctly longer than wide, tapering towards incisor. Incisor usually with 5 blunt teeth; *lacinia mobilis* on left mandible only, with 5 teeth and often a group of small setae; right mandible with serrated spine-like seta instead of *lacinia mobilis*; posterior of this seta, respectively *lacinia mobilis* a row of 2-3 serrated and 2-4 setulated or simple stout setae. Molar cylindrical, apically truncated, surface oval, concave, framed by a raised cuticular ledge facing the incisor, that ends in a prominent tooth on one side or sometimes both sides, and a row of acute teeth of varying size averted from the incisor, only in *Haploniscus ampliatus* Lincoln, 1985b a second cuticular ledge is present instead of the tooth row; right mandible with a row of accessory teeth and a group of small setae posterior of cuticular ledge; both mandibles with several setulated setae posterior of tooth row. Palp elongated, slender; article 1 usually with a simple seta distally; article 2 longest, with 2 or 3 spine-like serrated setae in the distal part and rows of setose scales; article 3 medially expanded, with numerous fine bristles and row of serrated spine-like setae; distal seta longest (Fig. 4.4).

Maxilla 1 outer endite slender, usually with 13 spine-like simple and serrated setae distally and some bristles on surface and margins; inner endite short, tapering distally, apically with several stout setae, margins with fine bristles.

Maxilla 2 outer lobe with 3-4 long, serrated or simple spine-like setae apically and numerous fine setae on margins; medial lobe with 2-3 long, serrated or simple spine-like setae and a shorter serrated spine-like seta, medial margin with row of simple spine-like setae; inner lobe broader than outer and medial lobe, apically with 2 short serrated spine-like setae and 3 robust simple setae, lateral margin with a simple spine-like seta, apical and lateral margins with numerous simple setae; basis usually with some long slender setae on medial margin.

Maxilliped endite subrectangular basally, longer than wide, distally as wide as proximally, lateral margin rounded distally, apical margin divided by a deep notch, medial part forming an acute process, bearing a serrated spine-like seta and a smaller spine-like mostly smooth but sometimes slightly serrated seta, a row of simple setae inserting posteriorly of spine-like setae, extending beyond apical margin of endite; close to apical notch a fan seta; apical margin laterally from notch with 2 smaller fan setae, sometimes accompanied by some small spine-like seta, and numerous small simple setae. Medial margin of endite vaulted ventrally, with numerous longer simple setae; 2-4 (mostly 3) retinacula present on medial margin; lateral margin with fringe of small bristles. Palp slender, articles 1-5 of decreasing width, each article

with several long simple setae. Epipod broad, triangular, sometimes with small bristles on margins, often ornamented with the overall cuticle structure of the body.

Pereopods: All ambulatory, increasing in length from 1-7, due to elongation of all articles, resulting in increasingly slender proportions. P1-4 inserting at anterior margin of appertaining pereonite, basis orientated posteriorly, P5-7 inserting at posterior margins of pereonites, basis directed anteriorly. Coxae reduced, forming a small sclerite around insertion of basis (Fig. 3.12), immovable, fused to pereonite. Basis elongated, slender, usually with broom setae dorsally on P2-7, ventrally with a varying number of simple setae. Ischium shorter than basis, with simple setae ventrally and dorsally. Merus shorter than ischium, with dorsal and ventral setae apically and sometimes ventral setae medially, setae simple, spine-like or flagellate. Carpus about as long as ischium, with comb-like scale rows ventrally (Fig. 3.12), often smaller on posterior pereopods, and several simple, spine-like or flagellate setae ventrally; distal part usually with a simple seta and a broom seta dorsally, on P5-7 often with a stout flagellate seta; P1 with single setose comb apically, only in *Hydroniscus lobocephalus* Lincoln, 1985a with two combs, P2-7 with two apical combs of varying size (Fig. 3.12), either both combs spinose or setose or one comb spinose and one comb setose, in several species also with apical dorsal combs, combs of P2-7 missing in *Hydroniscus vitjazi*. Propodus about as long as and more slender than carpus, with comb-like scale rows like carpus and simple spine-like or flagellate setae ventrally (Fig. 3.12), scale rows in several species also on surface of propodus; distalmost part with a broom seta and several simple setae dorsally, broom seta often biflagellate. Dactylus shorter than propodus, often with ventral scale rows, ventral claw reduced, forming a small flat, often apically bifid scale; dorsal claw usually about as long as dactylus, slightly curved ventrally, with ventral fold; several simple setae close to insertion of claws.

Pleopods: Male Plp1 of most species with broad proximal and slender distal part, mostly proximal part tapering slightly, only in *Haploniscus hamatus* Lincoln, 1985b and the undescribed species *H. sp. 12* the distal part distinctly extended laterally and broader than proximal part; lateral margins distally of broadest part often concave, distal part spatulate, bearing several setae, sometimes with distolateral processes or prolonged medial part; penes adjacent to ventral midline of pereonite 7, set in a deep notch in ventral margin of pleopod 1. Plp2 basipod tapering distally, with numerous long simple setae; endopod typically short and stout, about as long as basipod, but sometimes elongated and slender and 2-4 times as long as basipod (Fig. 3.11); exopod forming a small process distally from endopod insertion. Plp 2 of the female usually subcircular (Fig. 3.11), seldom longer than wide or wider than long (*Antennuloniscus latoperculus*) and triangular in *Abyssoniscus ovalis*, slightly vaulted ventrally,

with numerous simple setae on distal and lateral margins. Plp3 endopod large, with rounded distal margin and three plumose setae, lateral seta usually longest; exopod distinctly shorter than endopod, triangular, single-articulated, lateral margin rounded, with dense fringe of bristles and 2 to approximately 20 simple setae. Plp4 endopod triangular, without setation; exopod triangular single-articulated, usually shorter, but in few species as long as or longer than endopod, slender, with fringe of setae on lateral margin and single plumose seta apically, seta slightly longer than exopod. Plp5 uniramous, triangular, without setation.

Uropods, uniramous, short, cylindrical except in *Aspidoniscus perplexus* Menzies & Schultz, 1968 (described as “clubshaped” by Menzies & Schultz), inserting in deep fold between posterolateral processes and anal valves, ramus with several broom setae and simple setae; absent in few species (*Abyssoniscus ovalis*, *Hydroniscus abyssi* Hansen, 1916).

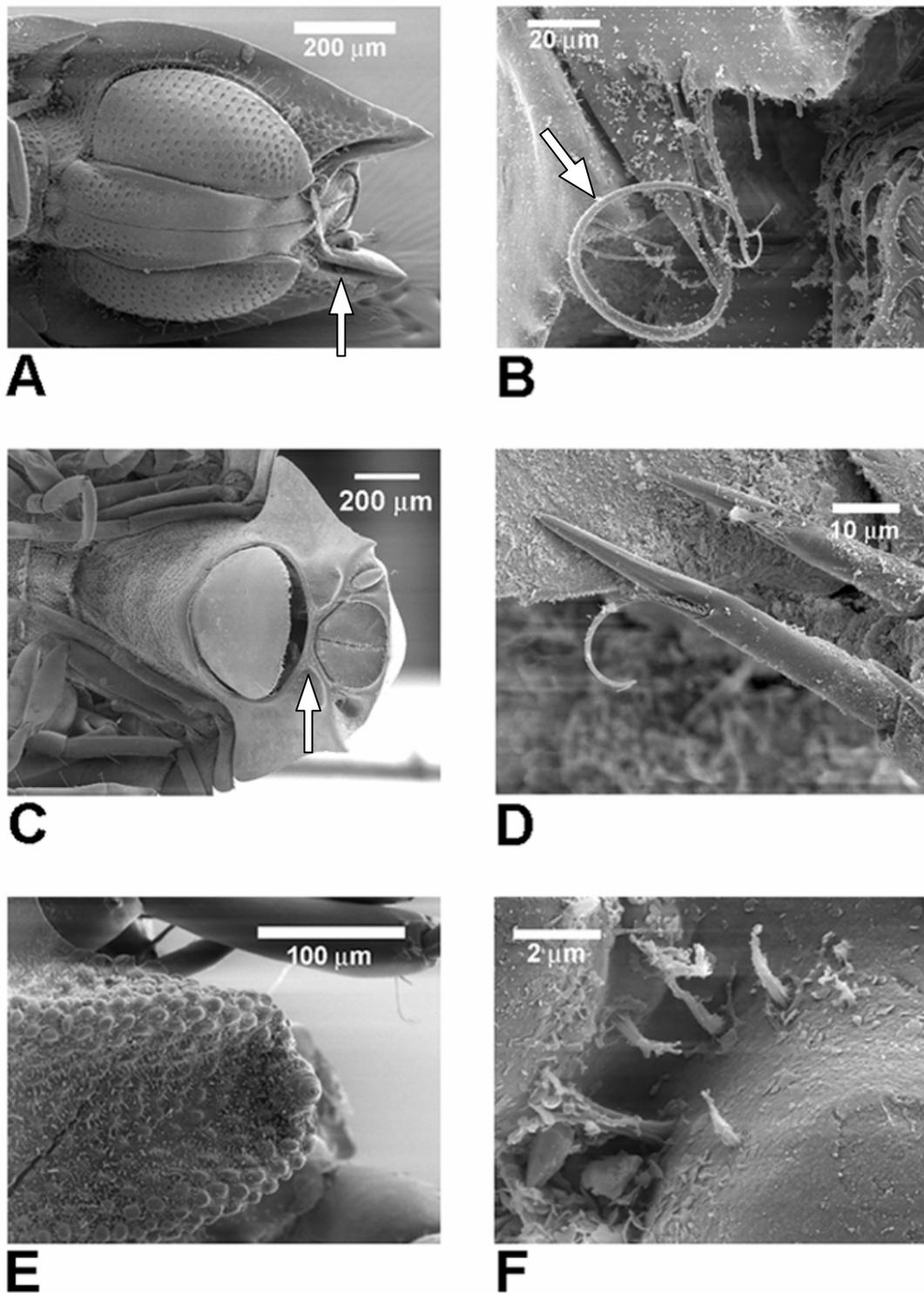


Figure 3.11: A *Mastigoniscus andeepi* n. sp., male, pleotelson, ventral view, arrow: ventral groove; B detail of A, with tip of pleopod 1 and endopod of pleopod 2 (arrow); C *Haploniscus cucullus* n. sp., female, pleotelson, ventral view, arrow: bulge around branchial chamber; D *Haploniscus weddellensis* n. sp., flagellate setae of carpus; E *Haploniscus cucullus* n. sp., rostrum, dorsal view; F detail of E, showing setae on tubercles.

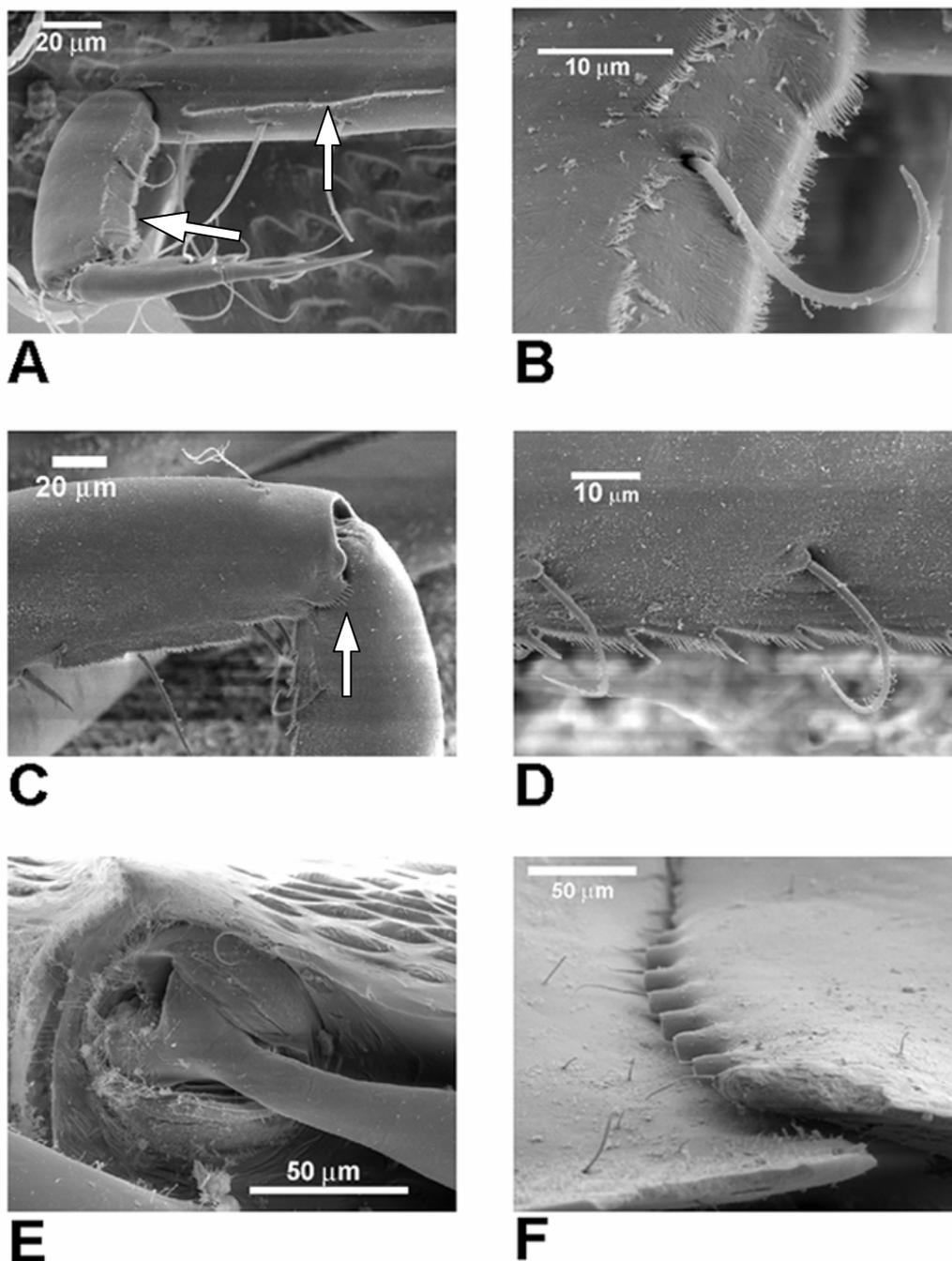


Figure 3.12: A *Antennuloniscus* sp. 1, carpus, propodus and dactylus, arrows: ventral combs of carpus and propodus; B detail of A, showing ventral combs and simple seta of propodus; C *Haploniscus cucullus* n. sp., carpus and propodus, arrow: apical comb of carpus; D detail of C, showing ventral combs and simple setae of propodus; E *Antennuloniscus* sp. 1, coxa; F *Haploniscus cucullus* n. sp., serrated margin of pereonite 5.

3.1.2.1 Intraspecific variability of characters

The intraspecific variability of characters was observed representative for 11 specimens of *Mastigoniscus andeepei* n. sp. and seven specimens of *H. cassilatus* n. sp. (see Tabs. 2 and 3)

Table 2: Intraspecific variability of some characters in *Mastigoniscus andeepei* n. sp.

<i>Mastigoniscus andeepei</i> ♂	HA30	HA122	HA123	HA124	HA125	HA126	HA201	HA202	HA203	HA204	HA205
Antenna 2 flagellar articles	14	14	14	14	14	12	14	14	14	14	14
Antenna 2 article 3 dorsal tooth number of jags	2	2	2	2	2	3	2	2	3	2	2
Md palp article 3 setae	6	?	5	5	5	5	5	6	6	5	7
LMd incisor serrated/simple setae	2/3	2/3	2/3	2/3	2/3	2/3	2/3	2/3	2/3	2/3	2/3
RMd incisor serrated/simple setae	3/3	3/4	3/3	3/4	3/4	3/3	3/3	3/4	3/4	3/3	3/4
Md molar number of teeth L/R	5/5	6/7	6/?	6/6	6/6	6/5	5/5	6/6	6/5	5/5	7/7
Md molar setulated setae L/R	4/6	4/5	?	4/5	3/6	2/5	4/5	5/6	4/4	6/5	4/6
Maxilla 2 outer lobe setae	3	4	4	4	4	4	3	4	4	4	4
Maxilla 2 medial lobe setae	4	3	3	3	3	3	3	3	4	4	3
P1-3 carpus ventral setae	3	3	3	3	3	3	3	3	3	3	3
P4 carpus ventral setae	2	2	2	2	2	2	2	2	2	2	2
P5-7 carpus ventral stout setae	2	2	2	2	2	2	2	2	2	2	2
P1p 3 exopod setae		2	2	3	3	?	3	2	2	2	2

Table 3: Intraspecific variability of some characters in *Haploniscus cassilatatus* n. sp.

<i>Haploniscus cassilatatus</i> ♀♀ and ♂	HA322 ♀	HA323 ♀	HA324 ♀	HA325 ♀	HA326 ♀	Ha 331 ♀	HA404 ♂
Antenna 2 flagellar articles	?	14	14	17	14	14	16
Antenna 2 article 3 dorsal tooth number of jags	0	0	0	0	0	0	0
Md palp article 3 setae	11	8	9	10	10	?	9
LMd incisor serrated/simple setae	2/4	2/4	2/4	2/4	2/4	2/4	2/4
RMd incisor serrated/simple setae	3/4	3/3	3/4	3/4	3/4	3/4	3/4
Md molar number of teeth L/R	7/6	6/5	5/5	5/5	6/5	5/6	5/6
Md molar setulated setae L/R	11/?	9/7	8/7	9/7	2/6	7/7	5/9
Maxilla 2 outer lobe setae	4	4	3	4	4	4	4
Maxilla 2 medial lobe setae	3	3	3	3	3	4	3
P1-4 carpus ventral flagellate setae	2-3	2-3	2	2-3	2	1-2	2-3
P5-7 carpus ventral flagellate setae	4	4	4	3-4	3-4	2-4	3-4
P1p 3 exopod setae	4	5	5	5	6	6	6

3.1.2.2 Genus *Antennuloniscus* Menzies, 1962

Type species: *Haploniscus dimeroceras* Barnard, 1920

Diagnosis

Head with anteriorly prolonged clypeus. Pereonites 5-7 fused with pleotelson, Antenna 2 article 1 small, in situ concealed by article 2; article 3 longer than wide, with longitudinal groove or suture; articles 5 and 6 fused, diffuse suture still visible, article 6 with terminal projection; flagellum small and slender, inserting subapically on peduncular article 6. Pleopod 1 with spine row near distal end of transverse groove. Pleopod 2 endopod short, stout, not or only slightly exceeding terminal margin of basipod.

Remarks

Antennuloniscus is one of the best defined genera of the Haploniscidae although the diagnosis given by Menzies and Schultz (1968) has to be modified. Most important characters are the anteriorly projecting clypeus (Fig. 4.4), which is unique in the family, and the highly modified antenna 2. Article 1 of antenna 2 is usually minute and concealed by article 2 in ventral view (Fig. 4.4): In all species described below, article 1 was found only after careful dissection of the antenna. In *A. simplex* Lincoln, 1985b it is slightly larger, but still smaller than in other genera of the family. With exception of *A. latoperculus*, the spine on article 3 of antenna 2 is short and often blunt; in the new species it is at least half as long as the width of the article. It is questionable if the longitudinal groove of article 3 really contains articles 4-6 when the antenna is folded caudally as described by Menzies and Schultz (1968). Article 3 is too short for articles 4-6 being inserted in that groove. As the peduncle of antenna 2 is relatively stout compared to other Haploniscidae, this groove probably helps in maintaining the mobility of the joints between articles 3, 4 and 5. In some species the groove is reduced and forms only a suture line (Fig. 4.4). Articles 5 and 6 are completely fused; the suture is still visible under the compound microscope but diffuse. The flagellum of antenna 2 is always small in comparison to the peduncle but comprises not always eight to ten articles as stated by Menzies and Schultz (1968); e. g., in *A. simplex* it has six articles. The male antenna 1 has five flagellar articles (flagellum defined as in Lincoln 1985a, b, which differs from the definition of Menzies and Schultz, (1968) who counted peduncular article 3 as first flagellar article) in most species, but not in *A. simplex*, where both males and females have a three-articulated flagellum. Often antenna 1 is reflexed caudally. In a number of species the maxilliped bears only two retinacula instead of three.

Although pereonites 5-7 are fused with each other and the pleotelson, the lateral margins of these segments are expressed and the sutures between pereonites 5-7 are usually distinct dorsally. The ventral surface of the posterior body shows a sexual dimorphism; usually the sutures between pereonites 5-7 and the pleotelson are clearly visible in males, while they may be absent or indistinct between pereonites 6 and 7 and the pleotelson in females.

Menzies and Schultz (1968) do not discuss the presence of an “intersex” specimen in their material of *A. subellipticus*, but this specimen is probably not an “intermediate” specimen as described by Wolff (1962: 212). Pleopod 2 of this individual has very few distal setae unlike the female operculum. Therefore it is probably a stage IV or IVa male (stages after Wolff, 1962). Sparsely setose pleopods 2 can be observed in other juvenile males of the Haploniscidae as well.

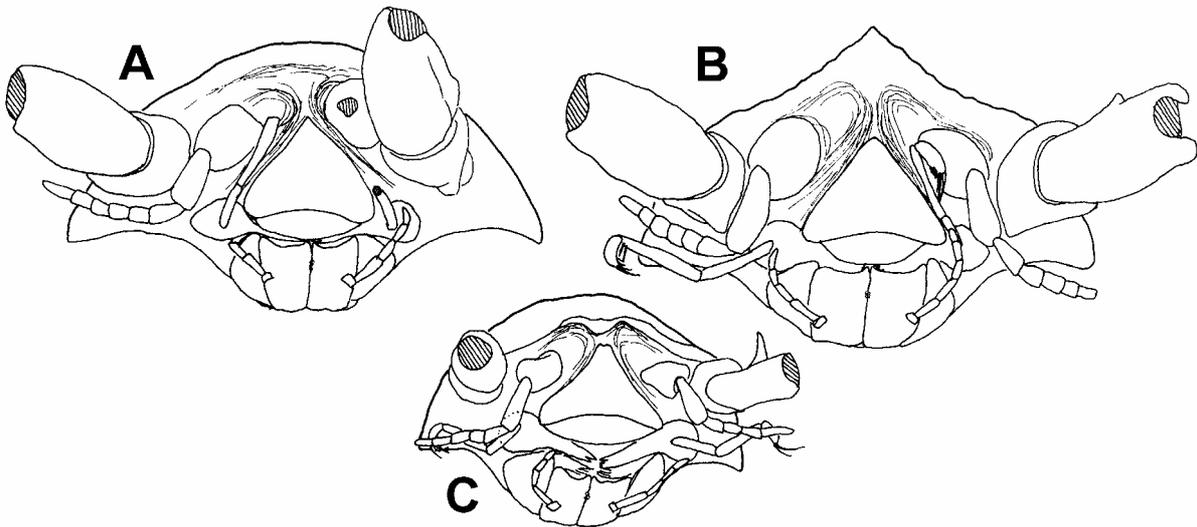


Figure 3.13: Fronteroventral view of anterior body: A *Antennuloniscus ornatus* Menzies, 1962, male; B *Antennuloniscus armatus* Menzies, 1962, male; C *Antennuloniscus latoperculus* n. sp., female.

3.1.2.2.1 *Antennuloniscus ornatus* Menzies, 1962

Figs 3.13-3.20

Material

Holotype: AMNH 12004, male, 2.0 mm, V-14-23, archipelagic apron of Menzies Seamount, southwest of South Georgia, eastern Scotia Sea, Atlantic, 55°29'S 37°57'W, 3770 m depth. ANDEEP material: Station 42-2, 59°40.30-40.32'S 57°35.42-42.64'W, 3689 m depth: two

males, 2.1 and 2.2 mm; five females, 1.9 – 2.3 mm; one ovigerous female, 2.0 mm; one juvenile, 1.1 mm long; ZMH K40723. Station 43-8, 60°27.13-27.19'S 56°05.12-04.81'W, 3962 m depth: one male, 2.0 mm; one female, 1.9 mm; ZMH 40724.

Diagnosis

Body broadly oval, 2 times as long as wide, head 2.1 times as wide as long, frontal margin convex; basis of pleotelson 1.8 times as wide as terminal margin in males, posterolateral processes short, not reaching terminal margin; antenna 2 peduncular article 3 with small dorsal tooth, longitudinal groove distinct, flagellum almost as long as articles 5 and 6, with 8 articles; carpus of P5–7 with numerous long simple setae ventrally; Plp1 1.7 times as long as wide, broadest part in the proximal fifth, 2.2 times broader than narrowest part, sympods separated at distal tip; Plp2 basipod 1.9 times as long as wide; endopod 0.8 times as long as basipod, sperm duct reaching from endopod tip almost to proximal third of article 2.

Description of male (ANDEEP specimen)

Body (Fig. 3.14) broadly oval, 2 times as long as wide. Head 2.1 times as wide as long, frontal margin convex. Margins of pereonites rounded, smooth; pereonite 5 broadest. Pleotelson 0.2 times as long as body, tapering slightly distally, basis 1.8 times as wide as terminal margin; lateral margins slightly convex, serrated, with numerous setae (broken off in illustrated specimen); terminal margin with median convex extension bearing the anus; posterolateral processes short, not reaching terminal margin; dorsal surface with 2 rounded longitudinal ridges, ventral surface with cuticular suture line surrounding the branchial chamber. Cuticle of body, pleopods 1 and 2, maxillipedal epipod and peduncular articles of antenna 2 with numerous small round depressions (Fig. 3.14 H).

Antenna 1 (Fig. 3.14) about 0.2 times as long as body, article 1 broadest, about 1.4 times as long as wide, article 2 slightly shorter, about half as wide as article 1, both articles with several broom and simple setae; article 3 0.6 times as long as article 2, with simple seta; flagellum with 5 articles of subequal length; article 1 with broom seta; article 2 with 1, article 3 with 2 aesthetascs, article 4 with 3 aesthetascs and 1 simple seta, terminal article with 1 lateral and 2 apical aesthetascs, 3 simple setae and 1 short broom seta.

Antenna 2 (Fig. 3.16) almost half as long as body, article 1 minute, in situ concealed by article 2, article 2 about as long as wide, article 3 about 2 times as long as wide, 1.3 times as long as article 2, with longitudinal groove and small, blunt dorsal tooth, article 4 short, 0.5 times as long as article 3, fused articles 5 and 6 together 1.2 times as long as article 3, with

numerous simple setae, some broom setae (broken off in illustrated specimen) and apical tooth; flagellum inserting subapically, slightly shorter than fused articles 5 and 6, with 8 articles of decreasing width, each with numerous simple setae.

Mandible (Fig. 3.17) incisor with five blunt teeth, *lacinia mobilis* of left mandible with five teeth, right mandible with stout serrated spine-like seta instead, spine row comprising 2 serrated and 2 simple spine-like setae; molar tooth row with 7 teeth and 4 setulated setae proximally, cuticular ledge tapering off forming a single tooth, right mandible with row of 6 indistinct accessory teeth proximally of cuticular ledge; palp article 2 with single serrated spine-like seta proximally of insertion of article 3, article 3 with 4 serrated spine-like setae of increasing length, distal seta about 3 times as long as proximal seta.

Maxilla 1 (Fig. 3.17) outer lobe with 8 simple and 4 serrated spine-like setae and several simple setae on lateral and medial margin and surface; inner lobe apically with 2 short spine-like setae and several simple setae.

Maxilla 2 (Fig. 3.17) outer lobe with 2 long and 1 short simple spine-like setae apically and rows of simple setae on lateral margin; medial lobe with 1 long and 1 shorter serrated spine-like seta and 1 simple seta apically and three spine-like setae on medial margin; inner lobe with 2 apical serrated spine-like setae, 3 stout apical simple setae and numerous simple setae on surface and medial margin.

Maxilliped (Fig. 3.18) endite apical margin with 2 small fan setae and 2 short spine-like setae, ventral surface with 1 spine-like and numerous simple setae, separated apical medial margin dorsally with 1 simple spine-like seta 1 serrated spine-like seta and row of simple setae, medial margin with 2 retinacula; epipod slightly longer than endite.

Pereopods (Figs 3.18-3.20): Basis of P1 only with 1 long simple seta ventrally, basis of P2-4 with 1 (P2 and 3) or 2 simple setae ventrally, 1 or 2 broom setae and 1 simple seta dorsally; basis of P5-7 with 2 long setae ventrally and a simple seta dorsally, P5 and 6 with 3 broom setae dorsally. Ischium with short simple setae on P1-4 and long simple setae ventrally on P5-7. Merus with 4 apical setae and 1 or 2 (P6 and 7) setae ventrally. Carpus with ventral comb-like scale rows and 3-4 long simple setae on P1-4, P5 with 4 simple setae and 1 stout seta ventrally, P6 and 7 with 6 respectively 7 simple setae and 1 stout seta; P7 with dorsal stout flagellate seta; apical comb on carpus of P1 small and setose, apical combs on P2-7 comprised of 1 small and 1 large spinose comb, decreasing in size on P6 and 7. Propodus with ventral row of comb-like scales and 2-5 simple setae ventrally, P5-7 with spine-like seta ventrally. Dactylus with 3 lateral setae on P1-4 and 1 lateral seta on P5-7; accessory tooth acute.

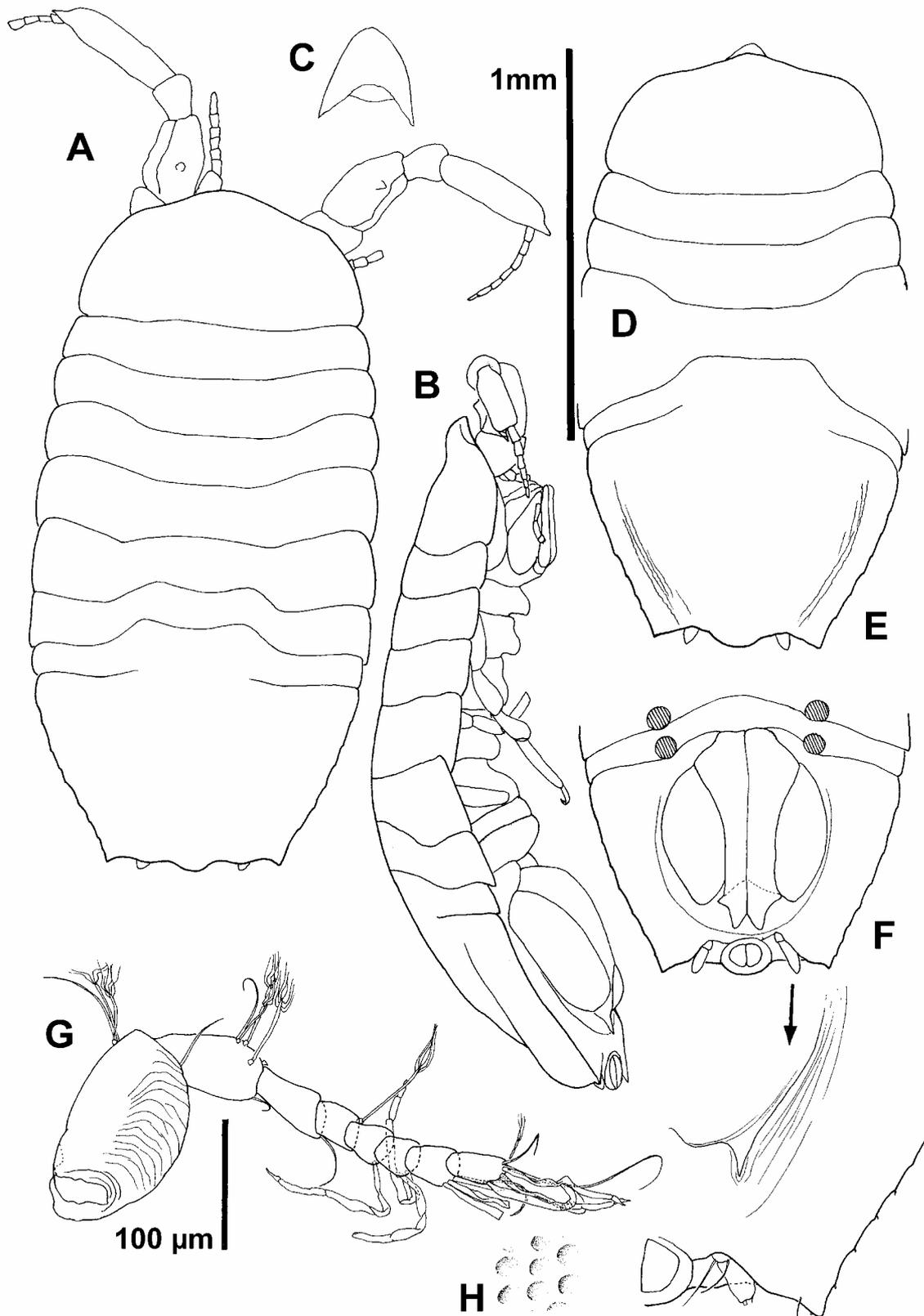


Figure 3.14: *Antennuloniscus ornatus* Menzies, 1962, ANDEEP male, 2.1 mm: A entire, dorsal view; B entire, lateral view; C prolonged clypeus with labrum, ventral view; D anterior part of body, dorsal view; E posterior body, dorsal view; F posterior body, ventral view; G antenna 1; H detail of cuticle structure.

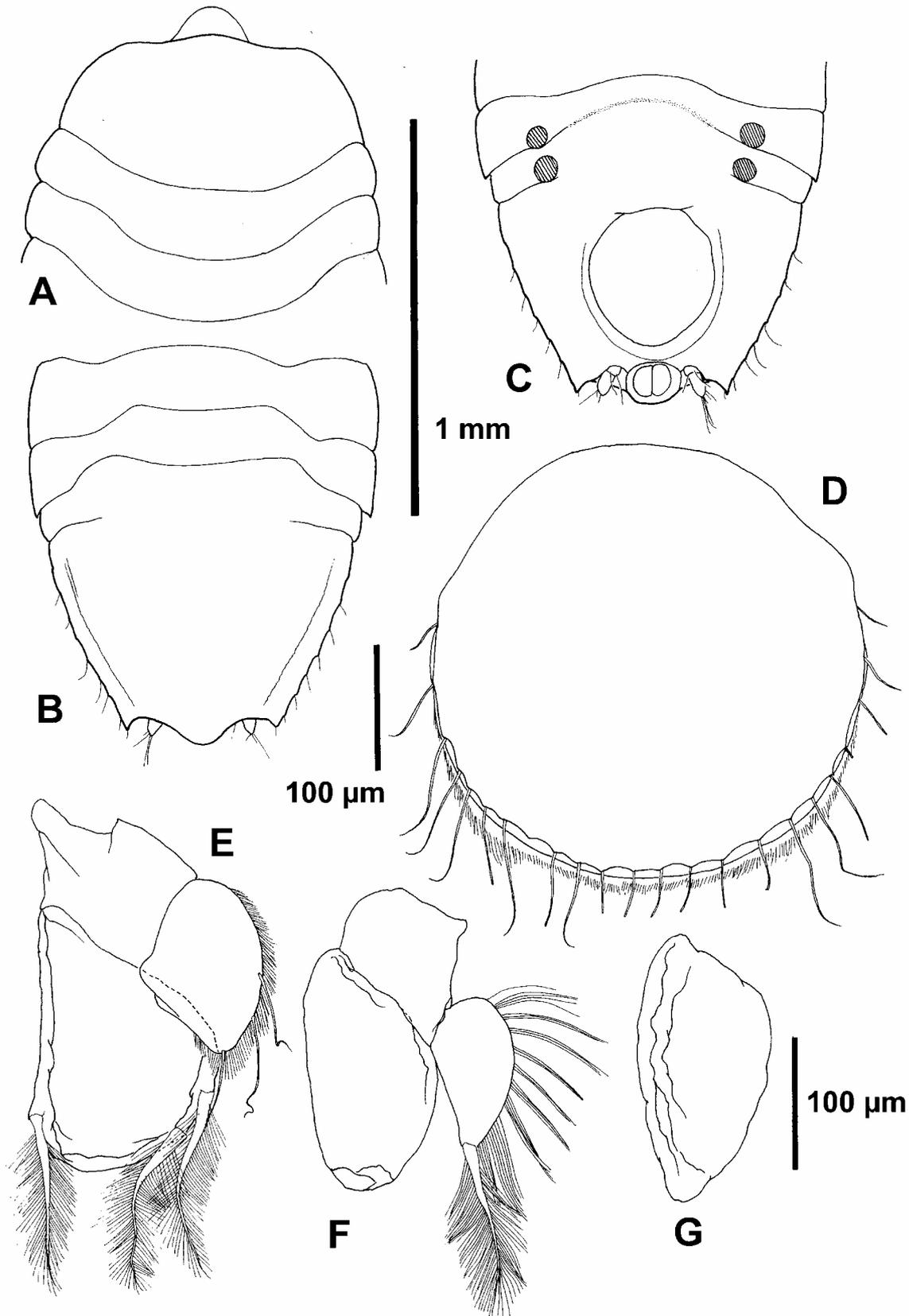


Figure 3.15: *Antennuloniscus ornatus* Menzies, 1962, ANDEEP female, 2.2 mm: anterior part of body, dorsal view; B posterior part of body, dorsal view; C posterior body, ventral view; D pleopod 2; ANDEEP male, 2.1 mm: E pleopod 3; F pleopod 4; G pleopod 5.

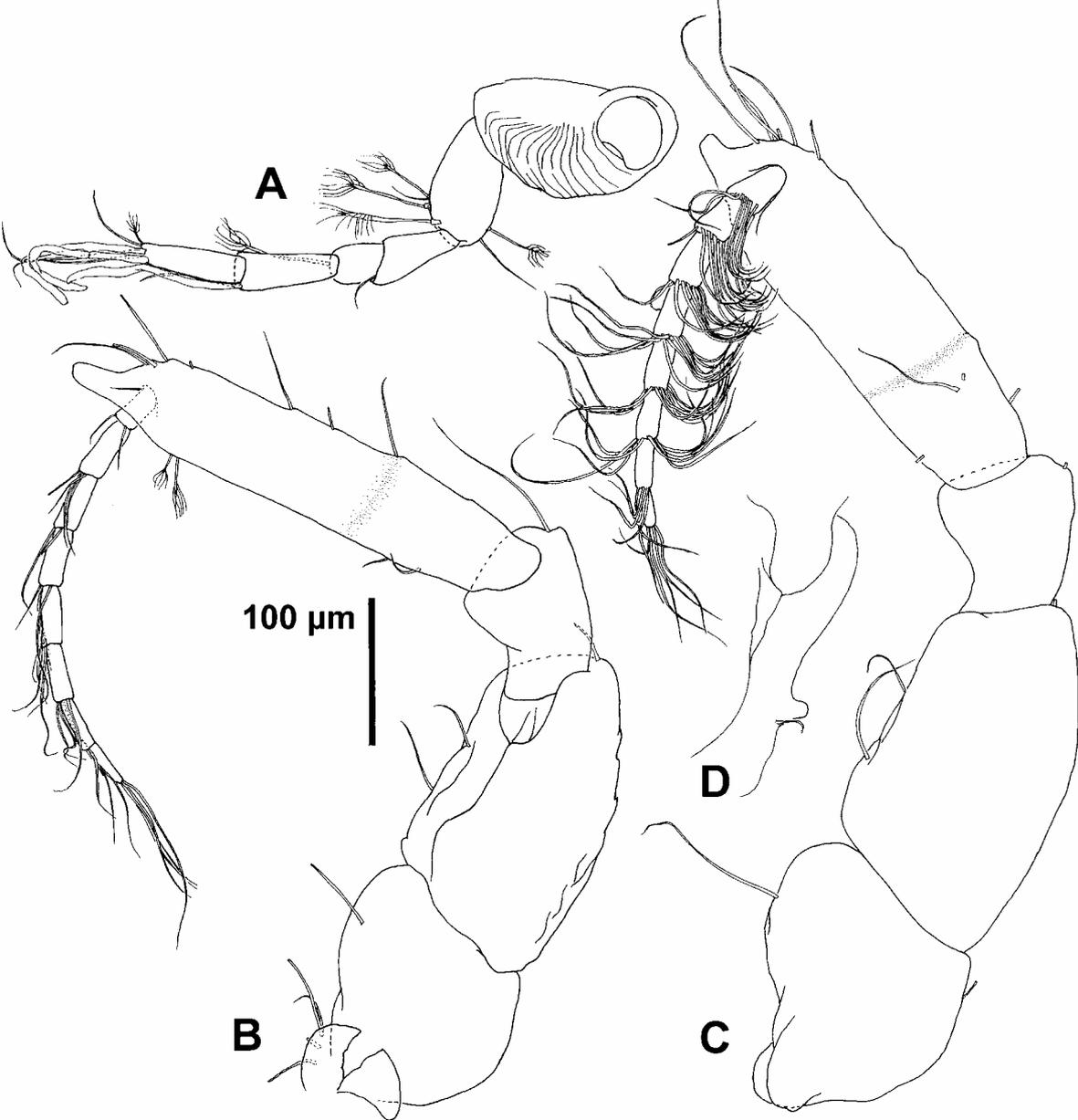


Figure 3.16: *Antennuloniscus ornatus* Menzies, 1962, ANDEEP female, 2.2 mm: A antenna 1; B antenna 2; male, 2.1mm: C antenna 2, female.

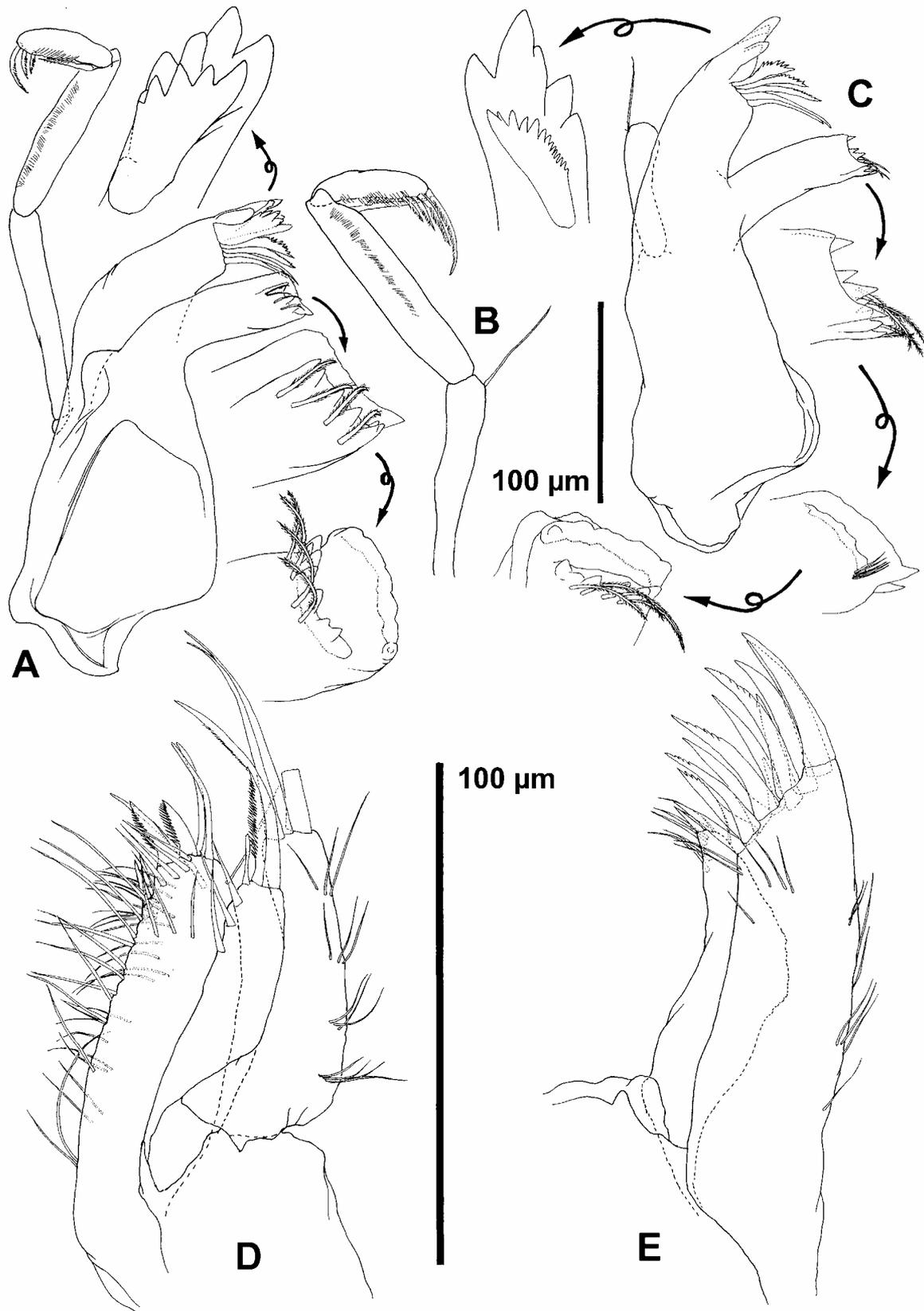


Figure 3.17: *Antennuloniscus ornatus* Menzies, 1962, ANDEEP male, 2.2 mm, female, 2.2 mm: A left mandible, female; B left mandibular palp, male; C right mandible, female; D maxilla 2; E maxilla 1.

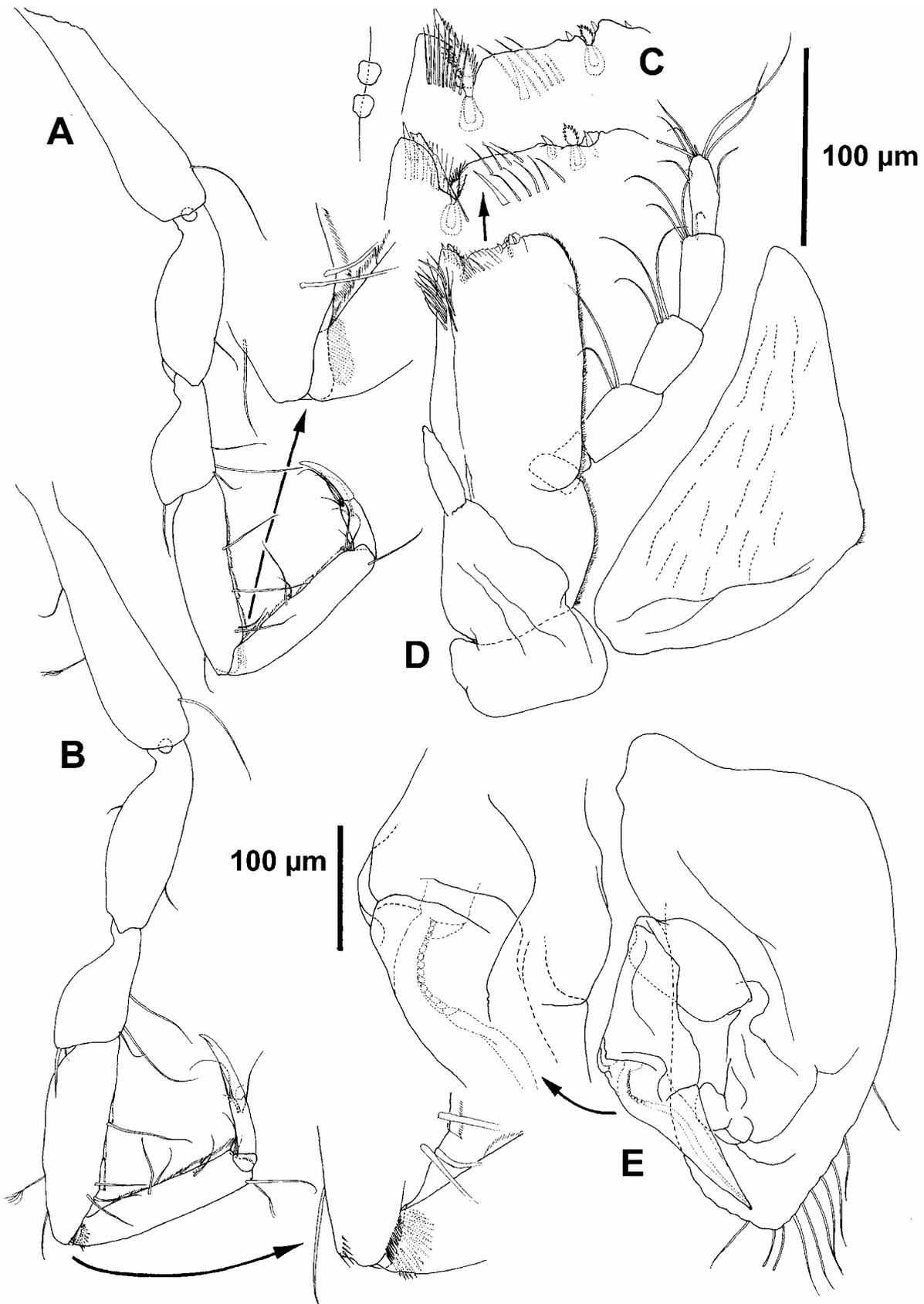


Figure 3.18: *Antennuloniscus ornatus* Menzies, 1962, ANDEEP male, 2.1 mm: A pereopod 1; B pereopod 2; C detail of left maxilliped, dorsal view; D right maxilliped, ventral view; E pleopod 2.

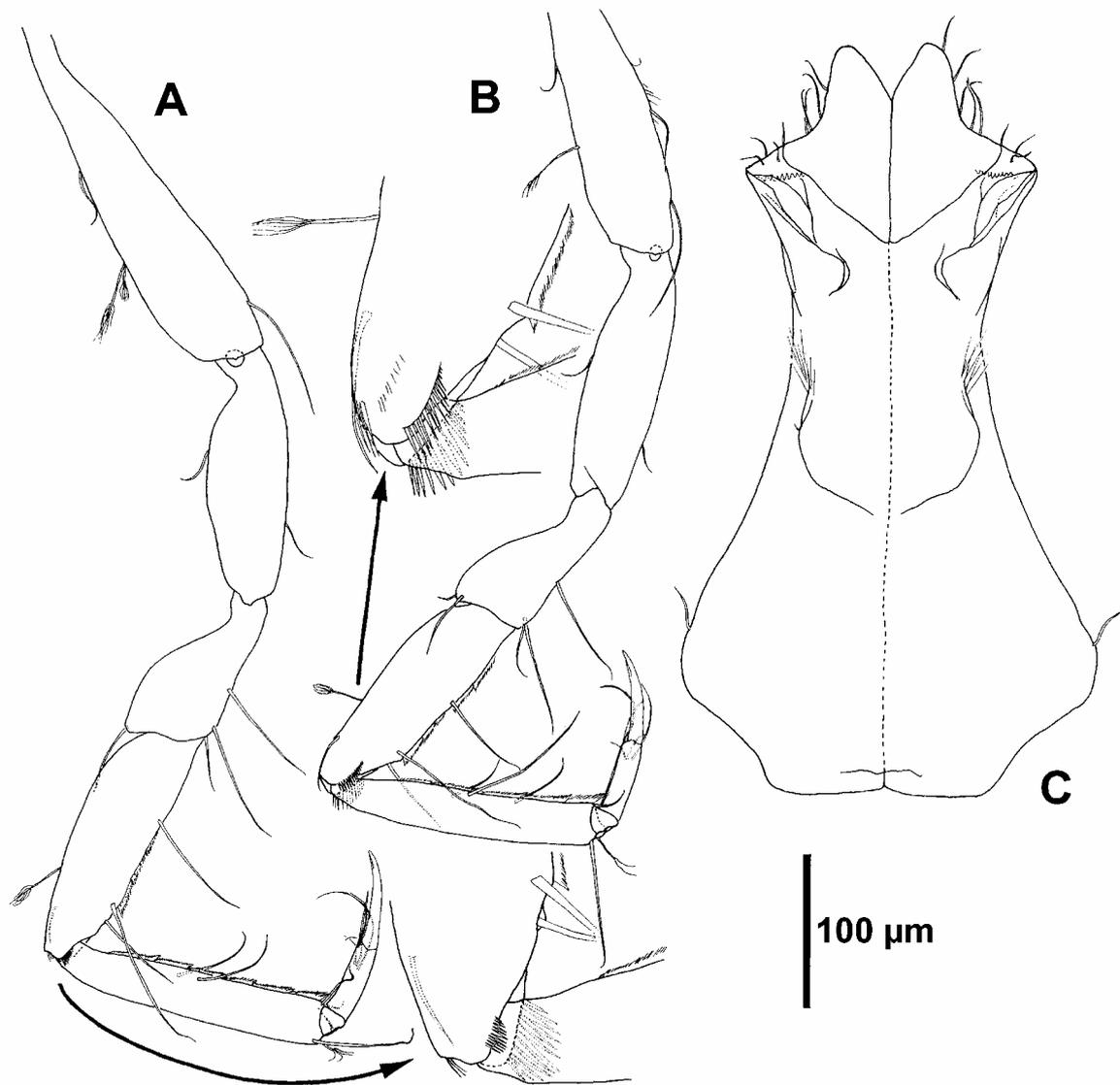


Figure 3.19: *Antennuloniscus ornatus* Menzies, 1962, ANDEEP male, 2.1 mm: A pereopod 3; B pereopod 4; C pleopod 1.

Pleopods (Figs 3.15, 3.18, 3.19): Plp1 1.7 times as long as wide, broadest part in the proximal fifth, 2.2 times broader than narrowest part, lateral margins with simple seta, distal margins with about 6 setae each, sympods separated at the distal tip, ventral surface with mediolateral bulges with several bristles and 2 transverse grooves in the distal third. Plp2 basipod 1.9 times as long as wide, with several simple setae in the distal part; endopod inserting in distal half of basipod, short, stout, 0.8 times as long as basipod, article 2 about 2 times as long as article 1, expanding in medial part, sperm duct reaching from endopod tip almost to proximal third of article 2, exopod small, inserting in the distal third of basipod. Plp3 endopod 1.3 times as long as wide, with rounded distal margin; exopod almost triangular, as

wide as long, 0.75 times as wide and half as long as endopod, lateral margin rounded, with 3 simple setae and fringe of fine bristles. Plp4 endopod oval, 1.8 times as long as wide; exopod 1.8 times as long as wide, 0.6 times as long and wide as endopod, lateral margin rounded with fringe of long bristles, plumose seta slightly longer than exopod. Plp5 2 times as long as wide.

Uropods (Fig.3.14) short, stout, not reaching terminal margin.

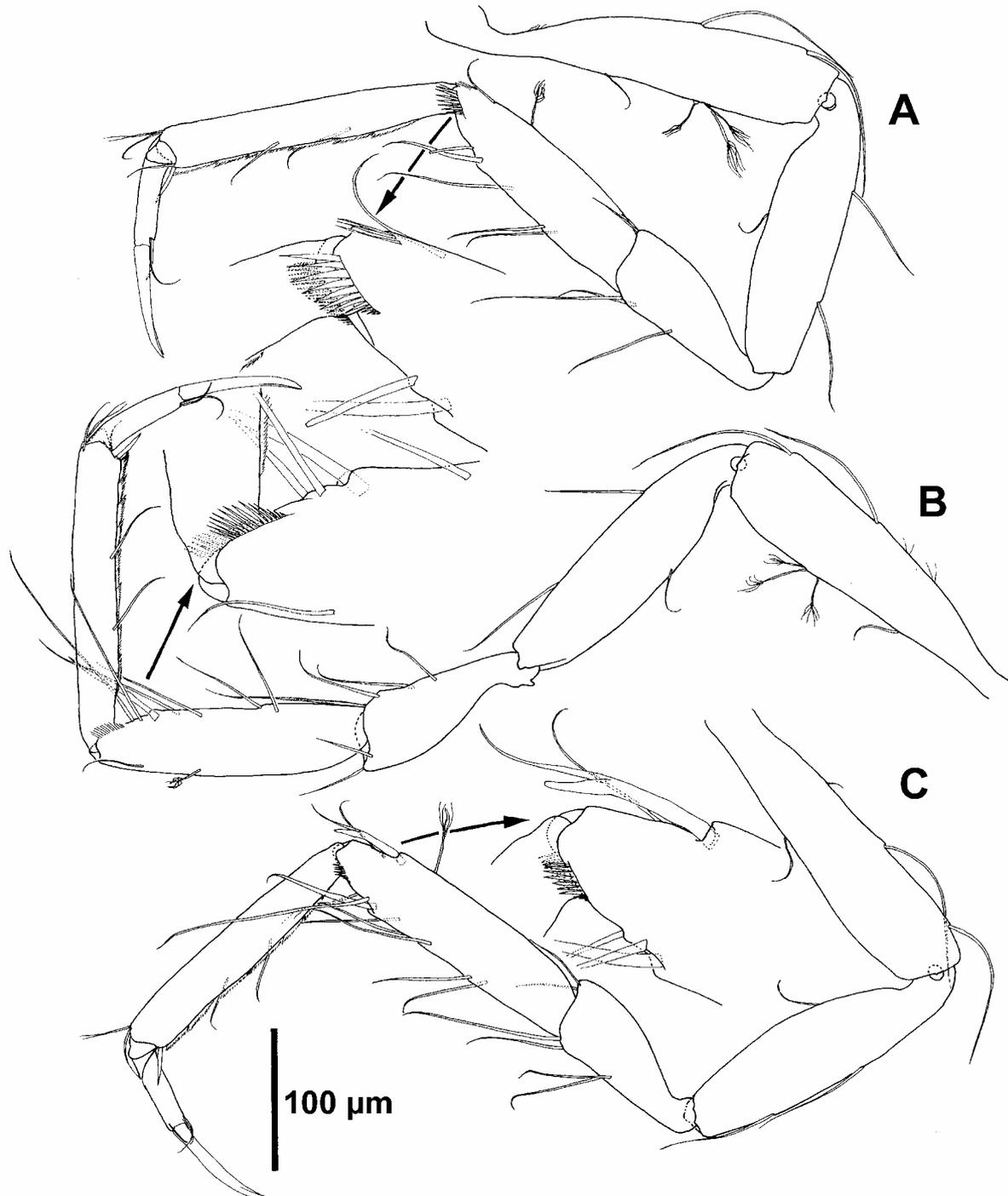


Figure 3.20: *Antennuloniscus ornatus* Menzies, 1962, ANDEEP male, 2.1 mm: A pereopod 5; B pereopod 6; C pereopod 7.

Description of female (ANDEEP specimen)

The female differs from the male in the following characters:

Sutures between pereonites 6 and 7 and pleotelson not distinct ventrally.

Basis of pleotelson (Fig. 3.15) 2 times as broad as terminal margin, longitudinal keels on dorsal surface less distinct, terminal margin slightly stronger produced.

Antenna 1 (Fig. 3.16) with 3 flagellar articles, article 2 with 1 aesthetasc, article 3 with 2 aesthetascs.

Antenna 2 (Fig. 3.16) more slender, flagellum with fewer setae.

Mandibular palp (Fig. 3.17) with 3 spine-like setae on article 3.

Operculum (Fig. 3.15) subcircular, with numerous simple setae on distal and lateral margins.

Remarks

The type specimens were found in the eastern Scotia Sea off South Georgia and off Cape Horn (55°31.2'S 64°7.5'W). The new specimens were found at two stations in the Drake Passage off Elephant Island. All three stations have a similar depth range. The original description by Menzies (1962) is not very detailed and also the redescription by Menzies and Schultz (1968) is rather inadequate, but the observation of the holotype revealed no differences between Menzies' and the new material.

Menzies (1962) stated that the closest relative of *A. ornatus* might be *A. dimeroceras* Barnard, 1920 based on the fact that both species are known from the South Atlantic and Menzies and Schultz (1986) follow his view. A comparison of the two species shows that they are rather morphologically different from each other and the occurrence of both species in the South Atlantic is not a satisfying reason to postulate a close relationship between them.

A. ornatus differs from the other species in the genus in having a broadly oval body. The pleotelson is similar to those of *A. armatus* and *A. subellipticus* Menzies and Schultz (1986), but broader and less tapering.

Whether the slight projection of the frontal margin of the head should be described as convex or bearing a rostral process is difficult to decide. The process is less distinct than in *A. armatus*, *A. diversus* Lincoln, 1985b, *A. dilatatus* Chardy, 1974 and the new species described below. Therefore it was not indicated as a rostrum above.

3.1.2.2.2 *Antennuloniscus armatus* Menzies, 1962

Figs 3.13, 3.21-3.26

Material

Holotype: AMNH 11997, female, 2.3 mm, V-14-28, western flank of Walvis Ridge, northwest of Meteor Seamount, Atlantic, 45°34'S 6°2'E, 4618 m depth.

ANDEEP material: Station 42-2, 59°40.30-40.32'S 57°35.42-42.64'W, 3689 m depth: seven subadult males, 2.1-2.5 mm; 15 females, 2.0-2.3 mm; six ovigerous females, 2.3-2.5 mm; ZMH K40725. Station 43-8, 60°27.13-27.19'S 56°05.12-04.81'W, 3962 m depth: two females, 2.1-2.2 mm; one ovigerous female, 2.4 mm; ZMH K40726.

Diagnosis

Body oval, 2.5 times as long as wide, head 2.3 times as wide as long, frontal margin slightly concave, with acute frontodorsally directed triangular rostrum; basis of pleotelson 2 times as wide as terminal margin in subadult males, posterolateral processes short, but exceeding terminal margin; antenna 2 peduncular article 3 with small, blunt dorsal tooth, longitudinal groove distinct, flagellum almost as long as articles 5 and 6, with 8 articles. Long simple setae ventrally on carpus of P1-4, moderately long simple setae ventrally on carpus of P5-7. Plp1 of subadult males 1.75 times as long as wide, broadest part in the proximal quarter, 2.25 times broader than narrowest part. Plp2 basipod 1.8 times as long as wide; endopod 0.85 times as long as basipod.

Description of subadult male (ANDEEP specimen)

Body (Fig. 3.21) oval, 2.5 times as long as wide; head 2.3 times as wide as long (without rostrum), frontal margin slightly concave, with acute frontodorsally directed triangular rostrum; margins of pereonites rounded, smooth; pereonite 4 broadest. Pleotelson 0.2 times as long as body, tapering distally, basis 2 times as wide as terminal margin; lateral margins slightly convex, serrated, with numerous setae (broken off in illustrated specimen); terminal margin with median convex extension bearing the anus; posterolateral processes short, exceeding terminal margin; dorsal surface with 2 rounded longitudinal ridges, ventral surface with cuticular suture line surrounding the branchial chamber. Cuticle of body, pleopods 1 and 2, maxillipedal epipod and peduncular articles of antenna 2 with numerous small round depressions.

Antenna 1 (Fig. 3.23) about 0.3 times as long as body length, article 1 broadest, about 1.3 times as long as wide, article 2 0.75 times as long and about half as wide as article 1, both articles with several broom setae; article 3 0.6 times as long as article 2, with simple seta; flagellum with 5 articles; article 1 shortest, with broom seta; articles 3 and 4 with 1 aesthetasc each, article 4 with 1 simple seta, terminal article longest, with 2 apical aesthetascs, 3 simple setae and 1 short broom seta.

Antenna 2 (Fig. 3.23) half as long as body, article 1 minute, in situ concealed by article 2, article 2 about as 1.2 times as long as wide, article 2 1.9 times as long as wide, 1.5 times as long as article 2, with longitudinal groove and small, blunt dorsal tooth, article 4 short, 0.5 times as long as article 3, fused articles 5 and 6 together 1.1 times as long as article 3, with numerous simple setae and apical tooth; flagellum inserting subapically, slightly shorter than fused articles 5 and 6, with 8 articles of decreasing width, each with numerous simple setae.

Mandible (Fig. 3.24) incisor with five blunt teeth, left mandible with *lacinia mobilis* with five teeth, right mandible with stout serrated spine-like seta instead, spine row comprising 2 serrated and 2 simple spine-like setae; molar tooth row with 6 teeth and 4 setulated setae proximally, cuticular ledge ending in a tooth on both sides, right mandible with cuticular ledge forming several blunt teeth and row of 4 blunt accessory teeth proximally; palp article 2 with 1 short and 1 longer serrated spine-like seta proximally of insertion of article 3, article 3 with 5 serrated spine-like setae of increasing length, distal seta about 4 times as long as proximal seta.

Maxilla 1 (Fig. 3.23) outer lobe with 10 simple and 3 serrated spine-like setae and several simple setae on lateral and medial margin and surface; inner lobe apically with short spine-like seta and several simple setae.

Maxilla 2 (Fig. 3.22) outer lobe with 2 long and 1 short simple spine-like setae apically and rows of simple setae on lateral and medial margin; medial lobe with 1 long simple and 1 shorter serrated spine-like seta and 1 simple seta apically and three spine-like setae on medial margin; inner lobe with 2 apical serrated spine-like setae, 3 stout apical simple setae and numerous simple setae on surface and margins.

Maxilliped (Fig. 3.24) endite apical margin with 2 small fan setae and 2 short spine-like setae, ventral surface with 1 spine-like and numerous simple setae, separated apical medial margin dorsally with 1 small and 1 larger serrated spine-like seta and row of simple setae, medial margin with 2 retinacula; epipod slightly longer than endite.

Pereopods (Figs 3.25, 3.26): Basis of P1–3 only with 1, of P4–7 with 2 long simple setae ventrally; P2–5 with 2, P6 with 3 and P7 with 1 broom seta dorsally (some broken of in

illustrated specimen); all pereopods with 1 simple seta dorsally. Ischium with short simple setae on P1–4 and long simple setae ventrally on P5–7. Merus with 4 apical and 1 ventral seta. Carpus with ventral comb-like scale rows slightly reduced on P5–7; ventrally 2–3 long simple setae on P1–4, on P5–7 1 simple seta and 2 stout setulated setae; P7 with dorsal stout flagellate seta; apical comb on carpus of P1 small and setose, apical combs on P2–7 composed of 1 small and 1 large spinose comb, on P5–7 both combs of subequal size, on P6 and 7 small. Propodus ventrally with row of comb-like scales and 3–4 simple setae on P1–4, on P5–7 with 2 simple and 1 spine-like seta ventrally. Dactylus with 3 lateral setae on P1–4 and 1 lateral seta on P5; accessory tooth acute.

Pleopods (Figs 3.22, 3.26): Plp1 1.75 times as long as wide, broadest part in the proximal quarter, 2.25 times broader than narrowest part, distal margins with about 5 setae each, ventral surface with mediolateral bulges. Plp2 basipod 1.8 times as long as wide, with several simple setae in the distal part; endopod inserting in distal half of basipod, short, stout, 0.85 times as long as basipod, article 2 about 1.7 times as long as article 1, slender, sperm duct not developed; exopod small, inserting close to endopod. Plp3 endopod 1.6 times as long as wide, with rounded lateral and distal margin; exopod almost triangular, 1.3 times as wide as long, 0.8 times as wide and half as long as endopod, lateral margin rounded, with 4 simple setae and fringe of fine bristles. Plp4 endopod 1.8 times as long as wide; exopod 2.3 times as long as wide, 0.5 times as long and 0.4 times as wide as endopod, lateral margin rounded with fringe of long bristles in the distal half, plumose seta slightly longer than exopod. Plp5 1.6 times as long as wide.

Uropods (Fig. 3.21) short, stout, extending beyond terminal margin, not reaching tips of posterolateral projections of pleotelson.

Description of female (ANDEEP specimen)

The female differs from the male in the following characters:

Suture between pereonite 7 and pleotelson not distinct ventrally.

Basis of pleotelson (Fig. 3.22) 2.3 times as broad as terminal margin, longitudinal keels on dorsal surface less distinct, terminal margin slightly stronger produced.

Antenna 1 (Fig. 3.23) with 3 flagellar articles, article 2 with 1 aesthetasc, article 3 with 2 aesthetascs.

Antenna 2 (Fig. 3.23) more slender, flagellum with fewer setae.

Mandibular palp (Fig. 3.24) with 4 spine-like setae on article 3.

Operculum (Fig. 3.22) subcircular, with numerous simple setae on distal and lateral margins.

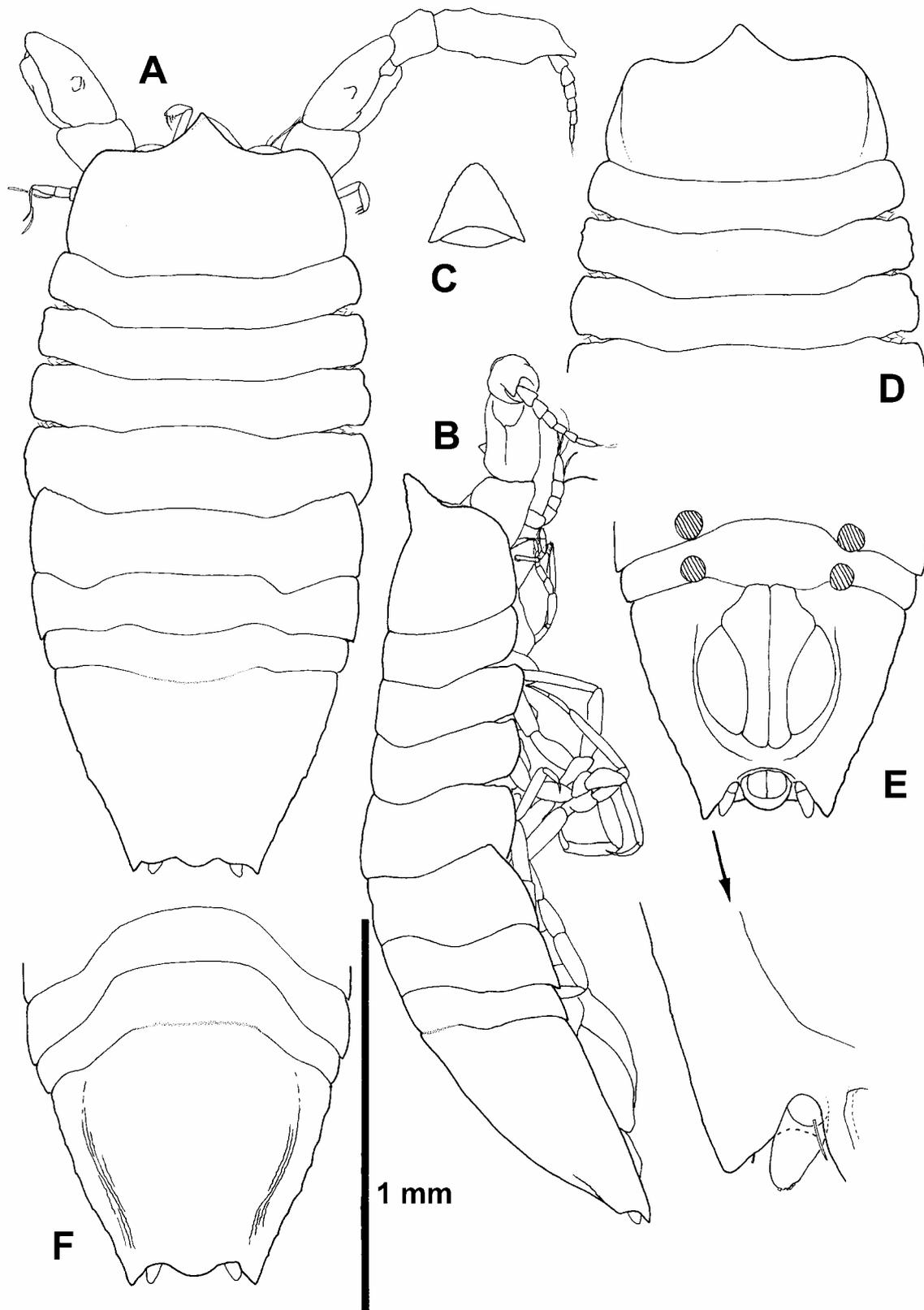


Figure 3.21: *Antennuloniscus armatus* Menzies, 1962, ANDEEP male, 2.2 mm: A entire, dorsal view; B entire, lateral view; C prolonged clypeus with labrum, ventral view; D anterior part of body, dorsal view; E posterior part of body, ventral view; F posterior part of body, dorsal view.

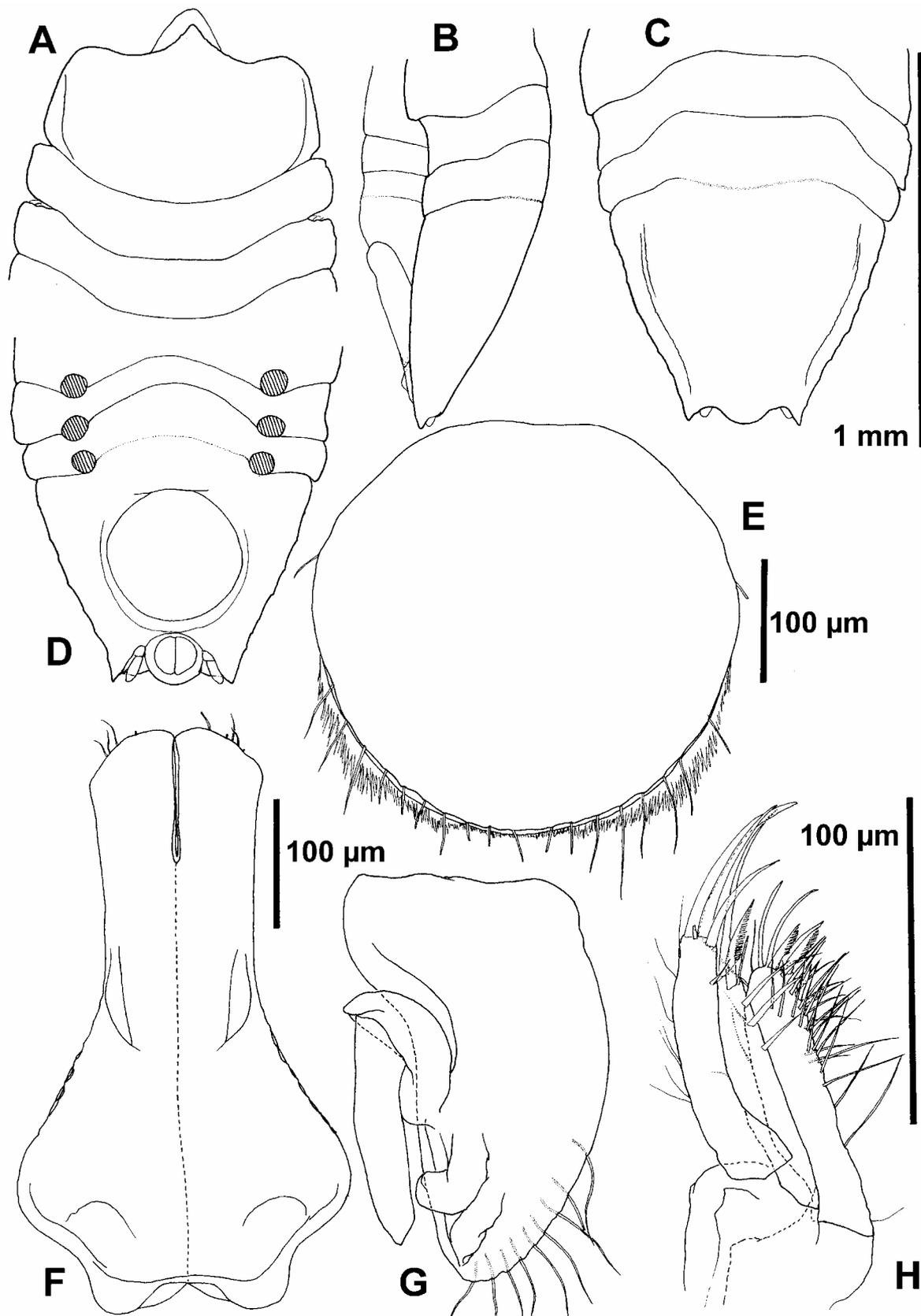


Figure 3.22: *Antennuloniscus armatus* Menzies, 1962, ANDEEP female, 2.1 mm: A anterior part of body, dorsal view; B posterior part of body, lateral view; C posterior part of body, dorsal view; D posterior part of body, ventral view; E pleopod 2; ANDEEP male, 2.2 mm: F pleopod 1; G pleopod 2; H maxilla 2.

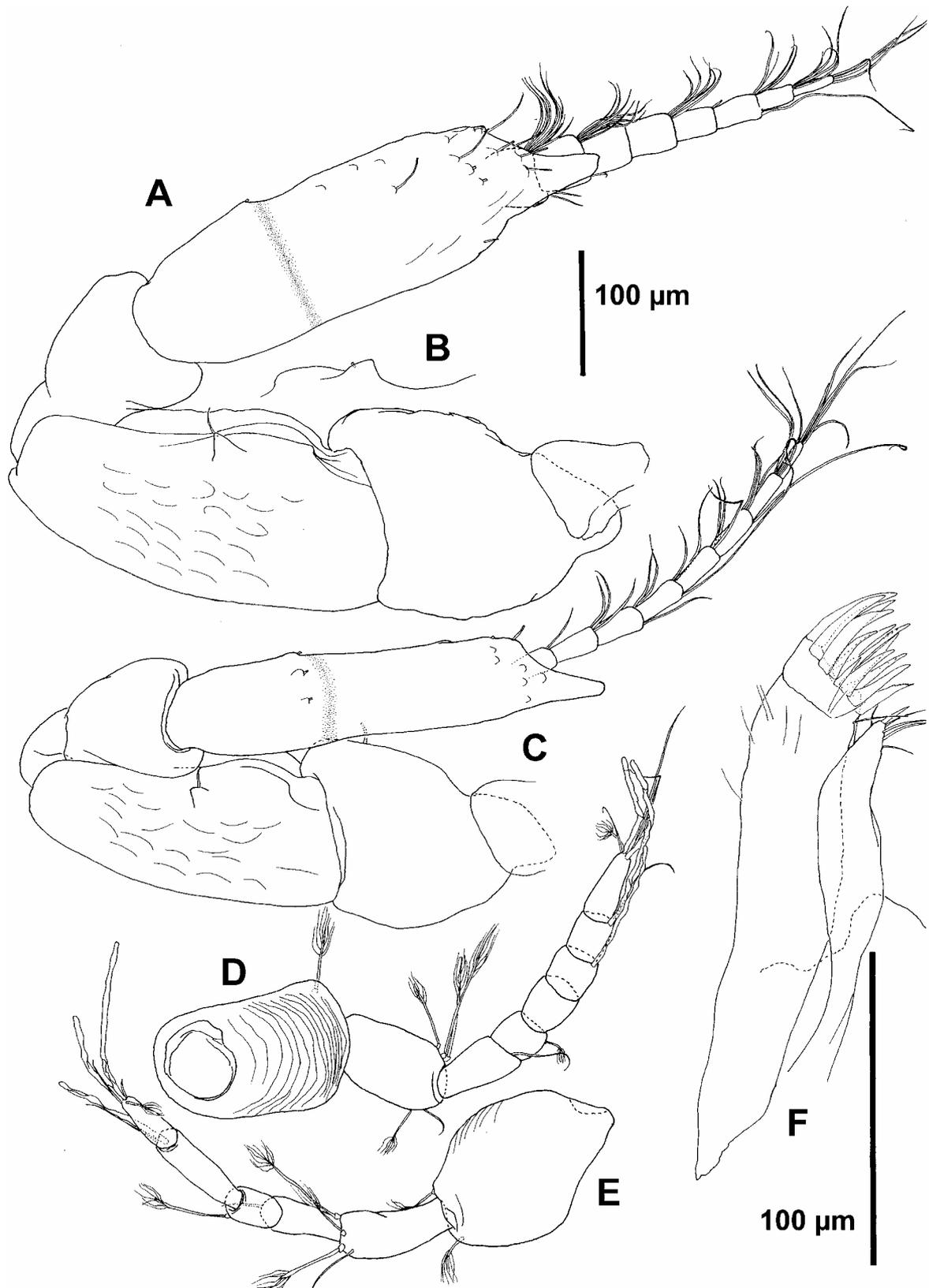


Figure 3.23: *Antennuloniscus armatus* Menzies, 1962, ANDEEP male, 2.2 mm, female, 2.1 mm: A antenna 2, male; B antenna 2, male, article 3 tooth, lateral view; C antenna 2, female; D antenna 1, male; E antenna 1, female; F maxilla 1.

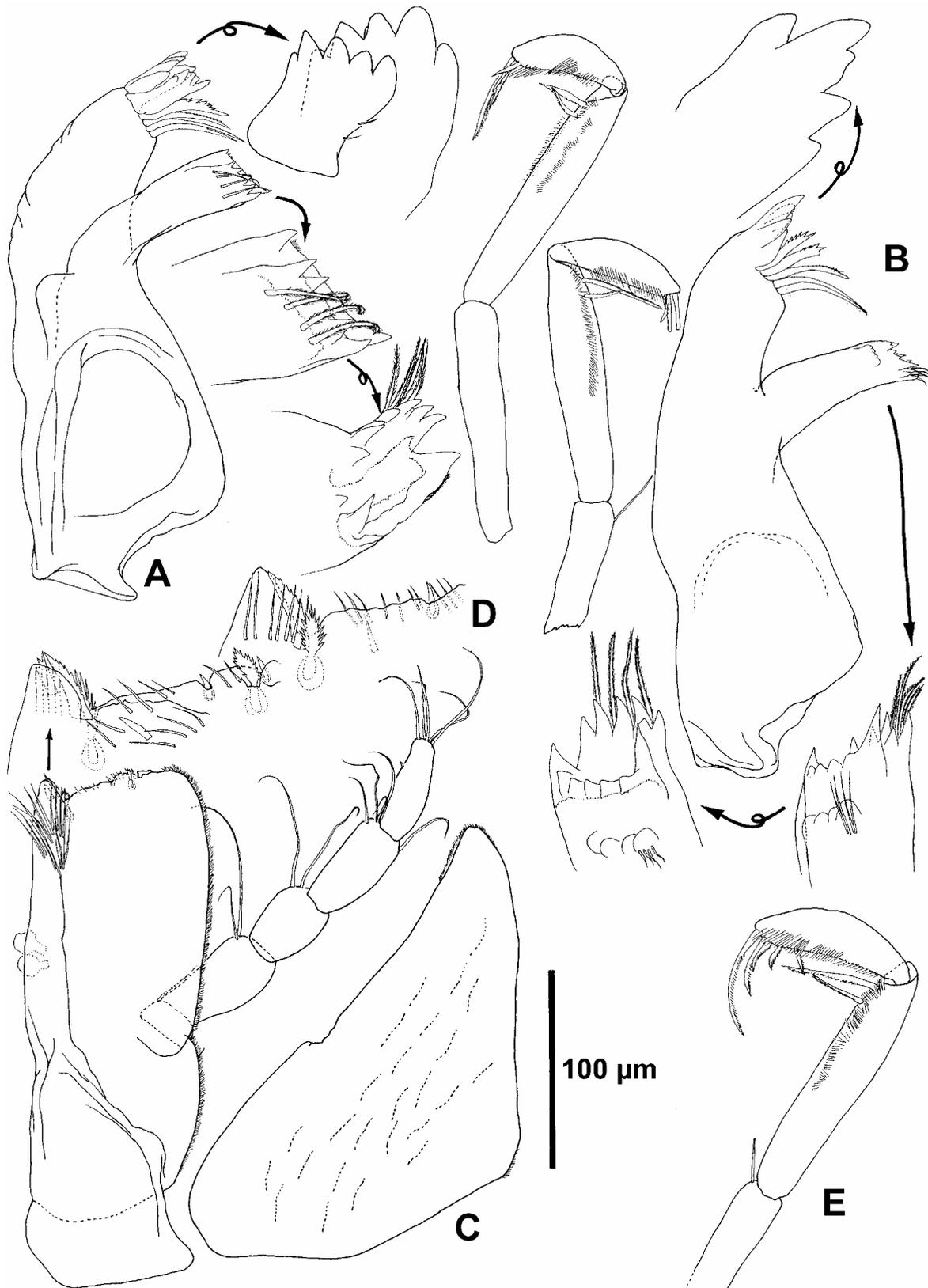


Figure 3.24: *Antennuloniscus armatus* Menzies, 1962, ANDEEP male, 2.2 mm, female, 2.1 mm: A left mandible, female; B right mandible, female; C right maxilliped, ventral view; D detail of left maxilliped, dorsal view; E left mandibular palp, male.

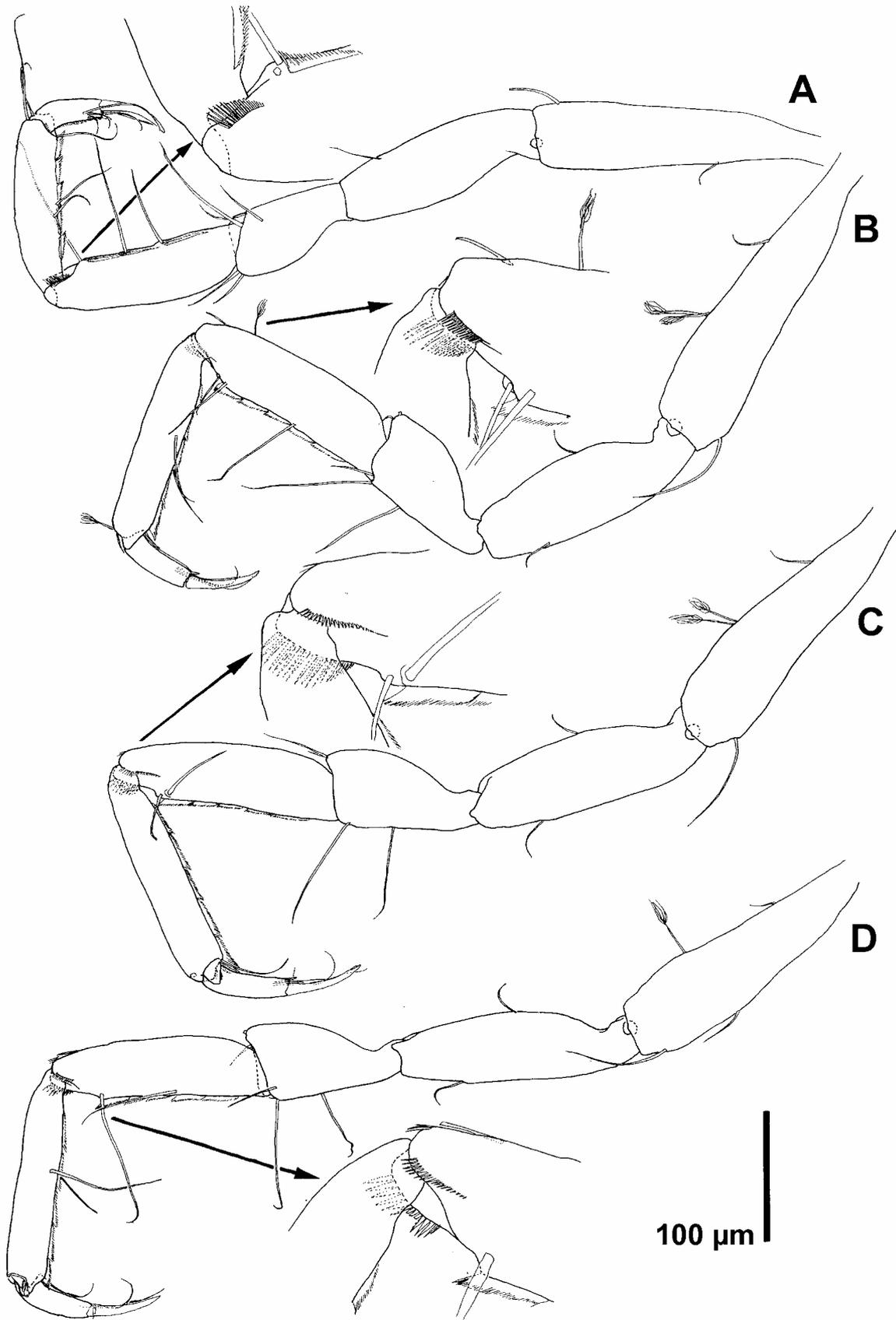


Figure 3.25: *Antennuloniscus armatus* Menzies, 1962, ANDEEP male, 2.2 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pereopod 4.

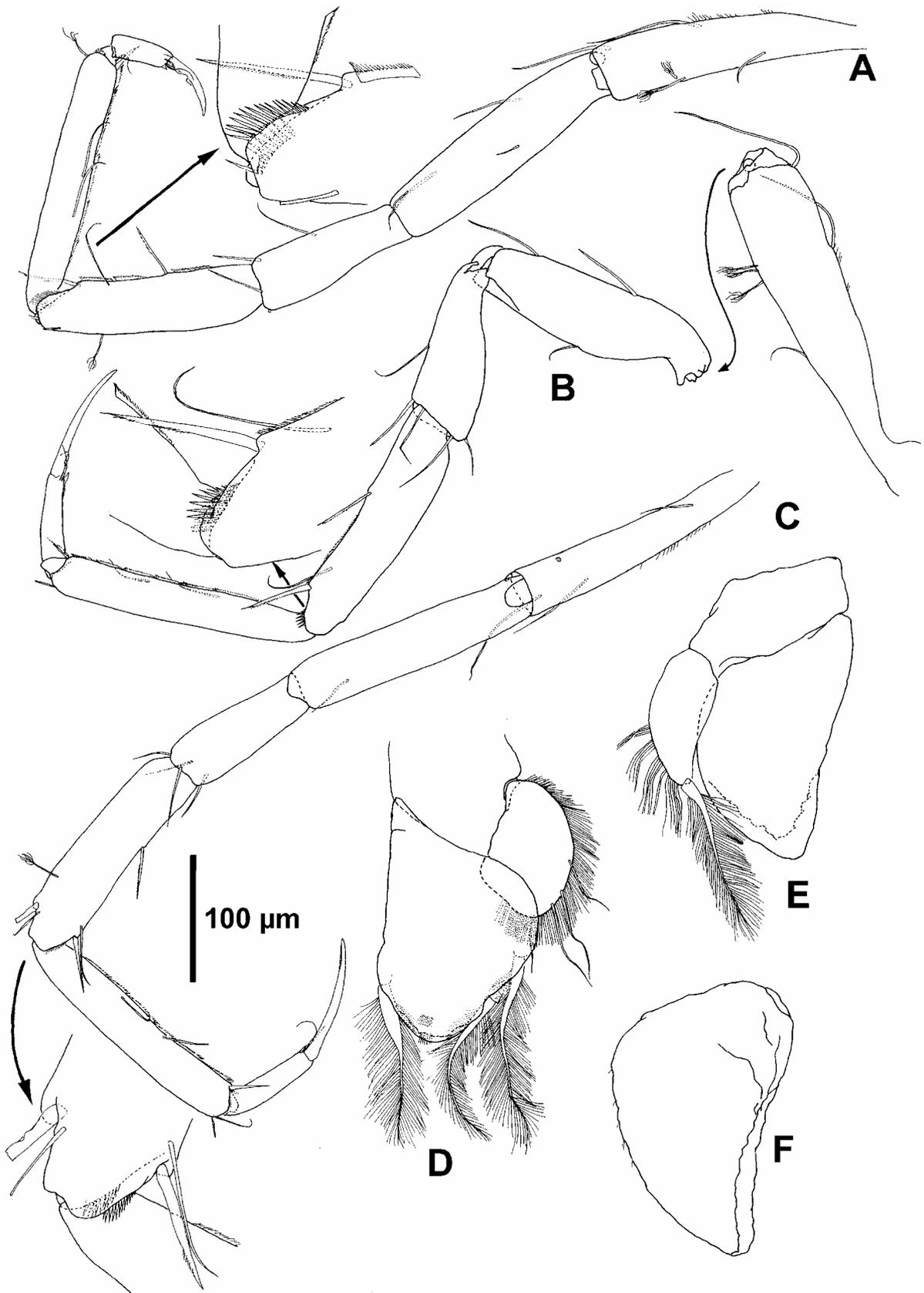


Figure 3.26: *Antennuloniscus armatus* Menzies, 1962, ANDEEP male, 2.2 mm: A pereopod 5; B pereopod 6; C pereopod 7; D pleopod 3; E pleopod 4; F pleopod 5.

Remarks

The holotype of the species is described from the Walvis Ridge, off Southern Africa, paratypes are recorded from off Cape of Good Hope (45°34'S 6°2'E, 41°3'S 7°49'E) (Menzies, 1962) whereas the ANDEEP specimens were found at two stations in the Drake Passage. Despite this long distance, the specimens are quite alike in all characters that were observable in the non-dissected holotype of Menzies (1962). The figures given by Menzies (1962) and Menzies and Schultz (1986) are not very detailed, but it seems that the illustrated male specimen is not fully mature, as was true for all males found during ANDEEP. Within the Haplioniscidae subadult males differ from the fully mature males mainly in the antennae and pleopods 1 and 2. Antenna 1 has fewer aesthetascs, the flagellar articles of antenna 2 are less setose in subadult males. Pleopods 1 and 2 are not fully developed, the tip of pleopod 1 has a very simple structure and lacks the transverse grooves. The endopod of pleopod 2 is simple, article 2 is slender and not expanded, the sperm duct is not developed. This means that several diagnostic characters can not be observed for this species. Important for the identification is the habitus, the rostrum, the shape of the pleotelson and the setation of the pereopods, which were disregarded in most of the previous studies of species belonging to the Haplioniscidae.

Menzies (1962) stated that *A. armatus* was closely related to *A. rostratus* Menzies, 1962. Since *A. rostratus* was transferred to *Haplioniscus* by Menzies and Schultz (1968), they postulated a relationship between *A. subellipticus* and *A. armatus*, based mainly on the proportions of the antennae of the females and the apex of the first male pleopods. However, the proportions of the antennae are similar in many species of the genus, while the two pleopods 1 cannot be compared due to the fact that the male specimen of *A. subellipticus* is fully mature, having a completely developed pleopod 1, which is quite unlike the premature pleopod 1 of the *A. armatus* males.

3.1.2.2.3 *Antennuloniscus latoperculus* n. sp.

Figs 3.13, 3.27-3.31

Material

Holotype: female, 1.6 mm; station 134-3, 65°19.20-19.05'S 48°03.77-02.92'W, 4069 m depth; ZMH K40727.

Paratypes: same locality as holotype: one female, 1.7 mm, ZMH K40728. Station 131-3, 65°19.83-19.99'S 51°31.61-31.23'W, 3053 m depth: four females 1.3-1.8 mm; one ovigerous female, 1.4 mm; ZMH K40729.

Etymology

From Latin *latus*, which means “broad”, referring to the unusual broad operculum of the species.

Diagnosis

Body almost oblong, 2.6 times as long as wide, all pereonites with equal width, head 1.6 times as wide as long, frontal margin slightly concave, broad, tapering, rostral process bent ventral, with rounded apex; basis of pleotelson 1.7 times as wide as terminal margin, posterolateral processes slender, acute, not reaching terminal margin; antenna 1 with 3 flagellar articles in females; antenna 2 peduncular article 3 with relatively large dorsal tooth, longitudinal groove distinct, flagellum almost as long as articles 5 and 6, with 8 articles. Carpus of P1–3 with long simple setae ventrally, shorter on P4–7. Plp2 of the female oval, wider than long.

Description of paratype female

Body (Fig. 3.27) almost oblong, 2.6 times as long as wide, all pereonites with equal width; head 1.6 times as wide as long, frontal margin slightly concave, broad, tapering, rostral process bent ventral, with rounded apex; margins of pereonites smooth; suture between pereonite 7 and pleotelson not distinct ventrally. Pleotelson 0.25 times as long as body, tapering slightly distally, basis 1.7 times as wide as terminal margin; lateral margins slightly convex, weakly serrated, with three setae each; terminal margin convex; posterolateral processes slender, acute, not reaching terminal margin; dorsal surface with 2 indistinct short longitudinal keels, ventral surface with cuticular suture line surrounding the branchial chamber. Cuticle of body, pleopods 1 and 2, maxillipedal epipod and peduncular articles of antenna 2 with numerous small round depressions.

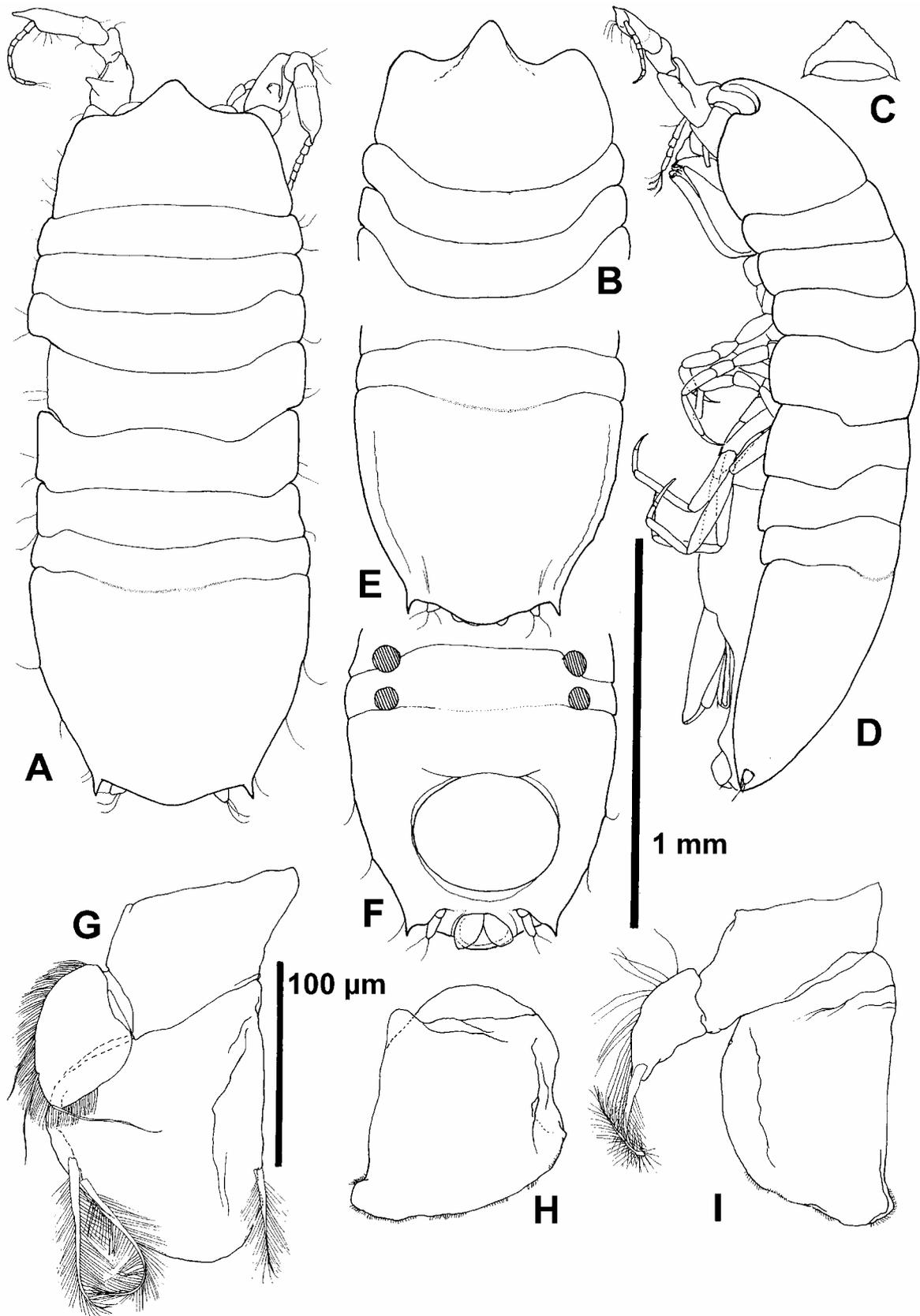


Figure 3.27: *Antennuloniscus latoperculus* n. sp., paratype female, 1.8 mm: A entire, dorsal view; B anterior part of body, dorsal view; C prolonged clypeus with labrum, ventral view; D entire, lateral view; E posterior part of body, dorsal view; F posterior part of body, ventral view; paratype female, 1.7 mm: G pleopod 3, H pleopod 5; I pleopod 4.

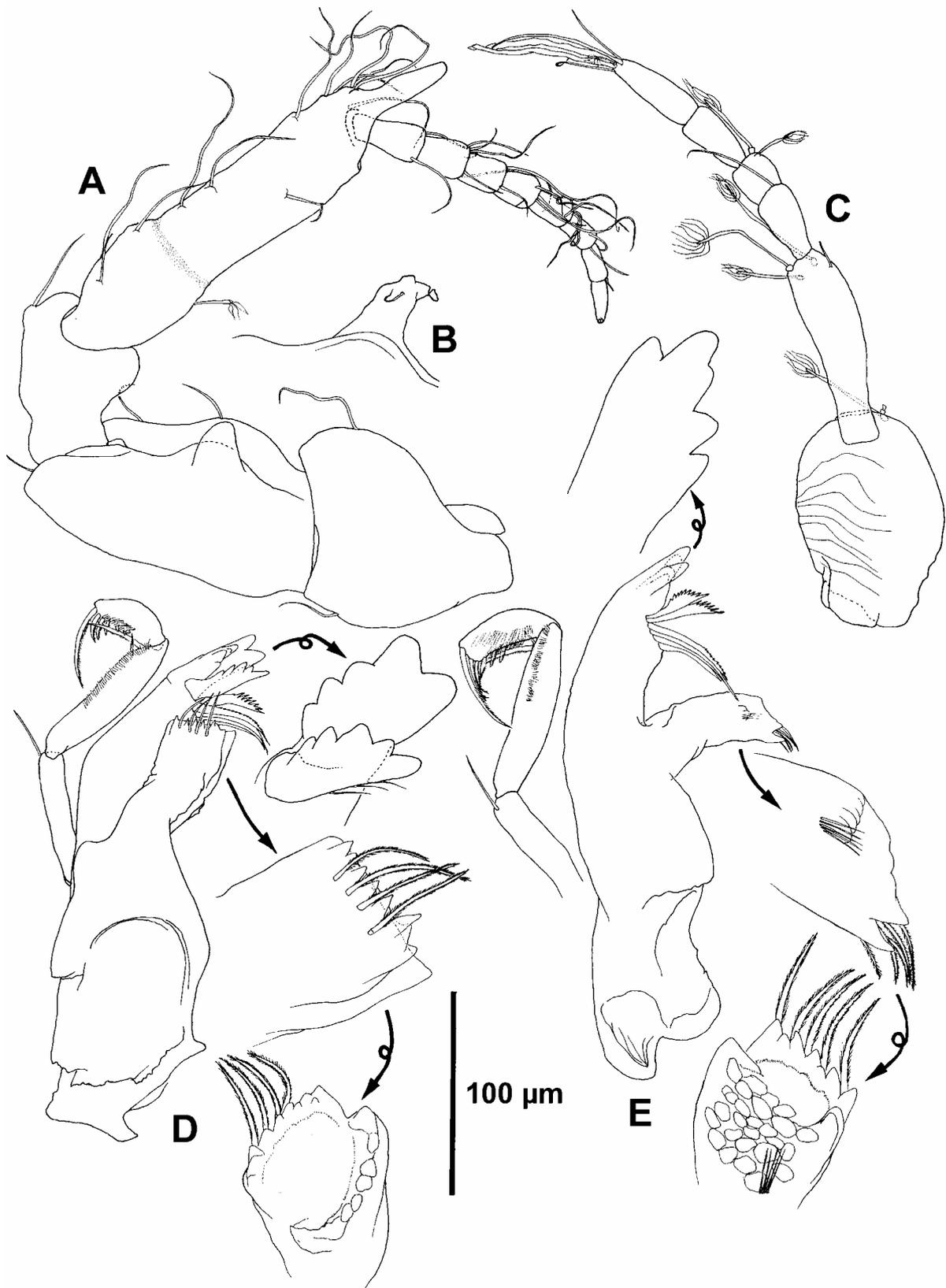


Figure 3.28: *Antennuloniscus latoperculus* n. sp., paratype female, 1.8 mm: A antenna 2; B antenna 2, article 3, dorsal tooth, lateral view; C antenna 1; D left mandible; E right mandible.

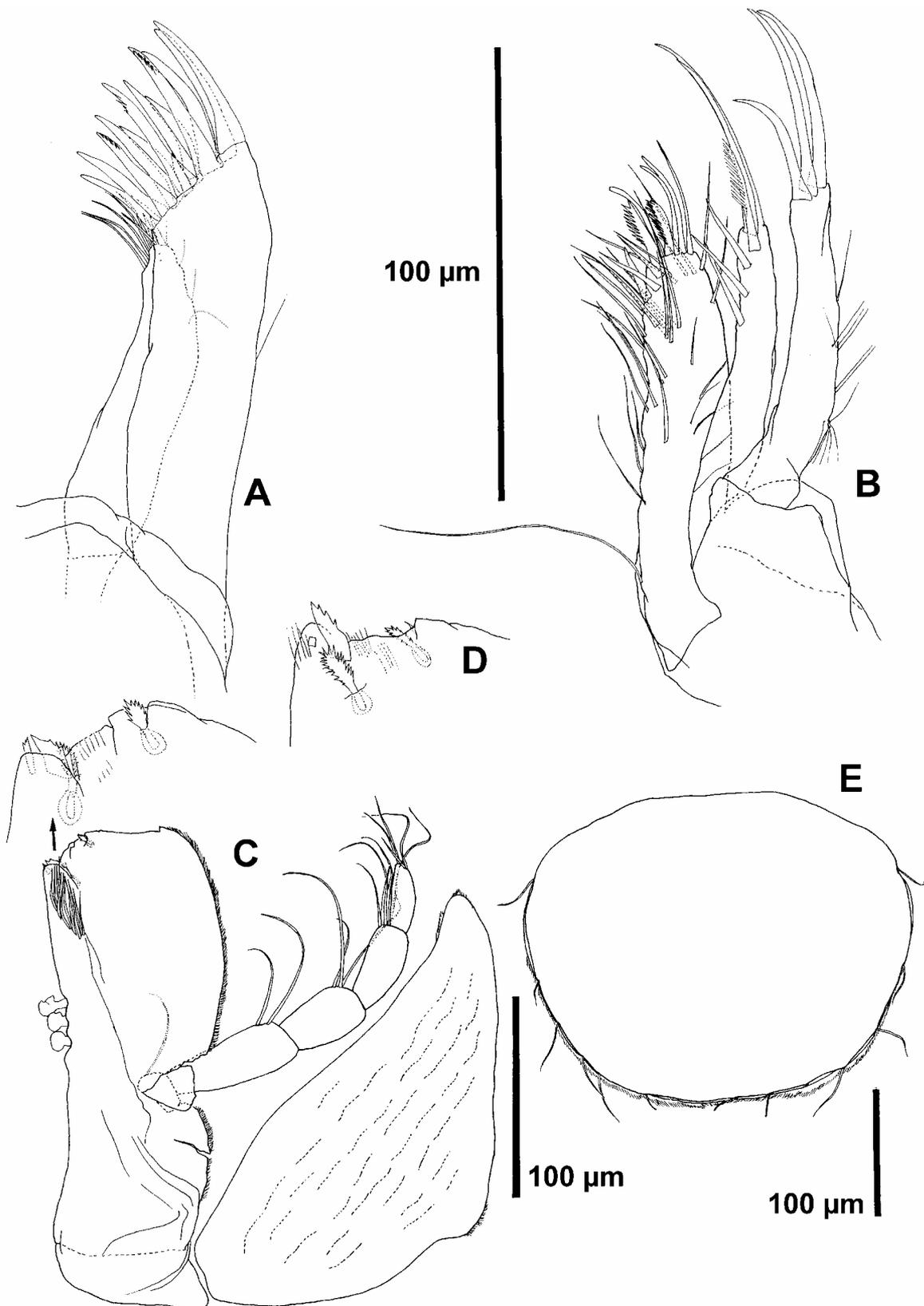


Figure 3.29: *Antennuloniscus latoperculus* n. sp., paratype female, 1.8 mm: A maxilla 1; B maxilla 2; C right maxilliped, ventral view; D detail of left maxilliped, dorsal view; E pleopod 2.

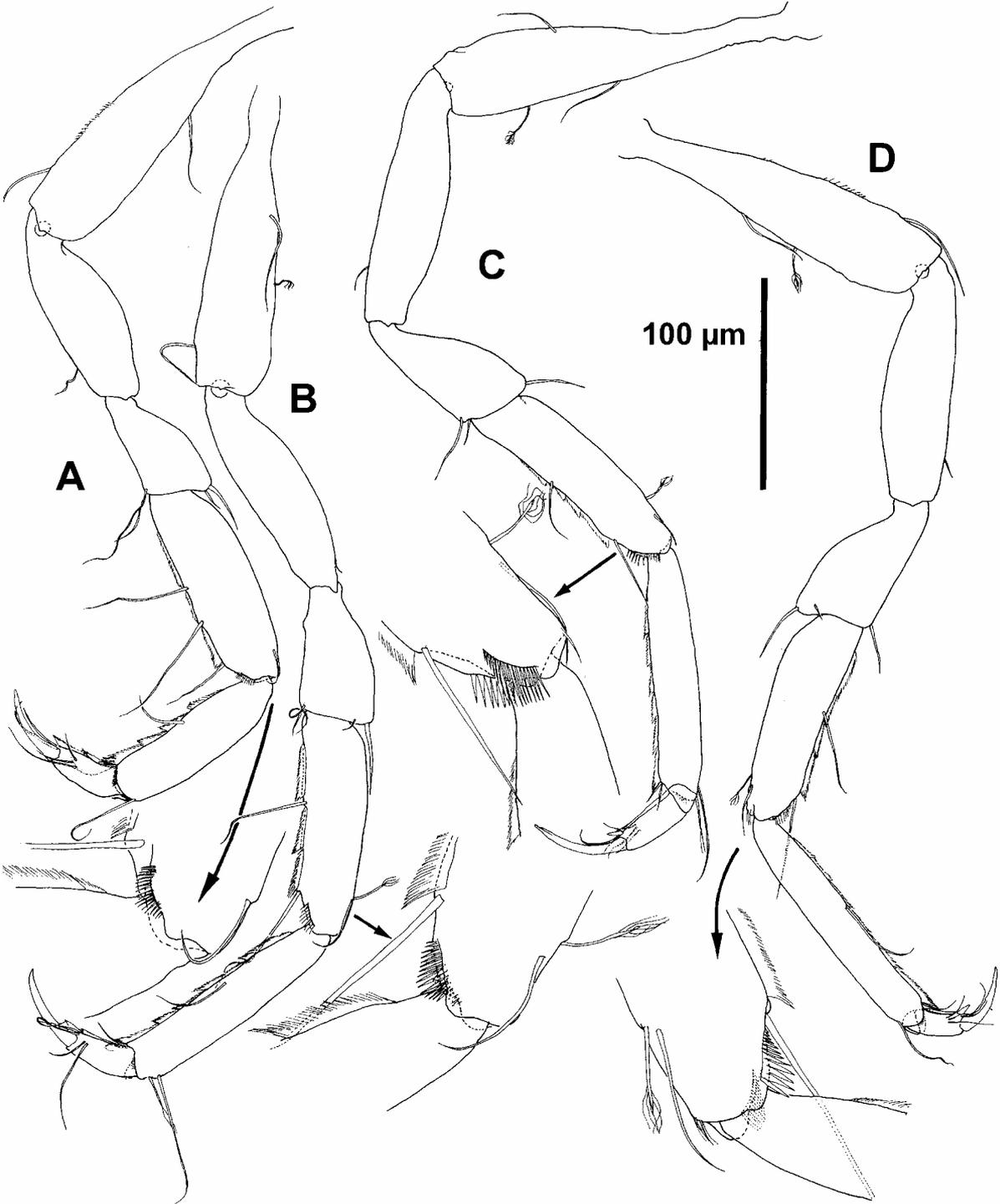


Figure 3.30: *Antennuloniscus latoperculus* n. sp., paratype female, 1.8 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pereopod 4.

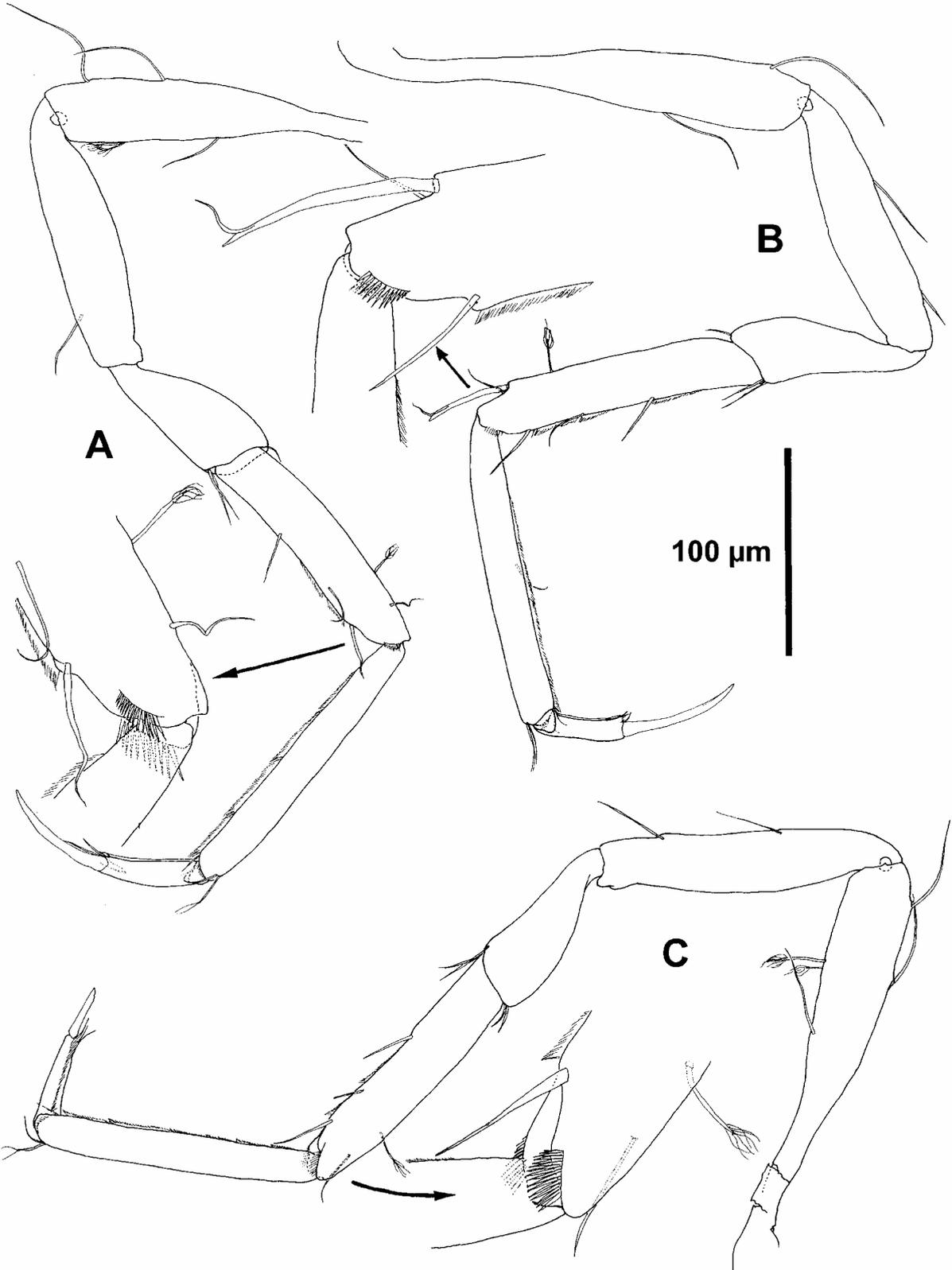


Figure 3.31: *Antennuloniscus latoperculus* n. sp., paratype female, 1.8 mm: A pereopod 5; B pereopod 6; C pereopod 7.

Antenna 1 (Fig. 3.28) about one fifth of body length, article 1 broadest, about 1.5 times as long as wide, article 2 slightly shorter, about 0.4 times as wide as article 1, both articles with several broom setae; article 3 0.4 times as long as article 2, with simple seta; flagellum with 3 articles; article 1 shortest, with 2 broom setae; article 3 1.6 times as long as article 2, article 3 more than twice as long as article 1, with 2 apical aesthetascs, 3 simple setae and 1 short broom seta.

Antenna 2 (Fig. 3.28) almost 0.35 times as long as body, article 1 minute, in situ concealed by article 2, article 2 about as long as wide, article 3 1.8 times as long as wide, 1.4 times as long as article 2, with longitudinal groove and large, acute dorsal tooth, article 4 short, half as long as article 3, fused articles 5 and 6 together (without apical tooth) 1.3 times as long as article 3, with numerous simple setae, at least 1 broom seta and long apical tooth; flagellum slightly shorter than fused articles 5 and 6, with 8 articles of decreasing width, each with several simple setae.

Mandible (Fig. 3.28) incisor with five blunt teeth, left mandible with *lacinia mobilis* with five teeth, right mandible with serrated spine-like seta instead, spine row comprising 2 serrated and 3 simple spine-like setae; molar tooth row with 8 teeth and 4 serrated setae proximally, cuticular ledge tapering off forming a single blunt tooth, right mandible with row of 6 indistinct accessory teeth proximally of cuticular ledge; palp article 2 with 1 long and 1 short serrated spine-like setae proximally of insertion of article 3, article 3 with 6 serrated spine-like setae of increasing length, distal seta about 10 times as long as proximal seta.

Maxilla 1 (Fig. 3.29) outer lobe with 10 simple and 3 serrated spine-like setae and several simple setae on lateral and medial margin; inner lobe apically with 2 short spine-like setae and several simple setae.

Maxilla 2 (Fig. 3.29) outer lobe with 2 long and 1 short simple spine-like setae apically and rows of simple setae on lateral margin; medial lobe with 2 long simple spine-like setae and 1 shorter serrated spine-like seta apically and 3 spine-like setae on medial margin; inner lobe with 2 apical serrated spine-like setae, 3 stout apical simple setae and numerous simple setae on surface and margins.

Maxilliped (Fig. 3.29) endite apical margin with 2 small fan setae and 1 short spine-like setae, ventral surface with numerous simple setae, separated apical medial margin dorsally with 1 small and 1 large serrated spine-like seta and row of simple setae, medial margin with 3 retinacula; epipod slightly longer than endite.

Pereopods (Figs 3.30, 3.31): Basis of P1–3 and 7 with 1, of P4–6 with 2 simple setae ventrally; dorsally with 1 simple seta, P2–4 with 1, P5 and 6 with 2 broom setae. Ischium with

1 short simple seta on P1-4 and 1–2 long simple setae ventrally on P5–7. Merus with 4 apical setae. Carpus with ventral comb-like scale rows slightly reduced on P5–7; carpus of P1 with three long simple setae ventrally, of P2–4 with 2 simple setae of decreasing length, carpus of P5–7 with 2 stout and 1 simple seta ventrally; P7 with dorsal stout flagellate seta; apical comb on carpus of P1 small and setose, apical combs on P2–7 comprised of 1 small and 1 large spinose comb, largest on P4–6. Propodus with ventral row of comb-like scales and 3 simple setae ventrally (some broken off in type specimen). Dactylus with 3 lateral setae on P1–4 and 1–2 lateral setae on P5–7; accessory tooth acute.

Pleopods (Figs 3.27, 3.29): Plp2 oval, 1.3 times as wide as long, margins with several simple setae. Plp3 endopod 1.3 times as long as wide, with rounded distal and lateral margin; exopod almost triangular, 1.2 times as long as wide, 0.5 times as wide and 0.4 times as long as endopod, lateral margin rounded, with 3 simple setae and fringe of fine bristles. Plp4 endopod 1.7 times as long as wide; exopod 1.5 times as long as wide, 0.4 times as long and wide as endopod, lateral margin rounded with fringe of long bristles. Plp5 almost as wide as long.

Uropods (Fig. 3.27) short, stout, not reaching terminal margin.

Remarks

This species is unique for the family in possessing an operculum which is wider than long and, corresponding to this, pleopods 3–5 tend to be rather short and broad. *A. latoperculus* also has an unusual large tooth on article 3 of antenna 1 compared to the other species of the genus, although in other genera, like *Chauliodoniscus*, this tooth might be much larger. Only three species within the genus *Antennuloniscus* possess a distinct rostrum: *A. armatus*, *A. dilatatus*, and *A. diversus*. While it is acute in *A. armatus* and *A. diversus*, only *A. dilatatus* has a rostrum similar to that of the new species. All three species can easily be distinguished from *A. latoperculus* by the shape of the pleotelson, which is rounded, with fairly produced but small posterolateral projections in the new species.

3.1.2.3 Genus *Mastigoniscus* Lincoln, 1985a

Type species: *Mastigoniscus pistus* Lincoln, 1985a

Diagnosis

Head without rostral process; pereonites 5-7 fused mediodorsally with each other and pleotelson, sutures more or less distinct; posterior body (pereonite 5-7 and pleotelson) longer than anterior one; pereonite 7 of adult specimens reduced, short, but with fully developed pereopod 7; males with strongly produced pleotelsonic processes, processes of females short; dorsal tooth of antenna 2 with jagged margin; pereopod 6 with strong spine-like seta dorsoapically on carpus; pleopods 1 and 2 of the male large, exceeding the size of the branchial chamber, covering most of the ventral surface of pleotelson, Plp1 extending from posterior margin of pereonite 7 to anterior margin of the anus; pleopod 2 of the female smaller; male pleopod 2 with strongly elongated endopod, article 1 curved backwards, article 2 much longer than article 1, forming the slender copulatory filament.

Remarks

Species of the genus show a pronounced sexual dimorphism, mainly concerning the shape and sculpture of the pleotelson. As the most important diagnostic characters are those of the pleotelson and pleopods 1 and 2 of the males, the identification of the females is difficult. To distinguish the females from each other and to allocate them to the males a combination of characters has to be used, like the shape of the head, the dorsal tooth on antenna 2, and some features of the mandibles. The shape of the pleotelson is a useful character as well, with regard to the different size and shape of the posterolateral processes of males and females.

The dorsal tooth of antenna 2 is an important diagnostic character, yet has to be treated carefully. As examinations of the intraspecific variability revealed, the number of jags might vary within one species; more important is the size and shape of the tooth itself.

The extremely elongated endopod of the male pleopod 2 is an important yet not unique character of the *Mastigoniscus* species. In situ the male filaments cross each other two times beneath the shelter of pleopod 1 in most species; only in *M. platovatus* Park, 2000 the filament is coiled beneath the basipod and pleopod 1. Most species of the genus possess longitudinal grooves extending from the branchial chamber to the tips of the pleotelsonic processes (Fig. 3.11). Lincoln (1985a) postulated that these grooves together with the grooves and processes on pleopod 1 serve as support for the copulatory filament. Indeed the filament was found resting in this groove in *Mastigoniscus polygomphios* n. sp. (Fig. 3.33).

3.1.2.3.1 *Mastigoniscus polygomphios* n. sp.

(Figs 3.32-3.38)

Material

Holotype: male, 2.9 mm, station 42-2, 59°40.30-40.32'S 57°35.42-42.64'W, 3689 m depth; ZMH K40778.

Paratypes: same locality as holotype: one male, 2.7 mm, three females, 2.7-3.3 mm; ZMH K40779.

Etymology

From Greek, *poly* meaning “many” and *gomphios* meaning “molar tooth”, referring to the molar process of the right mandible with its many teeth.

Diagnosis

Body 2.7 times as long as wide; head 3 times as wide as long in males, 2.6 times as wide as long in females, pereonite 5 broadest, body narrowing slightly posteriorly and anteriorly, pleotelson 0.3 times as long as body, lateral margins convex, terminal margin slightly concave in males, slightly convex in females, posterolateral processes of males elongated, about half as long as pleotelson in males, about 0.1 times as long as pleotelson in females, ventral surface of pleotelson with 2 deep grooves extending from the branchial chamber to tips of posterolateral processes, antenna 1 article 2 not as wide as article 1, with 4 flagellar articles in both sexes, antenna 2 dorsal tooth with 4 jags on distal margin, mandibular palp article 3 with 6 serrated spine-like setae, pleopod 1 2.7 times as long as wide, distal margins with about 11 setae each, male pleopod 2 endopod 3.9 times as long as basipod, uropods extending well beyond terminal margin.

Description of male paratype

Body 2.7 times as long as wide; head 3 times as wide as long, frontal margin slightly convex; pereonite 5 broadest, body narrowing slightly posteriorly and anteriorly; posterior margin of pereonite 4 and anterior margin of pereonite 5 serrated in intersegmental gap; pereonites 5-7 fused mediodorsally with each other and pleotelson; pleotelson (Fig. 3.33) 0.3 times as long as body, tapering distally, basis 1.4 times as wide as terminal margin; lateral margins convex; terminal margin slightly concave; posterolateral processes elongated, about half as long as pleotelson, distance between processes 0.4 times as long as pleotelson width;

dorsal surface of pleotelson smooth, ventral surface with two deep grooves extending from posterior margin of branchial chamber to tips of posterolateral processes. Cuticle of body, maxillipedal epipod and peduncular articles of antenna 1 and 2 with numerous small round depressions (Fig. 3.32 E).

Antenna 1 (Fig. 3.34) 0.3 times as long as body, article 1 broadest, about 1.2 times as long as wide, article 2 1.6 times as long and 0.75 times as wide as article 1, both articles with several broom setae; article 3 0.3 times as long as article 2, with simple seta; flagellum with 4 articles; article 1 short, with 1 broom seta; articles 2 and 3 3 times as long as article 1, each with 1 aesthetasc and 1 simple seta, article 4 with 2 lateral and 2 apical aesthetascs, 3 simple setae and 1 short broom seta.

Antenna 2 (Fig. 3.34) about half as long as body, articles 1 and 2 short, with 1 simple seta each; article 3 1.6 times as long as wide, distal margin of well developed dorsal tooth with 4 jags; article 4 short, 0.4 times as long as article 3; article 5 1.4 times as long and as wide as article 3, 2 times as long as wide, with broom seta; article 6 1.1 times as long as article 3, 3.1 times as long as wide, with at least 2 broom setae and 2 apical teeth; flagellum 2.3 times as long as peduncular article 6, with 14 articles of decreasing width, each with numerous simple setae.

Mandible (Fig. 3.34) incisor with 5 blunt teeth, left mandible with *lacinia mobilis* with 5 teeth, right mandible with stout serrated spine-like seta instead, spine row comprising 2 serrated and 3 simple spine-like setae; molar tooth row of right mandible with 5 larger and 5 smaller teeth, 5 setulated setae proximally, tooth row of left mandible with 6 larger and 7 smaller teeth, 6 setulated setae proximally; cuticular ledge with 2 teeth on either side; right mandible with numerous teeth, left mandible with row of 6 teeth on surface of molar process; right mandible with row of 6 accessory teeth proximally of cuticular ledge; palp article 2 with 3 serrated spine-like setae in distal quarter, article 3 with 6 serrated spine-like setae of increasing length, distal seta almost 4 times as long as proximal seta.

Maxilla 1 (Fig. 3.35) outer lobe with 8 simple and 4 serrated spine-like setae and several simple setae on lateral and median margin and surface; inner lobe apically with 2 short spine-like setae and several simple setae.

Maxilla 2 (Fig. 3.35) outer lobe with 2 long and 1 short serrated spine-like setae and 2 simple setae apically and numerous simple setae on lateral margin, median margin with 5 spine-like setae; medial lobe with 2 long and 1 shorter serrated spine-like setae apically and several spine-like setae on median margin; inner lobe with 2 serrated and 1 simple spine-like setae, 3 stout simple setae apically and numerous simple setae on surface and median margin.

Maxilliped (Fig. 3.35) endite apical margin with 3 small fan setae and 2 short spine-like setae, ventral surface with numerous simple setae, separated apical median margin dorsally with 1 simple spine-like seta, 1 stout serrated spine-like seta and row of simple setae, median margin with 3 retinacula; epipod about as long as endite.

Pereopods (Figs 3.36, 3.37): Basis of P1-3 and P7 with 1 simple seta ventrally, basis of P4-6 with 2 simple setae ventrally; P2-4 and P6 with 2, P5 with 3 and P7 with 1 broom seta dorsally; all pereopods with 1 simple seta dorsally. Ischium with 1-2 short simple setae ventrally and dorsally. Merus of P1 with 6, of P6-7 with 4 apical setae, ventral seta slightly stouter on P5-7. Carpus with ventral comb-like scale rows, slightly smaller on P5-7, and 3 simple setae ventrally on P1-4. P5-7 with 2 stout setae, distal one bifid on P7, and 1-2 simple seta ventrally; P6 with dorsal stout setulated seta; apical comb on carpus of P1 setose, apical combs on P2-7 comprised of 1 smaller and 1 larger lateral and 1 dorsal slightly spinose comb. Propodus with ventral row of comb-like scales, slightly smaller on P5-7, and 3-5 simple setae ventrally. Dactylus with 3 lateral setae; accessory tooth blunt.

Pleopods (Figs 3.33, 3.35, 3.36): Plp1 2.1 times as long as wide, evenly broadening proximally, broadest part in the proximal half, 2.3 times broader than narrowest part, distal margins with 3 setae each, sympods separated at the distal tip, ventral surface with mediolateral bulges and 2 transversal grooves in the distal third, extending from the suture to the tips of the subapical, distolaterally directed, slender processes; distal ventral surface with single seta on either side; dorsal surface with 2 setae near insertion of each process. Plp2 basipod about 2 times as long as wide, with numerous simple setae on lateral and distal margin; endopod inserting in distal half of basipod, long, slender, 3.9 times as long as basipod, article 1 short, curved backwards, article 2 about 8 times as long as article 1, with slight expansion near joint, containing the sperm duct opening, stylet tapering strongly in the proximal seventh, then narrowing continuously, thin membrane extending over the proximal two thirds of article; exopod small, inserting in the distal third of basipod. Plp3 endopod 1.8 times as long as wide; exopod 2.7 times as long as wide, 0.6 times as wide and 0.9 times as long as endopod, lateral margin rounded, with 2 simple setae and fringe of fine bristles. Plp4 endopod 2.7 times as long as wide; exopod 3.5 times as long as wide, 0.7 times as wide and 0.9 times as long as endopod, margins with fringe of long bristles, plumose seta about as long as exopod. Plp5 2.7 times as long as wide.

Uropods (Fig. 3.32) extending well beyond terminal margin, not reaching posterolateral processes of pleotelson.

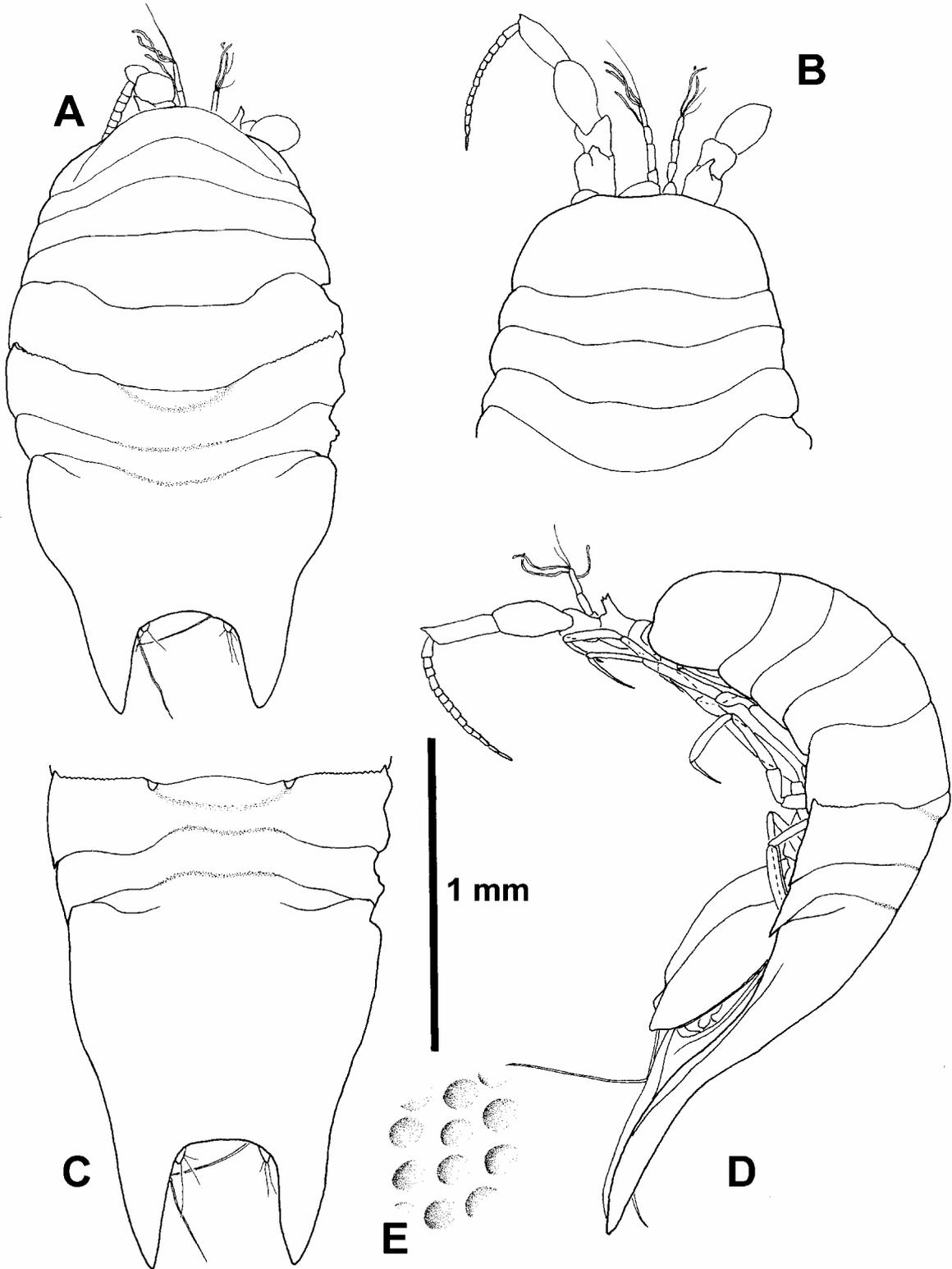


Figure 3.32: *Mastigoniscus polygomphios* n. sp., holotype, male, 2.9 mm: A entire, dorsal view; B anterior body, dorsal view; C posterior body, dorsal view; D entire, lateral view; E detail of cuticle structure.

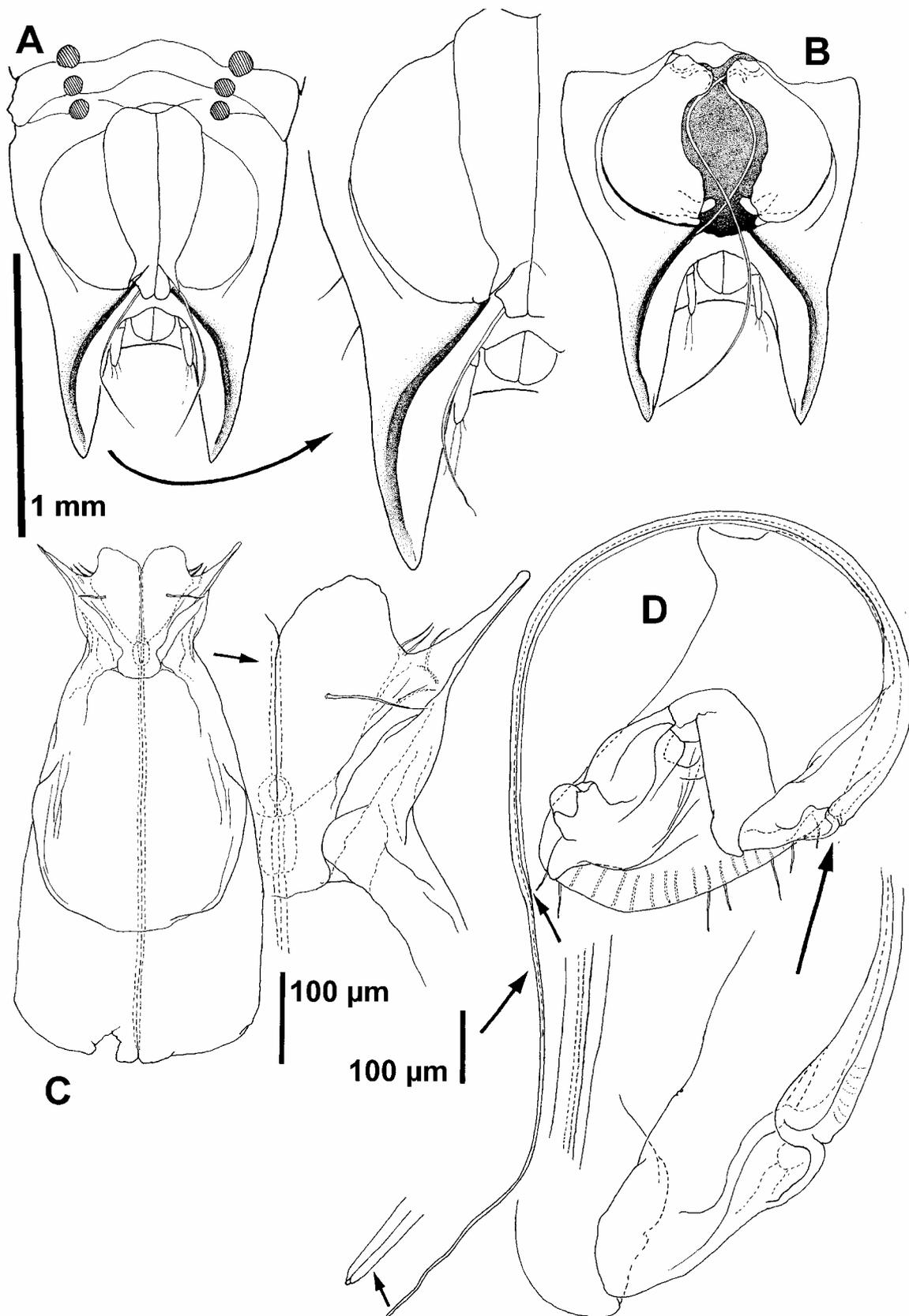


Figure 3.33: *Mastigoniscus polygomphios* n. sp., holotype, male, 2.9 mm: A posterior body, ventral view; paratype, male, 2.7 mm: B posterior body, ventral view (pleopod 1 removed); C pleopod 1; D pleopod 2.

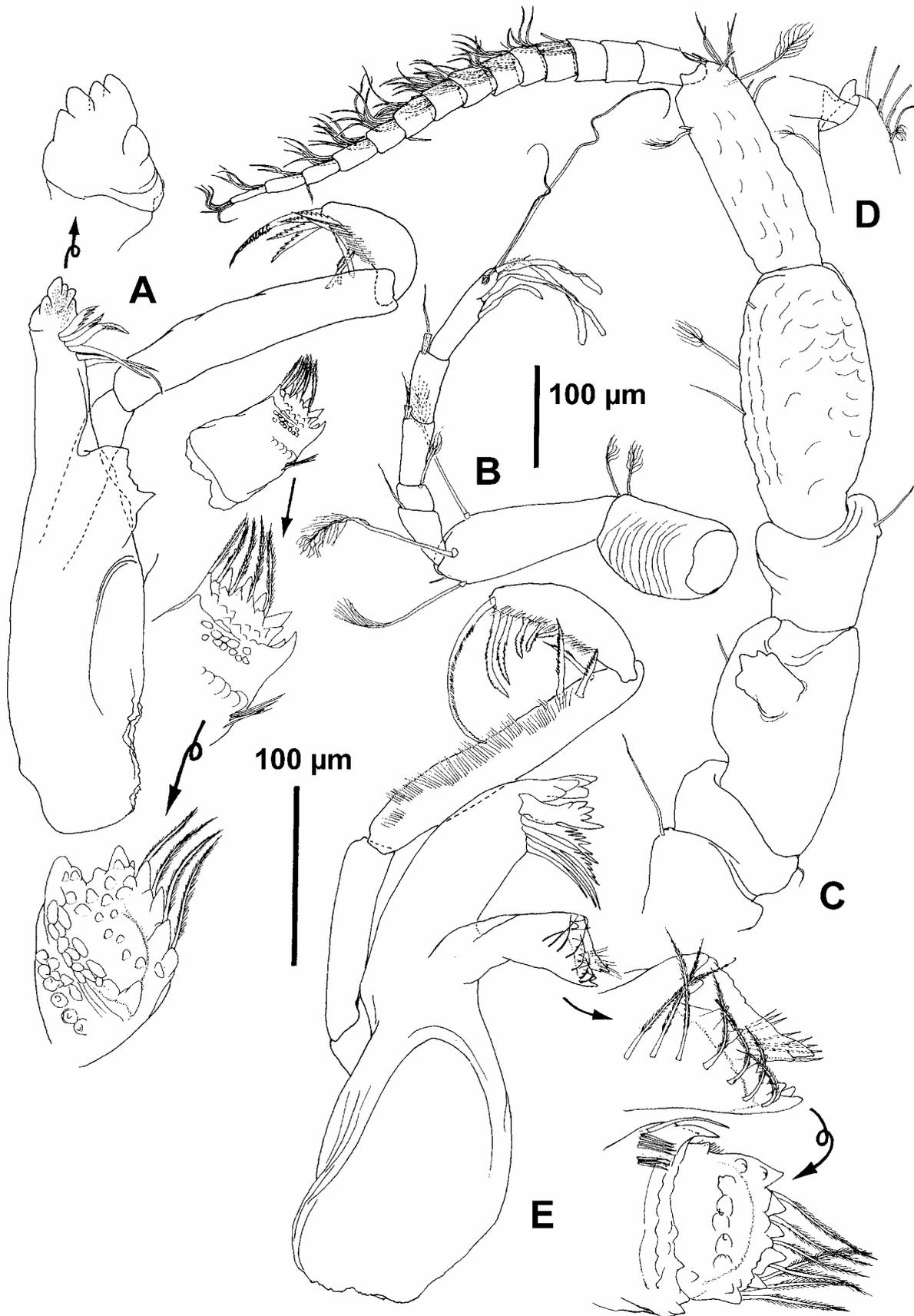


Figure 3.34: *Mastigoniscus polygomphios* n. sp., paratype, male, 2.7 mm: A right mandible; B antenna 1; C left antenna 2; D right antenna 2, article 6; E left mandible.

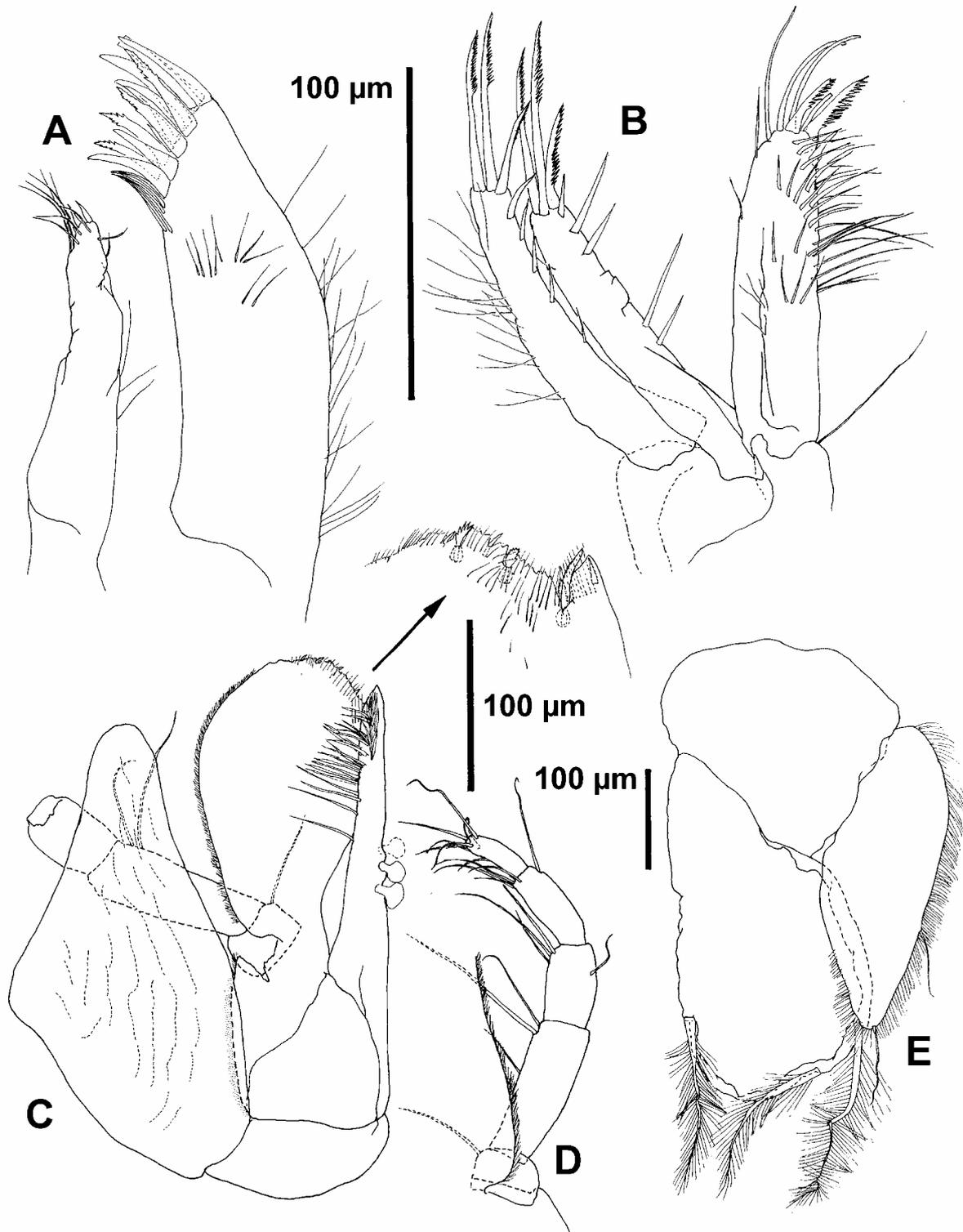


Figure 3.35: *Mastigoniscus polygomphios* n. sp., paratype, male, 2.7 mm: A maxilla 1; B maxilla 2; C left maxilliped; D right maxilliped, palp; E pleopod 3.

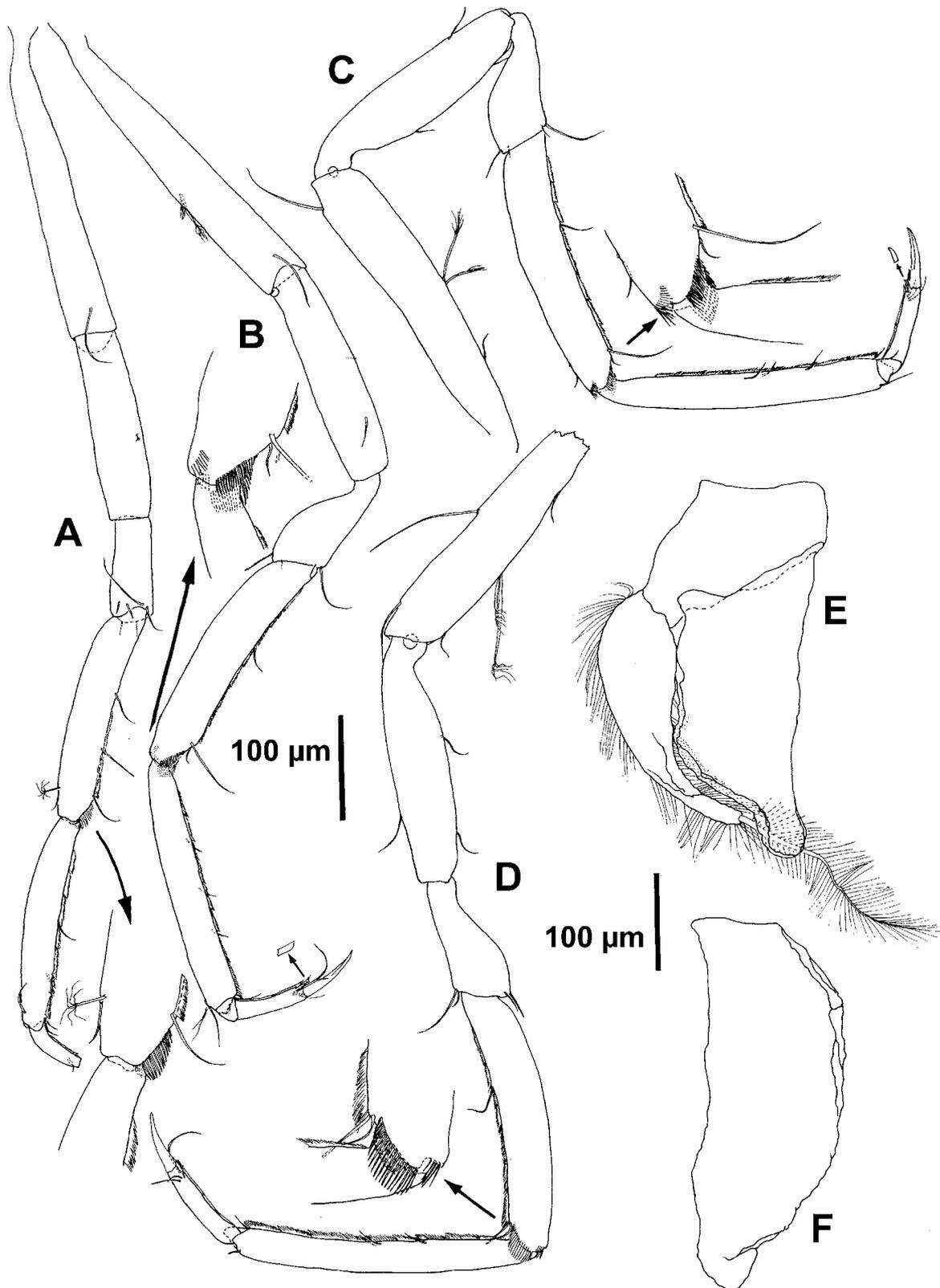


Figure 3.36: *Mastigoniscus polygomphios* n. sp., paratype, male, 2.7 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pereopod 4; E pleopod 4; F pleopod 5.

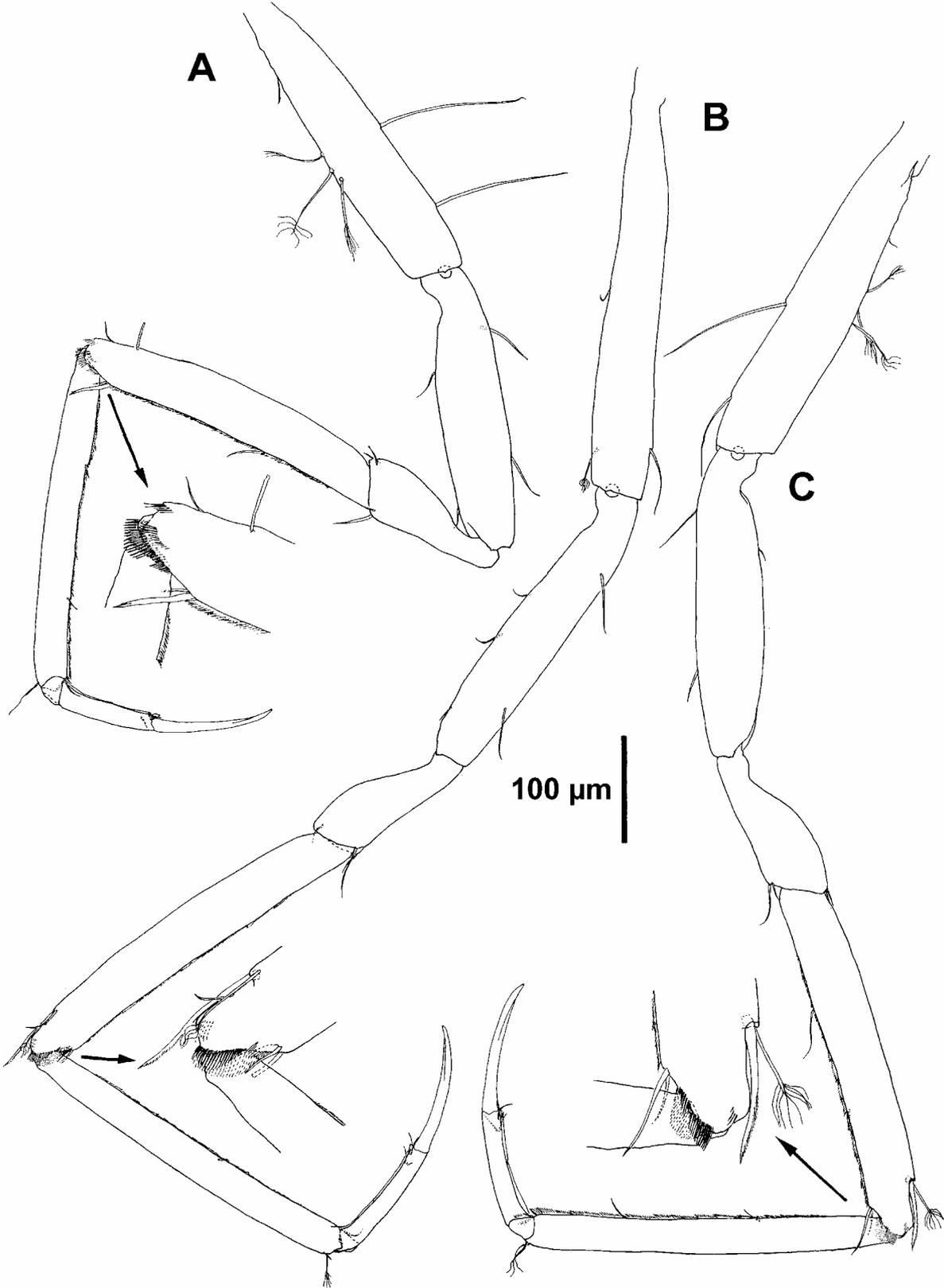


Figure 3.37: *Mastigoniscus polygomphios* n. sp., paratype, male, 2.7 mm: A pereopod 5; B pereopod 7; C pereopod 6.

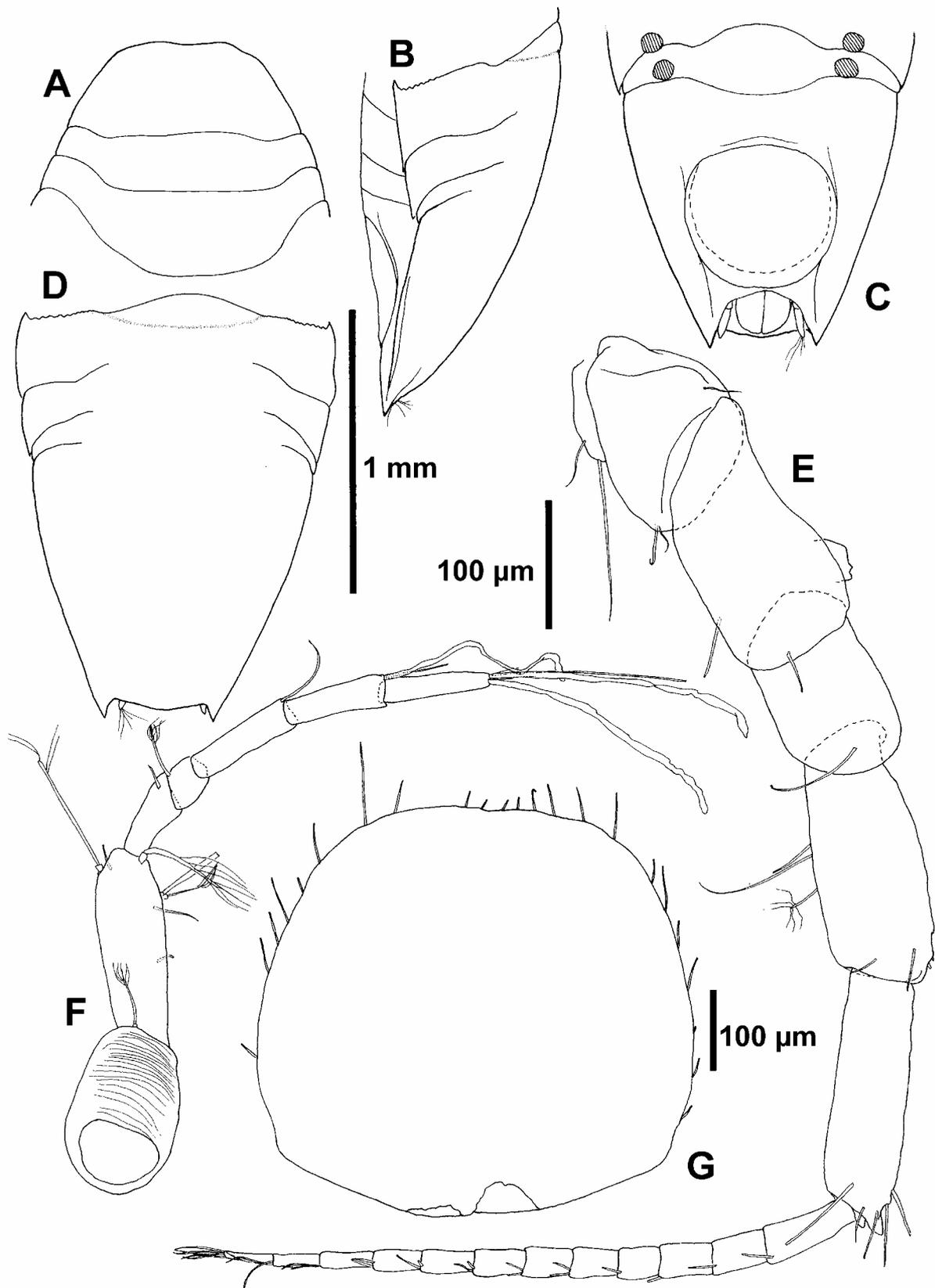


Figure 3.38: *Mastigoniscus polygomphios* n. sp., paratype, female, 3.0 mm: A anterior body, dorsal view; B posterior body, lateral view; C posterior body, ventral view; D posterior body, dorsal view; E antenna 2; F antenna 1; G pleopod 2.

Description of female

The female (Fig. 3.38) differs from the male in the following characters:

Head trapezoidal, 2.6 times as wide as long.

Basis of pleotelson 2.1 times as broad as terminal margin; terminal margin slightly convex; posterolateral processes small, about 0.1 times as long as pleotelson; ventral surface without grooves but with two indistinct longitudinal keels extending from branchial chamber to posterolateral processes

Antenna 1 with 4 flagellar articles, article 3 with 1 aesthetasc, article 4 with 2 aesthetascs.

Antenna 2 more slender, flagellum, with 12 articles, with fewer setae.

Operculum subcircular, with numerous simple setae on distal and lateral margins.

Remarks

The species resembles *M. stenocephalus* Park, 2000 regarding the shape of the pleotelson with the elongated processes and the grooves on the ventral surface. This is present in most species of the genus, but differs clearly in the shape of the head, the dorsal surface of the pleotelson which has two tubercles in the latter species, the shape of the dorsal tooth on antenna 2 and the multitoothed molar of the right mandible. Pleopods 1 and 2 are slightly broader in *M. polygomphios*. *M. concavus* Menzies and George, 1972 has similar processes like the new species, but can be distinguished by the shape of the pleotelson and the head. All other species differ in the shape and size of the pleotelsonic processes. Females can be identified by the combination of the shape of head and pleotelson, the dorsal spine of antenna 2 and the unique molar process of the right mandible.

3.1.2.3.2 *Mastigoniscus andeepi* n. sp.

(Figs 3.39-3.45)

Material

Holotype: male, 2.2 mm, station 42-2, 59°40.30-40.32'S 57°35.42-42.64'W, 3689 m depth; ZMH K40780.

Paratypes: same locality as holotype: 32 males, 2.2-2.5 mm, 42 females, 2.3-2.6 mm; ZMH K40781.

Etymology

The species is named after the ANDEEP project.

Diagnosis

Body 2.8 times as long as wide; head 2.1 times as wide as long, trapezoidal, frontal margin straight, pereonites of subequal width, pereonite 5 broadest, pereonites 5-7 fused mediodorsally with each other and pleotelson, pleotelson 0.3 times as long as body, lateral margins convex, terminal margin slightly convex, posterolateral processes moderately elongated, about 0.2 times as long as pleotelson, dorsal surface of pleotelson with 2 longitudinal keels, ventral surface with 2 deep grooves extending from the branchial chamber to tips of posterolateral processes, antenna 1 article 2 almost as wide as article 1, with 4 flagellar articles in males, antenna 2 dorsal tooth with 2 jags on anterior margin, mandibular palp article 3 with 7 serrated spine-like setae in males, pleopod 1 2.7 times as long as wide, distal margins with 3 setae each, pleopod 2 endopod 2.4 times as long as basipod, uropods extending well beyond terminal margin.

Description of paratype male

Body 2.8 times as long as wide; head 2.1 times as wide as long, trapezoidal, base 2.4 times as wide as frontal margin, frontal margin straight; pereonites of subequal width, pereonite 5 broadest, posterior margin of pereonite 4 and anterior margin of pereonite 5 serrated in intersegmental gap; pereonites 5-7 fused mediodorsally with each other and pleotelson; pleotelson 0.3 times as long as body, tapering distally, basis 1.5 times as wide as terminal margin; lateral margins convex; terminal margin slightly convex; posterolateral processes moderately elongated, about 0.2 times as long as pleotelson, distance between processes 0.4 times as long as pleotelson width; dorsal surface of pleotelson with two longitudinal keels, ventral surface with two deep grooves extending from posterior margin of branchial chamber to tips of posterolateral processes. Cuticle of body, maxillipedal epipod and peduncular articles of antenna 1 and 2 with numerous small round depressions.

Antenna 1 (Fig. 3.40) 0.2 times as long as body, article 1 broadest, about 1.6 times as long as wide, article 2 slightly longer, almost as wide as article 1, both articles with several broom setae and article 2 with some simple setae; article 3 0.3 times as long as article 2, with simple seta; flagellum with 4 articles of increasing length; article 1 with 1 broom seta and 1 simple seta; article 2 with 1, article 3 with 2 aesthetascs, article 4 with 2 lateral and 2 apical aesthetascs, 3 simple setae and 1 short broom seta.

Antenna 2 (Fig. 3.40) 0.4 times as long as body, article 2 1.4 times as wide as long; article 3 1.4 times as long as wide, almost 2 times as long as article 2, frontal margin of well developed dorsal tooth with 2 jags, tooth acute; article 4 short, 0.6 times as long as article 3; article 5 widest, 1.3 times as long as article 3, 1.7 times as long as wide, with broom seta; article 6 1.2 times as long as article 3, 2.5 times as long as wide, with broom seta; flagellum 2.6 times as long as peduncular article 6, with 14 articles of decreasing width, each with numerous simple setae.

Mandible (Fig. 3.41) incisor with 5 blunt teeth, left mandible with *lacinia mobilis* with 5 teeth, right mandible with stout serrated spine-like seta instead, spine row comprising 2 serrated and 3 simple spine-like setae; molar tooth row with 5 teeth and 4 or 5 setulated setae proximally, cuticular ledge forming a tooth on either side and with additional tooth on one side; right mandible with row of 6-7 accessory teeth proximally of cuticular ledge; palp article 2 with 3 serrated spine-like seta in the distal quarter, article 3 with 7 serrated spine-like setae of increasing length, distal seta almost 4 times as long as proximal seta.

Maxilla 1 (Fig. 3.40) outer lobe with 9 simple and 4 serrated spine-like setae and several simple setae on lateral and median margin; inner lobe apically with 2 short spine-like setae and several simple setae.

Maxilla 2 (Fig. 3.40) outer lobe with 2 long and 1 short serrated spine-like setae and 2 simple setae apically and rows of simple setae on lateral margin; medial lobe with 1 long and 3 shorter serrated spine-like seta apically and 6 spine-like setae on median margin; inner lobe with 2 serrated and 1 simple spine-like setae, 3 stout simple setae apically and numerous simple setae on surface and median margin.

Maxilliped (Fig. 3.41) endite apical margin with 2 small fan setae and 2 short spine-like setae, ventral surface with numerous simple setae, separated apical median margin dorsally with 1 simple spine-like seta, 1 stout serrated spine-like seta and row of simple setae, median margin with 3 retinacula; epipod about as long as endite; palp articles 4 and 5 with fringe of small bristles and distal inner margin.

Pereopods (Figs 3.42, 3.43): Basis of P1-3 and P7 with 1 simple seta ventrally, basis of P4-6 with 2 simple setae ventrally; P2-4 and P6 with 2, P5 with 3 and P7 with 1 broom seta dorsally; all pereopods with 1 simple seta dorsally. Ischium with 1-2 short simple setae ventrally and dorsally. Merus with 3 apical setae, ventral seta stout on P5-7. Carpus with ventral comb-like scale rows, slightly smaller on P5-7, and 2-3 simple setae ventrally on P1-4. P5-7 with 2 stout setae and 1 simple seta ventrally; P6 with dorsal stout flagellate seta; apical comb on carpus of P1 small and setose, apical combs on P2-7 comprised of 2 lateral and 1

dorsal slightly spinose combs, both lateral combs of subequal size. Propodus with ventral row of comb-like scales, slightly smaller on P5-7 and 3-5 simple setae ventrally, P5-7 with spine-like seta ventrally. Dactylus with 3 lateral setae on P1-4; accessory tooth blunt.

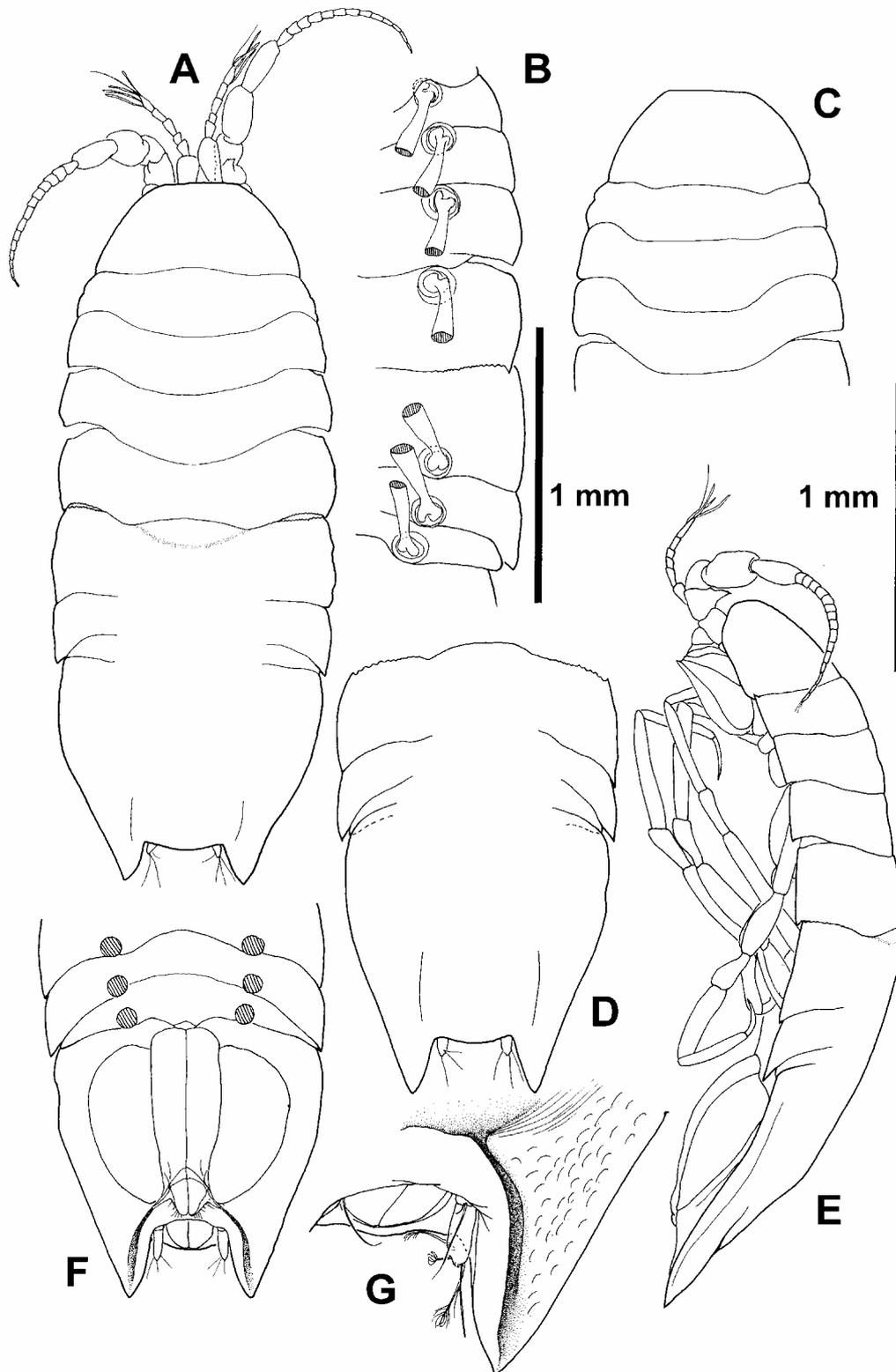


Figure 3.39: *Mastigoniscus andepi* n. sp., holotype, male, 2.2 mm: A entire, dorsal view; B pereopod insertion; C anterior body, dorsal view; D posterior body, dorsal view; E entire, lateral view; F posterior body, ventral view; paratype, male, 2.4 mm: G detail of posterior body.

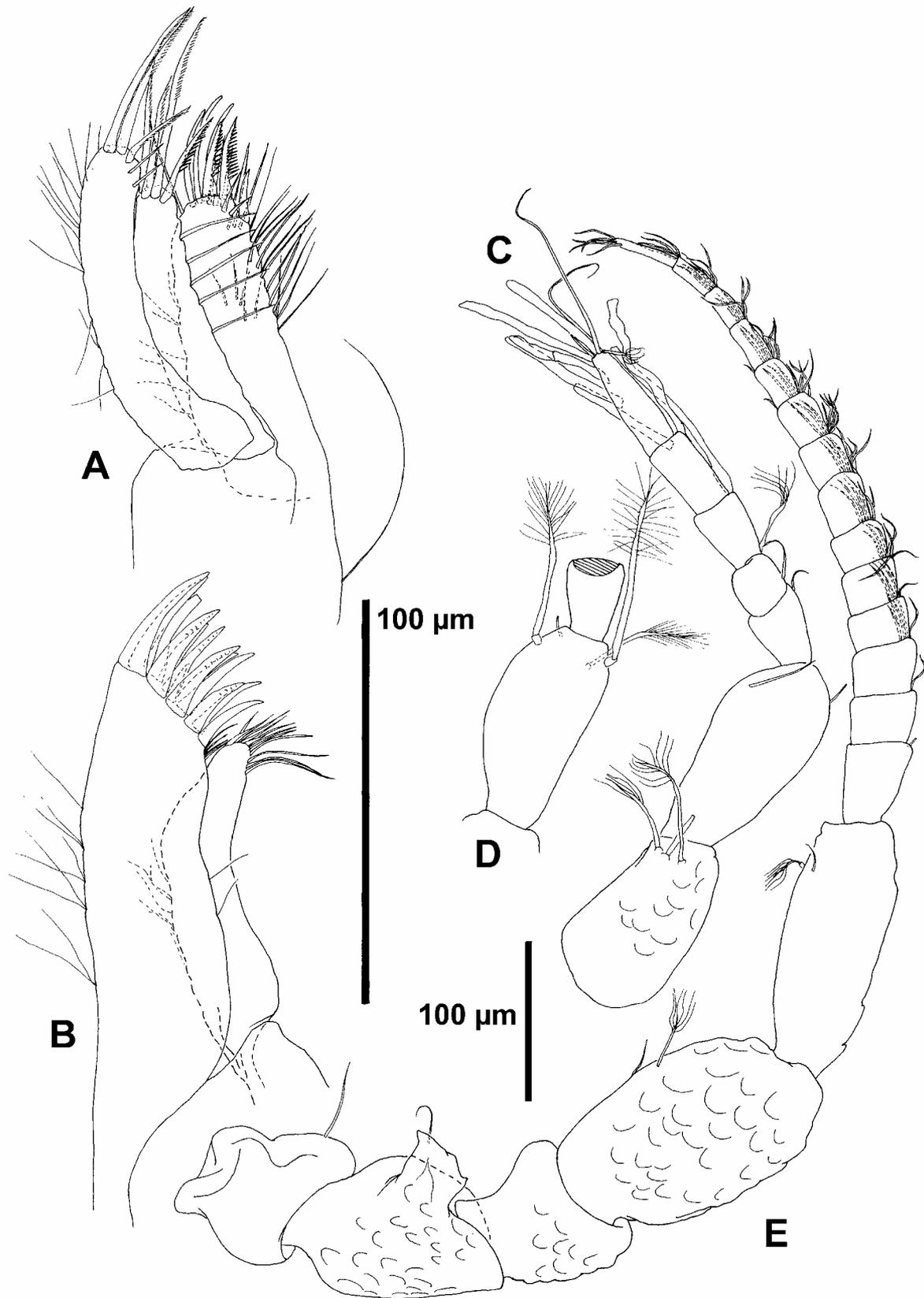


Figure 3.40: *Mastigoniscus andeepi* n. sp., paratype, male, 2.4 mm: A maxilla 2; B maxilla 1; C left antenna 1; D right antenna 1, article 2; E antenna 2.

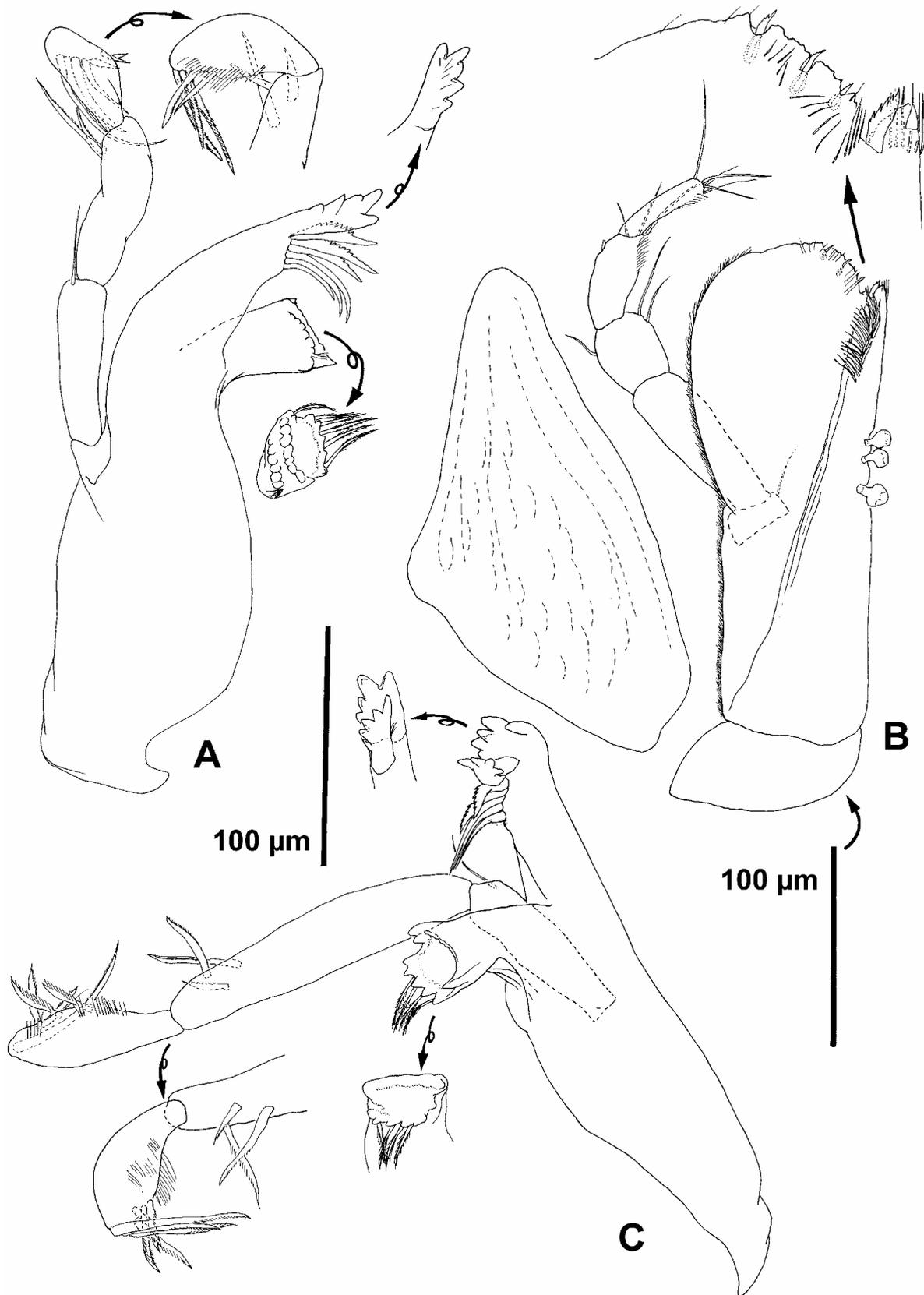


Figure 3.41: *Mastigoniscus andeepi* n. sp., paratype, male, 2.4 mm: A right mandible; B maxilliped; C left mandible.

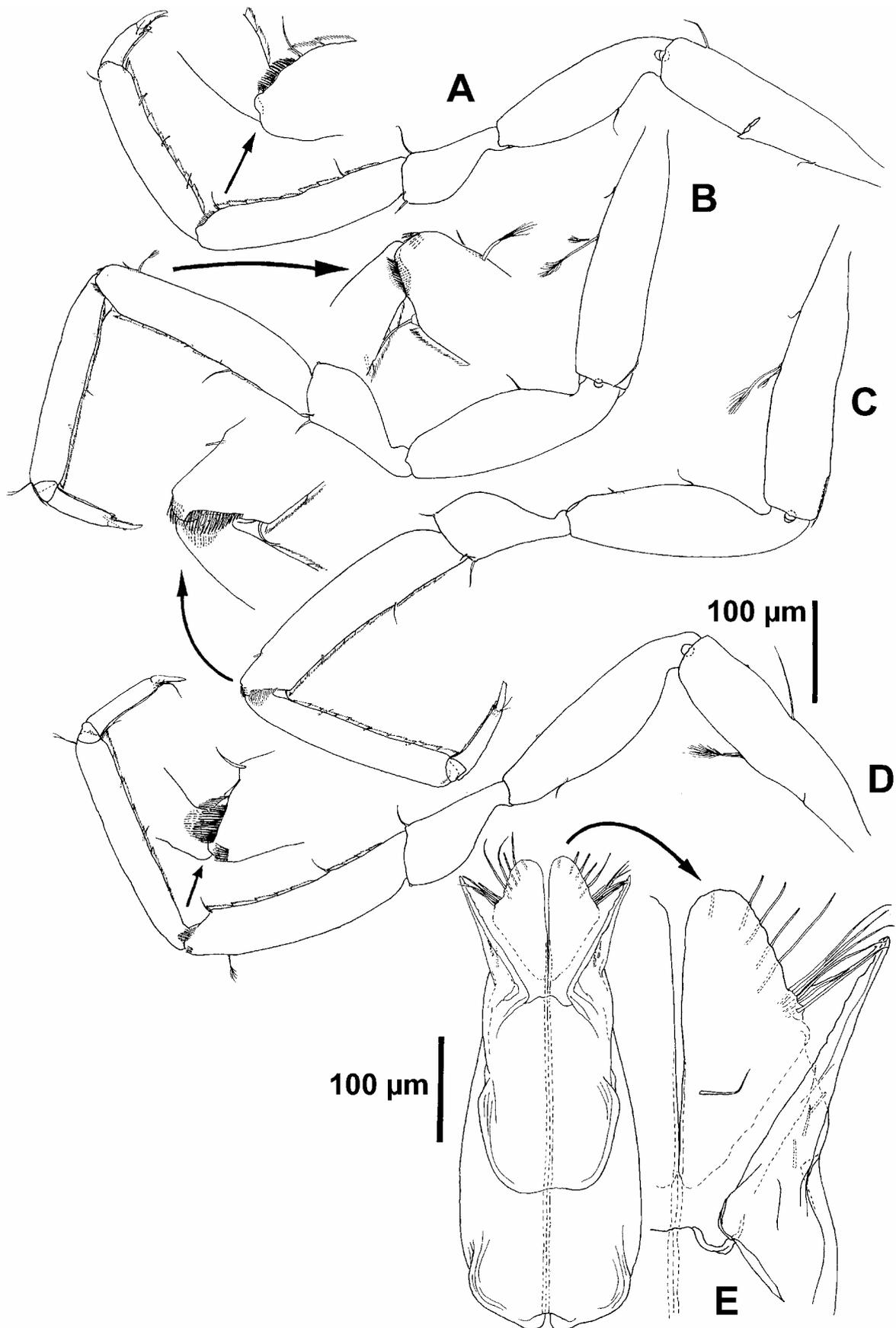


Figure 3.42: *Mastigoniscus andeepi* n. sp., paratype, male, 2.4 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pereopod 4; E pleopod 1.

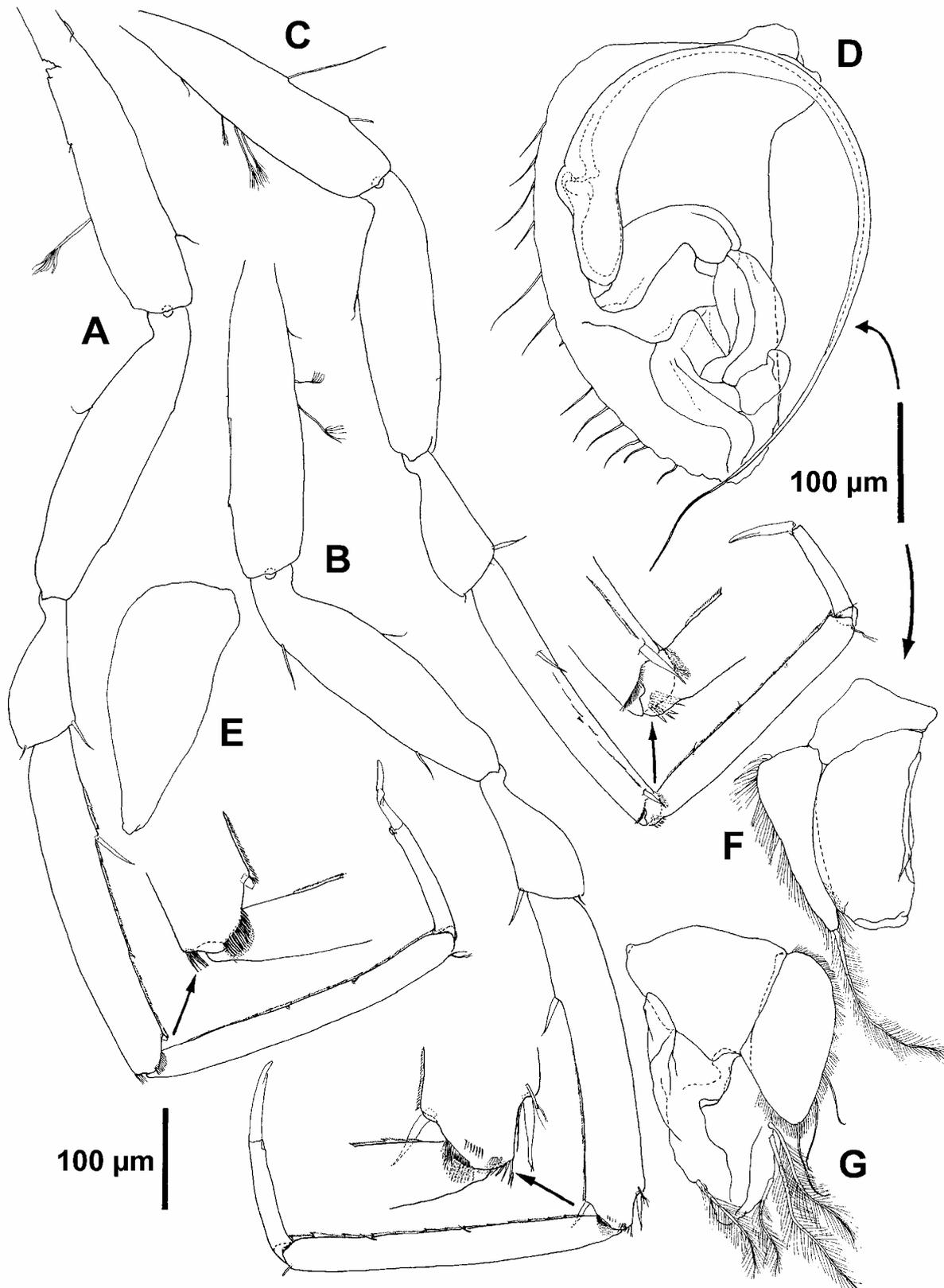


Figure 3.43: *Mastigoniscus andeepei* n. sp., paratype, male, 2.4 mm: A pereopod 7; B pereopod 6; C pereopod 5; D pleopod 2; E pleopod 5; F pleopod 4; G pleopod 3.

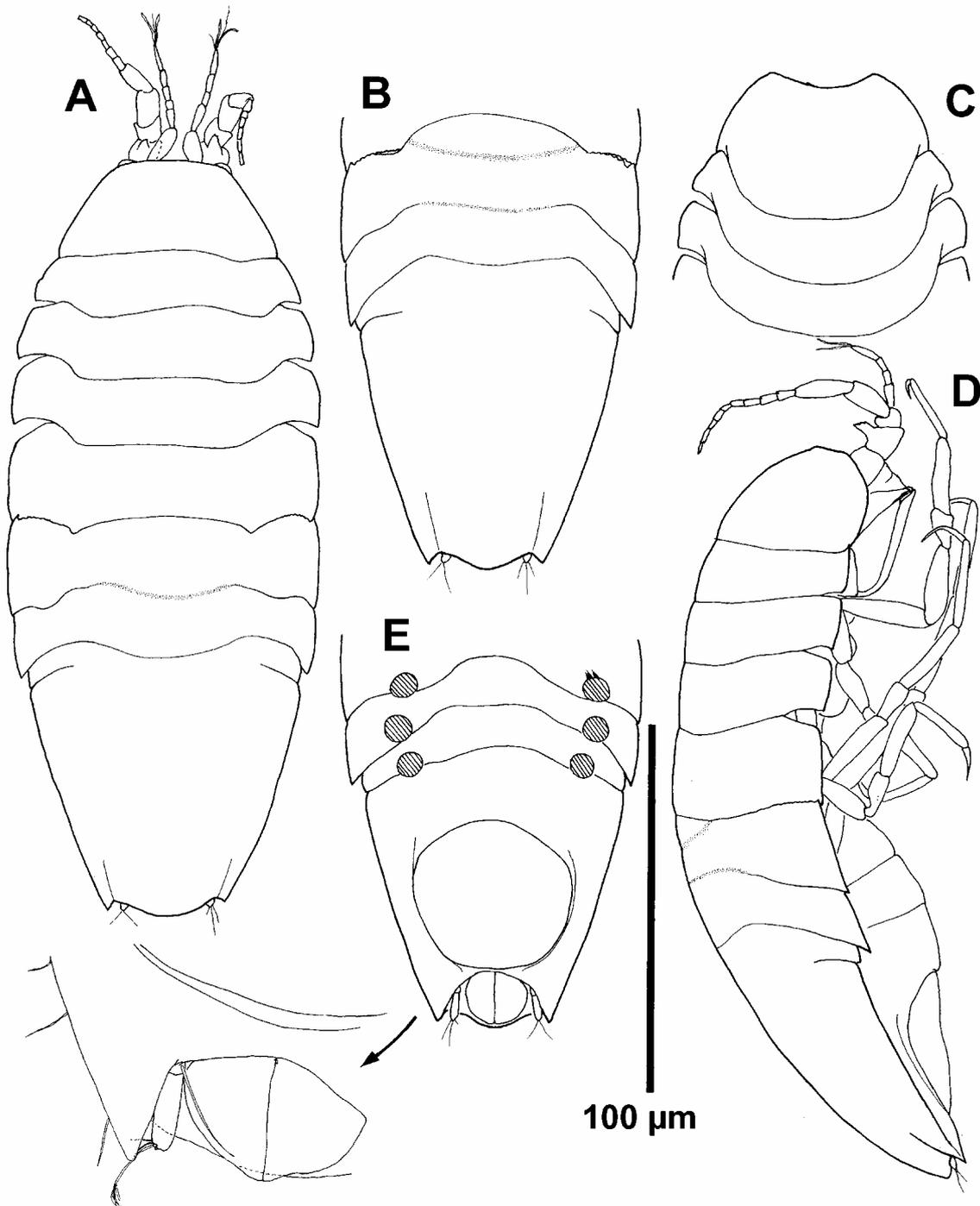


Figure 3.44: *Mastigoniscus andeepi* n. sp., paratype, female, 2.5 mm: A entire, dorsal view; B posterior body, dorsal view; C anterior body, dorsal view; D entire, lateral view; E posterior body, ventral view.

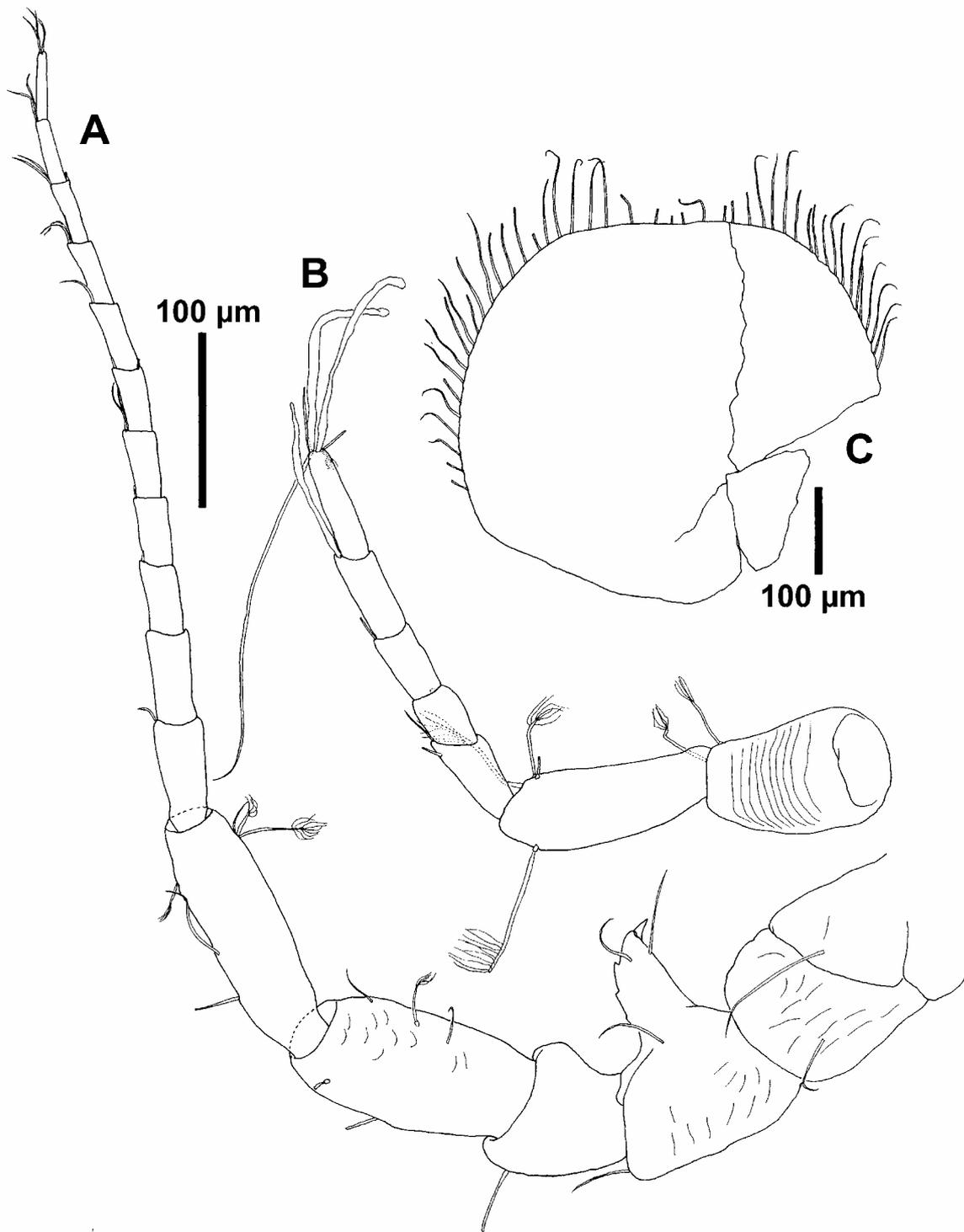


Figure 3.45: *Mastigoniscus andeepi* n. sp., paratype, female, 2.5 mm: A antenna 2; B antenna 1; C pleopod 2.

Pleopods (Figs 3.42, 3.43): Plp1 2.7 times as long as wide, evenly broadening proximally, broadest part in the proximal third, 1.7 times broader than narrowest part, distal margins with about 11 setae each, sympods separated at the distal tip, ventral surface with mediolateral

bulges and 2 transversal grooves in the distal third, extending from the suture to the tips of the subapical, distolaterally directed processes; distal ventral surface with single seta on either side; dorsal surface with several setae near each groove. Plp2 basipod about 2 times as long as wide, with numerous simple setae on lateral and distal margin; endopod inserting in proximal half of basipod, long, slender, 2.4 times as long as basipod, article 1 short, curved backwards, article 2 about 7 times as long as article 1, with slight expansion in the proximal eighth, containing the sperm duct opening, stylet tapering continuously; exopod small, inserting in the distal third of basipod. Plp3 endopod 2 times as long as wide; exopod 2 times as long as wide, 0.8 times as wide and long as endopod, lateral margin rounded, with 3 simple setae and fringe of fine bristles. Plp4 endopod 2 times as long as wide; exopod 3.1 times as long as wide, 0.6 times as wide and as long as endopod, lateral margin with fringe of long bristles, plumose seta about as long as exopod. Plp5 2.5 times as long as wide.

Uropods (Fig. 3.39) extending well beyond terminal margin, not reaching posterolateral processes of pleotelson.

Description of female

The female differs from the male in the following characters:

Posterolateral processes of pleotelson (Fig. 3.44) small, not reaching terminal margin.

Antenna 1 (Fig. 3.45) with 4 flagellar articles, article 3 with 1 aesthetasc, article 4 with 2 aesthetascs.

Antenna 2 (Fig. 3.45) more slender, flagellum, with 11 articles, with fewer setae.

Operculum (Fig. 3.45) subcircular, with numerous simple setae on distal and lateral margins.

Remarks

M. andeepi can be distinguished from the other species of the genus by the shape of the head, the male pleotelson, the shape of the dorsal tooth of antenna 2, and male pleopods 1 and 2. It is similar to *M. elegans* Park, 2000 but the latter lacks the characteristic grooves on the ventral surface of the pleotelson and has different pleopods.

As Park (2000) pointed out, an identification of manca and juveniles of *Mastigoniscus* is difficult if not impossible. Concerning *M. andeepi* and *M. pseudoelegans* this might apply to the females as well. More than 40 females were found at station 42-2. While the females of *M. polygomphios* can easily be distinguished by the shape of the head and pleotelson, as well as the unique molar process, the remaining females do not show any characteristic differences

that could be used to allocate them to two different species. Because males of *M. andeepi* were much more abundant than those of *M. pseudoelegans*, the females probably belong to the first species and therefore are described as *M. andeepi*. However it is possible that females of both species are among this material, which can not be identified by morphological means. For a satisfying identification a genetic fingerprint might prove to be a useful tool.

3.1.2.3.3 *Mastigoniscus pseudoelegans* n. sp.

(Figs 3.46-3.50)

Material

Holotype: male, 2.4 mm, 42-2, 59°40.30-40.32'S 57°35.42-42.64'W, 3689 m depth; ZMH K40782.

Paratypes: Same locality as holotype: three males, 2.4-2.5 mm; ZMH K40783.

Etymology

The name refers to the similarity of the new species with *M. elegans*.

Diagnosis

Body 3 times as long as wide; head 2 times as wide as long, trapezoidal, frontal margin straight, pereonite 5 broadest, body narrowing slightly posteriorly and anteriorly, pereonites 5-7 fused mediodorsally with each other and pleotelson, suture line between pereonites 5 and 6 indistinct, between pereonites 6 and 7 clearly visible, pleotelson 0.25 times as long as body, lateral margins slightly convex, terminal margin convex, posterolateral processes relatively small, about 0.1 times as long as pleotelson in males, smaller in females, dorsal surface of pleotelson with 2 longitudinal keels, ventral surface without grooves, antenna 1 article 2 almost as wide as article 1, with 4 flagellar articles in both sexes, antenna 2 dorsal tooth with 3 jags on anterior margin, mandibular palp article 3 with 5 serrated spine-like setae in males, pleopod 1 2.7 times as long as wide, distal margins with about 10 setae each, pleopod 2 endopod 2.5 times as long as basipod, uropods almost reaching terminal margin.

Description of paratype male

Body 3 times as long as wide; head 2 times as wide as long, trapezoidal, base 2.2 times as wide as frontal margin, frontal margin straight; pereonite 5 broadest, body narrowing slightly

posteriorly and anteriorly; posterior margin of pereonite 4 and anterior margin of pereonite 5 serrated in intersegmental gap; pereonites 5-7 fused mediodorsally with each other and pleotelson, suture line between pereonites 5 and 6 indistinct, between pereonites 6 and 7 clearly visible; pleotelson 0.25 times as long as body, tapering distally, basis 1.9 times as wide as terminal margin; lateral margins slightly convex; terminal margin convex; posterolateral processes relatively small, about 0.1 times as long as pleotelson, distance between processes 0.4 times as long as pleotelson width; dorsal surface of pleotelson with 2 longitudinal keels. Cuticle of body, maxillipedal epipod and peduncular articles of antenna 1 and 2 with numerous small round depressions.

Antenna 1 (Fig. 3.47) 0.2 times as long as body, article 1 broadest, about 1.5 times as long as wide, article 2 slightly longer and almost as wide as article 1, with several broom setae; article 3 0.4 times as long as article 2, with 2 simple setae; flagellum with 4 articles; article 1 short, with 1 broom seta; article 2 2.7 times as long as article 1, with 1 aesthetasc and 1 simple seta, article 3 2.2 times as long as article 1, with 2 aesthetascs and 1 simple seta, article 4 with 2 lateral and 2 apical aesthetascs, 3 simple setae and 1 short broom seta.

Antenna 2 (Fig. 3.47) 0.4 times as long as body, articles 1 and 2 short, with 1 simple seta each; article 3 1.2 times as long as wide, frontal margin of well developed dorsal tooth with 3 jags, tooth acute; article 4 short, 0.7 times as long as article 3; article 5 1.2 times as long and about as wide as article 3, 1.3 times as long as wide, with at least 2 broom setae; article 6 1.5 times as long as article 3, 2.5 times as long as wide, with at least 3 broom setae; flagellum 3 times as long as peduncular article 6, with 13 articles of decreasing width, each with numerous simple setae.

Mandible (Fig. 3.47) incisor with 5 blunt teeth, *lacinia mobilis* of left mandible with 5 teeth, right mandible with stout serrated spine-like seta instead, spine row comprising 2 serrated and 4 simple spine-like setae; molar tooth row with 6 larger and 6 or 7 smaller teeth, 4 or 5 setulated setae proximally; cuticular ledge of right mandible with 1 respectively 2 teeth, of left mandible with 2 teeth on either side; right mandible with 1 small additional tooth on surface near cuticular ledge, left mandible with row of 5 teeth on surface of molar process; right mandible with row of 6 accessory teeth proximally of cuticular ledge; palp article 2 with 3 serrated spine-like seta in distal quarter, article 3 with 5 serrated spine-like setae of increasing length, distal seta 6 times as long as proximal seta.

Maxilla 1 (Fig. 3.48) outer lobe with 8 simple and 4 serrated spine-like setae and several simple setae on lateral and median margin; inner lobe apically with 2 short spine-like setae and several simple setae.

Maxilla 2 (Fig. 3.48) outer lobe with 2 long and 1 short serrated spine-like setae and numerous simple setae on lateral margin, median margin with 5 spine-like setae; medial lobe with 2 long and 1 or 2 shorter serrated spine-like setae and 1 short simple spine-like seta apically and several spine-like setae on median margin; inner lobe with 2 serrated and 1 simple spine-like setae, 3 stout simple setae apically and numerous simple setae on surface and median margin.

Maxilliped (Fig. 3.48) endite apical margin with 3 small fan setae, ventral surface with numerous simple setae, separated apical median margin dorsally with 1 simple spine-like seta, 1 stout serrated spine-like seta and row of simple setae, median margin with 3 retinacula; epipod about as long as endite.

Pereopods (Figs 3.49, 3.50): Basis of P1-3 and P7 with 1 simple seta ventrally, basis of P4-6 with 2 long setae ventrally; P2-4 with 2, P5 and 6 with 3 and P7 with 1 broom seta dorsally; all pereopods with 1 simple seta dorsally. Ischium with 1-3 short simple setae ventrally and dorsally. Merus with 4 apical setae, ventral seta stout on P5-7, and several comb-like scales on surface. Carpus with ventral comb-like scale rows, smaller on P5-7, and 2-3 simple setae ventrally on P1-4. P5-7 with 2 stout setae, and 1 simple seta ventrally; P6 with dorsal stout flagellate seta; apical comb on carpus of P1 setose, apical combs on P2-7 comprised of 1 smaller and 1 larger lateral and 1 dorsal spinose comb, lateral combs largest on P5. Propodus with ventral row of comb-like scales, slightly smaller on P5-7, and 3-6 simple setae ventrally. Dactylus with 2-3 lateral setae; accessory tooth blunt.

Pleopods (Figs 3.48-3.50): Plp1 2.7 times as long as wide, evenly broadening proximally, broadest part in the proximal third, 1.7 times broader than narrowest part, distal margins with about 10 setae each, sympods separated at distal tip, ventral surface with mediolateral bulges and 2 transversal grooves in the distal third, extending from the suture to the tips of the subapical, distolaterally directed processes; distal ventral surface with single seta on either side. Plp2 basipod about 2 times as long as wide, with numerous simple setae on lateral and distal margin; endopod inserting in distal half of basipod, long, slender, 2.5 times as long as basipod, article 1 short, curved backwards, article 2 4.8 times as long as article 1, with slight expansion in the proximal seventh, containing the sperm duct opening, stylet tapering continuously; exopod small, inserting in the distal third of basipod. Plp3 endopod 1.7 times as long as wide; exopod 2.1 times as long as wide, half as wide and 0.6 times as long as endopod, lateral margin rounded, with 2 simple setae and fringe of fine bristles. Plp4 endopod about 1.8 times as long as wide; exopod 3.5 times as long as wide, margins with fringe of long bristles, plumose seta about as long as exopod. Plp5 2.1 times as long as wide.

Uropods (Fig. 3.46) extending almost to terminal margin, not reaching posterolateral processes of pleotelson.

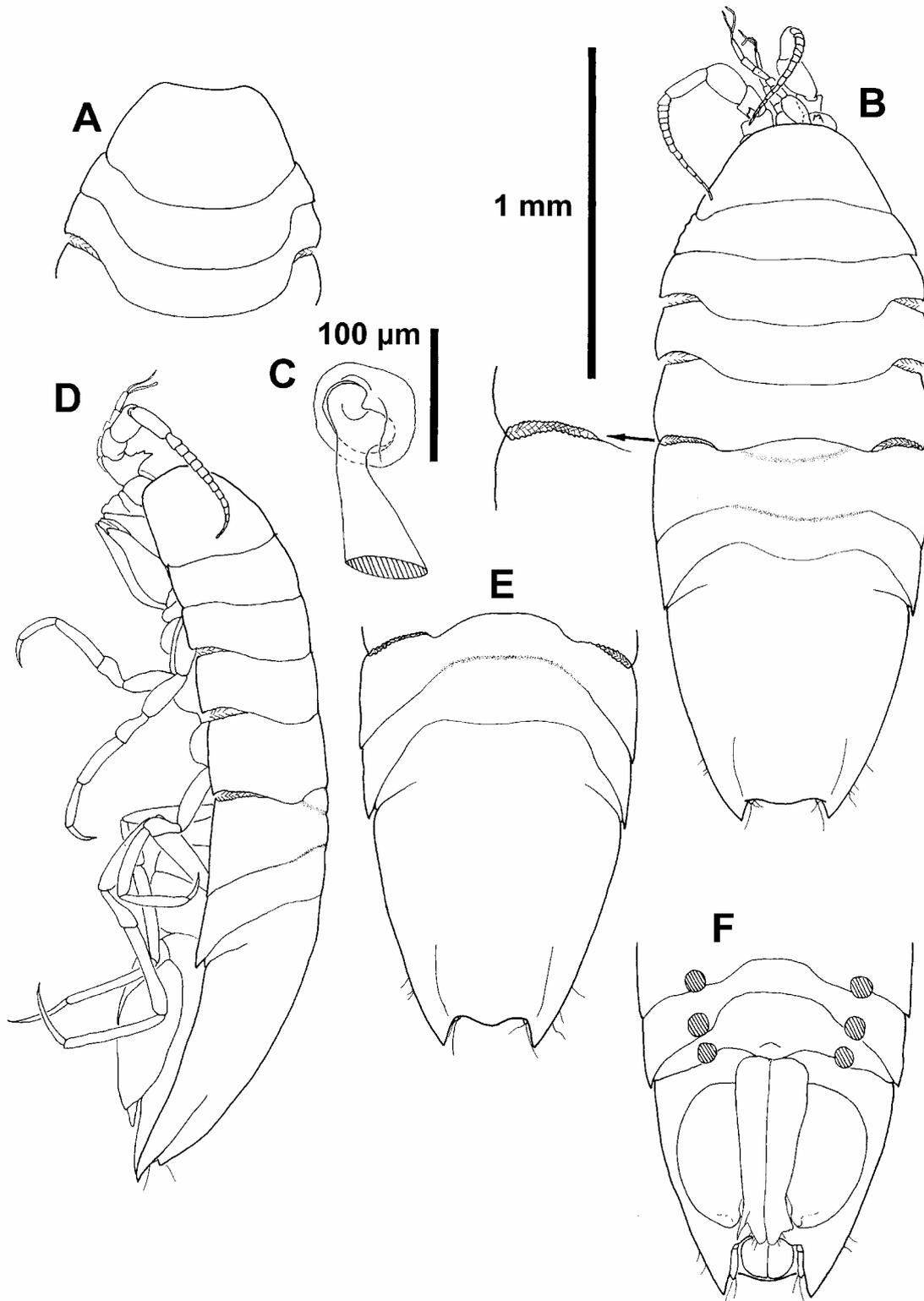


Figure 3.46: *Mastigoniscus pseudoelegans* n. sp., holotype, male, 2.4 mm: A anterior body, dorsal view; B entire, dorsal view; C insertion of pereopod 5; D entire, lateral view; E posterior body, dorsal view; F posterior body, ventral view.

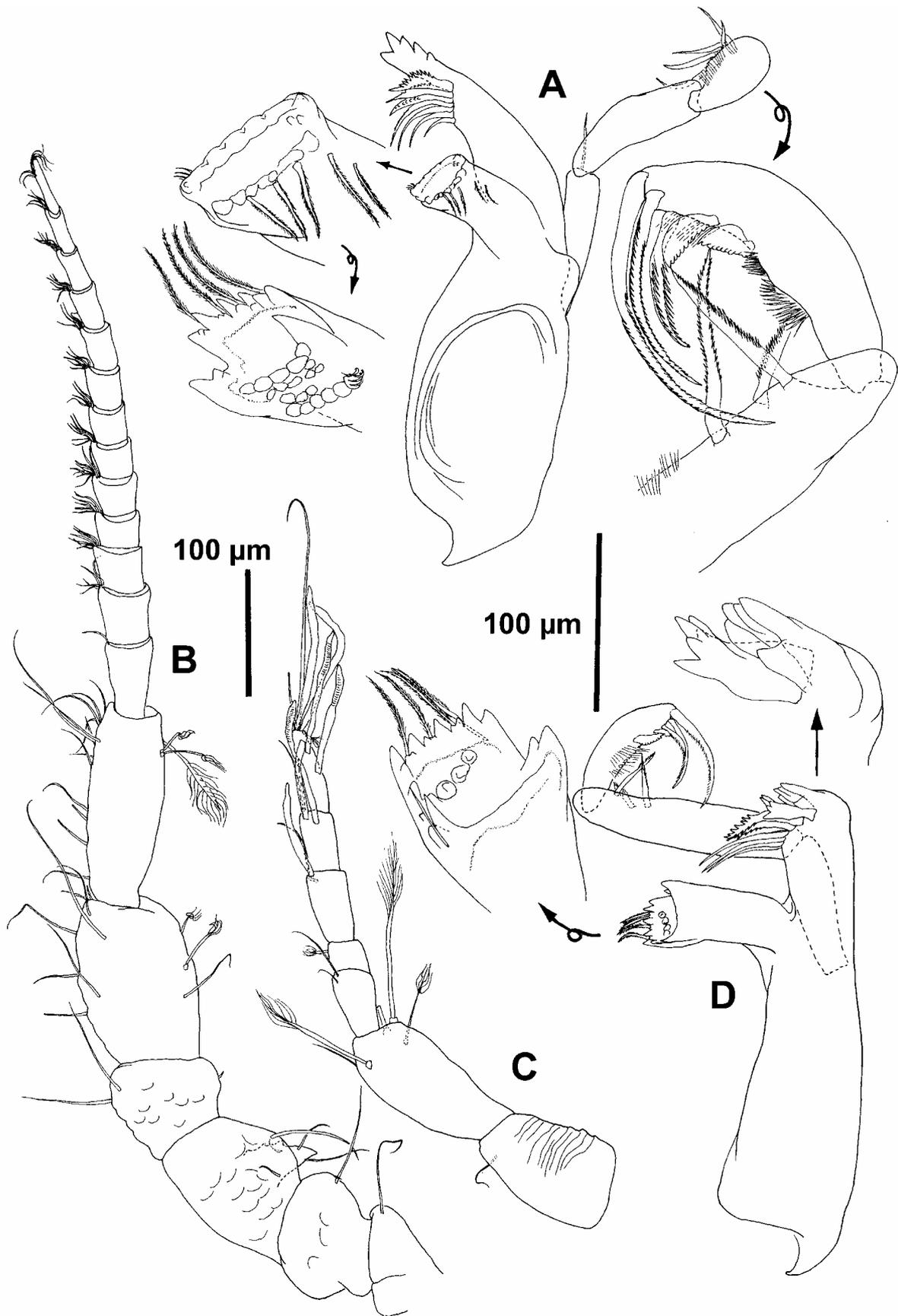


Figure 3.47: *Mastigoniscus pseudoelegans* n. sp., paratype, male, 2.5 mm: A right mandible; B antenna 2; C antenna 1; D left mandible.

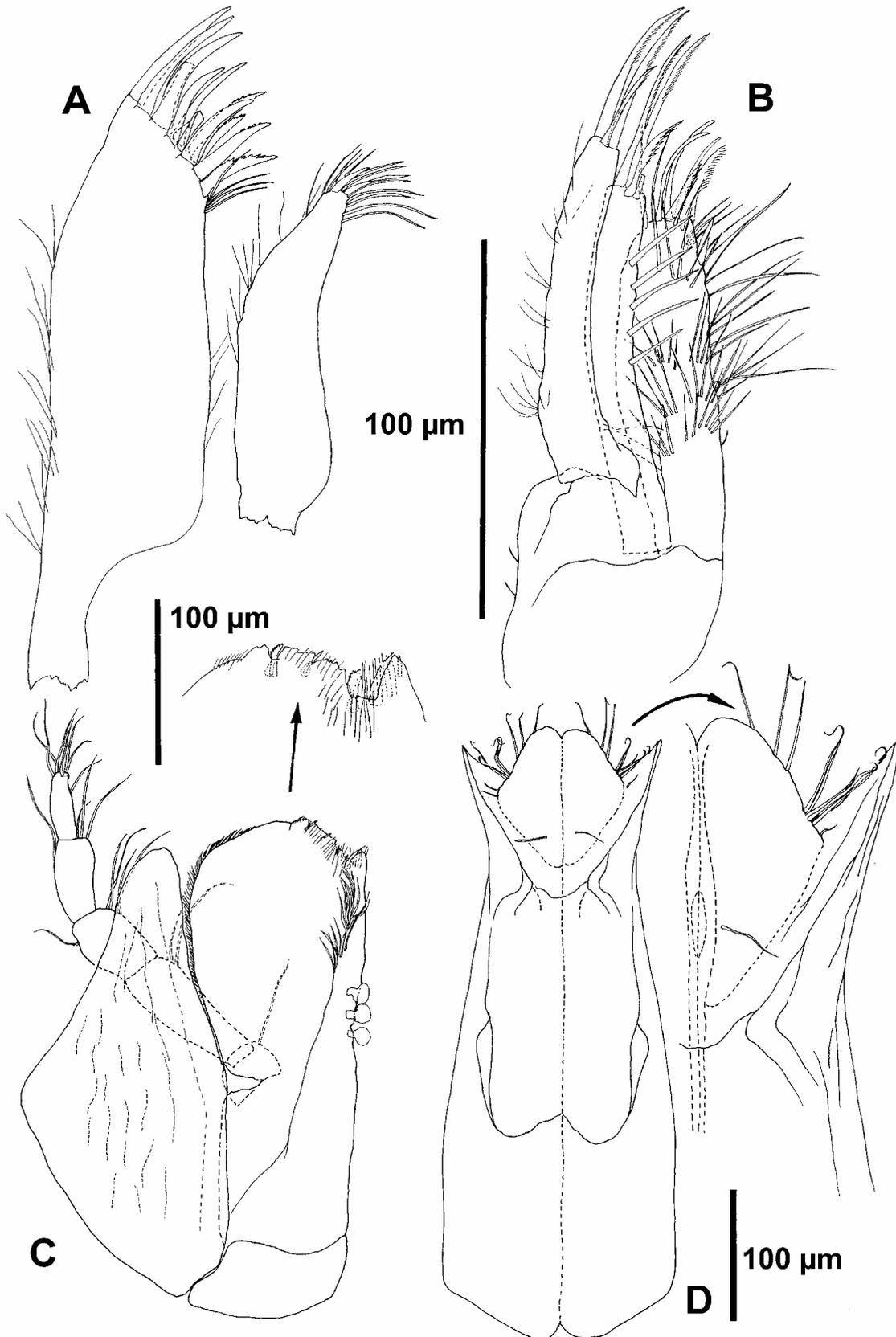


Figure 3.48: *Mastigoniscus pseudoelegans* n. sp., paratype, male, 2.5 mm: A maxilla 1; B maxilla 2; C maxilliped; D pleopod 1.

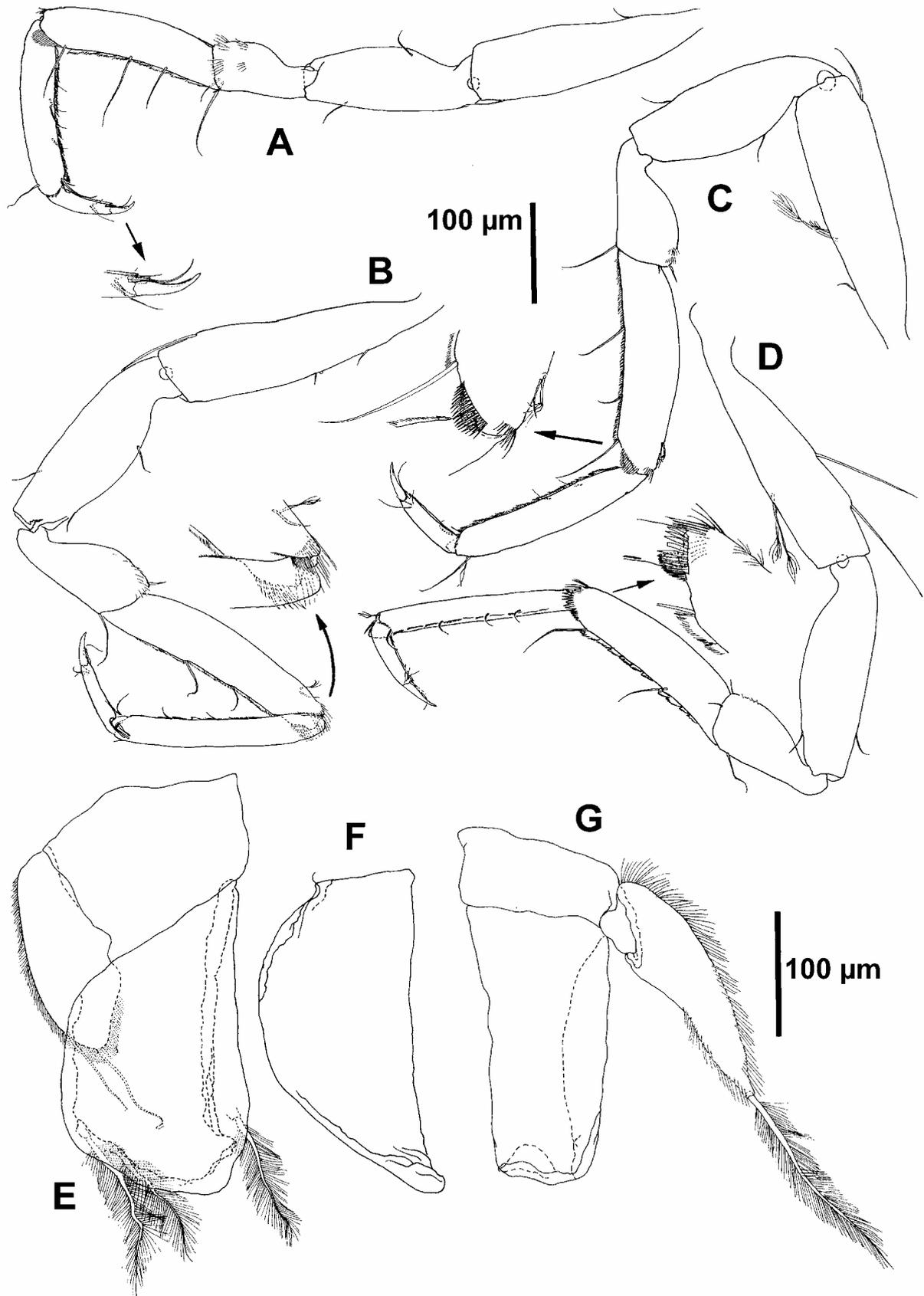


Figure 3.49: *Mastigoniscus pseudoelegans* n. sp., paratype, male, 2.5 mm: A pereopod 1; B pereopod 3; C pereopod 2; D pereopod 4; E pleopod 3; F pleopod 5; G pleopod 4.

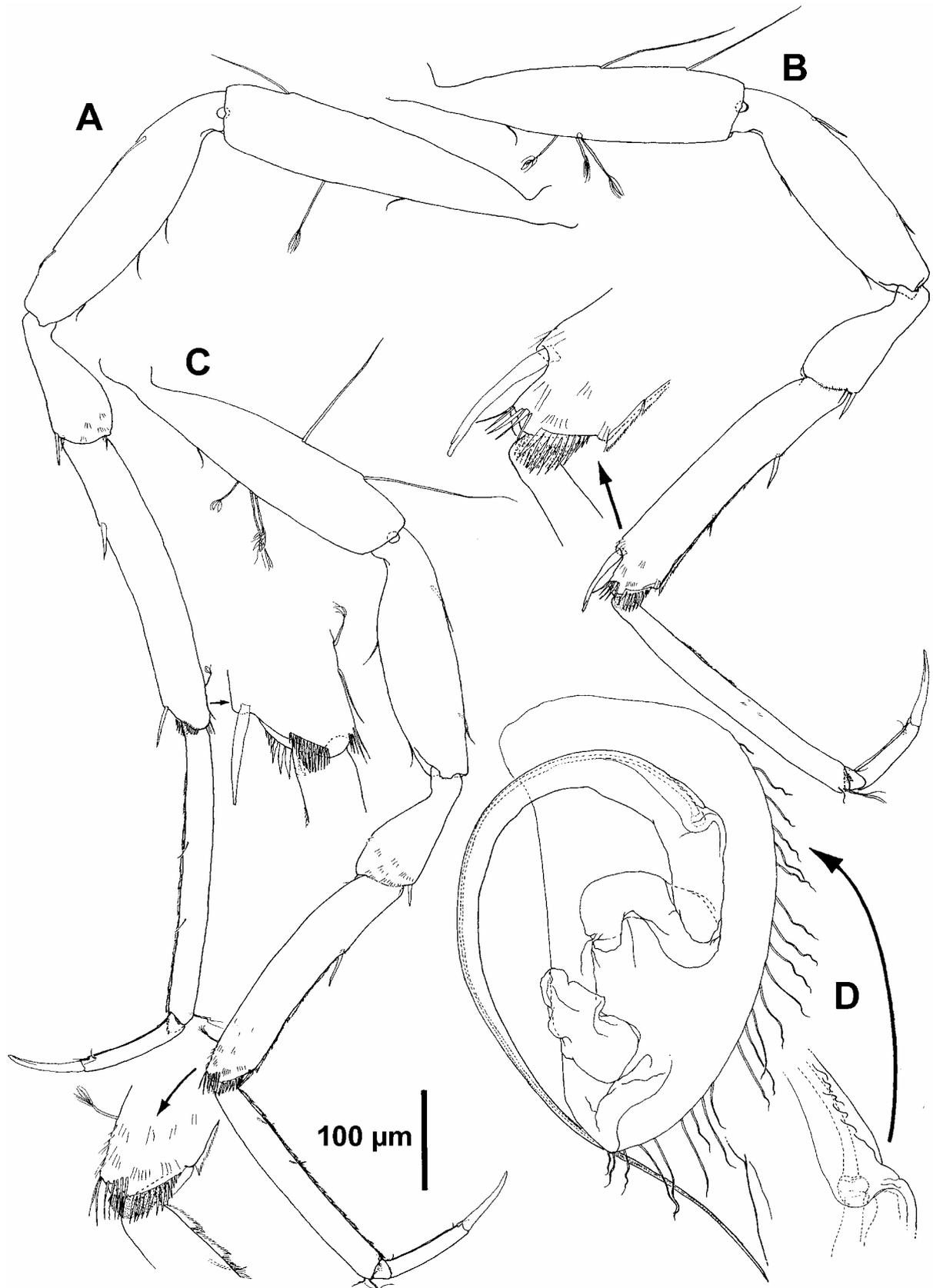


Figure 3.50: *Mastigoniscus pseudoelegans* n. sp., paratype, male, 2.5 mm: A pereopod 7; B pereopod 6; C pereopod 5; pleopod 2.

Remarks

This species resembles *M. elegans* in the shape of the body and the head, but has shorter pleotelsonic processes, a more slender pleopod 1, a shorter endopod of pleopod 2 and lacks the characteristic groove between the branchial chamber and the anus. The species is clearly distinguished from the above described species as well as from *M. concavus*, *M. generalis* Menzies and George, 1972, *M. platovatus* and *M. stenocephalus* by lacking the longitudinal grooves on the ventral surface of the pleotelson. As discussed above the females of this species are either unknown or indiscernible from females of *M. andeepi* (see above).

3.1.2.3.4 *Mastigoniscus* sp. A

(Figs 3.51-3.55)

Material

Station 131-3, 65°19.83-19.99'S 51°31.61-31.23'W, 3053 m depth: One juvenile male (stage IV), 2.7 mm; ZMH K40784.

Diagnosis

Body 2.9 times as long as wide; head 2.4 times as wide as long, frontal margin straight, pereonite 5 broadest, body narrowing slightly posteriorly and anteriorly, pereonites 5-7 fused mediodorsally with each other and pleotelson, pleotelson 0.3 times as long as body, lateral margins and terminal margin almost straight, posterolateral processes about 0.15 times as long as pleotelson, dorsal and ventral surface of pleotelson smooth, antenna 1 article 2 not as wide as article 1, with 3 flagellar articles in the juvenile male, antenna 2 dorsal tooth with 2 jags on anterior margin, mandibular palp article 3 with 7 serrated spine-like setae in males, uropods extending well beyond terminal margin.

Description of juvenile male (stage IV)

Body (Fig. 3.51) 2.9 times as long as wide; head 2.4 times as wide as long, frontal margin straight; pereonite 5 broadest, body narrowing slightly posteriorly and anteriorly; posterior margin of pereonite 4 and anterior margin of pereonite 5 serrated in intersegmental gap; pereonites 5-7 fused mediodorsally with each other and pleotelson; pleotelson 0.3 times as long as body, tapering distally, basis 1.9 times as wide as terminal margin; lateral margins and terminal margin almost straight; posterolateral processes about 0.15 times as long as

pleotelson, distance between processes 0.4 times as long as pleotelson width; dorsal surface of pleotelson smooth. Cuticle of body, maxillipedal epipod and peduncular articles of antenna 1 and 2 with numerous small round depressions.

Antenna 1 (Fig. 3.52) 0.2 times as long as body, article 1 broadest, about 1.5 times as long as wide, article 2 1.2 times as long and 0.8 times as wide as article 1, both articles with several broom setae; article 3 0.3 times as long as article 2, with simple seta; flagellum with 3 articles; article 1 with 1 broom seta; article 2 3.4 times as long as article 1, with 1 simple seta, article 3 2.6 times as long as article 1, with 2 aesthetascs, 2 simple setae and 1 short broom seta.

Antenna 2 (Fig. 3.52) 0.4 times as long as body, articles 1 and 2 short; article 3 1.5 times as long as wide, frontal margin of well developed dorsal tooth with 2 jags, tooth acute; article 4, 0.7 times as long as article 3; article 5 1.3 times as long as article 3, about 1.7 times as long as wide, with broom seta; article 6 1.4 times as long as article 3, 3 times as long as wide, with 2 broom setae; flagellum 2.4 times as long as peduncular article 6, with 9 articles of decreasing width, each with several simple setae.

Mandible (Fig. 3.52) incisor with 5 blunt teeth, *lacinia mobilis* of left mandible with 5 teeth, right mandible with stout serrated spine-like seta instead, spine row comprising 2 serrated and 3 simple spine-like setae; molar tooth row with 7 teeth on left mandible, with 6 large teeth and 2-3 additional smaller teeth on right mandible; 5 setulated setae proximally; cuticular ledge forming a tooth on either side; right mandible with about 4 indistinct teeth on surface of molar process and row of 6-7 accessory teeth proximally of cuticular ledge; palp article 2 with 3 serrated spine-like seta in the distal quarter (one broken off in type specimen), article 3 with 5 serrated spine-like setae of increasing length, distal seta almost 5 times as long as proximal seta.

Maxilla 1 (Fig. 3.53) outer lobe with 9 simple and 4 serrated spine-like setae and several simple setae on lateral and median margin; inner lobe apically with 2 short spine-like setae and several simple setae.

Maxilla 2 (Fig. 3.53) outer lobe with 2 long and 1 short serrated spine-like setae and 1 simple seta apically and numerous simple setae on lateral margin; medial lobe with 2 long and 1 shorter serrated spine-like seta apically and 6 spine-like setae on median margin, surface with several setae; inner lobe with 2 serrated and 1 simple spine-like setae, 3 stout simple setae apically and numerous simple setae on surface and median margin.

Maxilliped (Fig. 3.53) endite apical margin with 3 small fan setae and 2 short spine-like setae, ventral surface with numerous simple setae, separated apical median margin dorsally

with 1 simple spine-like seta, 1 stout serrated spine-like seta and row of simple setae, median margin with 2 retinacula; epipod slightly shorter than endite.

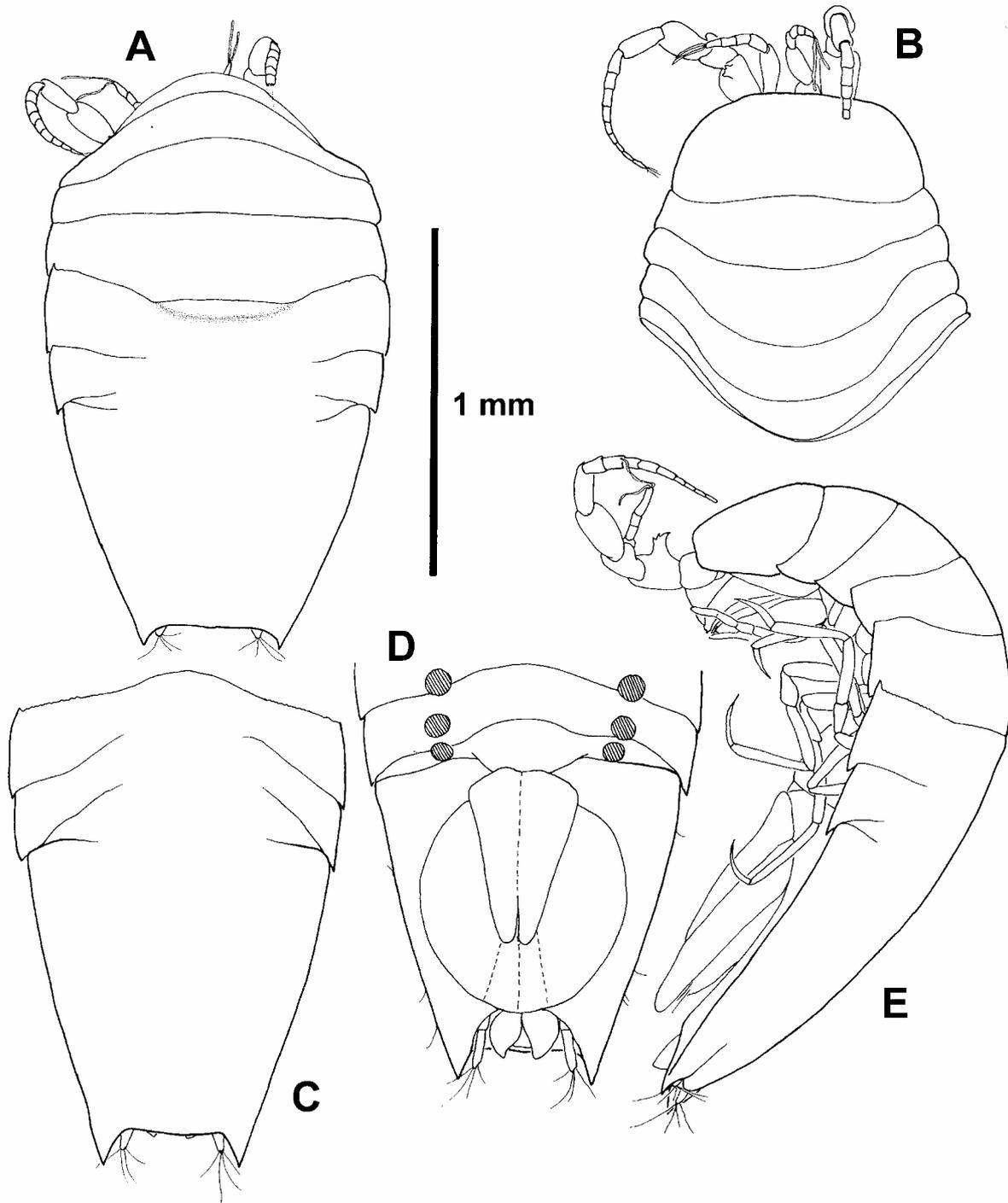


Figure 3.51: *Mastigoniscus* sp. A, male, 2.7 mm: A entire, dorsal view; B anterior body, dorsal view; C posterior body, dorsal view; D posterior body, ventral view; E entire, lateral view.

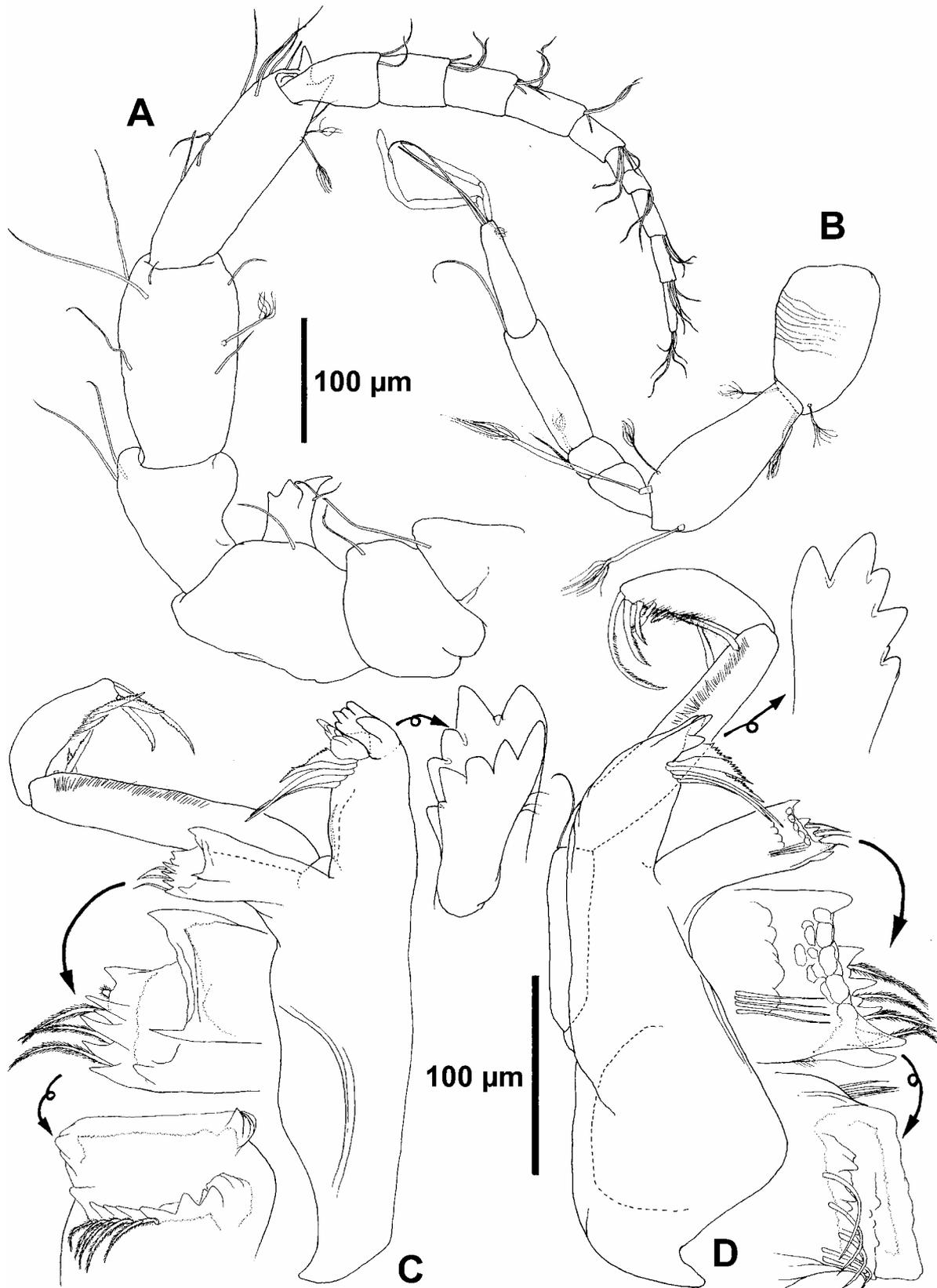


Figure 3.52: *Mastigoniscus* sp. A, male, 2.7 mm: A antenna 2; B antenna 1; C left mandible; D right mandible.

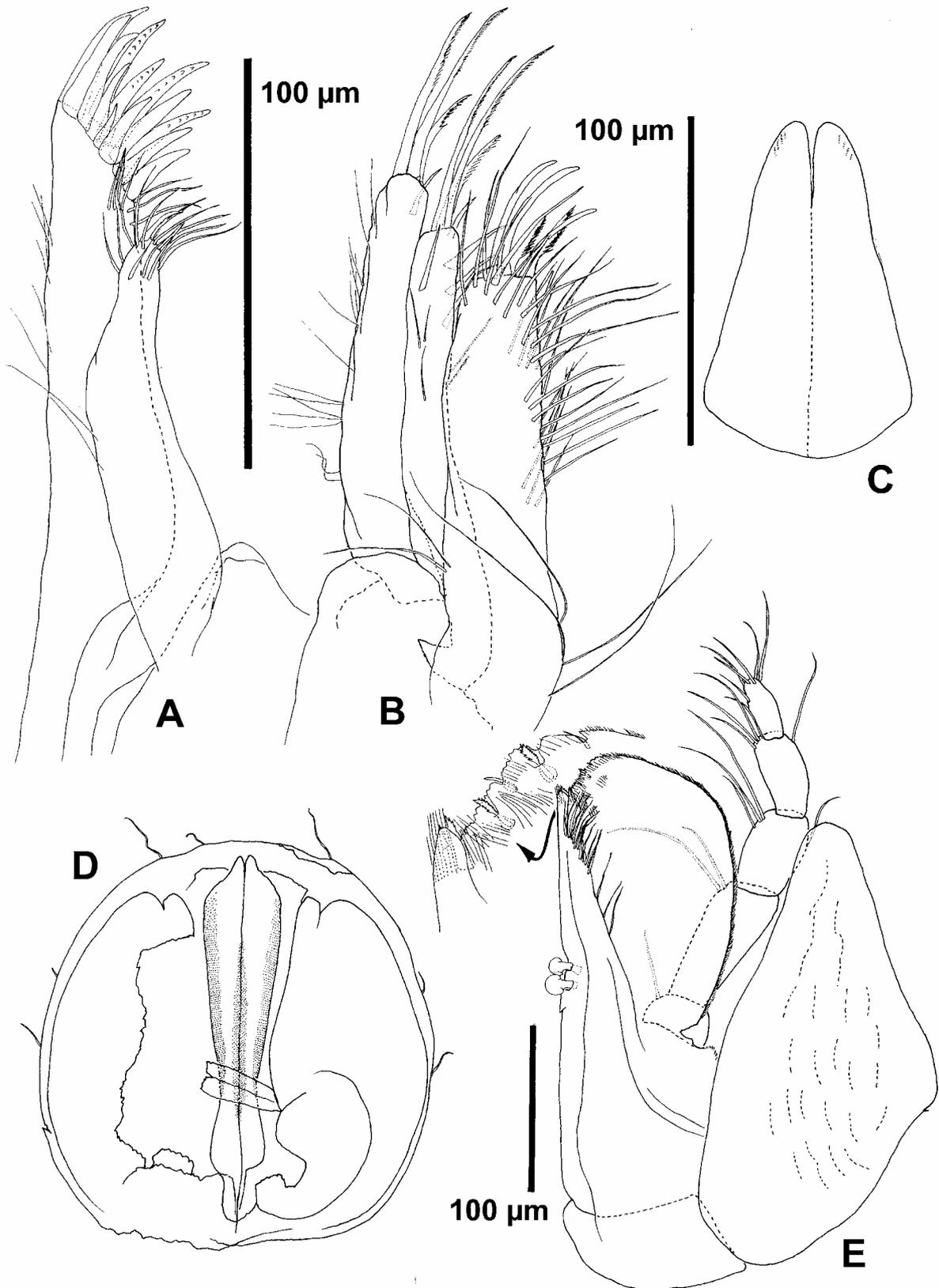


Figure 3.53: *Mastigoniscus* sp. A, male, 2.7 mm: A maxilla 1; B maxilla 2; C pleopod 1; D pleopod 2; E maxilliped.

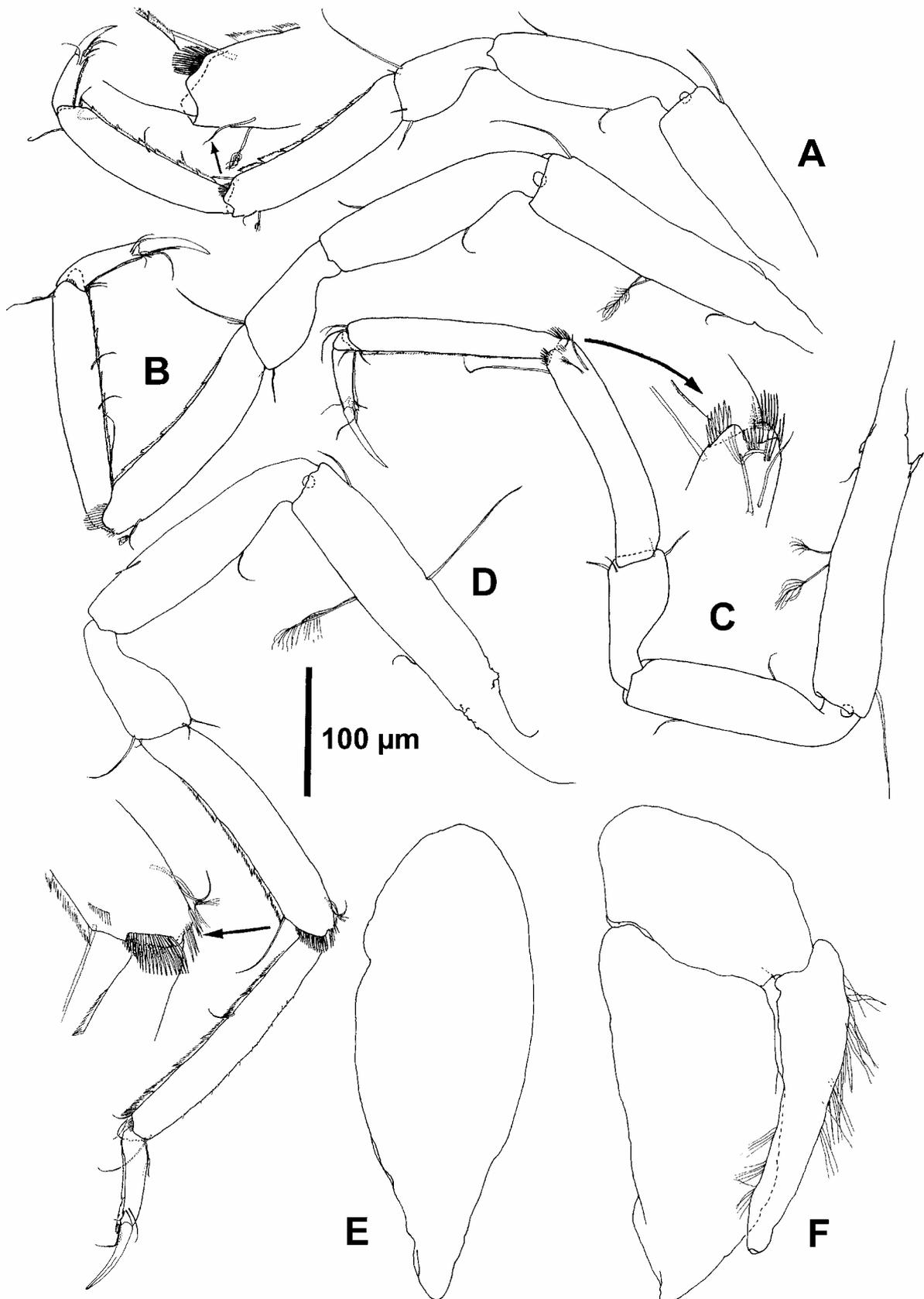


Figure 3.54: *Mastigoniscus* sp. A, male, 2.7 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pereopod 4; E pleopod 5; F pleopod 4.

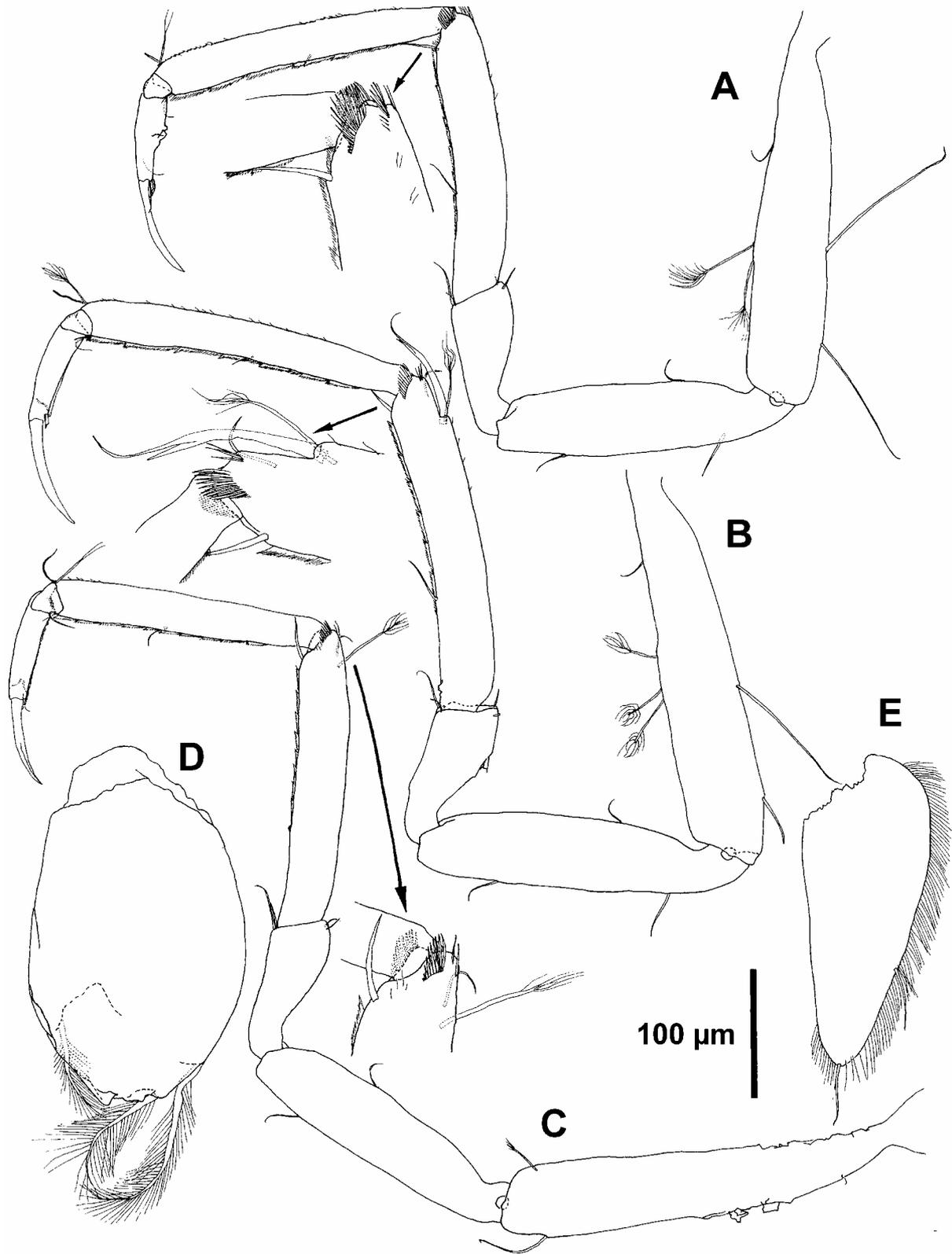


Figure 3.55: *Mastigoniscus* sp. A, male, 2.7 mm: A pereopod 5; B pereopod 6; C pereopod 7; D endopod of pleopod 3; E exopod of pleopod 3.

Pereopods (Figs 3.54, 3.55): Basis of P1-3 and P7 with 1 simple seta ventrally, basis of P4-6 with 2 long setae ventrally; P2-5 with 2, P6 with 3 and P7 with 1 broom seta dorsally; all pereopods with 1 simple seta dorsally. Ischium with 1-2 short simple setae ventrally and dorsally. Merus with 4 apical setae. Carpus with ventral comb-like scale rows and 1-2 simple setae ventrally, on P5-7 the apical seta spine-like; P6 with dorsal stout flagellate seta; apical comb on carpus of P1 small and setose, apical combs on P2-7 comprised of 1 larger and 1 smaller lateral and 1 small dorsal slightly spinose comb, lateral combs largest on P4 and 5. Propodus with ventral row of comb-like scales, slightly smaller on P5-7, and 3-5 simple setae ventrally, on P5-7 apical seta spine-like. Dactylus with 2-3 lateral setae on P1-4; accessory tooth blunt.

Pleopods (Figs 3.53-3.55): Plp1 premature 1.6 times as long as wide, evenly broadening proximally, broadest part in the proximal sixth, sympods separated at the distal tip. Plp2 forming a subcircular operculum, suture between left and right pleopod visible, endopods developed at ventral surface of operculum (destroyed during dissection). Plp3 endopod about 1.7 times as long as wide; exopod 2.5 times as long as wide, lateral margin rounded, with 2 simple setae and fringe of fine bristles. Plp4 endopod 2.3 times as long as wide; exopod 4.3 times as long as wide, 0.4 times as wide and 0.8 times as long as endopod, lateral margin with fringe of long bristles. Plp5 2.7 times as long as wide.

Uropods (figs 3.51) extending well beyond terminal margin, not reaching posterolateral processes of pleotelson.

Remarks

This species remains unnamed because it is only known by the instar IV juvenile male and does not possess most of the species-specific characters of the adult males. It resembles the female of *M. polygomphios*, but differs in the shape of the head, pleotelson and the dorsal tooth of antenna 2 and lacks the characteristic teeth on the molar surface.

3.1.2.3.5 *Mastigoniscus* sp. B

(Figs 3.56-3.60)

Material

Station 142-6, 58°50.78-50.44'S 23°57.75-57.59 W', 4221 m depth: One juvenile female, 2.4 mm; ZMH K40755.

Diagnosis

Body 2.9 times as long as wide; head 2.2 times as wide as long, trapezoidal, pereonite 4 broadest, body narrowing slightly posteriorly and anteriorly, pereonites 5-7 fused mediodorsally with each other and pleotelson, pleotelson 0.3 times as long as body, lateral margins slightly convex, terminal margin convex, posterolateral processes short, reaching terminal margin, dorsal surface of pleotelson smooth, antenna 1 article 2 not as wide as article 1, antenna 2 dorsal tooth with 2 jags on anterior margin, mandibular palp article 3 with 7 serrated spine-like setae in males, pereopods stout, uropods not reaching terminal margin of pleotelson.

Description of juvenile female

Body (Fig. 3.56) 2.9 times as long as wide; head 2.2 times as wide as long, trapezoidal, frontal margin straight; pereonite 4 broadest, body narrowing slightly posteriorly and anteriorly; posterior margin of pereonite 4 and anterior margin of pereonite 5 serrated in intersegmental gap; pereonites 5-7 fused mediodorsally with each other and pleotelson; pleotelson 0.3 times as long as body, tapering distally, basis 2.3 times as wide as terminal margin; lateral margins slightly convex; terminal margin convex; posterolateral processes short, reaching terminal margin, distance between processes 0.4 times as long as pleotelson width; dorsal surface of pleotelson smooth. Cuticle of body more or less smooth.

Antenna 1 (Fig. 3.57) 0.2 times as long as body, article 1 broadest, about 1.5 times as long as wide, article 2 about as long and 0.7 times as wide as article 1, both articles with several broom setae; article 3 0.4 times as long as article 2, with simple seta; flagellum with 3 articles; article 1 with 1 broom seta; article 2 2.4 times as long as article 1, article 3 1.8 times as long as article 1 with simple seta, with 2 aesthetascs, 3 simple setae and 1 short broom seta.

Antenna 2 (Fig. 3.57) 0.4 times as long as body, articles 1 and 2 short; article 3 1.3 times as long as wide, frontal margin of well developed dorsal tooth with 2 jags, posterior margin with 1 jag, tooth blunt; article 4 0.6 times as long as article 3; article 5 as long as article 3, about 1.3 times as long as wide; article 6 1.2 times as long as article 3, 2.2 times as long as wide, with at least 1 broom seta; flagellum 2.5 times as long as peduncular article 6, with 10 articles of decreasing width, each with several simple setae.

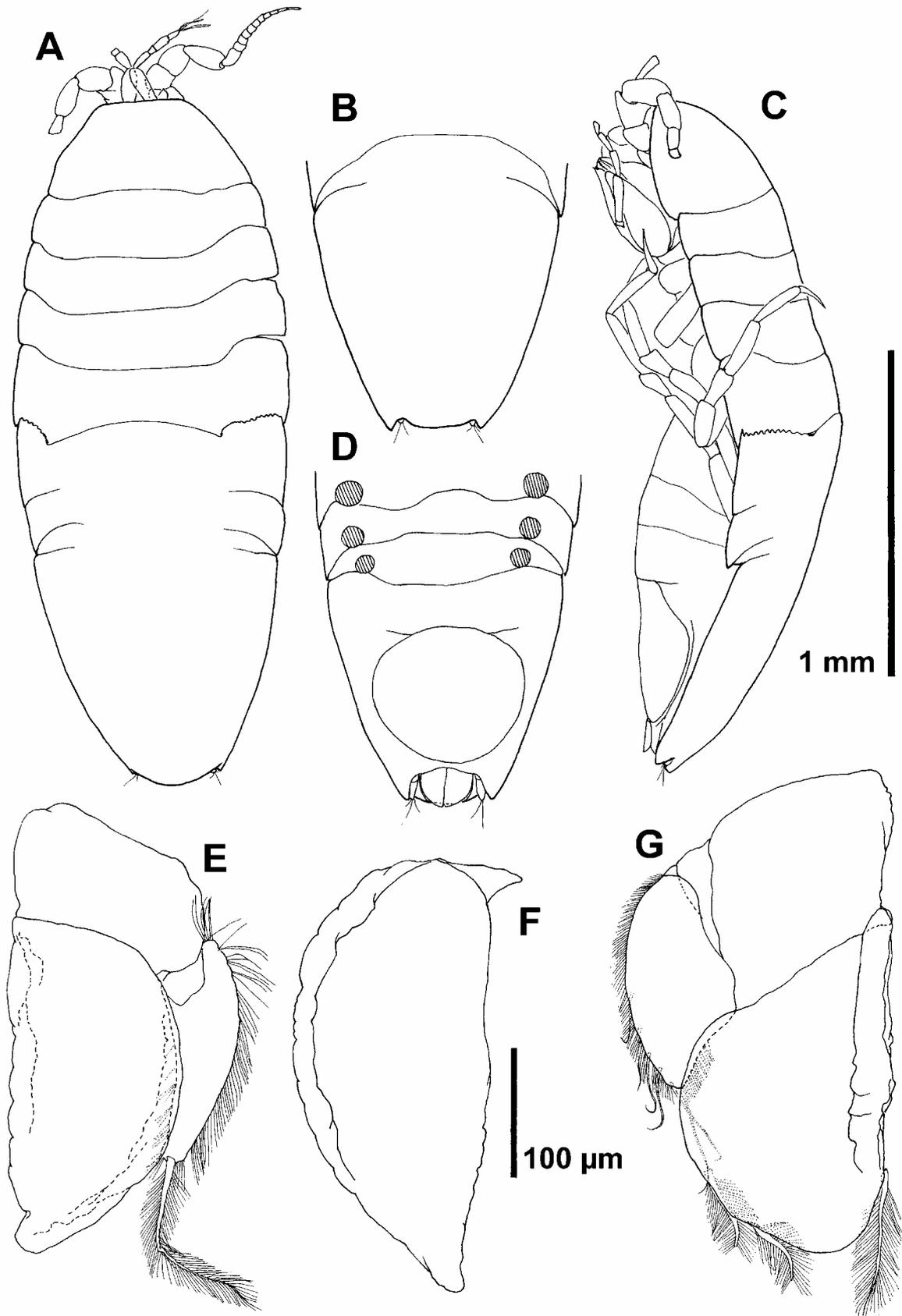


Figure 3.56: *Mastigoniscus* sp. B, female, 2.4 mm: A entire, dorsal view; B posterior body, dorsal view; C entire, lateral view; D posterior body, ventral view; E pleopod 3; F pleopod 5; G pleopod 3.

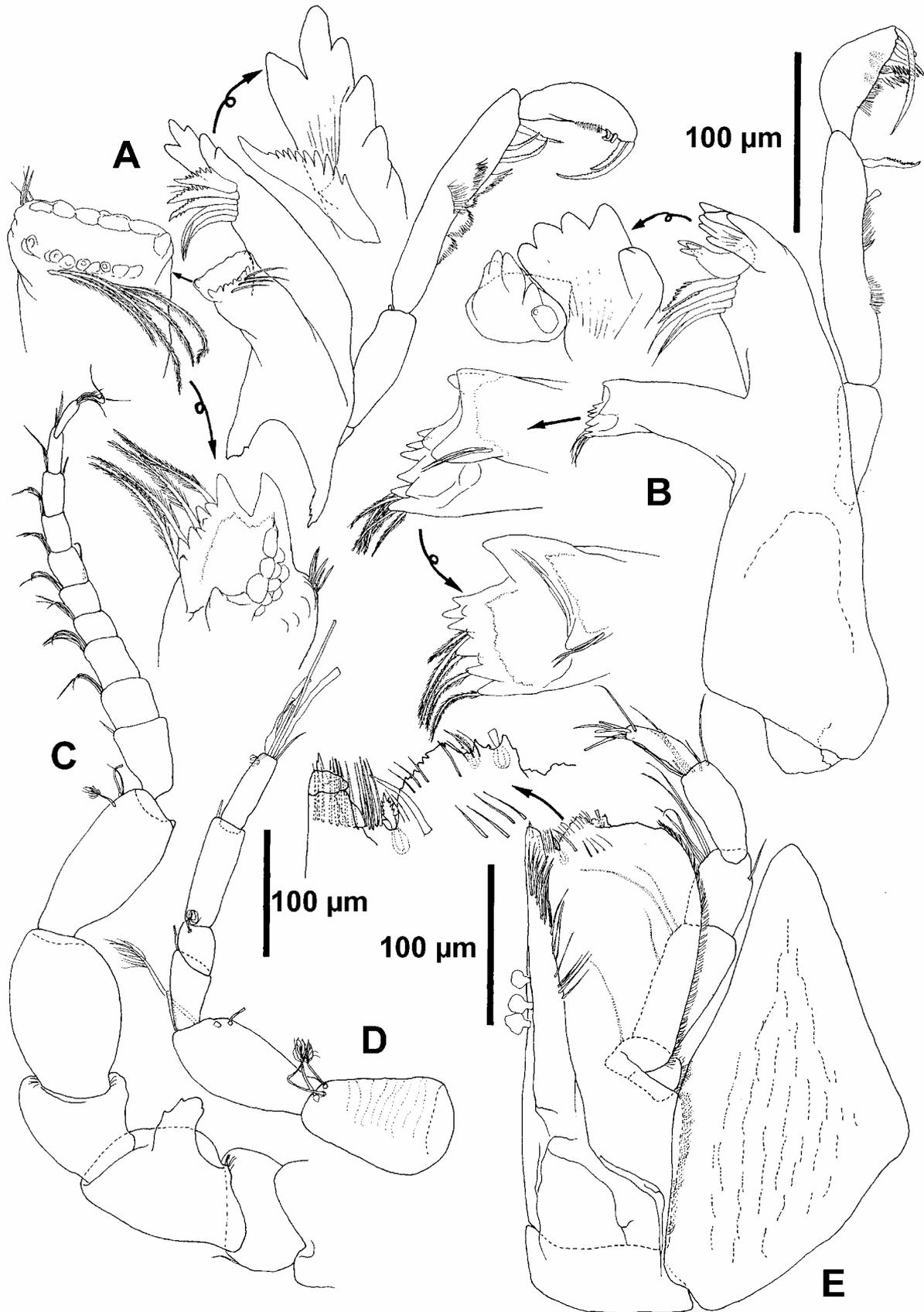


Figure 3.57: *Mastigoniscus* sp. B, female, 2.4 mm: A right mandible; B left mandible; C antenna 2; D antenna 2; E maxilliped.

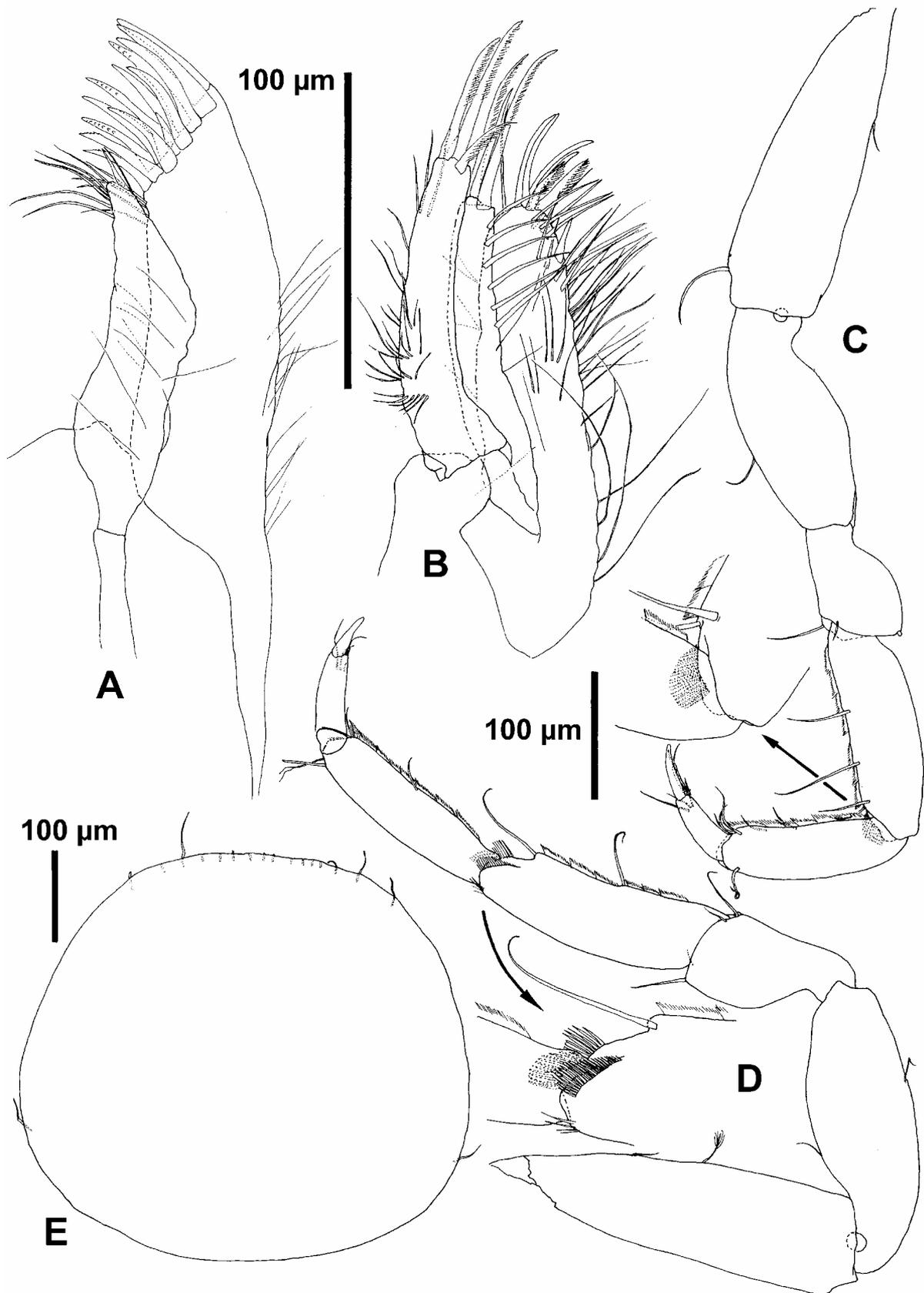


Figure 3.58: *Mastigoniscus* sp. B, female, 2.4 mm: A maxilla 1; B maxilla 2; C pereopod 1; D pereopod 2; E pleopod 2.

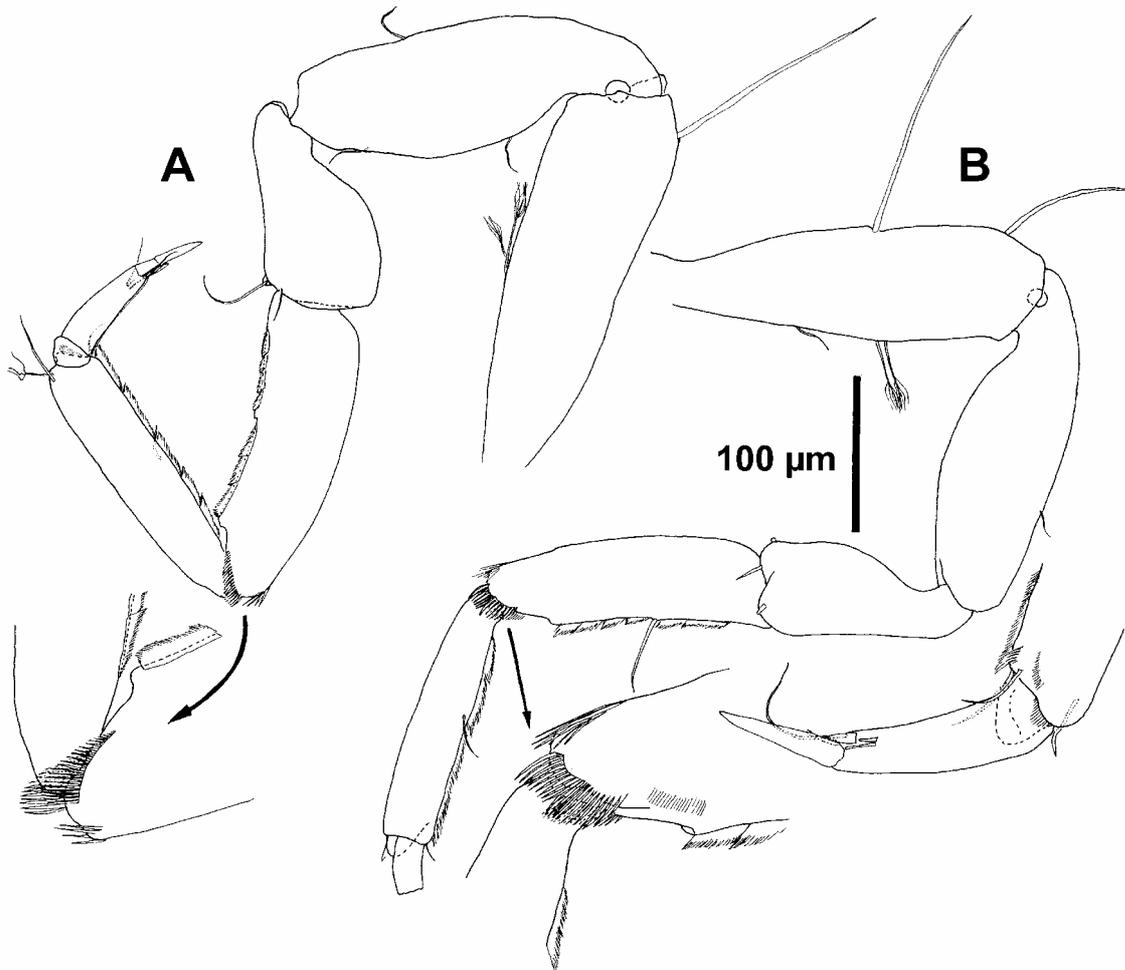


Figure 3.59: *Mastigoniscus* sp. B, female, 2.4 mm: A pereopod 3; B pereopod 4.

Mandible (Fig. 3.57) incisor with 5 blunt teeth, *lacinia mobilis* of left mandible with 5 teeth, right mandible with stout serrated spine-like seta instead, spine row comprising 2 serrated and 3 simple spine-like setae; molar tooth row with 6 larger and 3 smaller teeth; 4 or 5 setulated setae proximally; cuticular ledge forming a tooth on either side; right mandible with row of 5-6 accessory teeth proximally of cuticular ledge; palp article 2 with 3 serrated spine-like seta in the distal quarter, article 3 with 5 serrated spine-like setae of increasing length, distal seta about 3 times as long as proximal seta.

Maxilla 1 (Fig. 3.58) outer lobe with 8 simple and 5 serrated spine-like setae and several simple setae on lateral and median margin; inner lobe apically with 2 short spine-like setae and several simple setae.

Maxilla 2 (Fig. 3.58) outer lobe with 2 long and 1 short serrated spine-like setae and rows of simple setae on lateral margin; medial lobe with 2 long and 1 shorter serrated spine-like seta apically and 6 spine-like setae on median margin; inner lobe with 2 serrated and 1 simple

spine-like setae, 4 stout simple setae apically and numerous simple setae on surface and median margin.

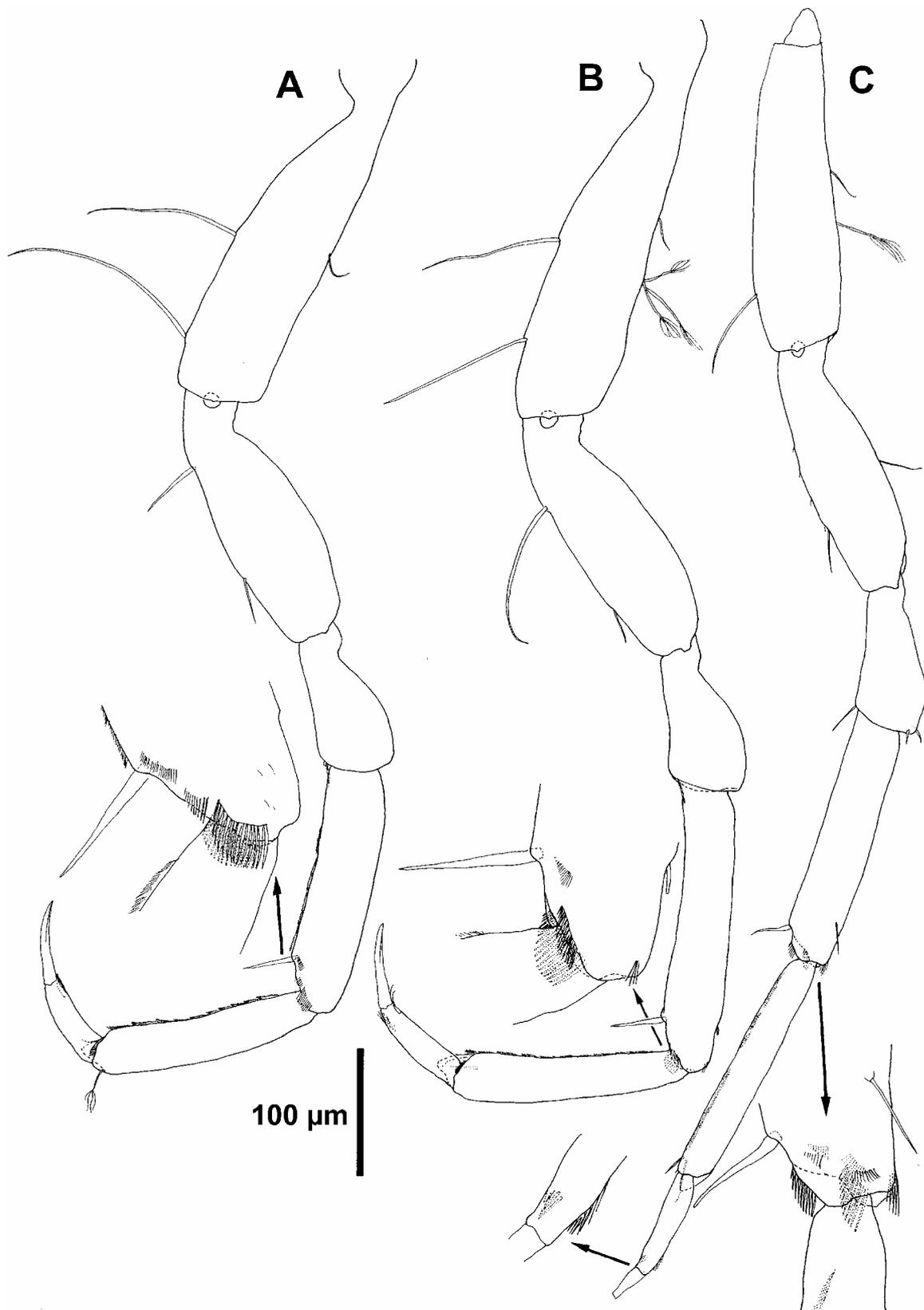


Figure 3.60: *Mastigoniscus* sp. B, female, 2.4 mm: A pereopod 5; B pereopod 6; C pereopod 7.

Maxilliped (Fig. 3.57) endite apical margin with 3 small fan setae, ventral surface 1 spine-like seta and numerous simple setae, separated apical median margin dorsally with 1 apically bifid spine-like seta, 1 stout serrated spine-like seta and row of simple setae, median margin with 3 retinacula; epipod slightly longer than endite.

Pereopods (Figs 3.58-3.60): Basis of P1-3 and P7 with 1 simple seta ventrally, basis of P4-6 with 2 long setae ventrally; P2-5 with 2, P6 with 3 and P7 with 1 broom seta dorsally (probably broken off in P2 and 5); all pereopods with 1 simple seta dorsally. Ischium with 1-2 short simple setae ventrally and dorsally on P 1-4 and 7, with stout, long seta on P5 and 7. Merus with 4 apical setae (some broken off in type specimen). Carpus with ventral comb-like scale rows, reduced on P6 and 7, on P1 with 4, on P2-4 with 2 simple setae ventrally, on P5-7 with 1 spine-like seta ventrally; P6 with dorsal stout flagellate seta (broken off in illustrated limb); apical comb on carpus of P1 setose, apical combs on P2-7 comprised of 1 larger and 1 smaller lateral and 1 small dorsal slightly spinose comb, lateral combs of almost the same size on P3, larger comb on P4 divided into two short combs. Propodus with ventral row of comb-like scales, slightly smaller on P5-7, and 2-5 simple setae ventrally, on P5-7 apical seta stout. Dactylus with 2-3 lateral setae and dorsal spinose scale.

Pleopods (Figs 3.56, 3.58): Operculum subcircular, lateral margins with single seta, distal margin with several setae. Plp3 endopod about 1.6 times as long as wide; exopod 2 times as long as wide, half as wide and 0.6 times as long as endopod, lateral margin rounded, with 6 simple setae and fringe of fine bristles. Plp4 endopod 2 times as long as wide; exopod 3 times as long as wide, 0.4 times as wide and 0.7 times as long as endopod, lateral margin with fringe of long bristles; plumose seta as long as exopod. Plp5 2.2 times as long as wide.

Uropods (Fig. 3.56) short, not reaching terminal margin of pleotelson.

Remarks

The flagellum of antenna 1 of the described specimen indicates that it is an instar IV juvenile female and therefore this species is not named. However it can be clearly distinguished from other species of the genus by the shape of the pleotelson and its posterolateral processes. The pereopods of this species are unusually stout for the genus *Mastigoniscus*, whose other members possess rather slender pereopods. This might be due to the fact that the specimen is not adult.

3.1.2.4 Genus *Haploniscus* Richardson, 1908

Type species: *Nannoniscus bicuspis* Sars, 1877

Remarks

By far the largest of the haploniscid genera, *Haploniscus* forms a depository for species that cannot be allocated to one of the more clearly defined genera (Lincoln, 1985a, b; Brökeland and Wägele, in press). Consequently the genus is defined only by the absence of those apomorphies, which characterize the remaining genera. Therefore a diagnosis for *Haploniscus* is redundant and not given here.

The genus contains species with a great variety of body shapes. Some species like *H. helgei* Wolff, 1962 are able to conglobate, like species of *Hydroniscus* and *Chauliodoniscus*. The variation includes also the differentiation of the limbs, for example the length of the third article of antenna 2 or the length of the endopod of pleopod 2, as well as the setation of the pereopods. Some species seem to be closely related to one of the other genera without possessing all characteristic apomorphies of these.

Since the erection of *Chauliodoniscus* and *Mastigoniscus* by Lincoln (1985a), to which several *Haploniscus* species were transferred, no further reasonable subdivision of *Haploniscus* was attempted. The genus *Chandraniscus*, established by George (2004) for some new and several *Haploniscus* species, has to be questioned (see 4.1.2).

The species described below are part of a complex of very similar species. Despite the morphological similarities, the genetic distances show that they belong to distinct species, which are closely related (Michael Raupach, pers. com). Because of the great similarity between the different species only the first one is described in detail; for the following species the differences to the first one are listed.

3.1.2.4.1 *Haploniscus cassilatus* n. sp.

(Figs 3.61-3.66, 3.99)

Material

Holotype: male, 3.9 mm; station 46-7, 60°38.33-38.06'S 53°57.38-57.51'W, 5639 m depth; ZMH K40756.

Paratypes: same locality as holotype: 4 males, 3.5-3.9 mm; 3 ovigerous females, 3.5-3.6; 21 females, 2.4-3.6 mm, 36 juveniles, 1.4-2.5 mm; ZMH K40757.

Etymology

The species is named after the prominent rostrum; from *cassis*, which means “helmet”, and *latus*, which means “carrying”.

Diagnosis

Body oval, 3 times as long as wide. Head about 2.5 times as wide as long, frontal margin concave, with prominent rostrum; rostrum covered with small tubercles, with dorsal depression and acute upturned frontal tooth, a deep ventral indentation between rostrum and frontal margin of head. Pereonites 3-5 broadest. Lateral margins of pleotelson convex, posterolateral processes short, not reaching terminal margin; dorsal surface of pleotelson with 2 sharp longitudinal keels, ventral surface with cuticular bulge surrounding the branchial chamber and tapering towards anus. Antenna 1 with 4 flagellar articles. Carpus with 1-3 flagellate spine-like setae, apical and ventral combs of carpus spinose, carpus of P5 and 6 with dorsal flagellate seta. Pleopod 1 with nearly continuous distal margin. Endopod of pleopod 2 as long as basipod. Uropods not reaching terminal margin.

Description of female paratype

Body oval, 3 times as long as wide. Head about 2.5 times as wide as long, frontal margin concave, with prominent rostrum; rostrum covered with small tubercles, with dorsal depression and acute upturned frontal tooth, a deep ventral indentation between rostrum and frontal margin of head. Margins of pereonites straight, smooth. Pereonites 3-5 broadest. Pleotelson 0.2 times as long as body, tapering distally, basis 1.8 times as wide as terminal margin; terminal margin convex. Cuticle of body smooth.

Antenna 1 (Fig. 3.62) about 0.3 times as long as body, article 1 broadest, about 1.5 times as long as wide, article 2 1.3 times as long and about half as wide as article 1, both articles with several broom and simple setae; article 3 0.4 times as long as article 2, with simple seta; flagellum with 4 articles; article 1 shortest, with broom seta; article 2-4 of subequal length, article 2 with simple seta, article 3 with 1 aesthetasc and 1 simple seta, article 4 with 2 aesthetascs and 2 simple setae.

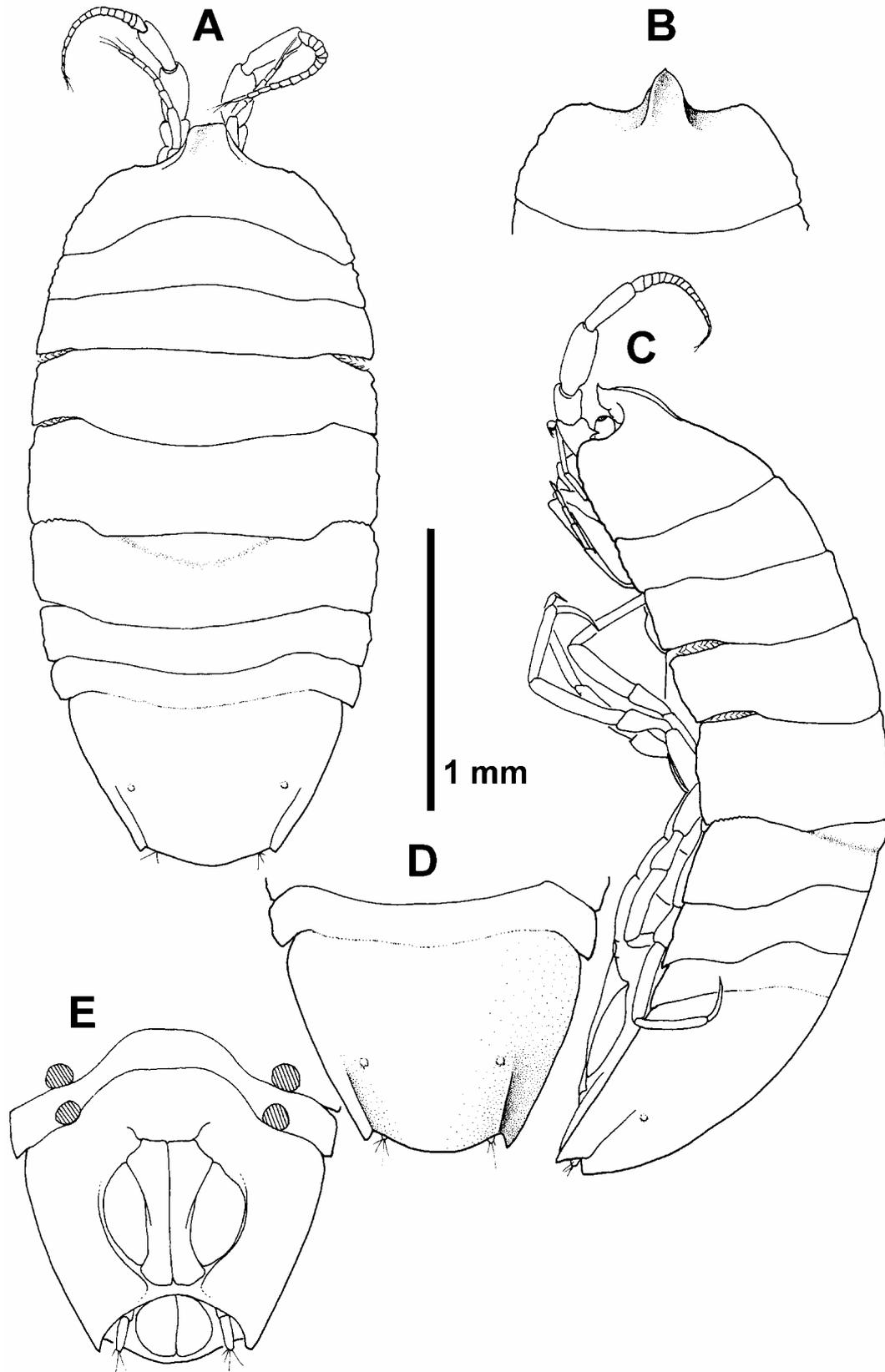


Figure 3.61: *Haploniscus cassilatus* n. sp., holotype, male, 3.9 mm: A dorsal view; B anterior body, dorsal view; C lateral view; D posterior body dorsal view; E Posterior body ventral view.

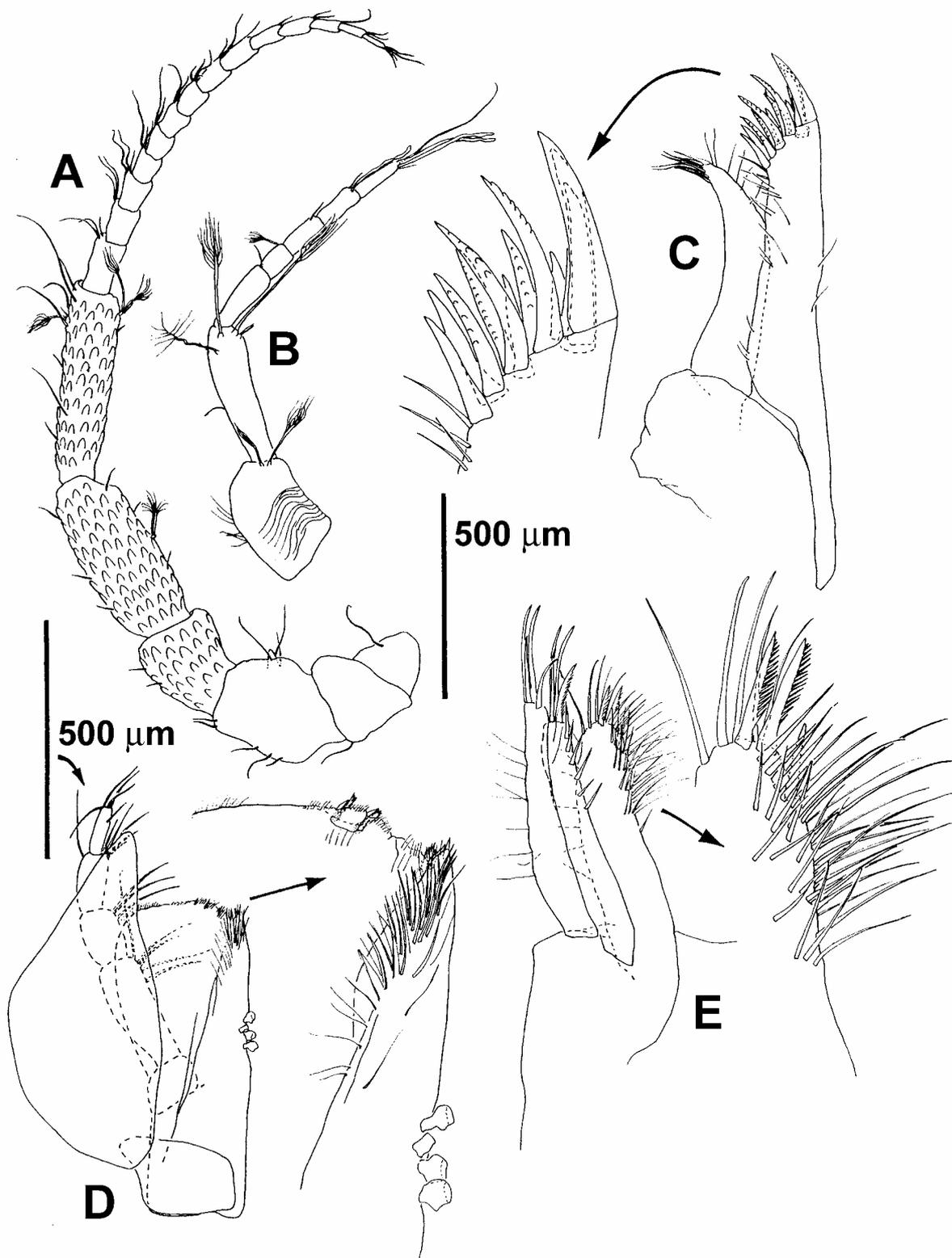


Figure 3.62: *Haploniscus cassilatus* n. sp., paratype, female, 3.6 mm: A antenna 2; B antenna 1; C maxilla 1; D maxilliped; E maxilla 2.

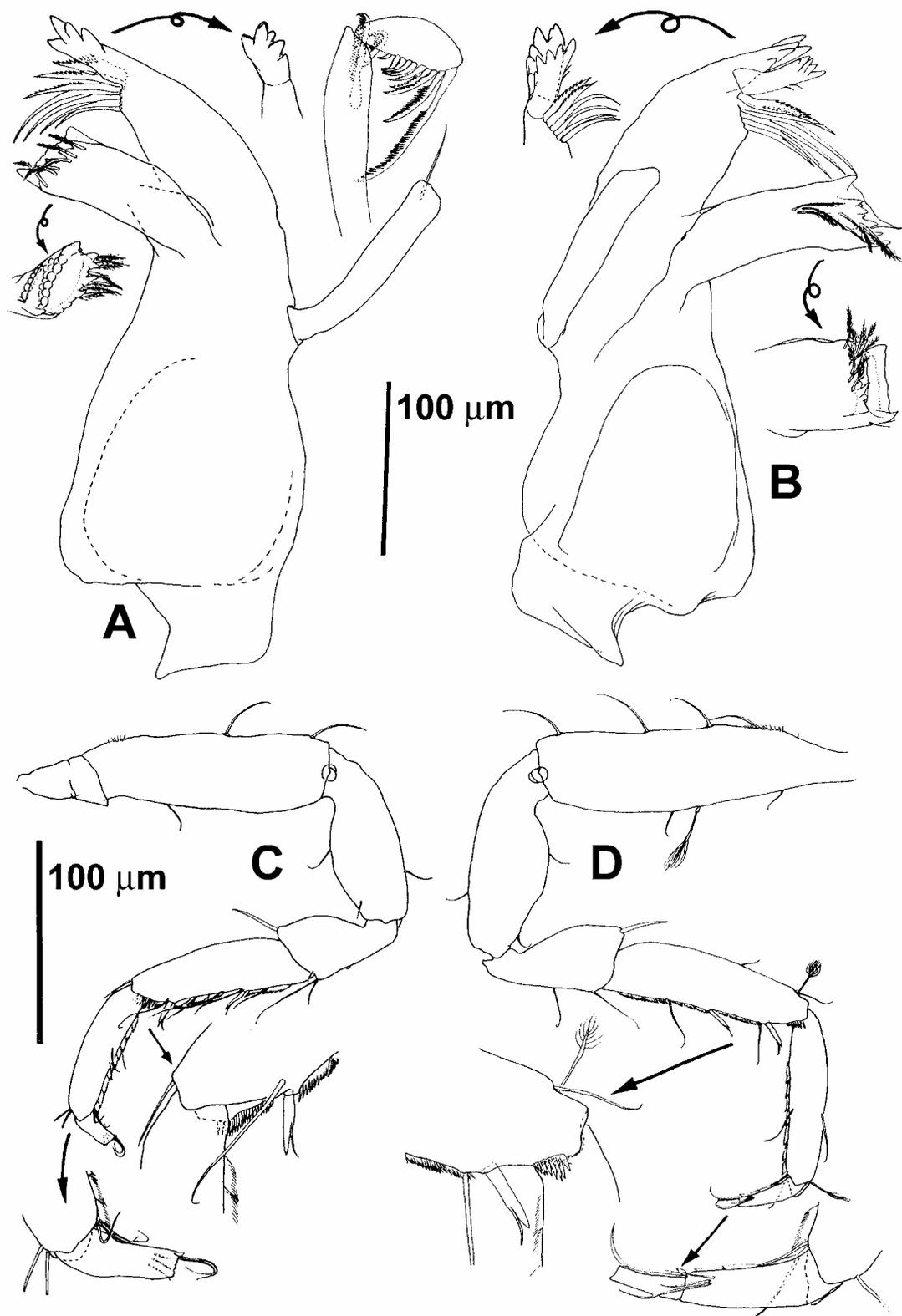


Figure 3.63: *Haploniscus cassilatus* n. sp., paratype, female, 3.6 mm: A right mandible; B left mandible; C pereopod 1; D pereopod 2.

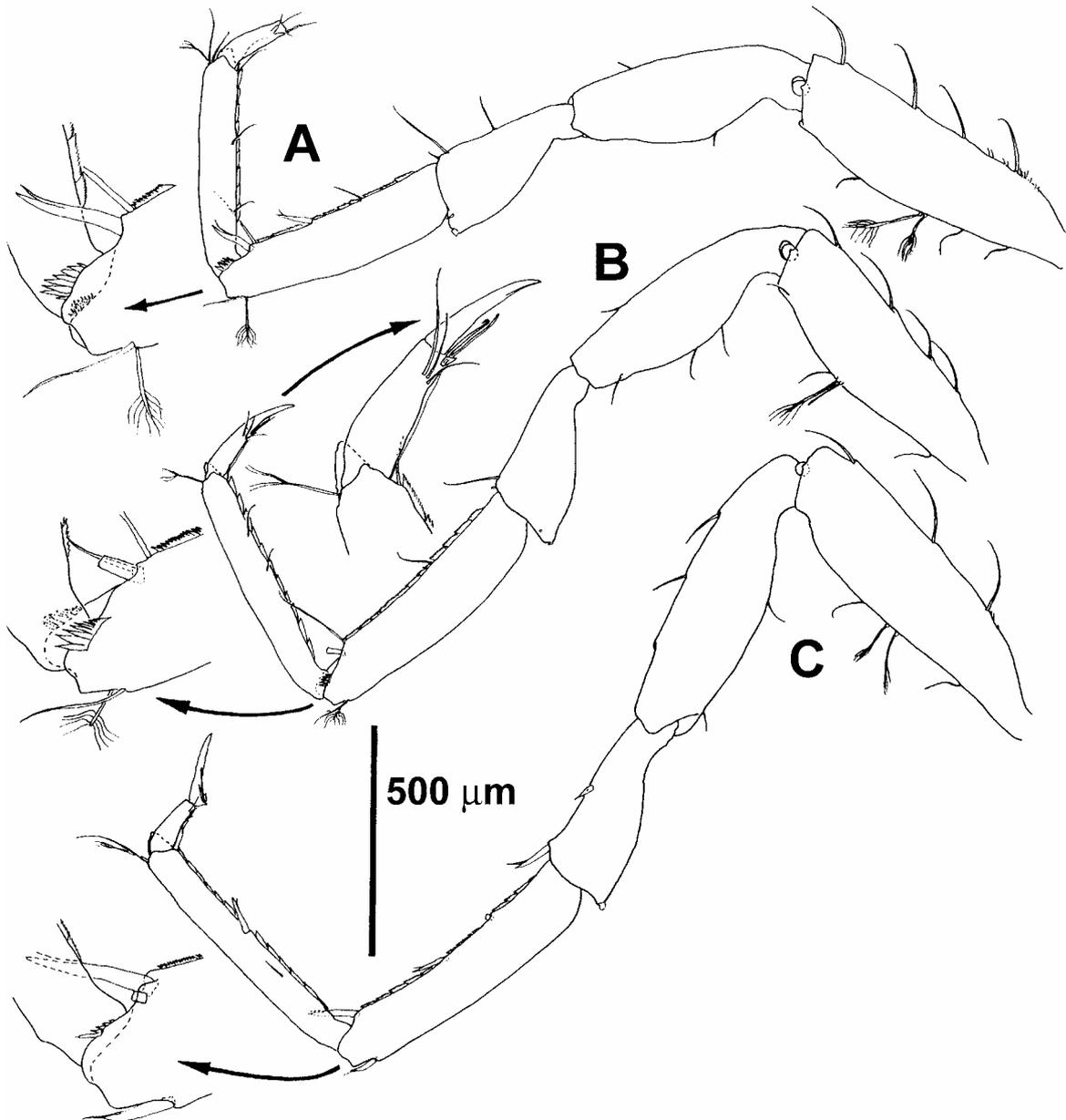


Figure 3.64: *Haploniscus cassilatus* n. sp., paratype, female, 3.6 mm: A pereopod 3; B pereopod 4; C pereopod 5.

Antenna 2 (Fig. 3.62) 0.7 times as long as body, articles 1 and 2 slightly wider than long, with simple seta, article 3 about as long as wide, 2 times as long as article 2, with short dorsal tooth and several simple setae, article 4 0.6 times as long as article 3, article 5 1.5 times, article 6 1.7 times as long as article 3, both articles with several simple and some broom setae, articles 4-6 covered with numerous triangular scales; flagellum 0.7 times as long as peduncle, 14-articulated, each article with several simple setae.

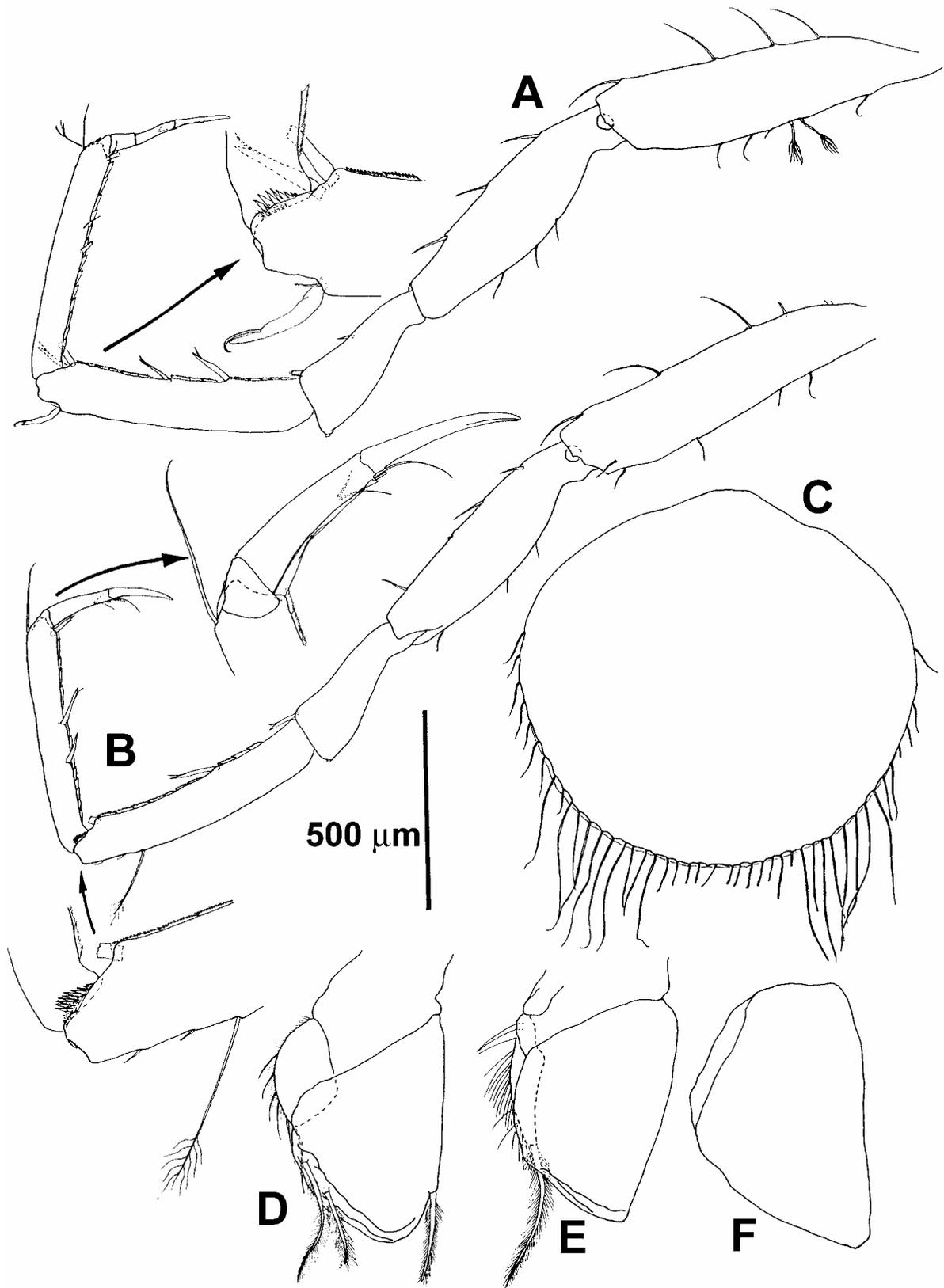


Figure 3.65: *Haploniscus cassilatus* n. sp., paratype, female, 3.6 mm: A pereopod 6; B pereopod 7; C pleopod 2; D pleopod 3; E pleopod 4; F pleopod 5.

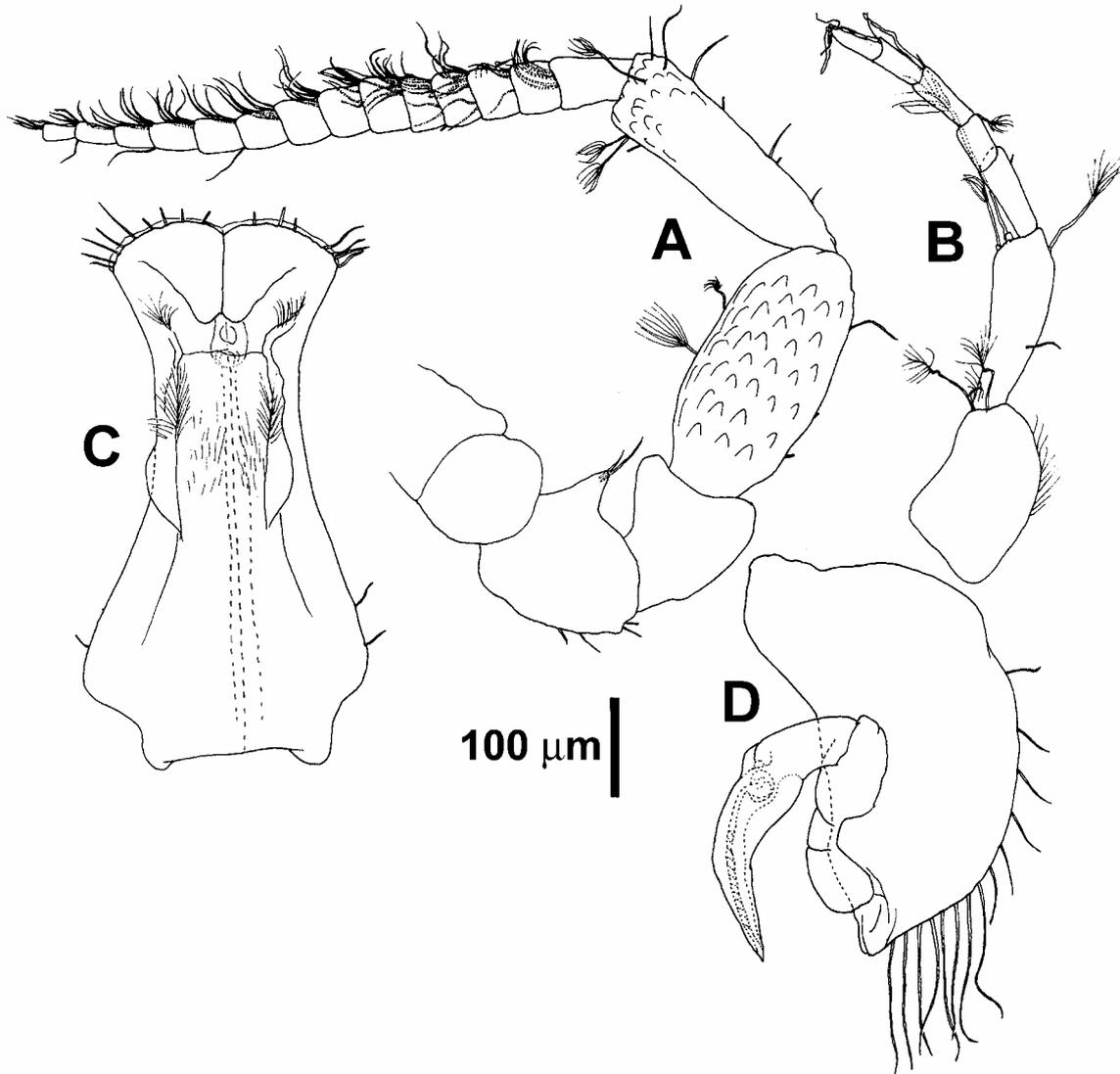


Figure 3.66: *Haploniscus cassilatus* n. sp., paratype, male, 3.9 mm: A antenna 2; B antenna 1; C pleopod 1; D pleopod 2.

Mandible (Fig. 3.63) incisor with five blunt teeth, *lacinia mobilis* of left mandible with five teeth, right mandible with stout serrated spine-like seta instead, spine row comprising 2 serrated and 4 simple spine-like setae; molar tooth row with about 7 teeth and 8 setulated setae proximally, cuticular ledge tapering off forming a tooth on both sides, right mandible with row of 6 accessory teeth proximally of cuticular ledge; palp article 2 with 3 serrated spine-like setae proximally of insertion of article 3, article 3 with 10 serrated spine-like setae of increasing length.

Maxilla 1 (Fig. 3.62) outer lobe with 7 simple and 5 serrated spine-like setae and several simple setae on lateral and medial margin and surface; inner lobe apically with several stout simple setae.

Maxilla 2 (Fig. 3.62) outer lobe with 2 long and 2 short simple spine-like setae apically several simple setae on lateral margin; medial lobe with 2 long and 1 shorter simple spine-like setae and 1 serrated seta apically, medial margin with 6 spine-like setae; inner lobe with 2 apical serrated spine-like setae, 3 stout apical simple setae and numerous simple setae on surface and medial margin.

Maxilliped (Fig. 3.62) endite apical margin with 3 small fan setae and 2 short spine-like setae, ventral surface with numerous simple setae, separated apical medial margin dorsally with 1 simple spine-like seta 1 serrated spine-like seta and row of simple setae, medial margin with 4 retinacula; epipod slightly longer than endite.

Pereopods (Figs 3.63-3.65): Basis with 3-4 long simple seta ventrally, basis of P2-6 with 1-2 broom setae dorsally. Ischium with 3 simple setae ventrally and dorsally (some broken off in type specimen). Merus with 3-4 setae apically and 1 simple setae ventrally, P5-7 with apical ventral flagellate seta, ventral seta on P5-7 spine-like. Ventral comb-like scale rows of carpus and propodus spinose; carpus with 1-3 flagellate setae and several simple setae, apical flagellate seta on P5 and 6; apical comb on carpus of P1 small and setose, apical combs on P2-7 comprised of 1 small and 1 larger spinose comb. Propodus with 2-6 simple setae ventrally, P5-7 with 2-3 flagellate spine-like seta ventrally, P1-4 with mediodorsal simple seta. Dactylus with 3 lateral setae; accessory tooth acute.

Pleopods (Figs 3.65): Plp 2 subcircular, with more than 40 setae on distal and lateral margins, longest setae on distal margin. Plp3 endopod 1.6 times as long as wide, with rounded distal margin; exopod small, as 1.8 times as long as wide, 0.4 times as wide and half as long as endopod, lateral margin rounded, with 6 simple setae and fringe of fine bristles. Plp4 endopod 1.6 times as long as wide; exopod 4.4 times as long as wide, 0.6 times as long and 0.2 times as wide as endopod, lateral margin rounded with fringe of long bristles, plumose seta slightly longer than exopod. Plp5 1.6 times as long as wide.

Uropods (Fig.3.61) not reaching terminal margin.

Description of male

The male (Fig. 3.61, 3.66, 3.99) differs from the female in the following characters:

Antenna 2 (Fig. 66) more stout, with more than 14 flagellar articles, flagellar articles with more setae.

Plp1 (Fig. 3.66) 1.9 times as long as wide, broadest part in the proximal quarter, 1.9 times broader than narrowest part, lateral margins with 2 simple setae, distal margins with about 9 setae each, sympods distal margin continuous, ventral surface with mediolateral bulges covered with numerous bristles, transverse grooves in the distal third with several bristles. Plp2 (Fig. 3.66) basipod 2.1 times as long as wide, with several simple setae on lateral and distal margin; endopod inserting in distal half of basipod, short, stout, as long as basipod, article 2 about 3 times as long as article 1, expanding in the medial part, sperm duct reaching from endopod tip almost to proximal third of article 2, exopod small, inserting in the distal third of basipod.

3.1.2.4.2 *Haploniscus cucullus* n. sp.

(Figs 3.67-3.73, 3.99)

Material

Holotype: subadult male, 5.3 mm; station 43-8, 60°27.13-27.19'S 56°05.12-04.81'W, 4782 m depth, ZMH K40758.

Paratypes: same locality as holotype: 1 ovigerous female, 5.4 mm; 1 female, 2.8 mm; 1 juvenile, 2.2 mm; ZMH K40759. Station 42-2, 59°40.30-40.32'S 57°35.42-42.64'W, 3689 m depth: 1 ovigerous female, 5.9 mm; 3 females, 3.4-3.6 mm; 8 juveniles, 3.3-3.6 mm; ZMH K40760.

Etymology

The name refers to the cap-like rostrum that is extra ordinary large in this species; the Latin *cucullus* means “cap” or “hood”.

Diagnosis

Body oval, about 3 times as long as wide. Head about 2.5 times as wide as long, frontal margin concave, with prominent rostrum; rostrum covered with small tubercles, with dorsal depression and acute upturned frontal tooth, a deep ventral indentation between rostrum and frontal margin of head. Pereonites 3-5 broadest. Lateral margins of pleotelson convex basally, concave distally, posterolateral processes short, not reaching terminal margin; dorsal surface of pleotelson with 2 sharp longitudinal keels, ventral surface with cuticular bulge surrounding the branchial chamber and tapering towards anus. Antenna 1 with 4 flagellar articles.

Maxilliped with 3 retinacula. Carpus of P1-4 with 3-4 ventral flagellate setae, P5-7 with 4-6 ventral flagellate setae, apical and ventral combs of carpus spinose, carpus of P5 and 6 with dorsal flagellate seta.

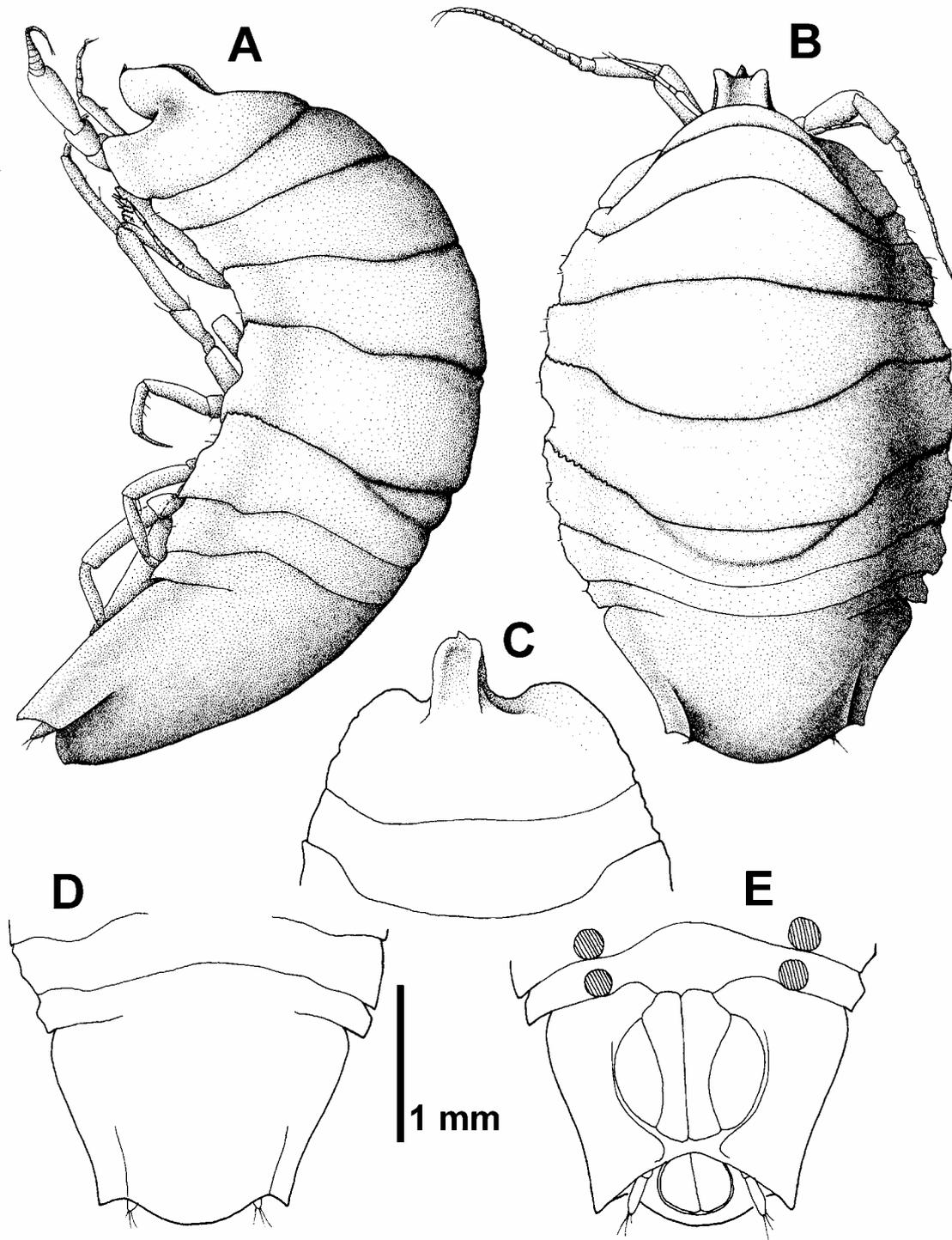


Figure 3.67: *Haploniscus cucullus* n. sp., holotype, male, 5.3 mm: A lateral view; B dorsal view; C anterior body, dorsal view; D posterior body, dorsal view; E posterior body, ventral view.

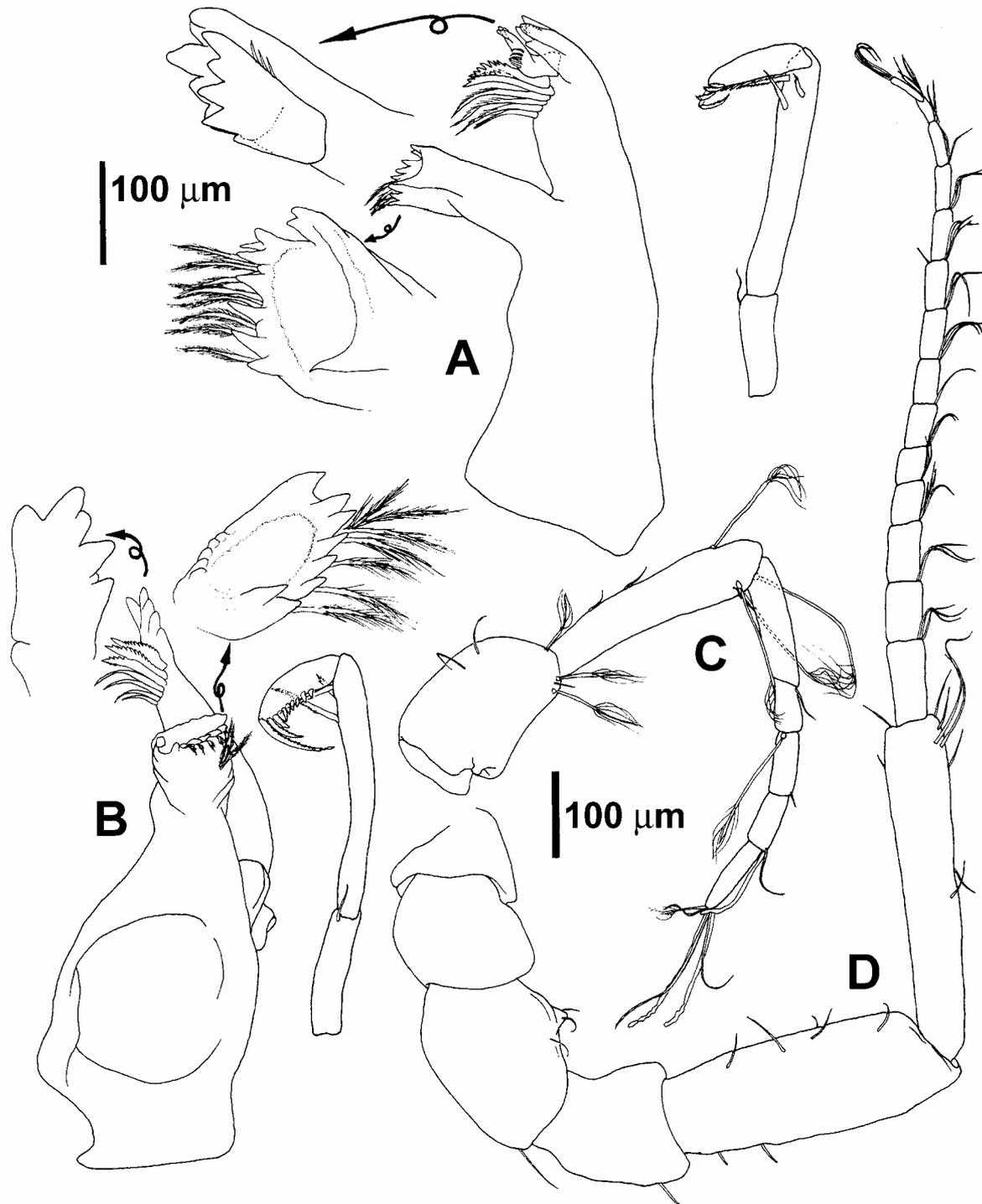


Figure 3.68: *Haploniscus cucullus* n. sp., paratype, female, 5.4 mm: A left mandible; B right mandible; C antenna 1; D antenna 2.

Description of female

H. cucullus differs from *H. cassilatus* in the following characters:

Rostrum (Fig. 3.72) slightly larger, less tapering distally, curved slightly stronger dorsally in lateral view.

Pleotelson (Fig. 3.72) lateral margin convex in basal half, concave in distal half, posterolateral processes slightly longer.

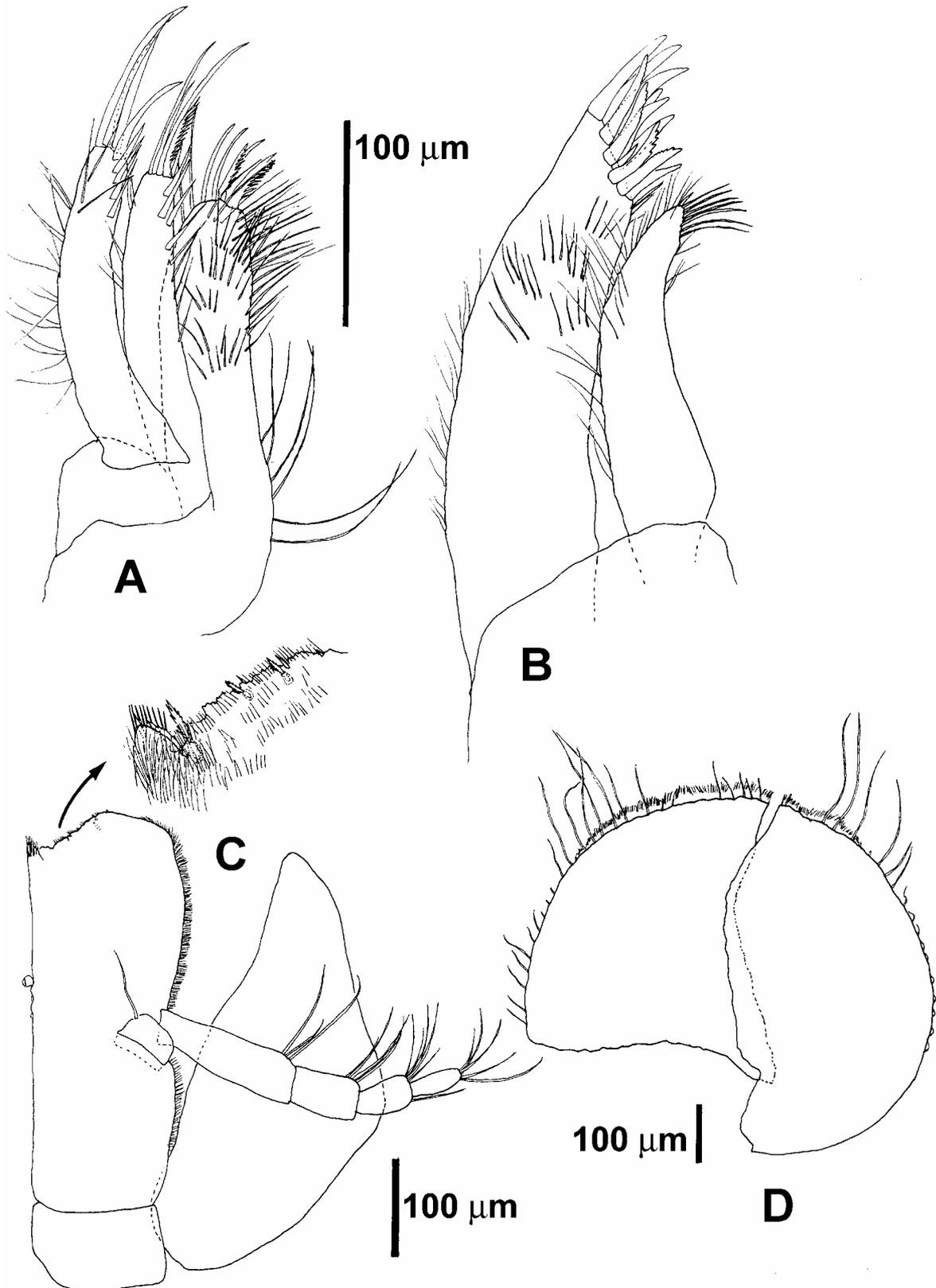


Figure 3.69: *Haploniscus cucullus* n. sp., paratype, female, 5.4 mm: A maxilla 2; B maxilla 1; C maxilliped; D pleopod 2.

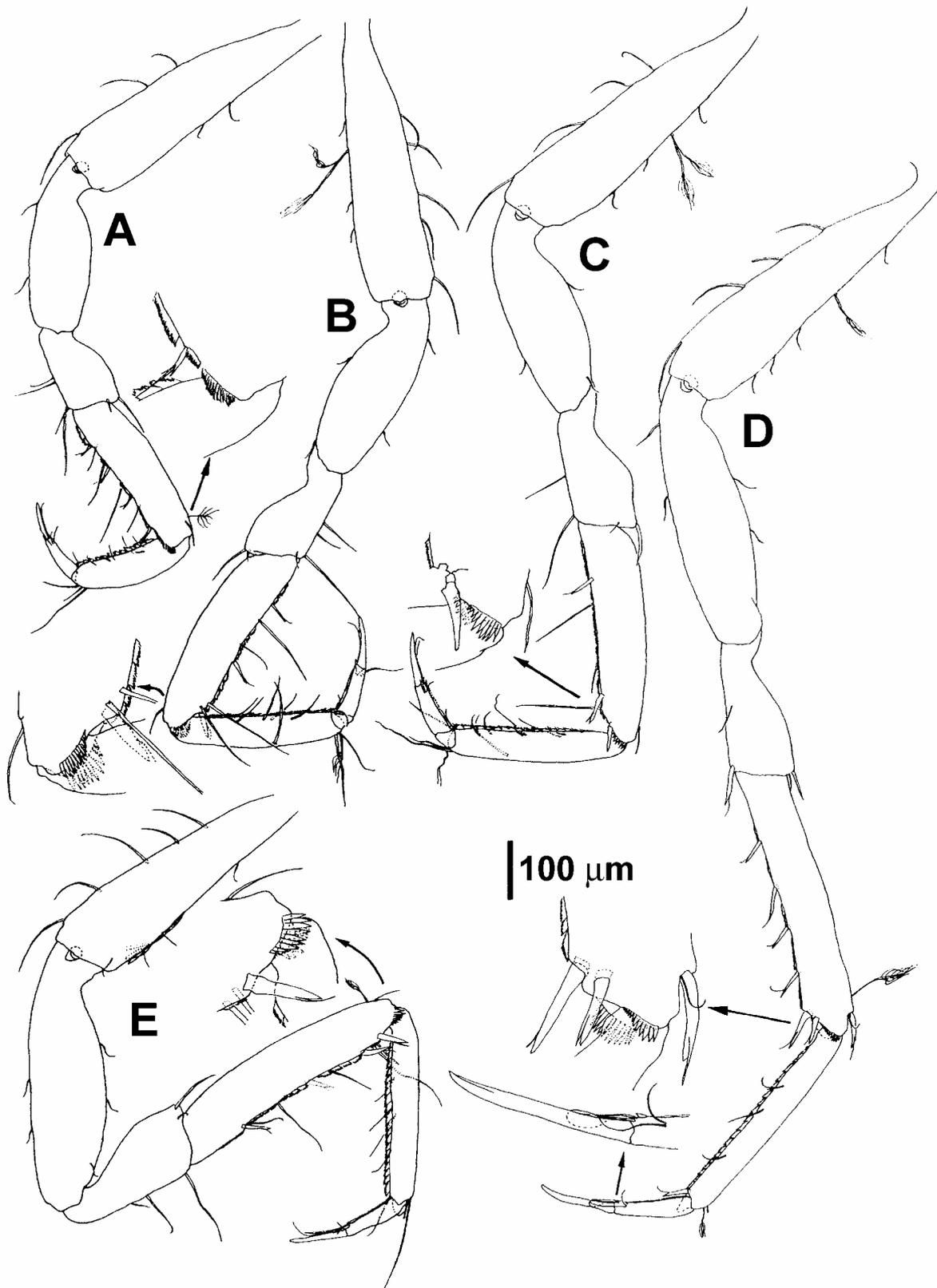


Figure 3.70: *Haploniscus cucullus* n. sp., paratype, female, 5.4 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pereopod 5; E pereopod 4.

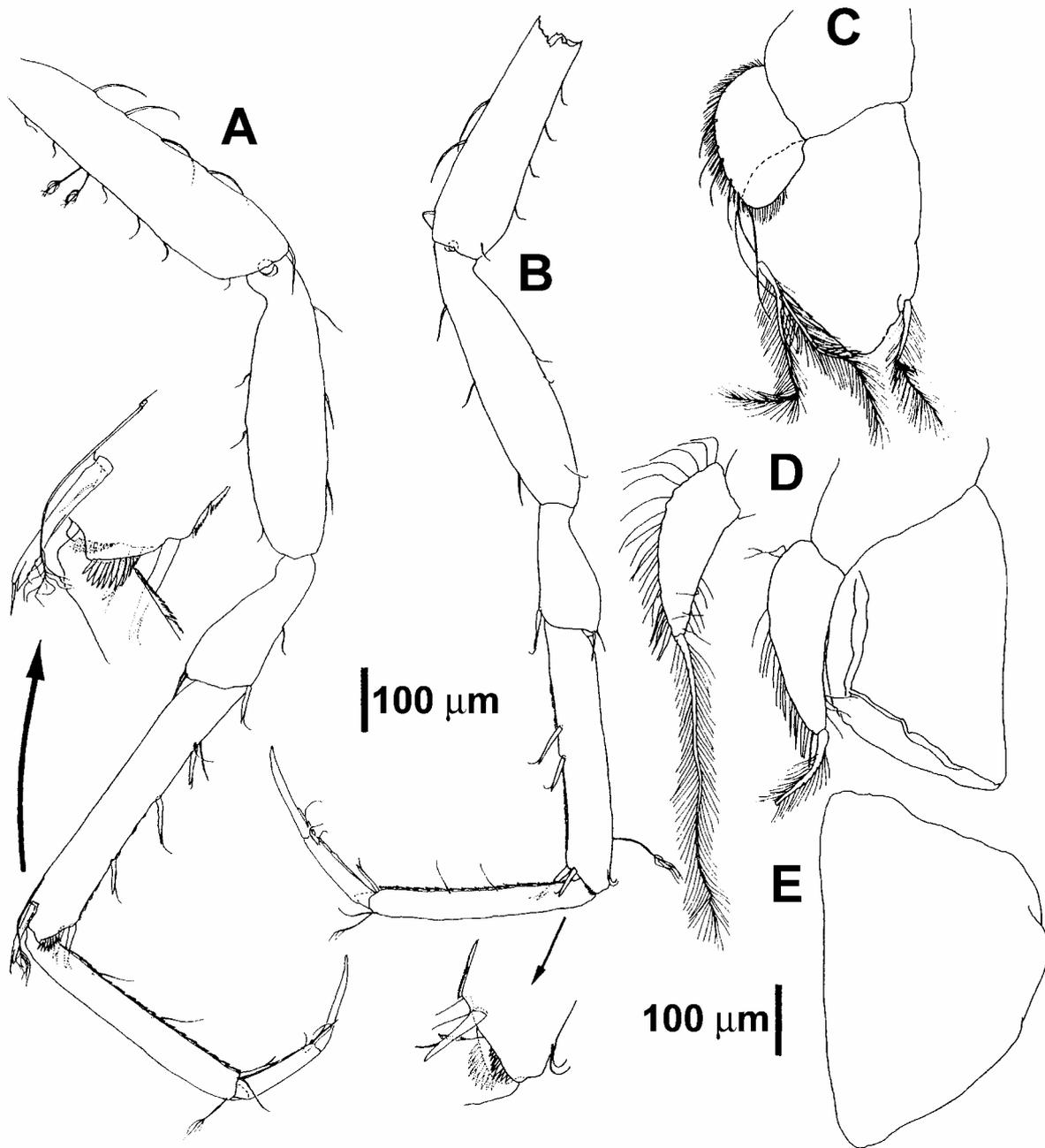


Figure 3.71: *Haploniscus cucullus* n. sp., paratype, female, 5.4mm: A pereopod 6; B pereopod 7; C pleopod 3; D pleopod 4; E pleopod 5.

Mandibular (Fig. 3.68) palp article 3 with about 10 serrated spines.

Maxilliped (Fig. 3.69) with 3 retinacula. Pereopods (Figs 3.70, 3.71): Basis with 3-5 ventral setae. Merus with 1-2 medioventral simple setae on P5-7. Carpus of P1-4 with 3-4 ventral flagellate setae, P5-7 with 4-6 ventral flagellate setae.

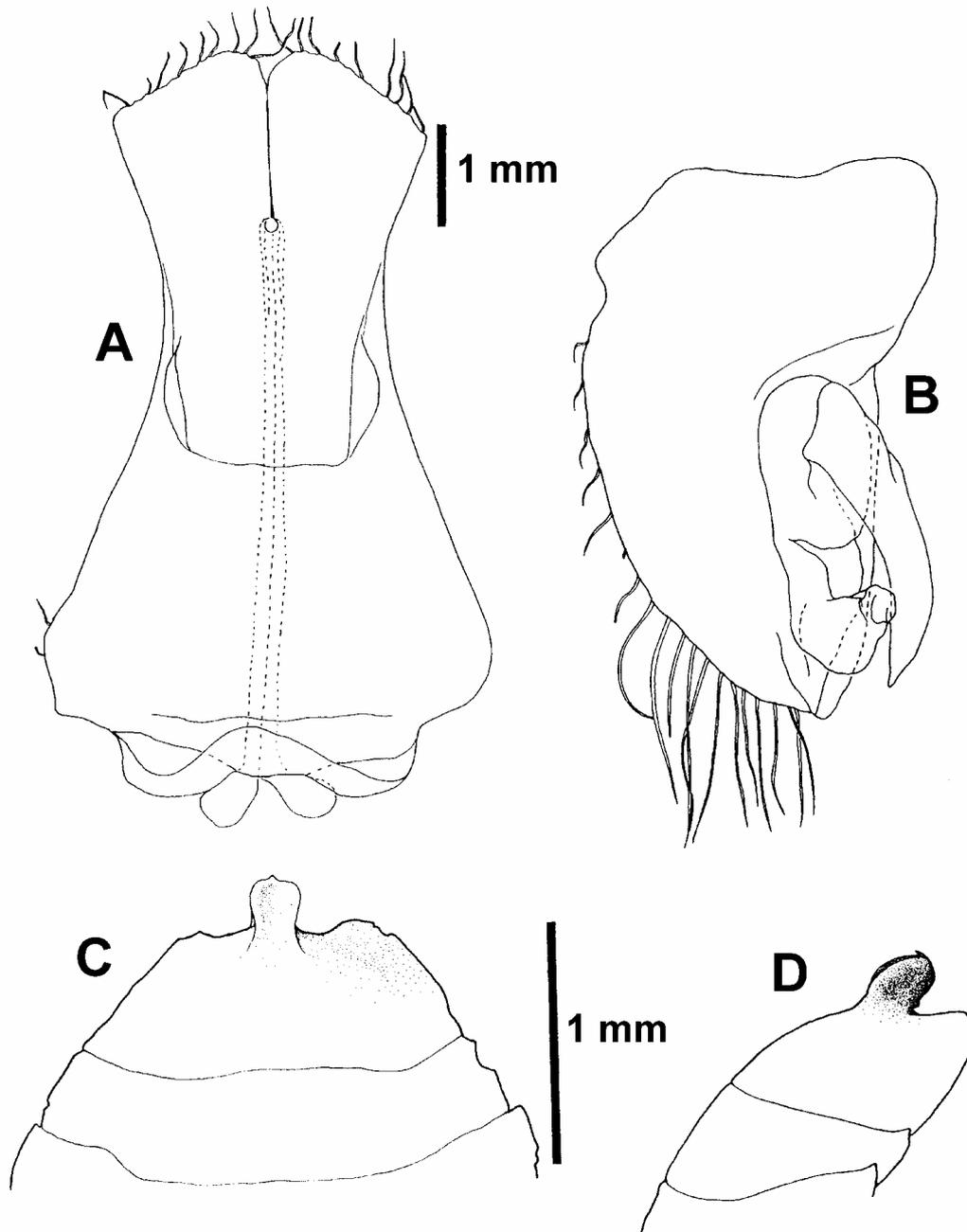


Figure 3.72: *Haploniscus cucullus* n. sp., holotype male, 5.3 mm: A pleopod 1; B pleopod 2; paratype female, 5.9 mm: C anterior body, dorsal view; D anterior body, lateral view.

Description of male

No adult males were found; the subadult male differs from the female in the following characters:

Pleopod 1 (Fig. 3.72) similar to that of *H. cassilatus*, but lacking the transversal grooves on the dorsal surface, due to immaturity. Penes present. Pleopod 2 sperm duct not developed.

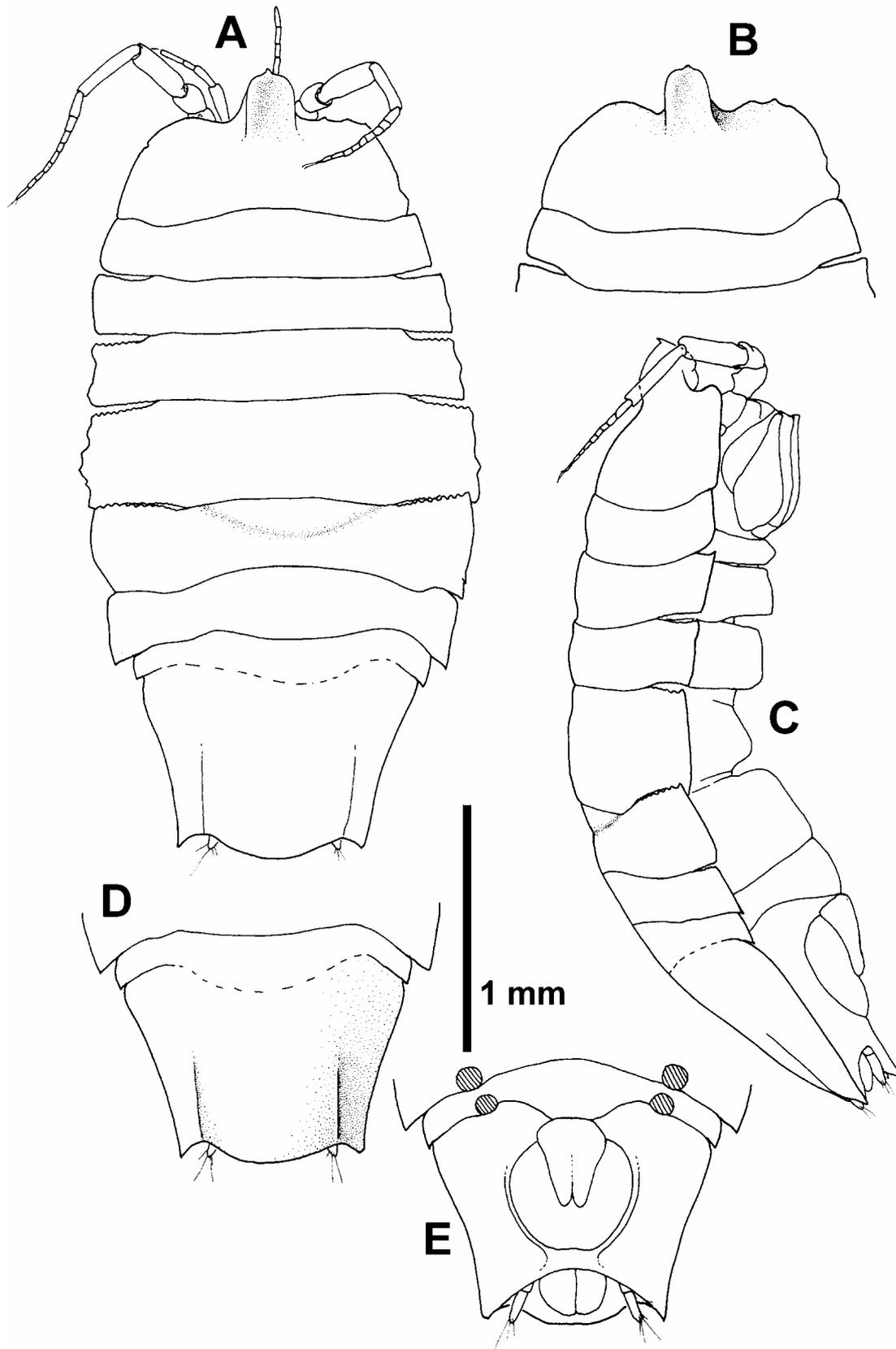


Figure 3.73: *Haploniscus cucullus* n. sp. paratype, juvenile male, 3.6 mm: A dorsal view; B anterior body, dorsal view; C lateral view (pereopods omitted); D posterior body, dorsal view; posterior body, ventral view.

3.1.2.4.3 *Haploniscus weddellensis* n. sp.

(Figs 3.74-3.78, 3.99)

Material

Holotype: male, 3.0 mm; station 133-3, 65°20.17-20.08'S 54°14.30-14.34'W, 1314 m depth, ZMH K40761.

Paratypes: same locality as holotype: 16 males, 2.6-3.0 mm; 3 ovigerous females 3.5-4.2 mm; 9 females, 2.3-2.9 mm; 11 juveniles, 1.2-2.3 mm; ZMH K40762.

Etymology

Named after the type locality in the Weddell Sea.

Diagnosis

Body oval, about 3 times as long as wide. Head about 2.5 times as wide as long, frontal margin concave, with prominent rostrum; rostrum covered with small tubercles, with shallow dorsal depression and acute upturned frontal tooth, a deep ventral indentation between rostrum and frontal margin of head. Pereonites 3-6 broadest. Lateral margins of pleotelson convex basally, concave distally, posterolateral processes exceeding terminal margin slightly; dorsal surface of pleotelson with 2 sharp longitudinal keels, ventral surface with cuticular bulge surrounding the branchial chamber and tapering towards anus. Antenna 1 with 4 flagellar articles. Carpus of P1-4 with 2-4 ventral flagellate setae, P5-7 with 2-3 ventral flagellate setae, apical and ventral combs of carpus spinose, carpus of P6 with dorsal flagellate seta.

Description of female

H. weddellensis differs from *H. cassilatus* in the following characters:

Rostrum (Fig. 3.75) shorter and broader, dorsal depression shallow. Pereonites 3-6 broadest. Pleotelson (Fig. 3.75) lateral margins convex basally, concave distally, posterolateral processes longer, exceeding terminal margin slightly.

Mandibular palp with about 8 serrated setae.

Carpus with 2-4 ventral flagellate setae, only carpus of P6 with dorsal flagellate seta.

Description of male

Pleopods 1 and 2 (Fig. 3.77) are more or less identical with the pleopods of *H. cassilatus*.

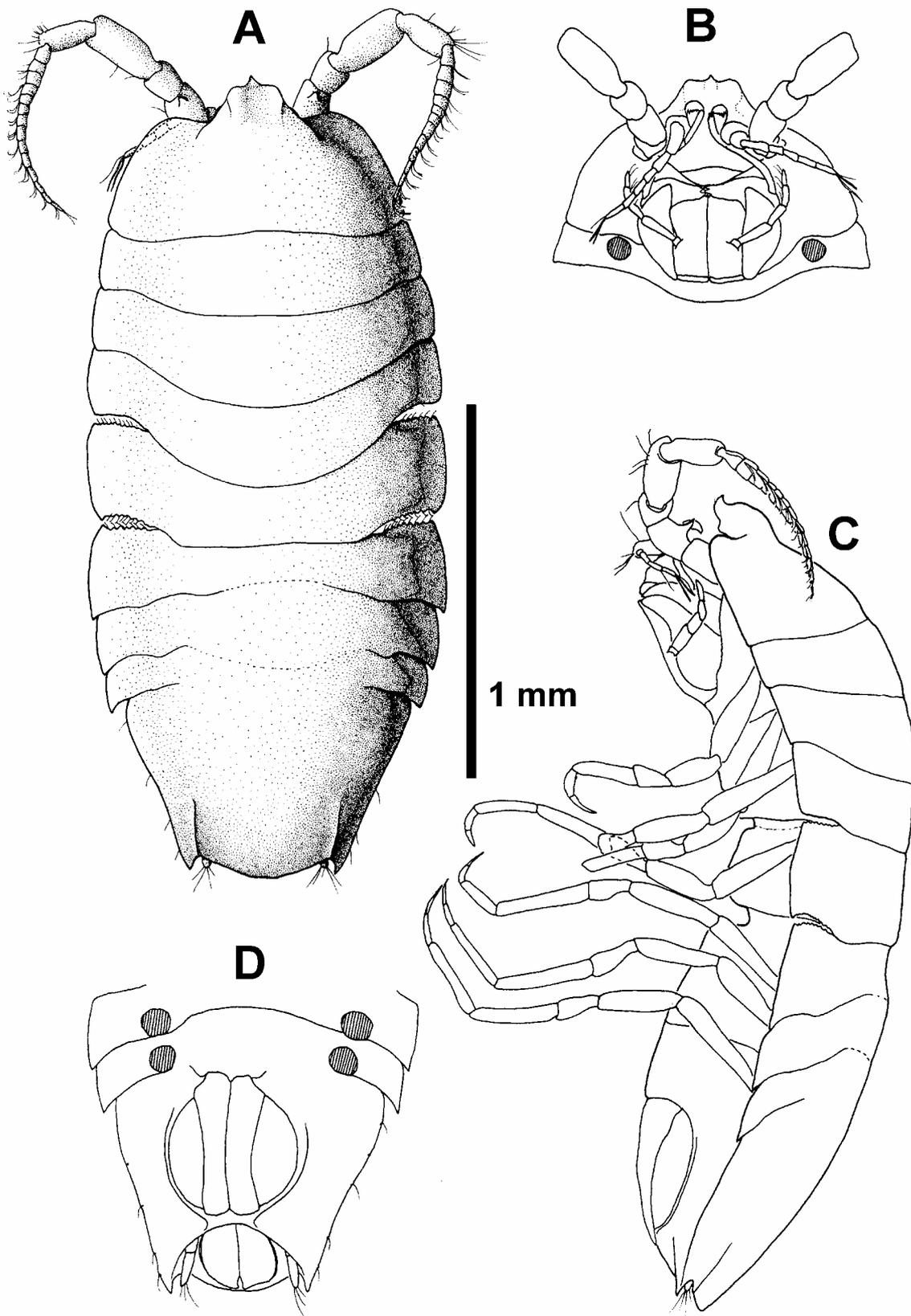


Figure 3.74: *Haploniscus weddellensis* n. sp., holotype, male, 3.0 mm: A dorsal view; B anterior body ventral view; C lateral view; D posterior body, ventral view.

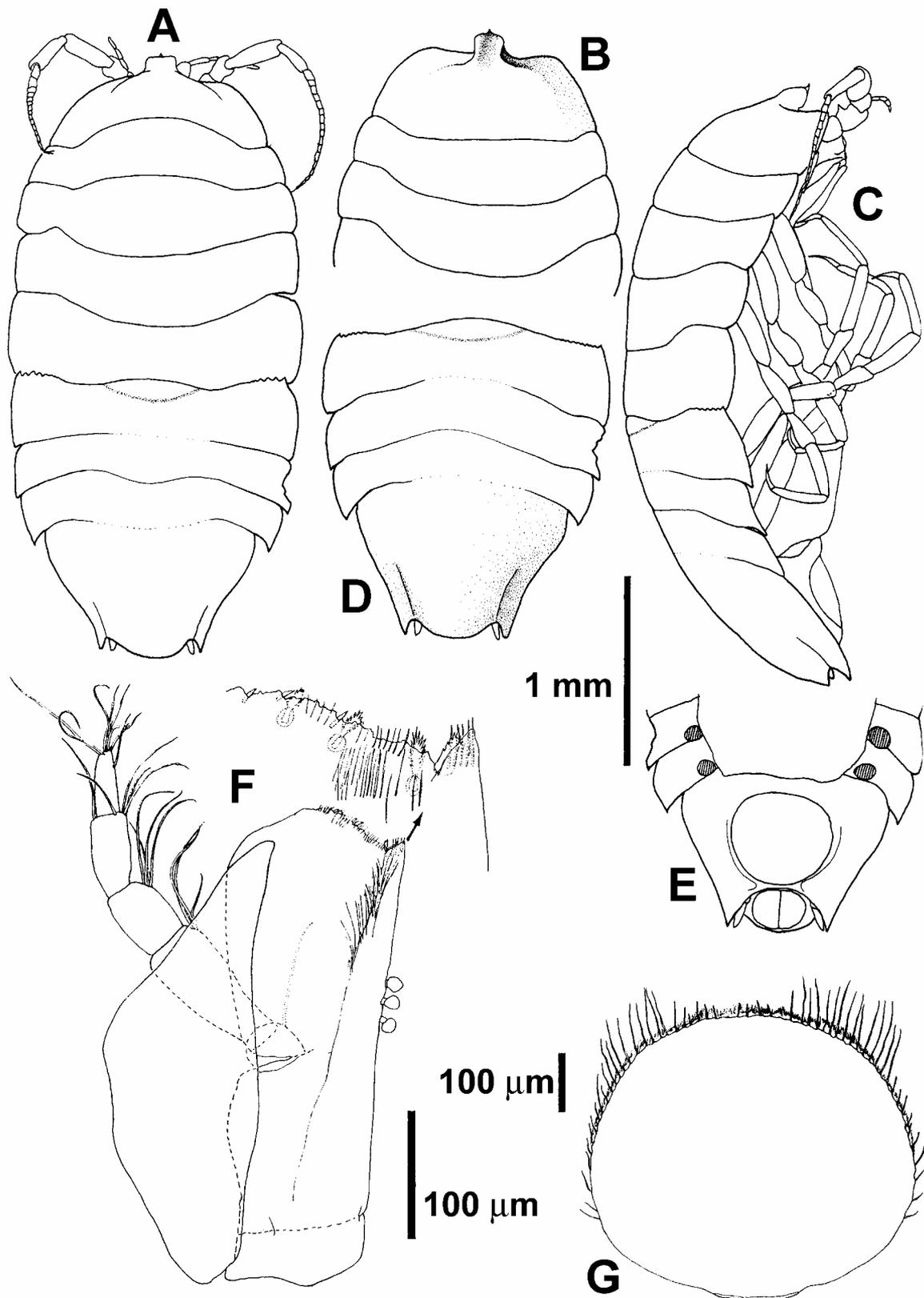


Figure 3.75: *Haploniscus weddellensis* n. sp., paratype, female, 4.2 mm: A dorsal view; B anterior body, dorsal view; C lateral view; D posterior body, dorsal view; E posterior body, ventral view; G pleopod 2; paratype, male, 2.8 mm: F maxilliped.

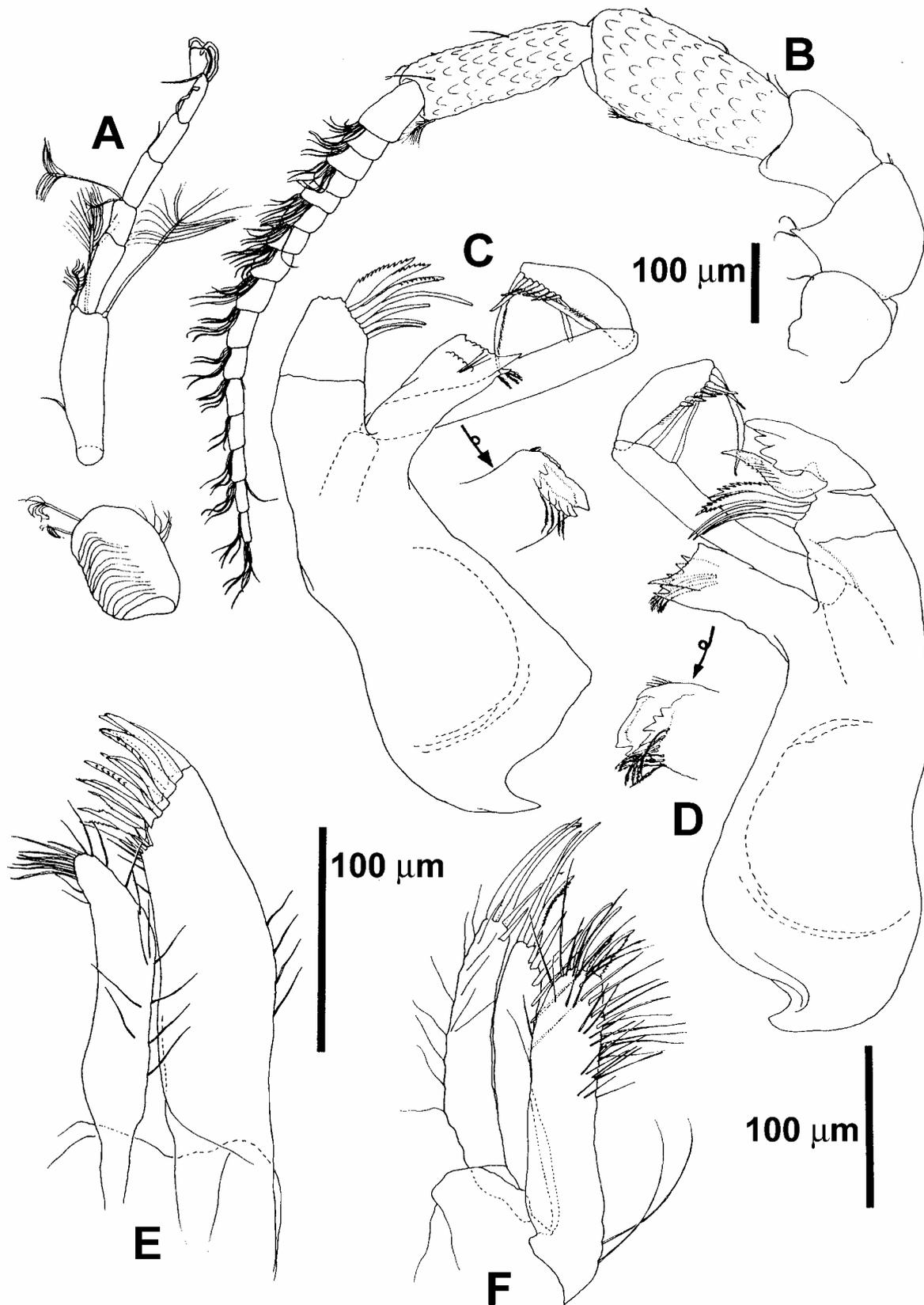


Figure 3.76: *Haploniscus weddellensis* n. sp., paratype, male, 2.8 mm: A antenna 1; B antenna 2; C right mandible; D left mandible; E maxilla 1; F maxilla 2.

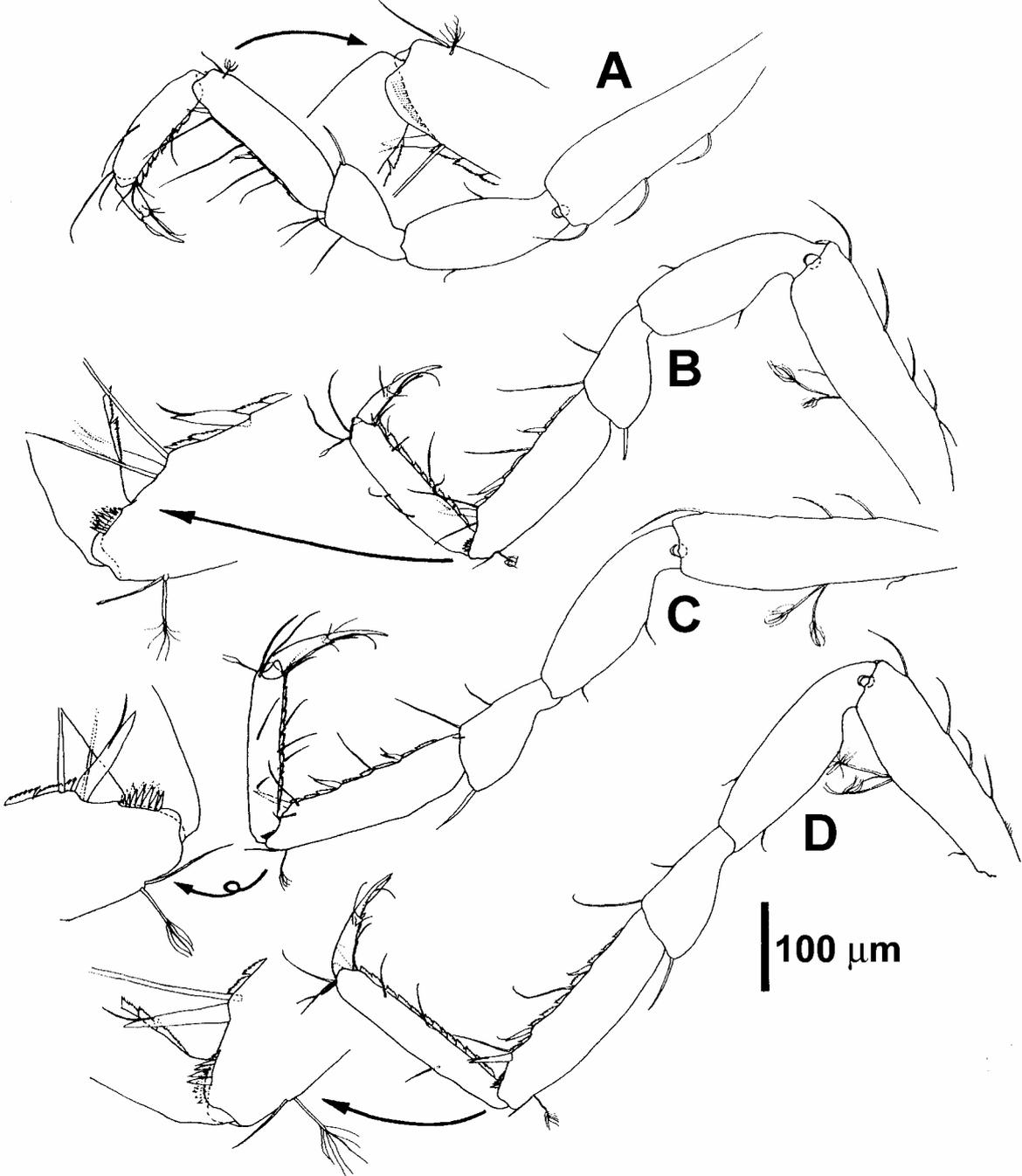


Figure 3.77: *Haploniscus weddellensis* n. sp., paratype, male, 2.8 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pereopod 4.

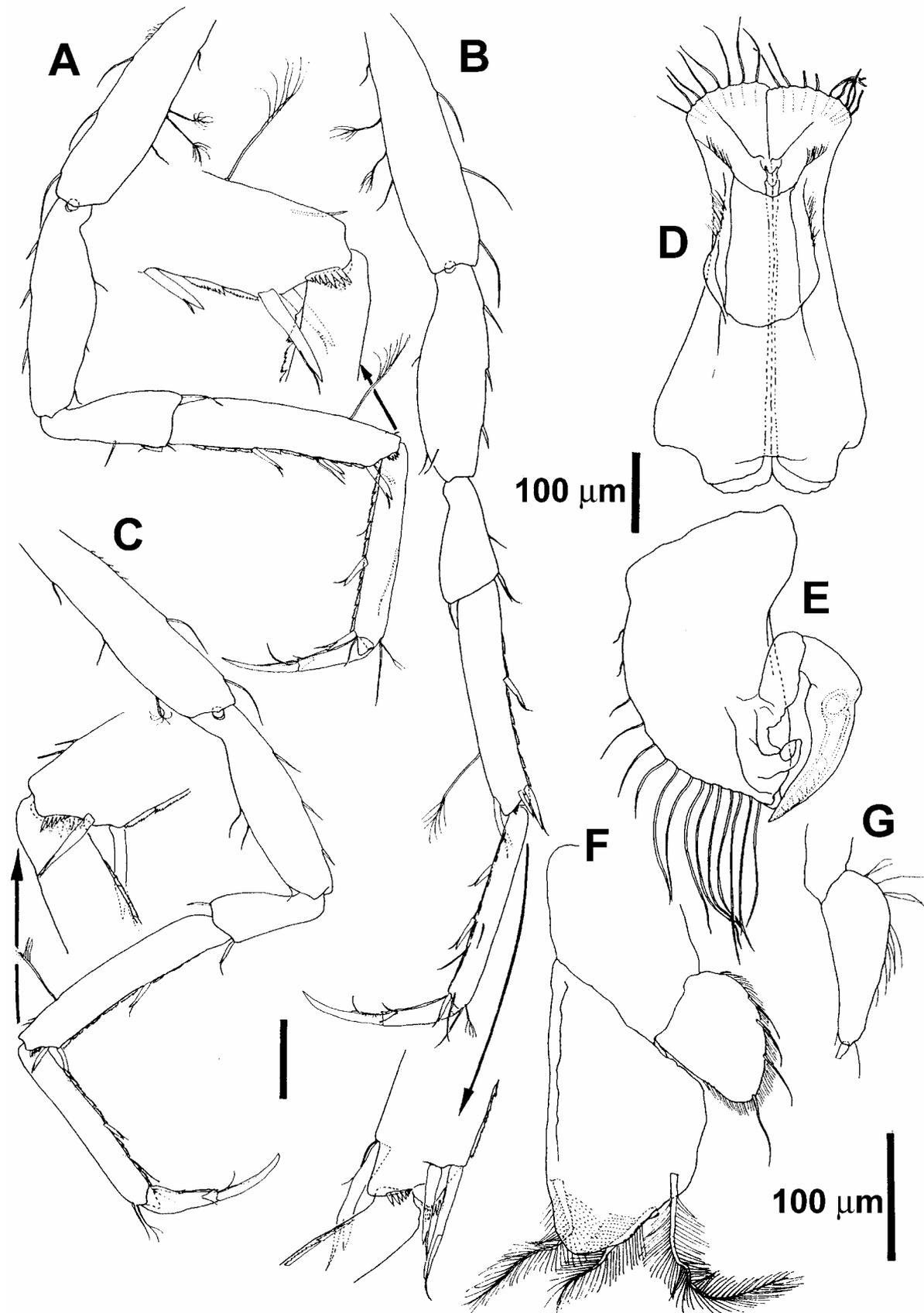


Figure 3.78: *Haploniscus weddellensis* n. sp., paratype, male, 2.8 mm: A pereopod 5; B pereopod 6; C pereopod 7; D pleopod 1; E pleopod 2; F pleopod 3; G pleopod 4, exopod.

3.1.2.4.4 *Haploniscus procerus* n. sp.

(Figs 3.79-3.84, 3.99)

Material

Holotype: female, 7.4 mm; station 131-3, 65°19.83-19.99'S 51°31.61-31.23'W, 3553 m depth; ZMH K40763.

Paratype: same locality as holotype: one female, 7.6 mm; ZMH K40764.

Etymology

The name refers to the rostrum that is elongated in this species; the Latin term *procerus* means “large”, “slender”, “long”.

Diagnosis

Body oval, about 3 times as long as wide. Head about 2.5 times as wide as long, frontal margin concave, with prominent rostrum; rostrum covered with small tubercles, with dorsal depression and acute upturned frontal tooth, a deep ventral indentation between rostrum and frontal margin of head. Pereonites 3-6 broadest. Lateral margins of pleotelson convex basally, concave distally, posterolateral processes exceeding terminal margin slightly; dorsal surface of pleotelson with 2 sharp, pronounced longitudinal keels, ventral surface with cuticular bulge surrounding the branchial chamber and tapering towards anus. Antenna 1 with 4 flagellar articles. Maxilliped with 3 retinacula. Carpus of P1-4 with 4-5, of P5-7 with 7-8 ventral flagellate setae, apical and ventral combs of carpus spinose, carpus of P5-7 with dorsal flagellate seta.

Description of female paratype

H. procerus differs from *H. cassilatus* in the following characters:

Rostrum slightly larger, less tapering, in lateral view curved slightly stronger dorsally.

Pereonites 3-6 broadest. Lateral margins of pleotelson convex basally, slightly concave distally, dorsal keels more pronounced, pleotelsonic processes exceeding terminal margin slightly.

Antenna 2 (Fig. 3.80) scales small, more numerous.

Mandibular (Fig. 3.80) palp with 12 serrated setae.

Maxilliped (Fig. 3.81) with 3 retinacula.

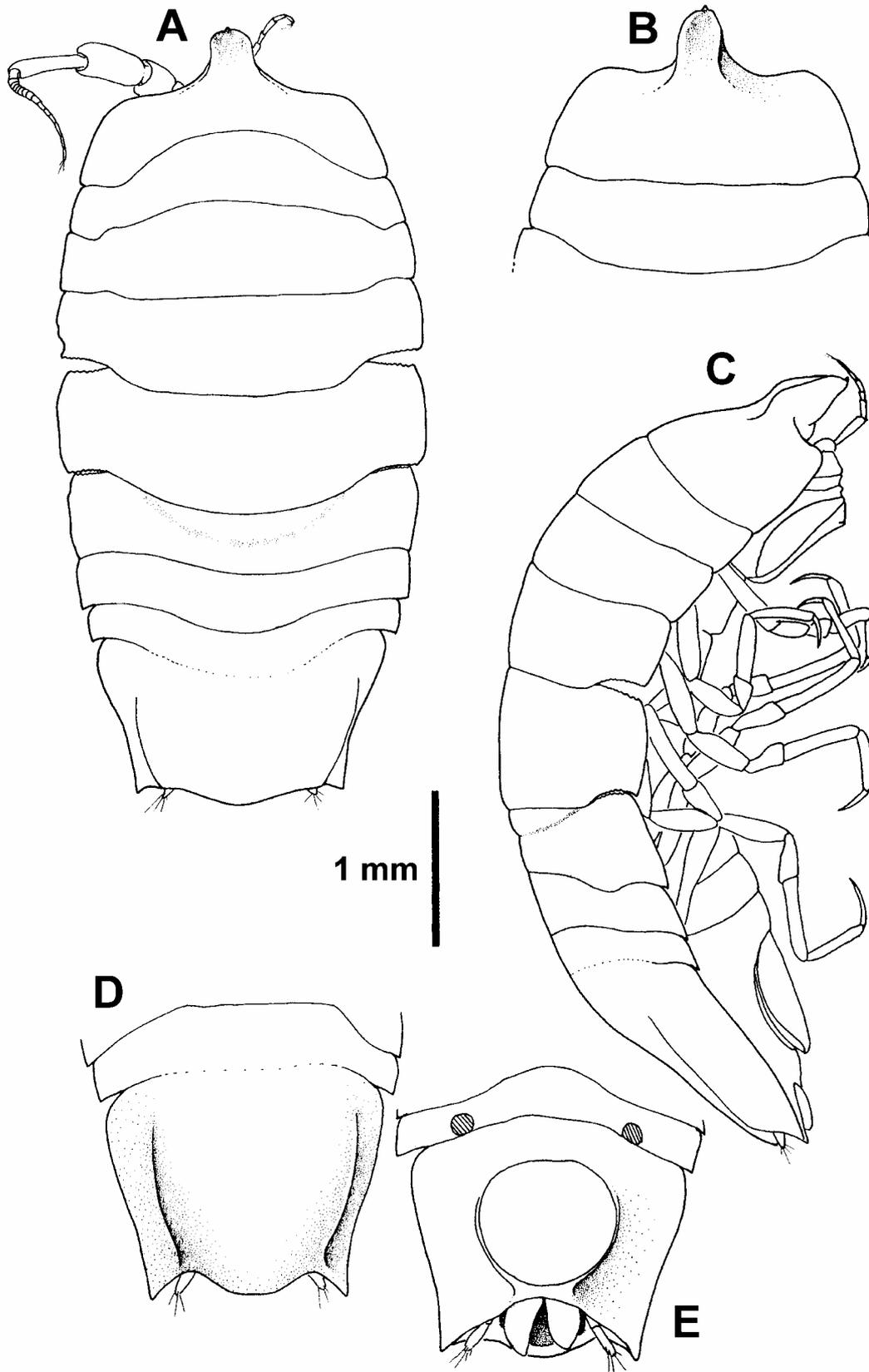


Figure 3.79: *Haploniscus procerus* n. sp., holotype, female, 7.4 mm: A dorsal view, B anterior body, dorsal view; C lateral view; D posterior body, dorsal view; E posterior body, ventral view.

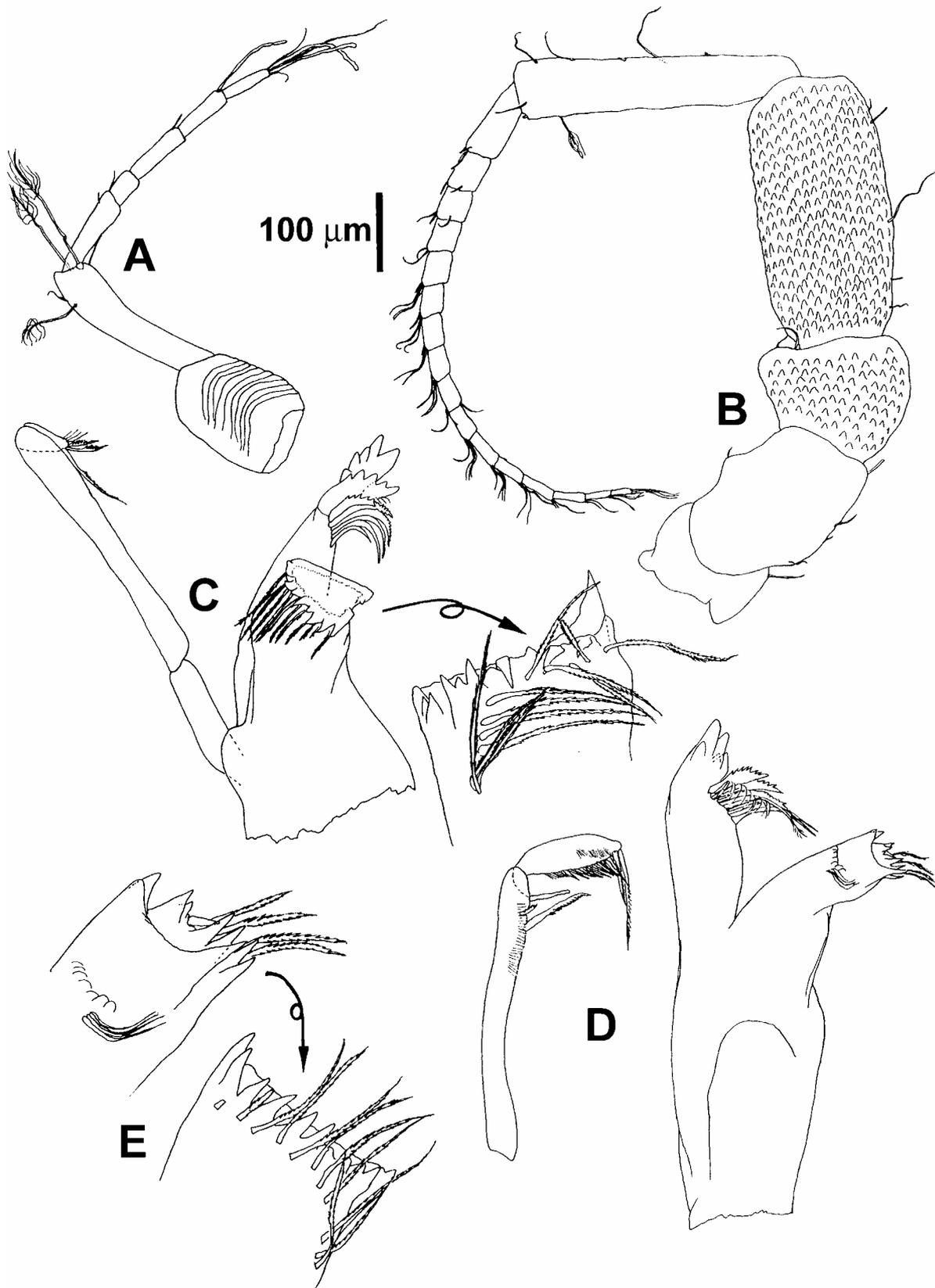


Figure 3.80: *Haploniscus procerus* n. sp., paratype, female, 7.6 mm: A antenna 1; B antenna 2; C left mandible; D right mandible; E right mandible, detail of molar process.

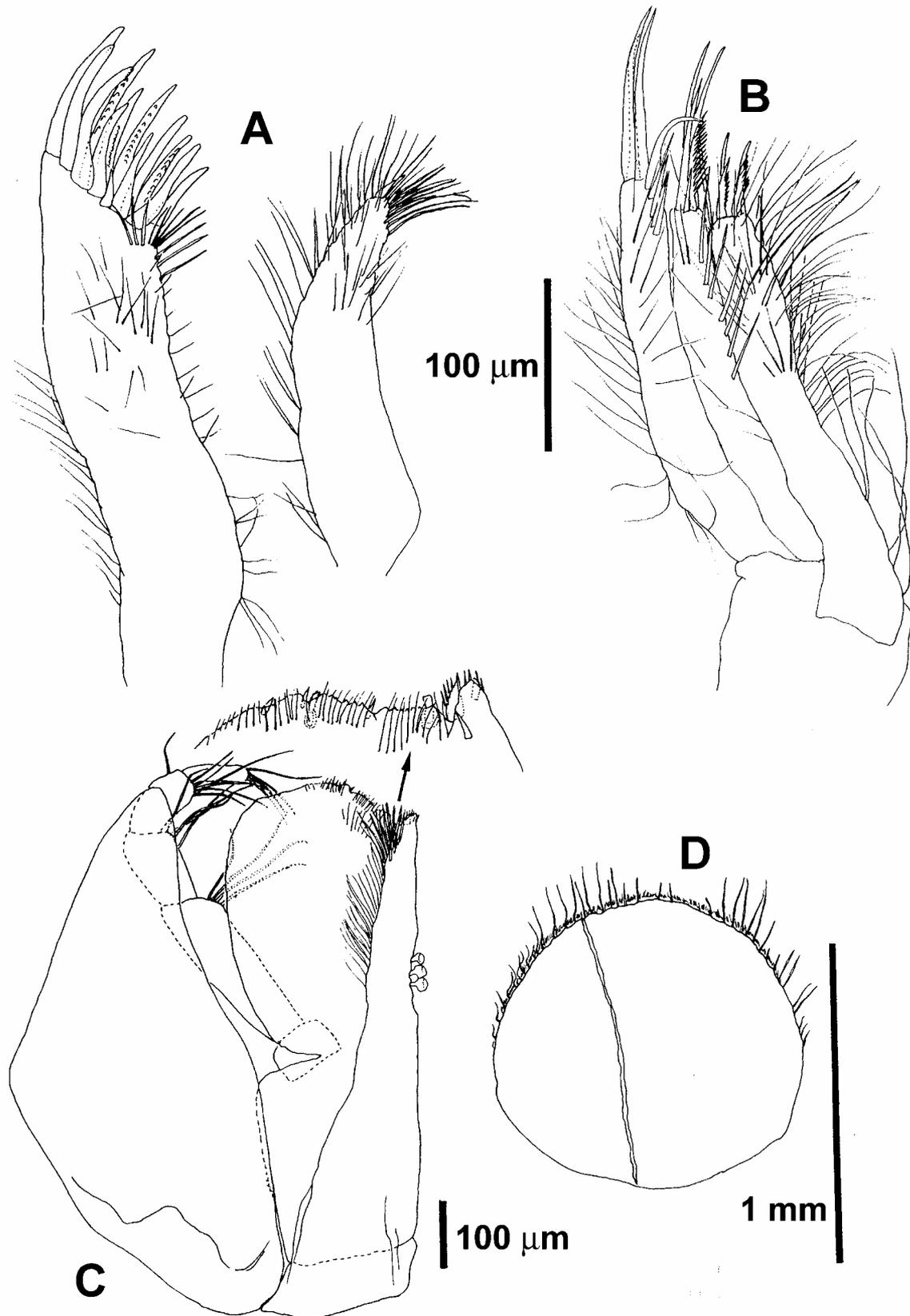


Figure 3.81: *Haploniscus procerus* n. sp., paratype, female, 7.6 mm: A maxilla 1; B maxilla 2; C maxilliped; D pleopod 2.

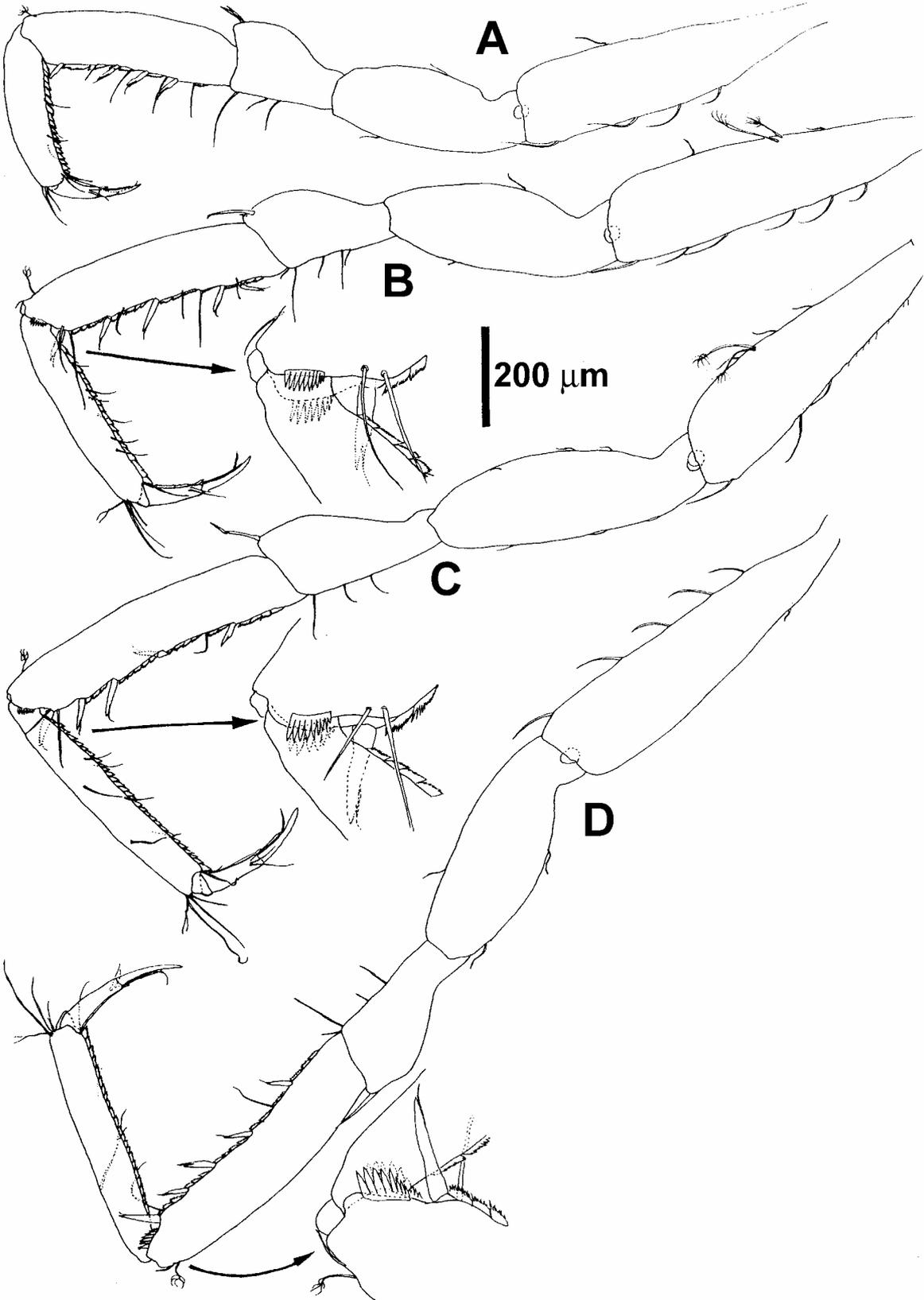


Figure 3.82: *Haploniscus procerus* n. sp., paratype, female, 7.4 mm: A pereopod 1; B pereopod 2; C pereopod 3; D pereopod 4.

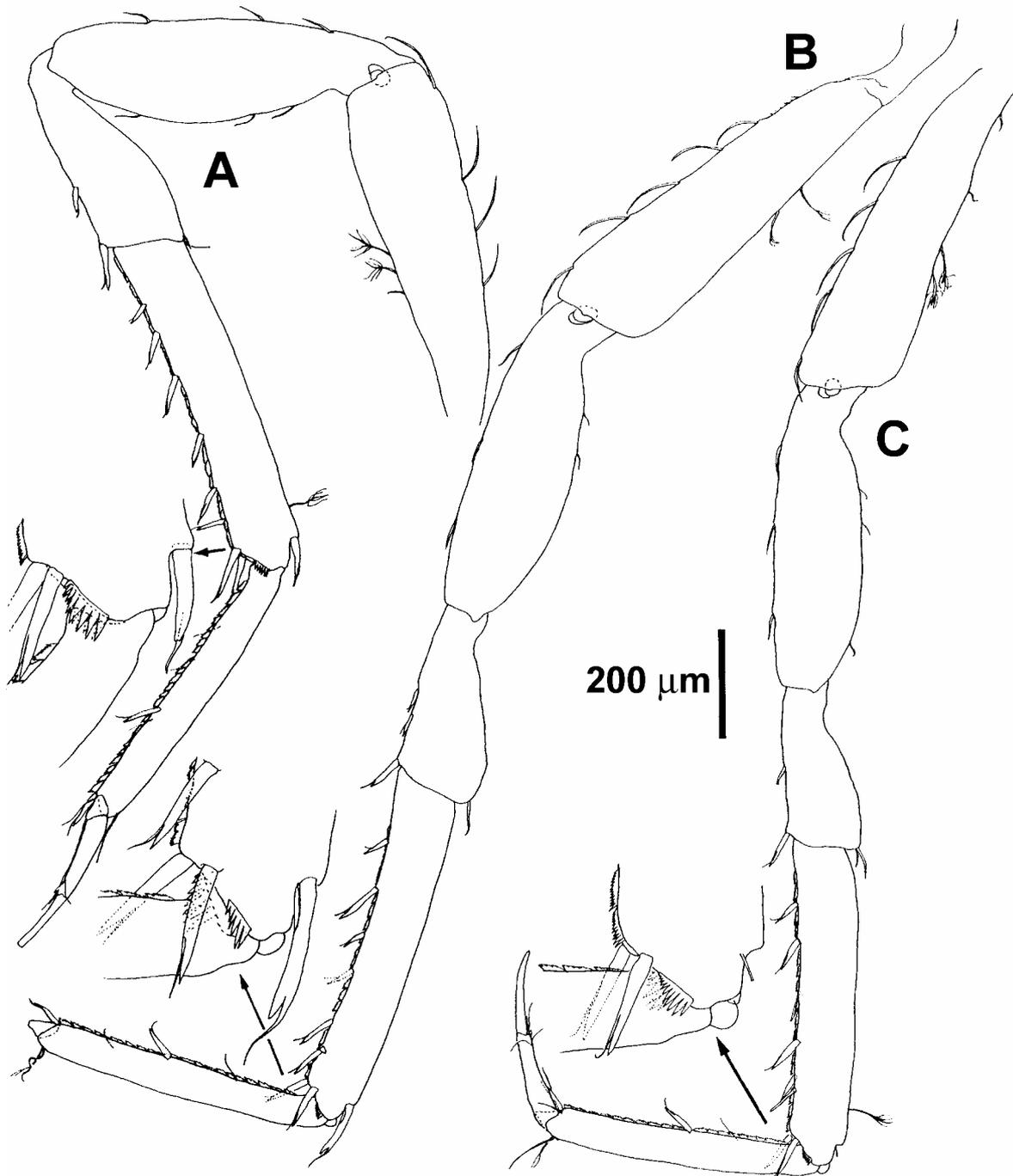


Figure 3.83: *Haploniscus procerus* n. sp., paratype, female, 7.4 mm: A pereopod 5; B pereopod 6; C pereopod 7.

Pereopods (Figs 3.82, 3.83): Basis with 4-6 setae ventrally. Merus of P1-4 with 2-3 simple medioventral setae, of P5-7 with 1-2 medioventral flagellate setae. Carpus of P1-4 with 4-5 ventral flagellate setae, of P5-7 with 7-8 ventral flagellate setae, dorsal apical flagellate seta on carpus of P5-7 (broken off on P7).

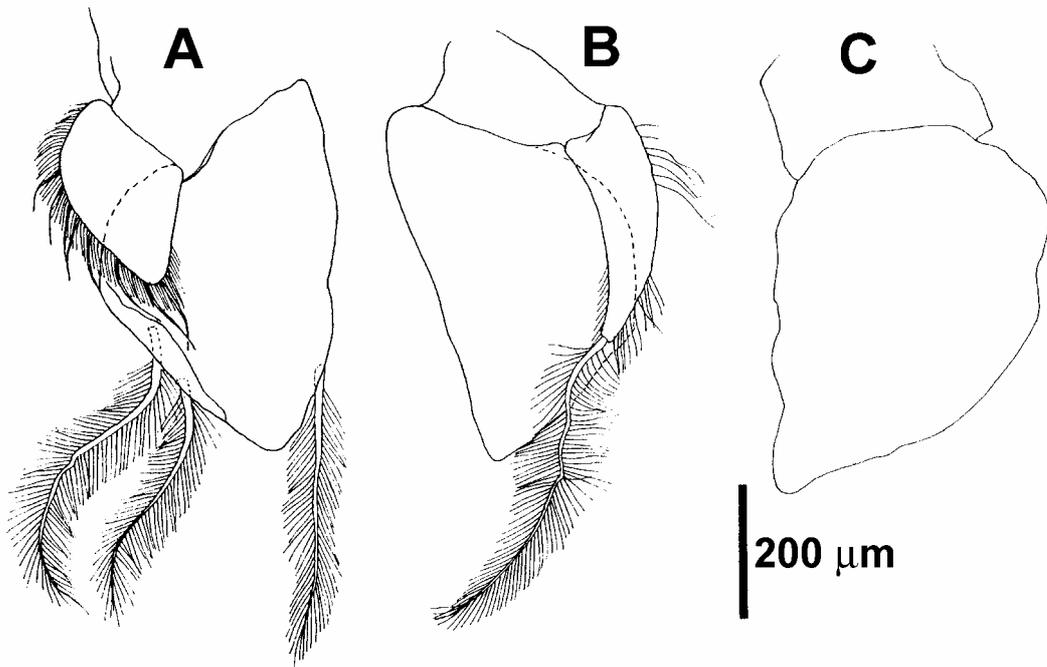


Figure 3.84: *Haploniscus procerus* n. sp., paratype female, 7.4 mm: A pleopod 3; B pleopod 4; C pleopod 5.

3.1.2.4.5 *Haploniscus kyrbasius* n. sp.

(Figs 3.85-3.90, 3.99)

Material

Holotype: male, 5.7 mm; station 141-10, 58°15.98-16.28'S 24°53.73-54.09'W, 4183 m depth; ZMH K40765.

Etymology

Kyrbasia is the name of a Persian hat with peaked crown; the name refers to the rostrum.

Diagnosis

Body oval, 3 times as long as wide. Head about 3.0 times as wide as long, frontal margin concave, with prominent rostrum; rostrum covered with small tubercles, with dorsal depression and acute upturned frontal tooth, a deep ventral indentation between rostrum and frontal margin of head. Pereonites 3-5 broadest. Lateral margins of pleotelson convex basally, concave distally, posterolateral processes short, not reaching terminal margin; dorsal surface of pleotelson with 2 sharp longitudinal keels, ventral surface with cuticular bulge surrounding the branchial chamber and tapering towards anus.

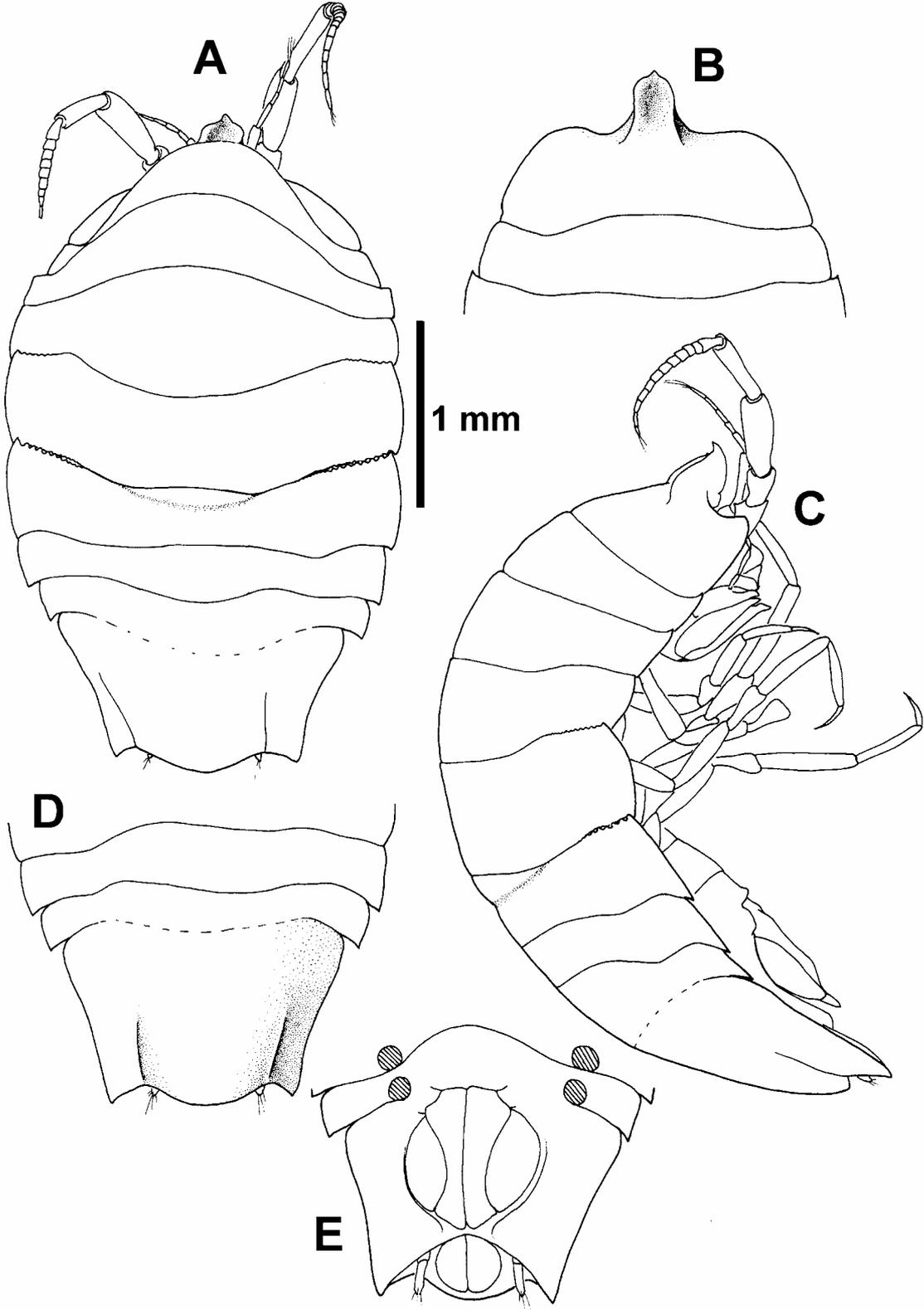


Figure 3.85: *Haploniscus kyrbasius* n. sp., holotype, male, 5.7 mm: A dorsal view; B anterior body, dorsal view; C lateral view; D posterior body, dorsal view; E posterior body, ventral view.

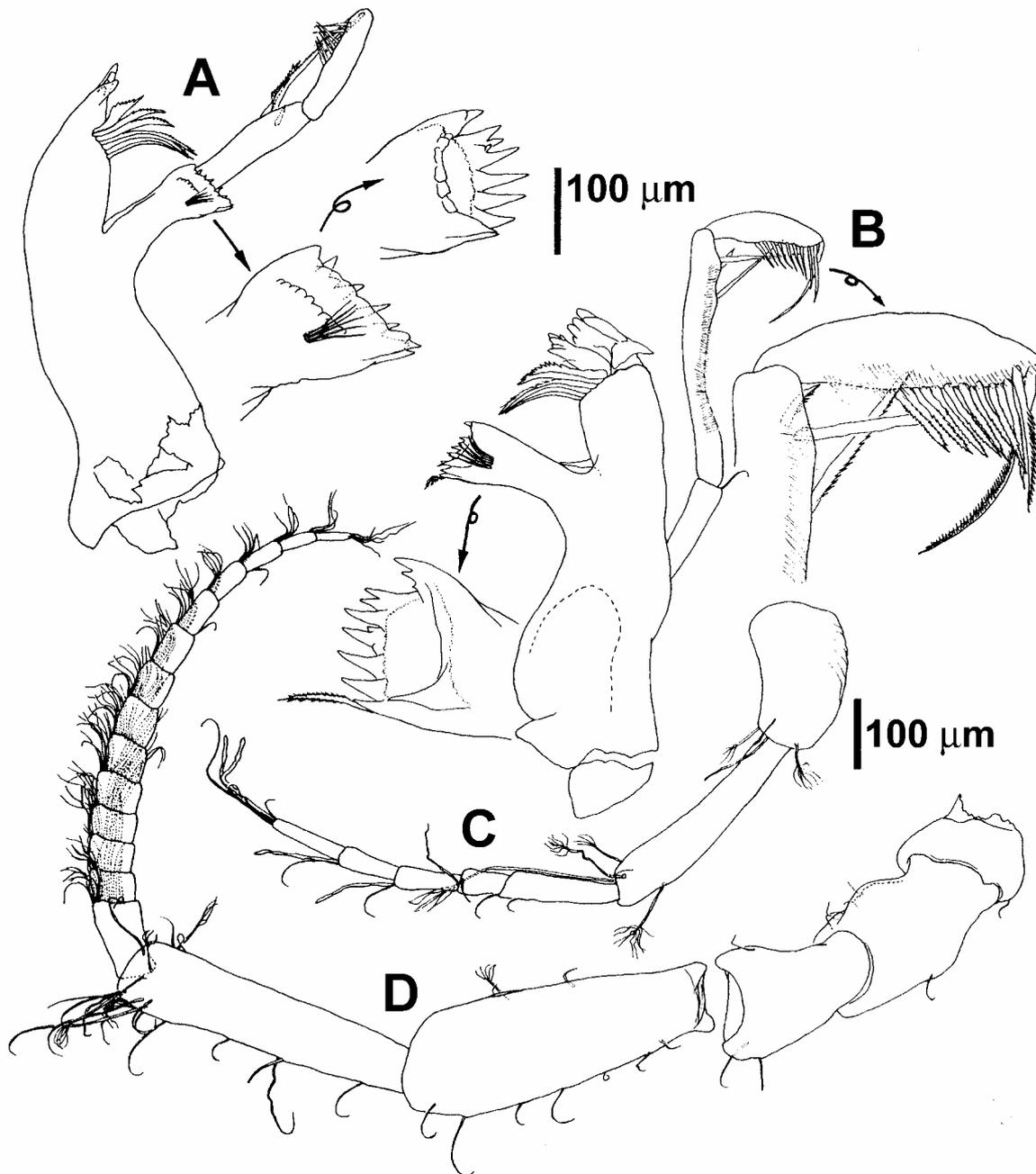


Figure 3.86: *Haploniscus kyrbasius* n. sp., holotype, male, 5.7 mm: A right mandible; B left mandible; C antenna 1; D antenna 2.

Antenna 1 with 4 flagellar articles. Maxilliped with 3 retinacula. Carpus of P1-4 with 4, of P5-7 with 5-6 flagellate setae, apical and ventral combs of carpus spinose, carpus of P5 and 6 with dorsal flagellate seta. Pleopod 1 with nearly continuous distal margin. Endopod of pleopod 2 as long as basipod.

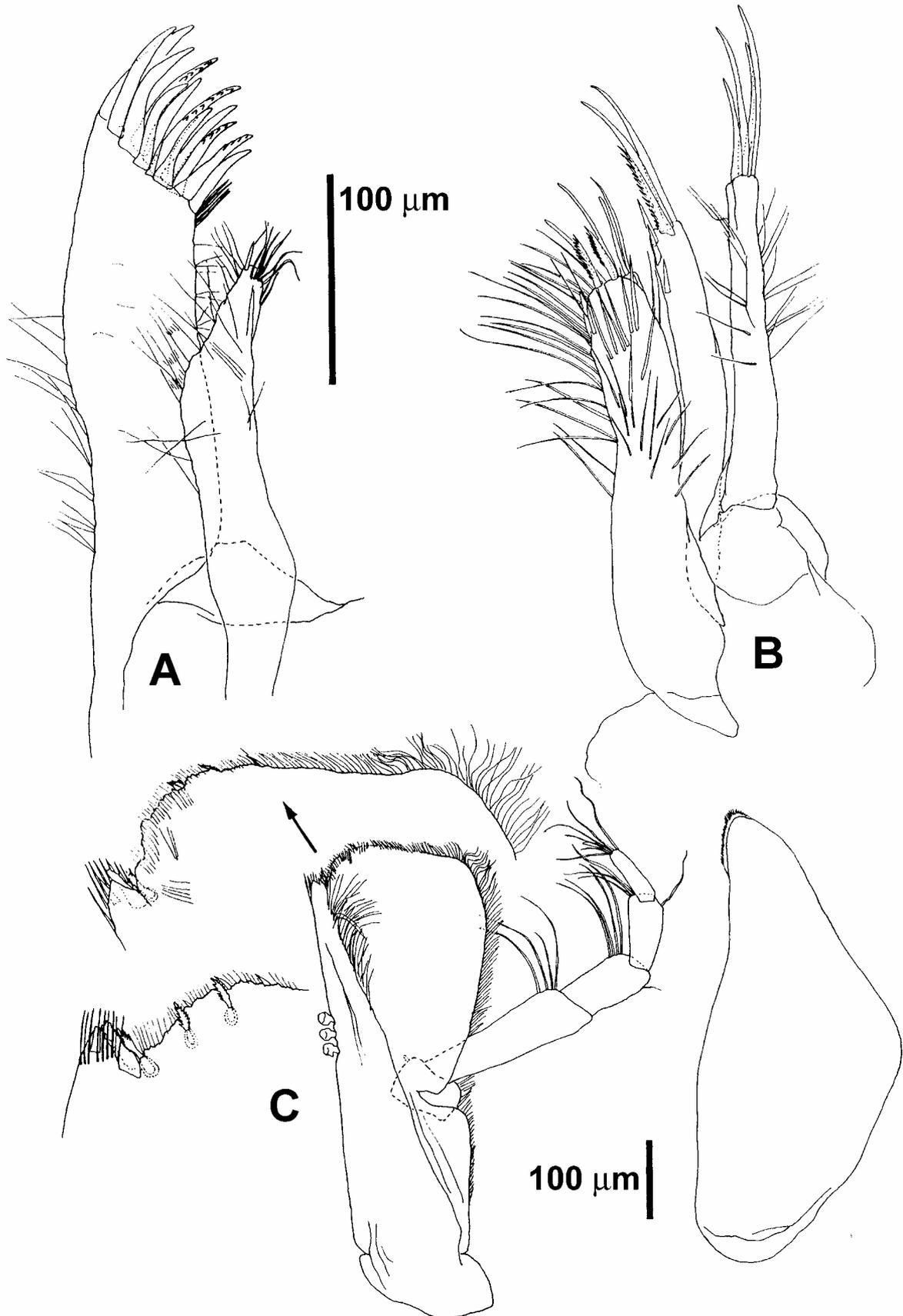


Figure 3.87: *Haploniscus kyrbasius* n. sp., holotype, male, 5.7 mm: A maxilla 1; B maxilla 2; C maxilliped, distal margin in dorsal and ventral view.

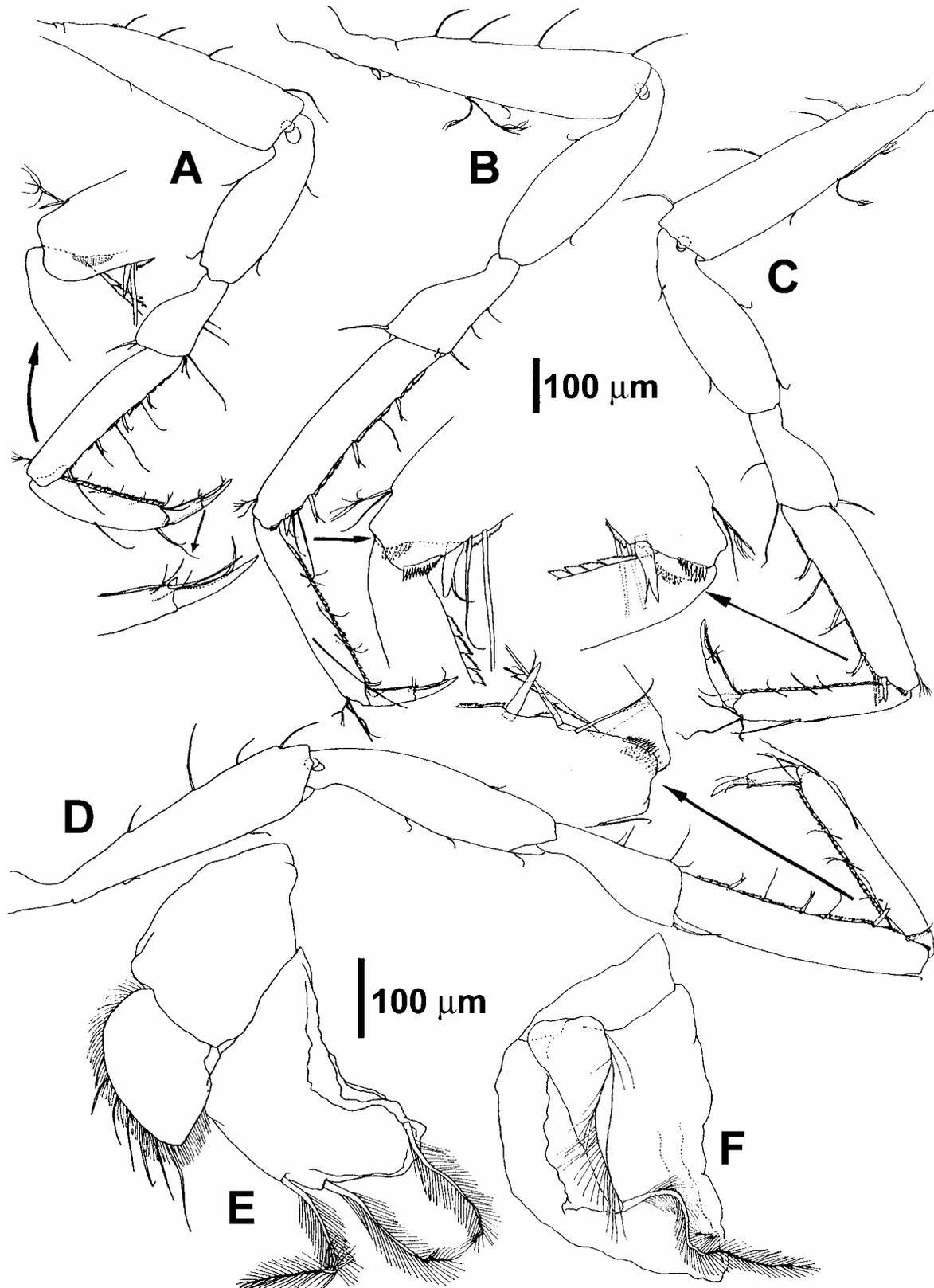


Figure 3.88: *Haploniscus kyrbasius* n. sp., holotype, male, 5.7 mm: A pereopod 1; B pereopod 3; C pereopod 2; D pereopod 4; E pleopod 3; F pleopod 4.

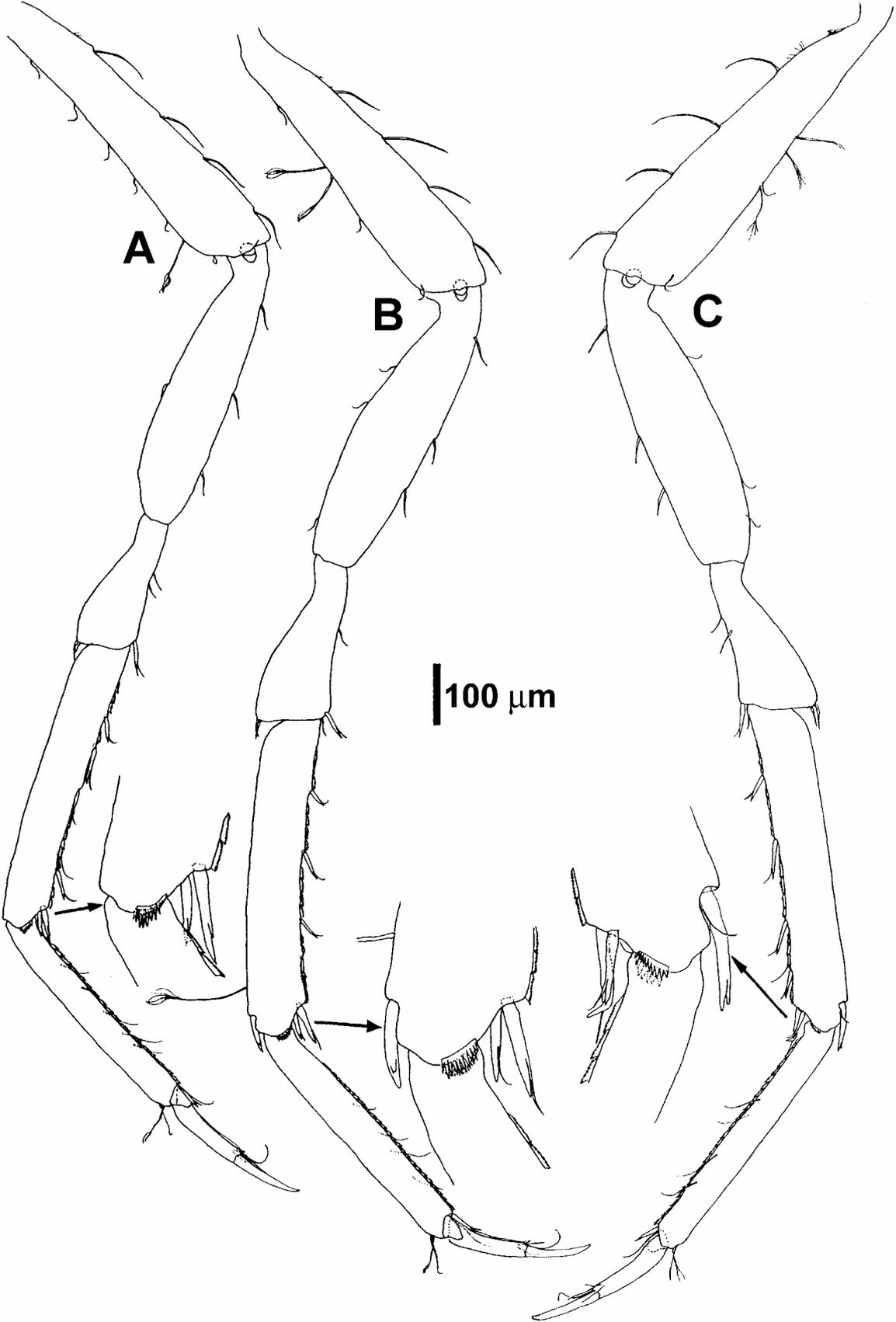


Figure 3.89: *Haploniscus kyrbasius* n. sp., holotype, male, 5.7 mm: A pereopod 7; B pereopod 5; C pereopod 6.

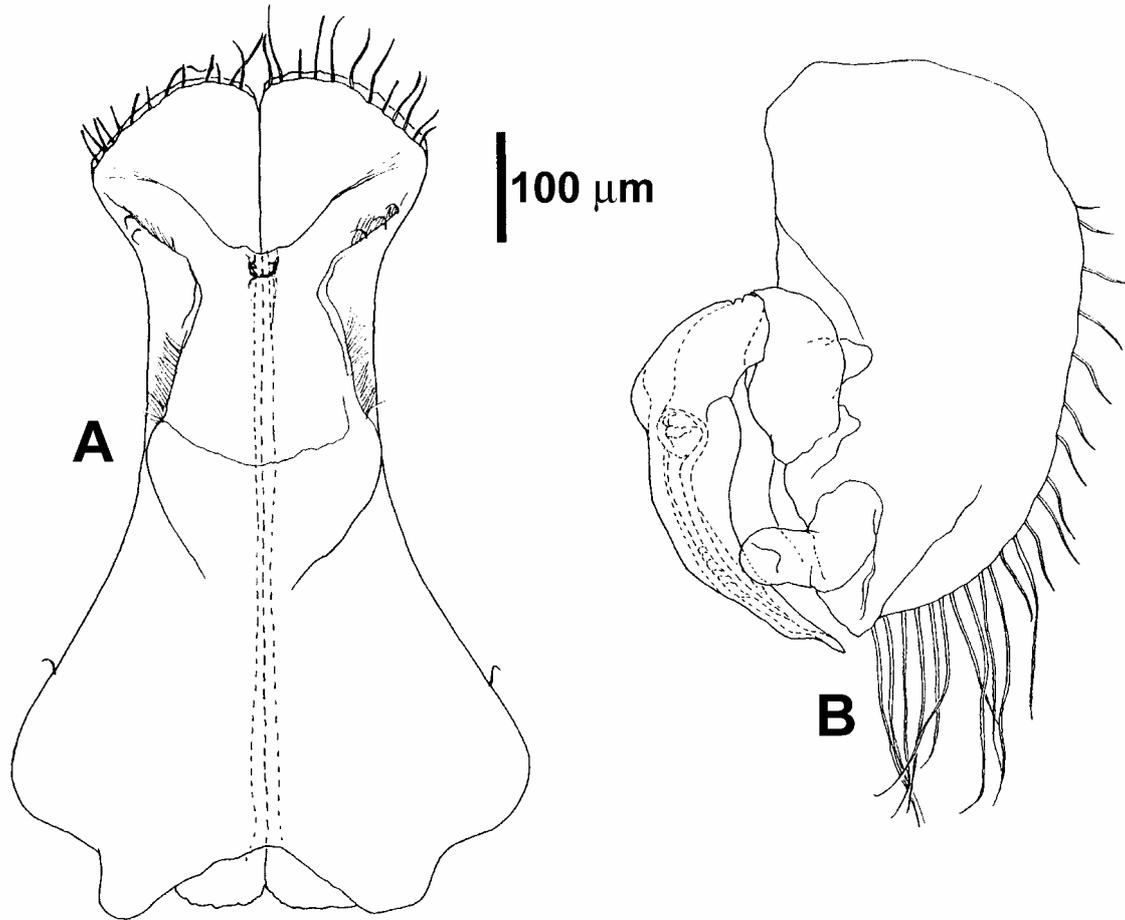


Figure 3.90: *Haploniscus kyrbasius* n. sp., holotype, male, 5.7 mm: A pleopod 1; B pleopod 2.

Description of male holotype

H. kyrbasius differs from *H. cassilatus* in the following characters:

Head (Fig. 3.85, 3.99) about 3 times as wide as long. Rostrum slightly larger, less tapering, curved slightly stronger dorsally in lateral view. Pleotelson (Fig. 3.85) lateral margins convex basally, concave distally.

Antenna 1 (Fig. 3.86) flagellar articles 3 and 4 with 1 aesthetasc each.

Mandibular palp article 3 with 10 serrated setae.

Maxilliped (Fig. 3.87) with 3 retinacula.

Pereopods (Fig. 3.88, 3.89): Basis with 4 ventral setae. Merus with 2 medioventral setae. Carpus of P1-4 with 4, of P5-7 with 5-6 flagellate setae. Propodus of P5-7 with 1 ventral flagellate seta.

3.1.2.4.6 *Haploniscus nudifrons* n. sp.

(Figs 3.91-3.94)

Material

Holotype: female, 11.3 mm; station 129-2, 59°52.21-52.20'S 59°58.75-58.63'W, 4076 m depth; ZMH K40766.

Etymology

The name refers to the absence of the rostrum that is characteristic for the other species of the *Haploniscus cucullus* complex; *nudus* meaning “naked”.

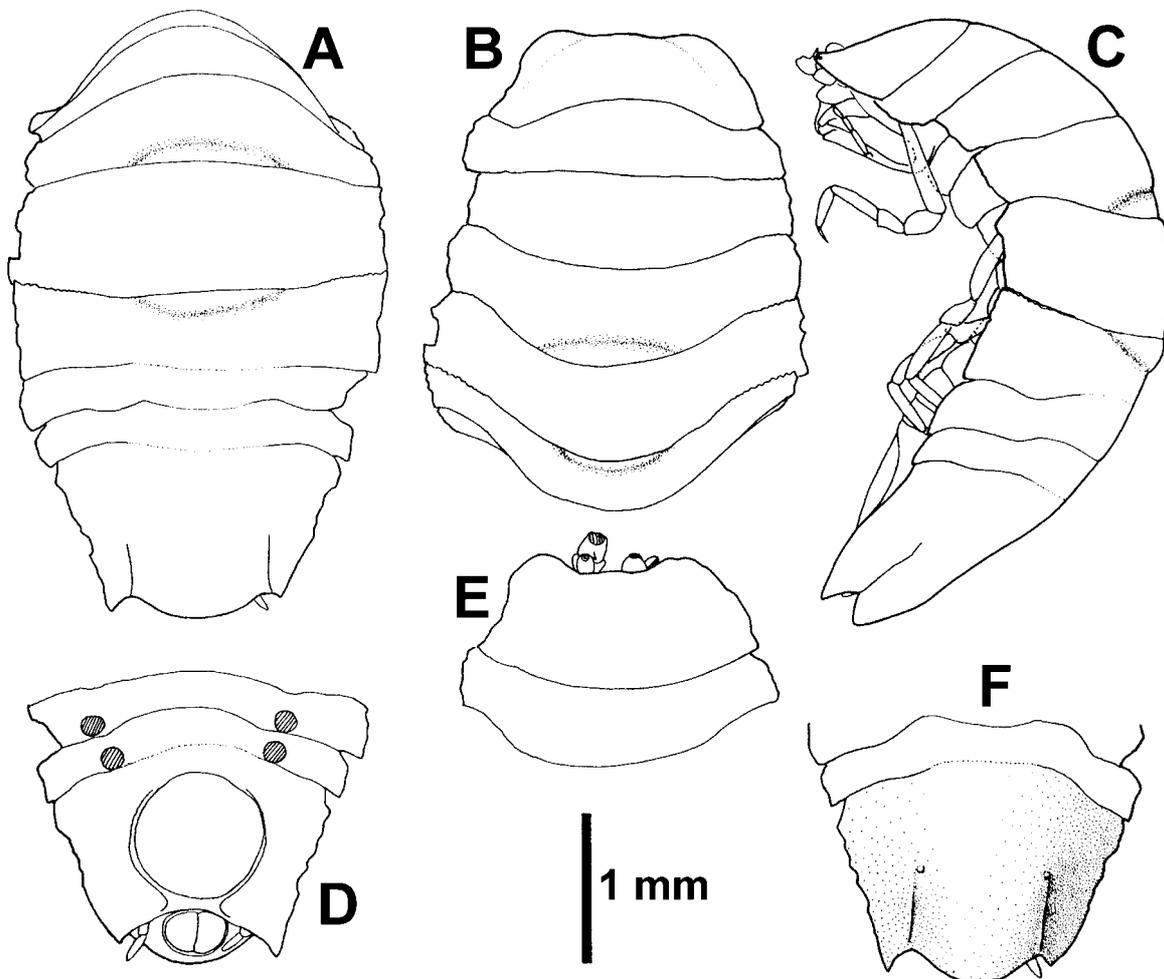


Figure 3.91: *Haploniscus nudifrons* n. sp., holotype, female, 11.3 mm: A posterior body, dorsal view, B anterior body, dorsal view; C lateral view; D posterior body, ventral view; E anterior body, dorsal view; F posterior body, dorsal view.

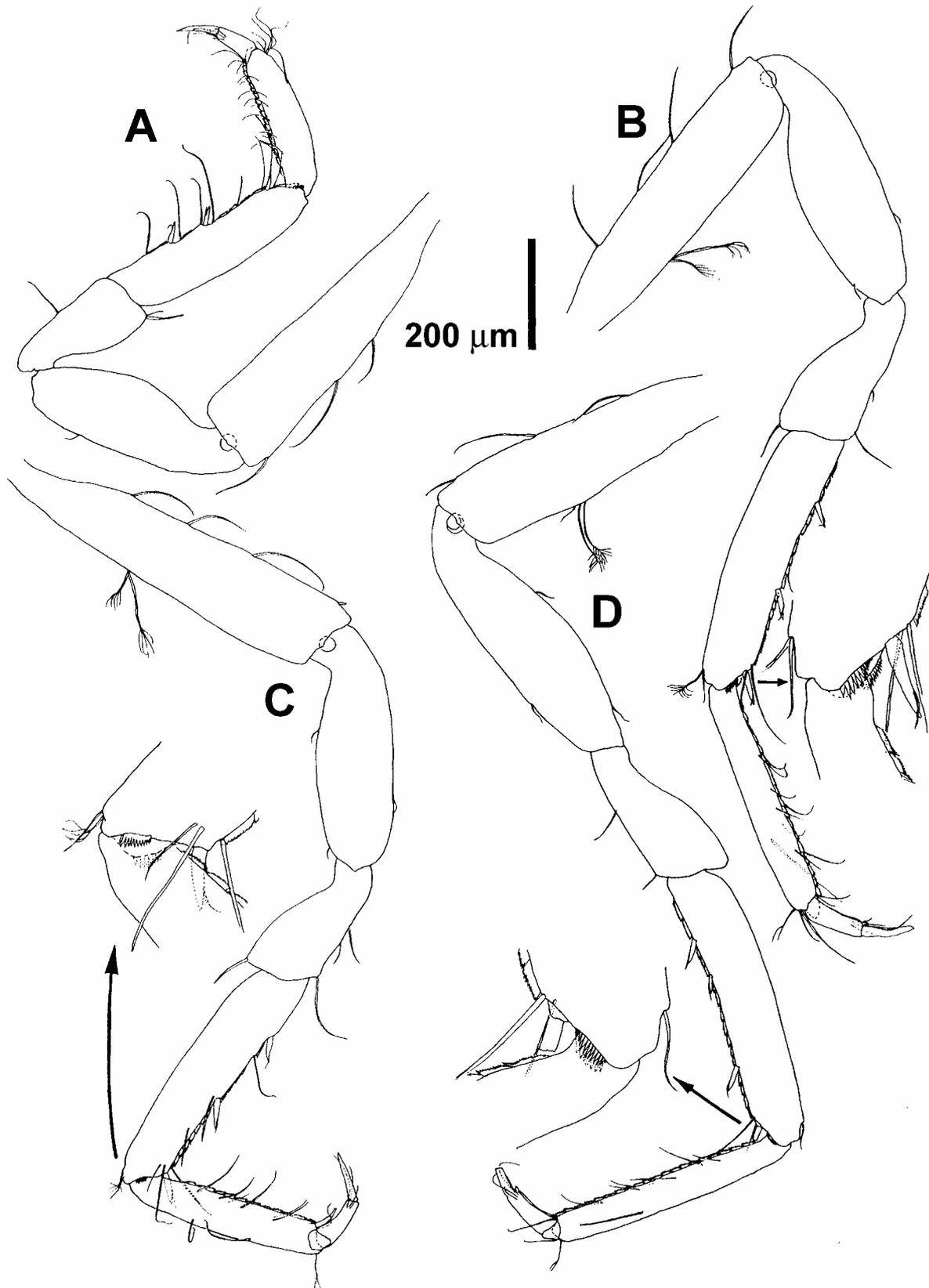


Figure 3.92: *Haploniscus nudifrons* n. sp., holotype, female, 11.3 mm: A pereopod 1; B pereopod 3; C pereopod 2; D pereopod 4.

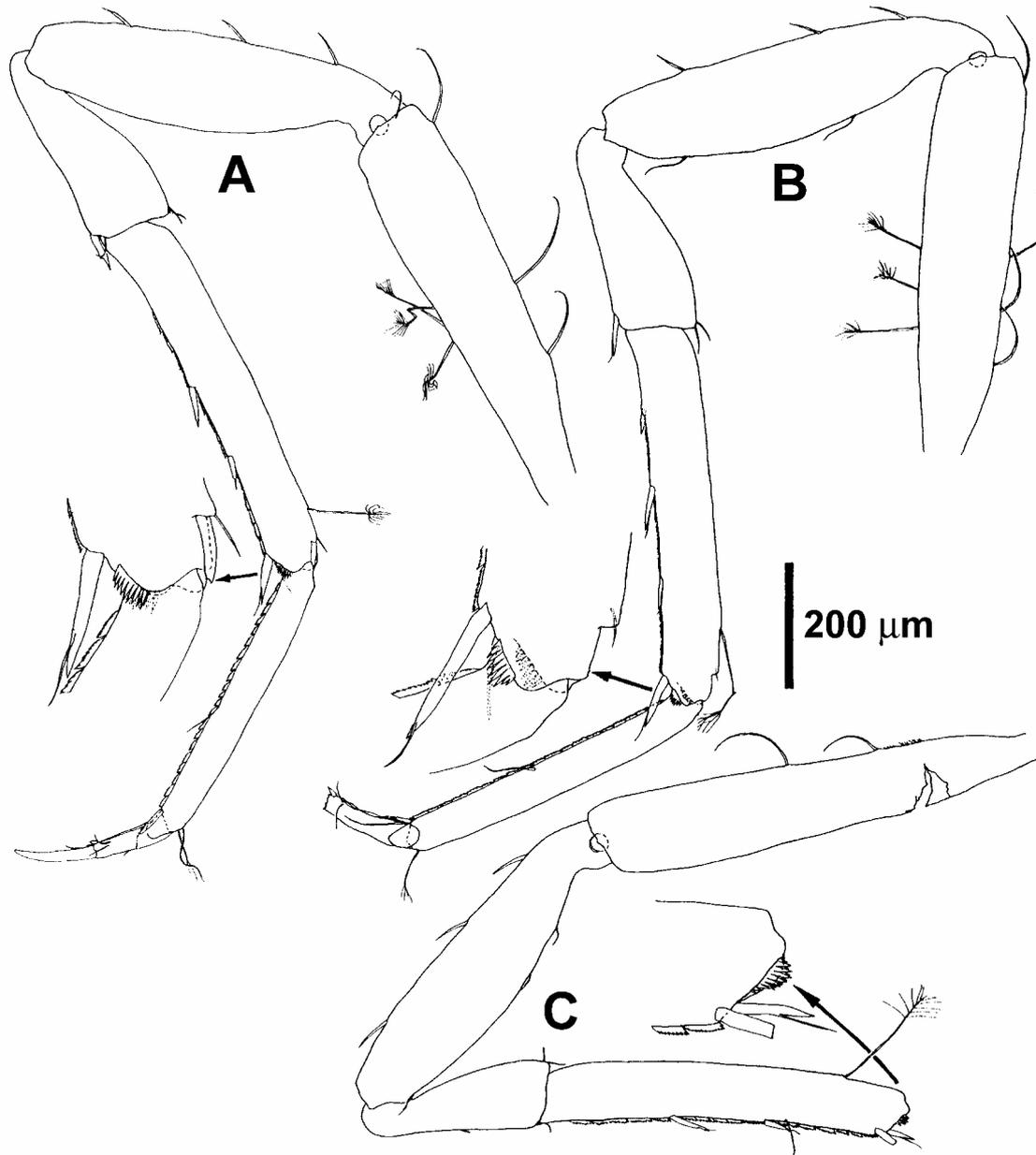


Figure 3.93: *Haploniscus nudifrons* n. sp., holotype, female, 11.3 mm: A pereopod 5; B pereopod 6; C pereopod 7.

Diagnosis

Body oval, 3 times as long as wide. Head about 2.5 times as wide as long, frontal margin concave, without rostrum. Pereonites 3-5 broadest. Lateral margins of pleotelson convex, posterolateral processes short, not reaching terminal margin; dorsal surface of pleotelson with 2 sharp longitudinal keels, ventral surface with cuticular bulge surrounding the branchial chamber and tapering towards anus. Carpus with 3-4 flagellate spine-like setae, apical and

ventral combs of carpus spinose, carpus of P5 and 6 with dorsal flagellate seta. Plp2 of female without setae on lateral margins. Uropods reaching terminal margin of pleotelson.

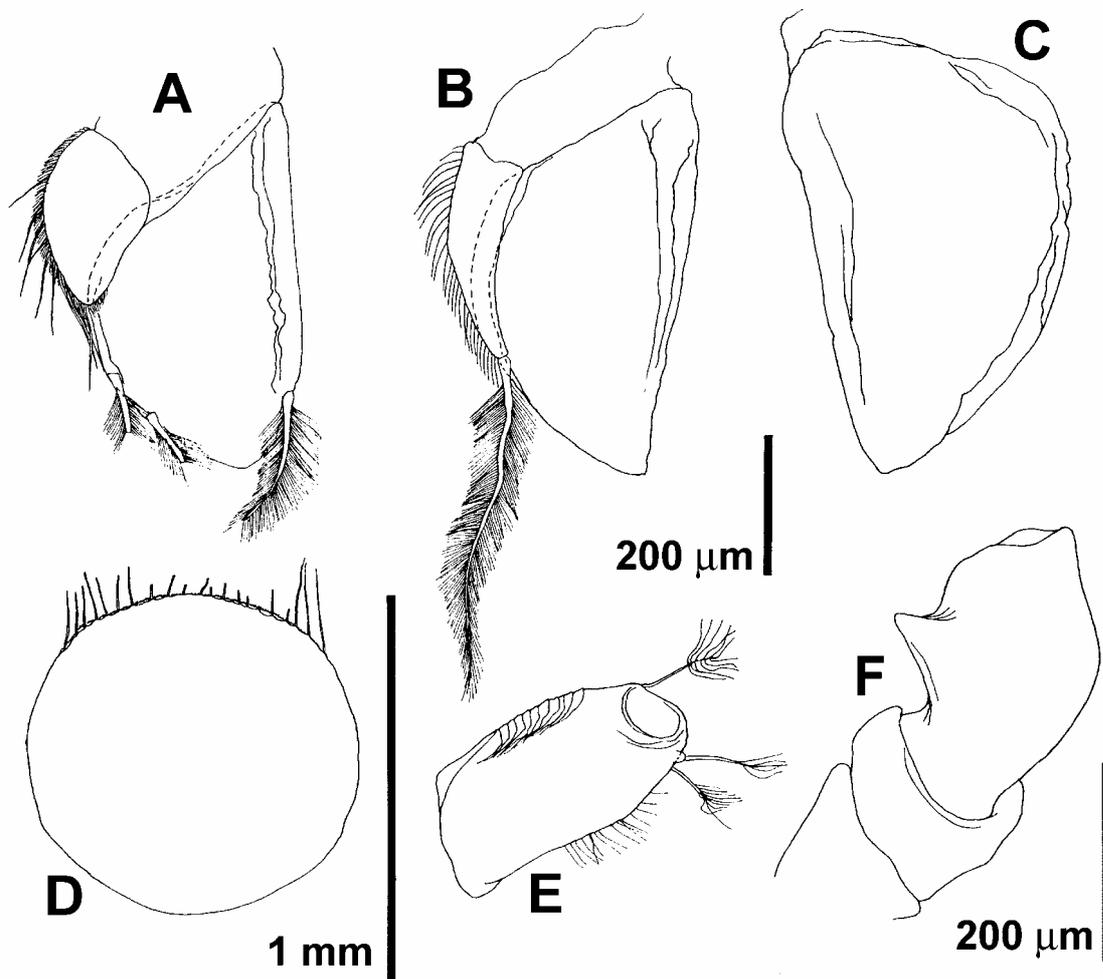


Figure 3.94: *Haploniscus nudifrons* n. sp., holotype, female, 11.3 mm: A pleopod; B pleopod 4; C pleopod 5; D pleopod 2; E antenna 1, article 1; F antenna 2, articles 1-3.

Description of female holotype

H. nudifrons differs from *H. cassilatus* in the following characters:

Head (Fig. 3.91) without rostrum.

Distal articles of antennae (Fig. 3.94) lost.

Maxilliped with 3 retinacula.

Pereopods (Fig. 3.92, 3.93): Merus with 1-2 medioventral setae. Carpus with 3-4 ventral flagellate setae.

Plp2 (Fig. 3.94) lateral margins, without setae, distal margin with about 20 setae.

Uropods (Fig. 3.91) reaching terminal margin of pleotelson.

3.1.2.4.7 *Haploniscus microkorys* n. sp.

(Figs 3.95-3.99)

Material

Holotype: male, 4.3 mm; station 134-3, 65°19.20-19.05'S 48°03.77-02.92'W, 4553 m depth; ZMH K40767.

Etymology

From the Greek words *micros* meaning small and *korys* meaning helmet; the name refers to the rostrum, which is smaller than in most species of the *Haploniscus cucullus* complex.

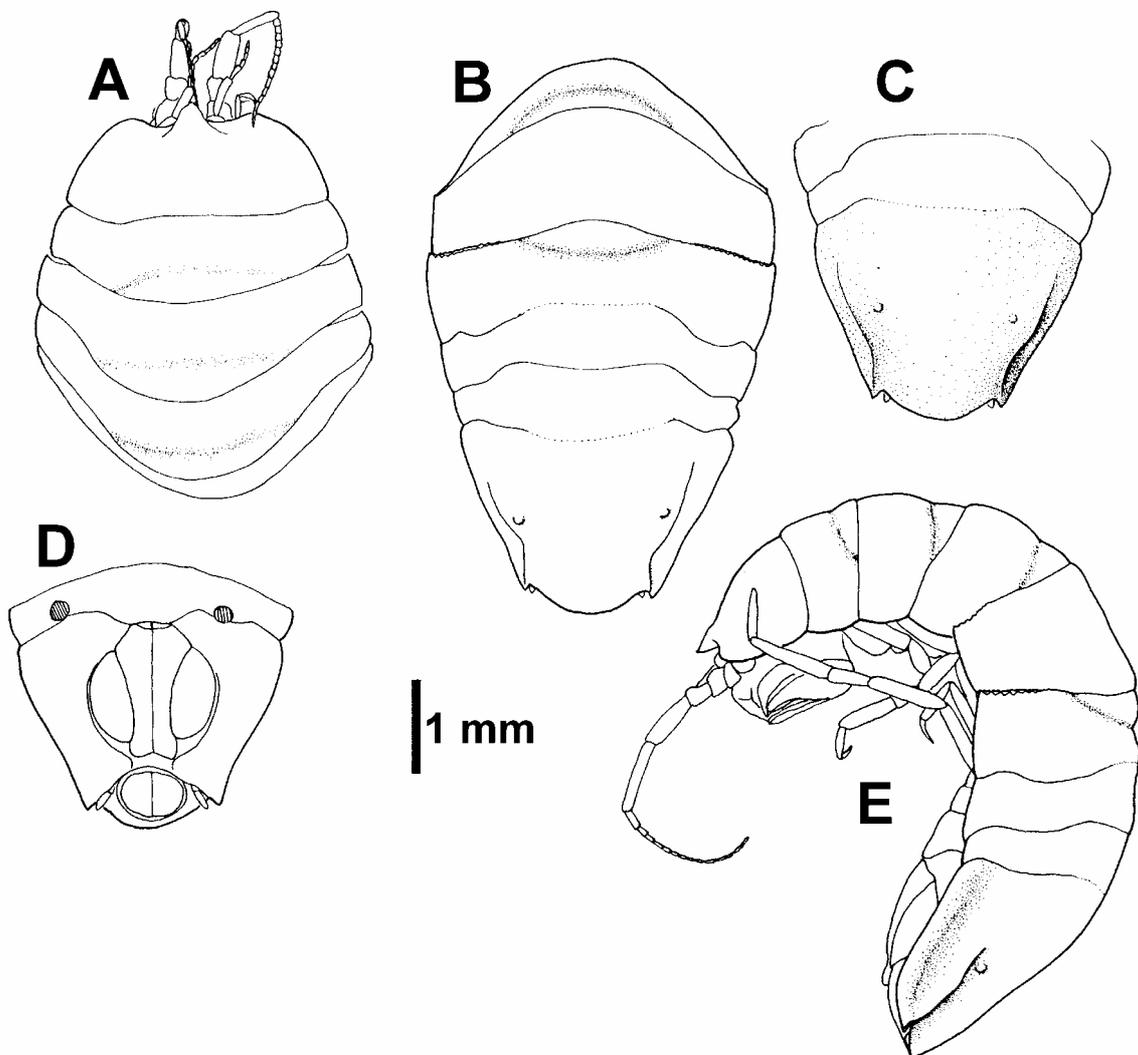


Figure 3.95: *Haploniscus microkorys* n. sp., holotype, male, 4.3 mm: A anterior body, dorsal view; B posterior body, dorsal view; C posterior body, dorsal view; D posterior body, ventral view; E lateral view.

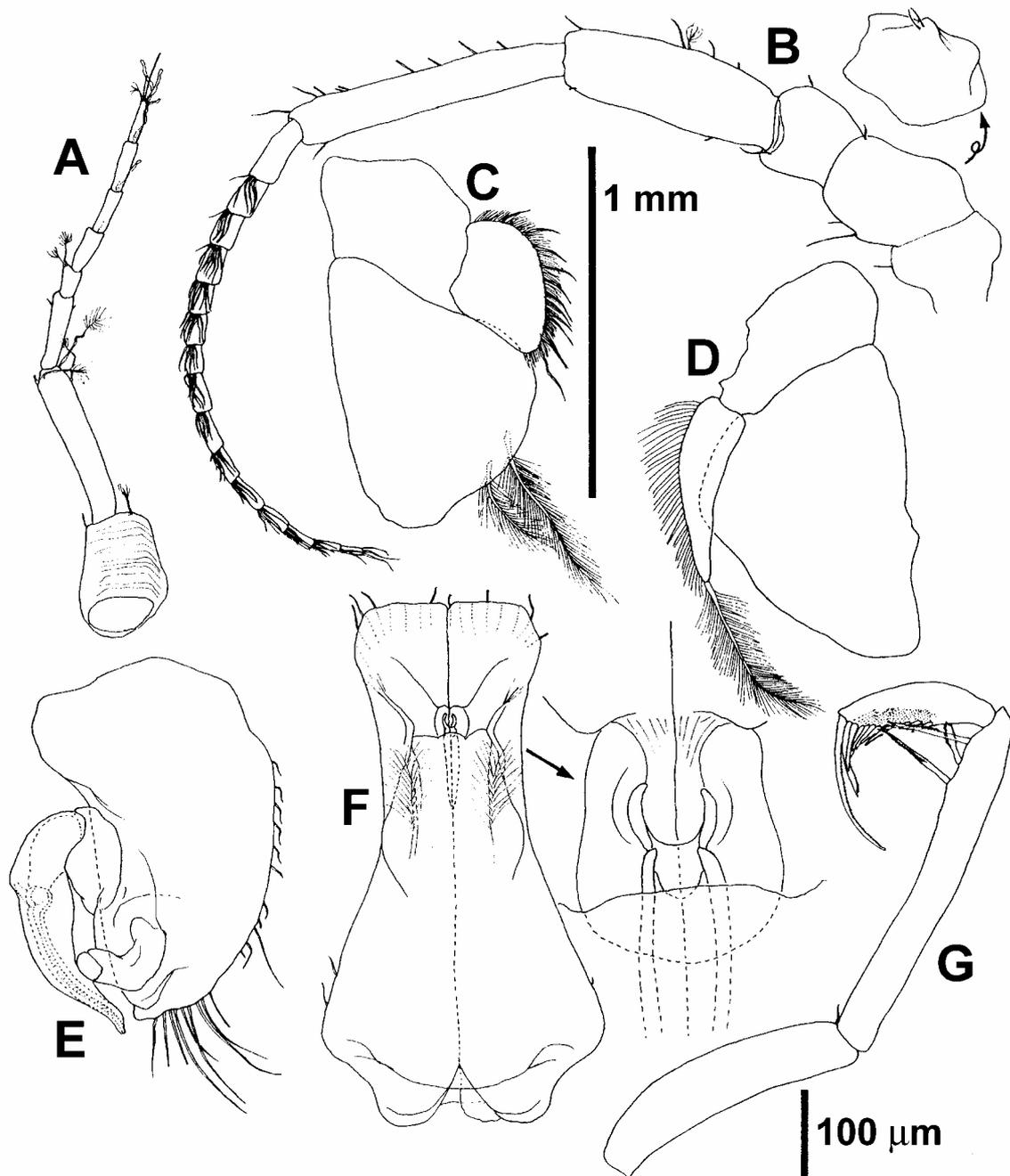


Figure 3.96: *Haploniscus microkorys* n. sp., holotype, male, 4.3 mm: A antenna 1; B antenna 2; C pleopod 3; D pleopod 4; E pleopod 2; F pleopod 1; G mandibular palp.

Diagnosis

Body oval, 3 times as long as wide. Head about 2.5 times as wide as long, frontal margin concave, with triangular rostrum; rostrum pointing ventrally with acute frontal tooth, a deep ventral indentation between rostrum and frontal margin of head. Pereonites 3-5 broadest. Lateral margins of pleotelson convex basally, concave distally, posterolateral processes short,

not reaching terminal margin; dorsal surface of pleotelson with 2 sharp longitudinal keels, ventral surface with cuticular bulge surrounding the branchial chamber and tapering towards anus. Antenna 1 with 5 flagellar articles. Maxilliped with 3 retinacula. Carpus of P1 with 6, of P2-7 with 7-11 ventral flagellate setae, apical and ventral combs of carpus spinose, carpus of P5 and 6 with dorsal flagellate seta. Pleopod 1 with nearly continuous distal margin. Endopod of pleopod 2 as long as basipod.

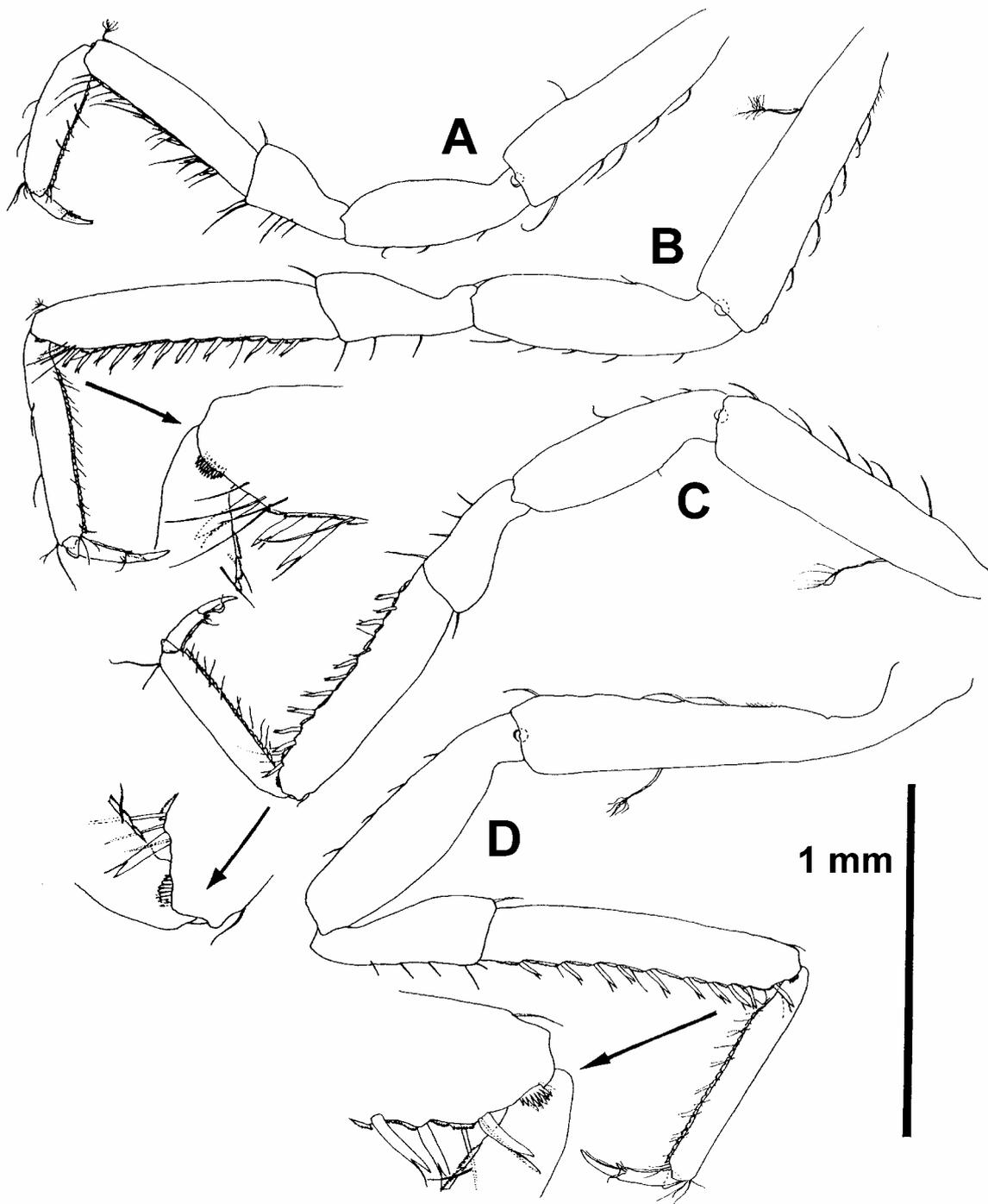


Figure 3.97: *Haploniscus microkorys* n. sp., holotype, male, 4.3 mm: A pereopod 1; B pereopod 3; C pereopod 2; D pereopod 4.

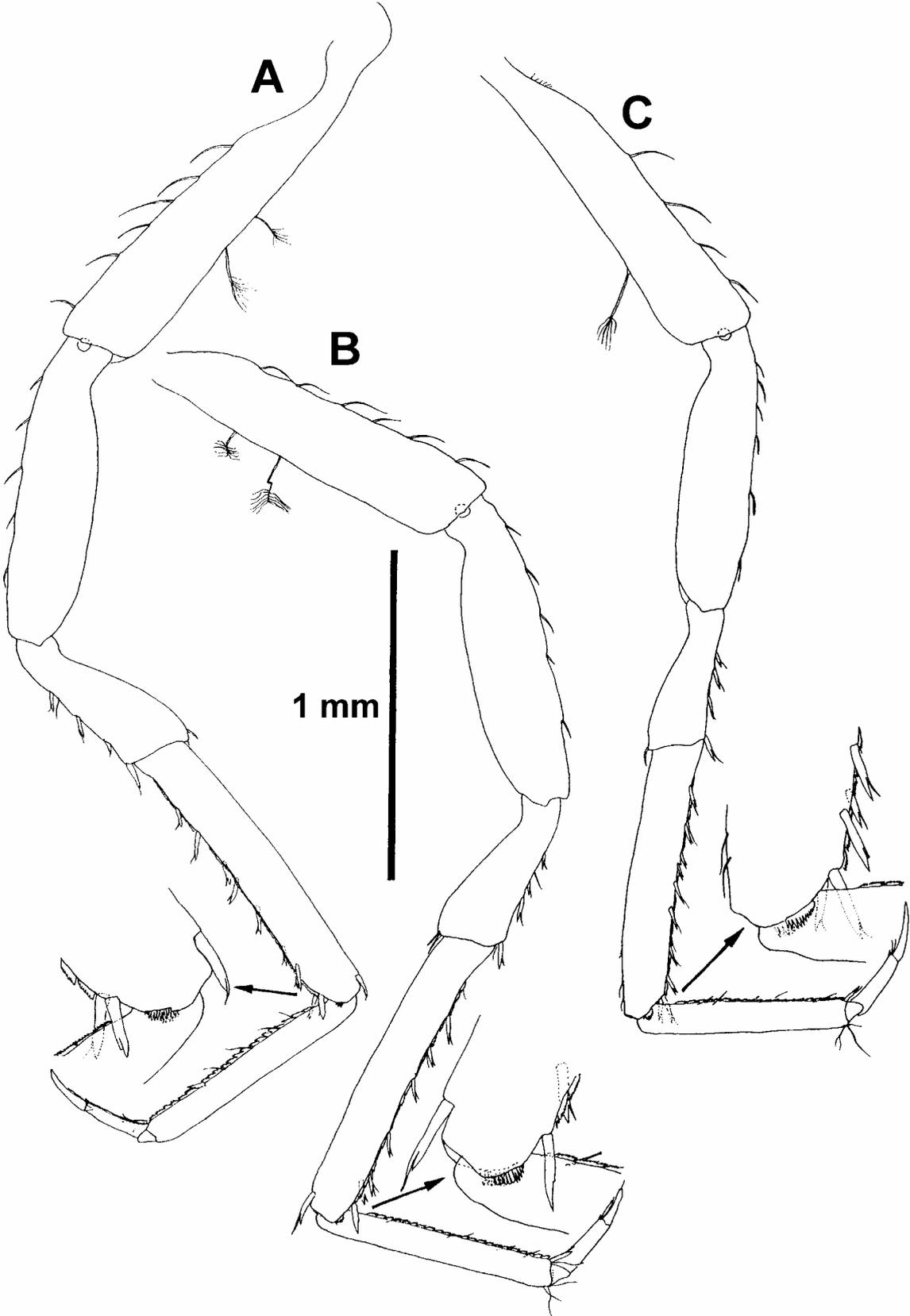


Figure 3.98: *Haploniscus microkorys* n. sp., holotype, male, 4.3 mm: A pereopod 5; B pereopod 6; C pereopod 7.

Description of male holotype

H. microkorys differs from *H. cassilatus* in the following characters:

Rostrum (Fig. 3.95, 3.99) smaller, pointing ventrally, triangular in dorsal view, without dorsal depression.

Lateral margins of pleotelson (Fig. 3.95) convex basally, concave distally.

Antenna 1 (Fig. 3.96) with 5 flagellar articles, articles 3 and 4 with 1 aesthetasc, article 5 with 2 aesthetascs.

Antenna 2 (Fig. 3.96) more slender.

Mandibular palp (Fig. 3.96) with 11 serrated setae.

Maxilliped with 3 retinacula.

Pereopods (Figs 3.97, 3.98): Basis with 4-7 ventral setae. Ischium with 3-6 ventral setae. Merus of P1-4 with 3-4 medioventral simple setae, of P5-7 with 3 medioventral flagellate setae. Carpus of P1 with 6, of P2-7 with 7-11 ventral flagellate setae. Propodus of P2-4 with almost 20 simple setae ventrally, propodus of P5-7 with 1-2 ventral flagellate setae and several simple setae.

Exopod of pleopod 3 (Fig. 3.96) with 12 setae.

Remarks

Because only a single specimen of *H. nudifrons* and *H. microkorys* was found, the mouthparts of these species were not dissected to avoid damaging of the important diagnostic features of the head in the holotypes. The mouthparts themselves were found to hold no important diagnostic characters, except for the mandibular palp, which was dissected carefully in *H. microkorys*, but was lost in *H. nudifrons*.

The *Haploniscus cucullus complex* is characterized by a broad body shape, the concave frontal margin of the head, the short posterolateral processes of the pleotelson and the characteristic setation of the pereopods; pleopod 1 of adult males is similar to that of subadult males, the endopod of the male pleopod 2 is short, the sexual dimorphism is restricted to the pleopods. The scales on the peduncular articles of antenna 2 seem to be a common character as well. Although they were not visible under the compound microscope in some species, e.g. *H. cucullus*, these scales were found in a specimen of *H. cucullus* that was prepared for SEM studies. The size and number of scales is subject of interspecific variation, but maybe also of intraspecific variation. The proportions of the peduncular articles of antenna 2 are variable as well; antenna 2 of *H. cassilatus* is relatively stout, antenna 2 of *H. microkorys* is more slender.

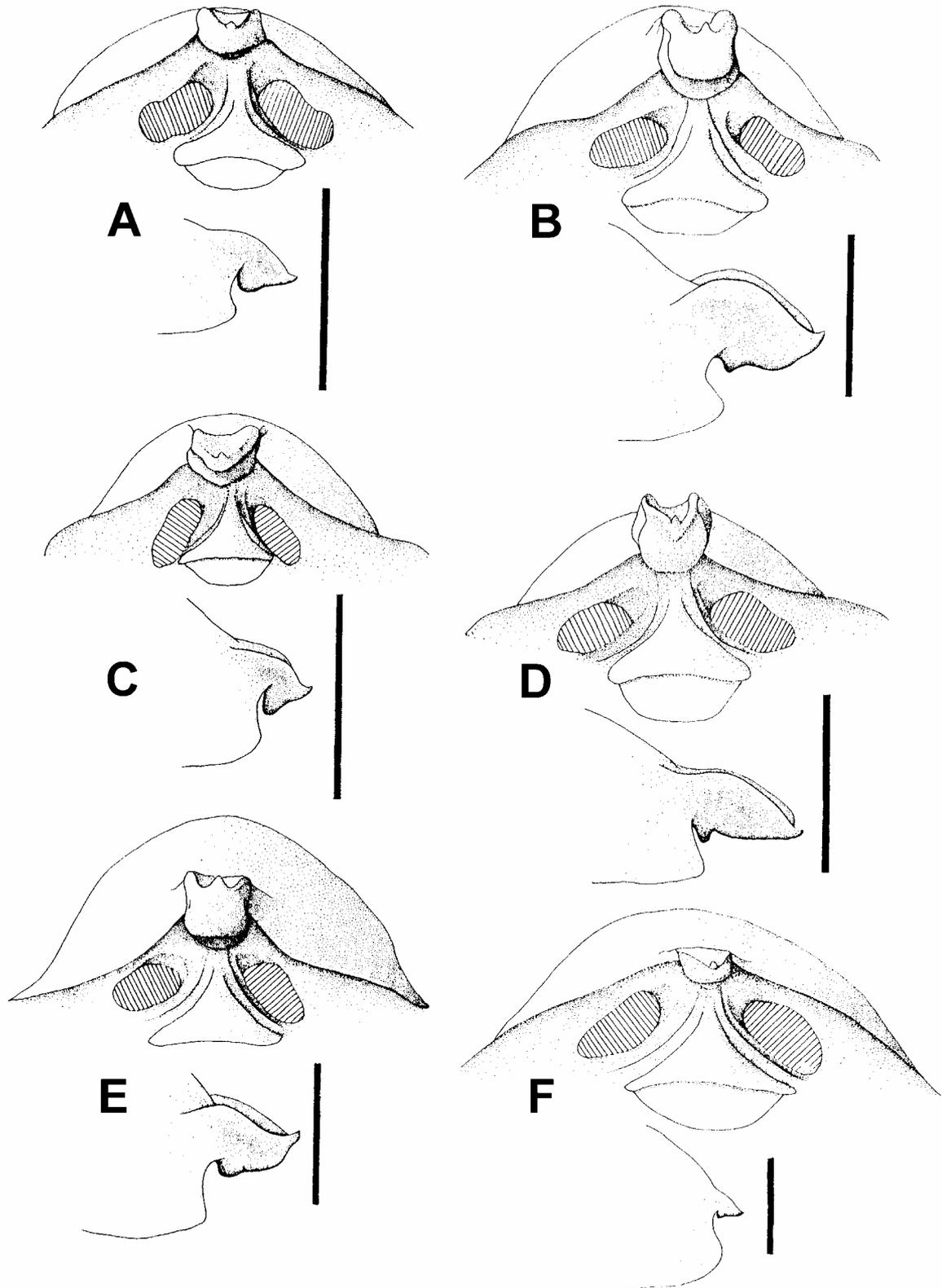


Figure 3.99: Frontal and lateral view of rostral processes: A *Haploniscus cassilatus* n. sp., paratype, male, 3.6 mm; B *H. cucullus* n. sp., holotype, male, 5.3 mm; C *H. weddellensis* n. sp., holotype, male, 3.0 mm; D *H. procerus* n. sp., holotype, female, 7.6 mm; E *H. kyrbasius* n. sp., holotype, male, 5.7 mm; F *H. microkorys* n. sp., holotype, male, 4.3 mm. Scale bars = 500 μ m.

While the setation of the flagellar articles of antenna 2 is usually more strongly developed in males, such a dimorphism could not be found in the two species, where adult males and females were present; *H. cassilatus* and *H. weddellensis*. This corresponds to the generally weakly expressed sexual dimorphism.

The size range of the *Haploniscus cucullus* complex is large; the smallest adult specimens belonged to *H. weddellensis*, with 11.3 mm length the biggest specimen was the *H. nudifrons* female. However, it is difficult to determine the size range of most species due to lack of material. Oviparous females seem to be among the largest specimens of each species.

The strongest interspecific variation within the *Haploniscus cucullus* complex can be observed in the size and shape of the rostrum and the setation of the pereopods. Fig. 3.99 shows the rostrum of the above described species in frontal and lateral view. The biggest rostrum is found in *H. cucullus*, while *H. microkorys* has the smallest rostrum. *H. nudifrons* is not illustrated in this figure, because the species does not possess a rostrum at all. Despite the considerably smaller or absent rostrum of *H. microkorys* and *H. nudifrons*, they are sistergroups to *H. cucullus* in a molecular phylogenetic analysis based on 16S rRNA sequences (Michael Raupach, pers. com.). This leads to the conclusion that the rostrum is a symplesiomorphy of the whole *Haploniscus cucullus* complex, and that its partial respectively complete reduction in *H. microkorys* and *H. nudifrons* is an autapomorphy. Besides interspecific variation of the rostrum, intraspecific variation of this structure can be observed. In relation to body size oviparous females possess a smaller rostrum than other specimens belonging to the same species. SEM pictures revealed that the rostrum is covered with small tubercles, each bearing several tiny sensory setae (Fig. 3.11).

The setation of the pereopods includes flagellate spine-like setae ventrally on carpus and propodus of all species, but their number varies within and between species. By far the most setae can be found in *H. microkorys*, while specimens of *H. cassilatus* possess only 1-3 flagellate setae on the ventral carpus.

Because of the intraspecific variation, the number of setae is problematic as a diagnostic character; to define discrete character states a statistical analysis would be necessary. This is not possible at the moment, because not enough specimens were found of most species. In those species, where adult males were found, pleopod 1 and 2 looked more or less alike. In contrast to most species of the Haploniscidae the pleopod of subadult and adult specimens does not differ greatly, it has to be dissected to identify the ontogenetic stage. In adult males the dorsal surface of pleopod 1 has two transversal grooves, which are only weakly indicated in stage V males.

Molecular results (Michael Raupach, pers. com.) as well as morphological results show that specimens from the stations 42-2 and 43-8 belong to the same species, *H. cucullus*. The two stations are located relatively closely together in the Scotia Sea and have similar depth. The other species were each found at one station only.

Besides the above described species three juvenile specimens of the *Haploniscus cucullus* complex were found at station 131, the station, where two adult specimens of *H. procerus* were sampled. These possess a much shorter rostrum than *H. procerus* and could not be allocated clearly to one of the newly described species.

Haploniscus charcoti Chardy, 1975 closely resembles the species of the *Haploniscus cucullus* complex, but apparently lacks the acute produced tip of the rostrum, and the two pereopods illustrated by Chardy seem to lack the typical flagellate setae. Besides it was found in the North Atlantic and while the different populations of this species complex sampled at close by stations in the Southern Ocean proved to belong to different species, it is hardly plausible that one of the species described above could belong to *H. charcoti*. However *H. charcoti* might turn out to be another member of this species complex.

H. tridens Menzies, 1962; *H. tricornis* Menzies, 1962 and *H. tricornooides* Menzies, 1962 also resemble species of the *Haploniscus cucullus* complex, but differ from the species described above in the shape of the rostrum.

3.1.2.5 Genus *Chauliodoniscus* Lincoln, 1985a

Type species: *Chauliodoniscus tasmanus* Lincoln, 1985a

Diagnosis

Head without rostrum; at least one of pereonites 2-4 with prolonged anterolateral angles; pereonite 5 not fused to pereonite 6; enrollment possible with frontal margin close to branchial chamber. Antenna 2 article 3 dorsal tooth as long as or longer than width of article, article 5 inflated, with convex lateral margins. Mandible with not more than seven serrated setae. Maxilliped with two retinacula.

Remarks

All species of the genus show a sexual dimorphism in the shape of pereonites 2-4. The anterior angles are usually more produced in males. However, the extent of the dimorphism varies between species. While it is pronounced in some species like in *C. tasmanus* Lincoln, 1985a, it is less conspicuous in other species, e. g. *C. armadilloides* (Hansen, 1916).

3.1.2.6 Genus *Hydroniscus* Hansen, 1916

Type species: *Hydroniscus abyssi* Hansen, 1916

Head with large lobe-like rostrum; pereonites 5-7 fused to pleotelson, only lateral sutures faintly visible; pereonite 7 completely reduced dorsally; enrollment possible with frontal margin close to terminal margin. Antenna 2 article 3 dorsal tooth absent. Mandibular palp article 3 with more than seven serrated setae. All pereopods with flagellate setae on carpus and propodus.

Remarks

The original generic diagnosis from Hansen (1916) included the absence of the uropods. Lincoln (1985a) already discussed the fact that this is not true for all species of the genus. Actually the type species *H. abyssi* Hansen, 1916 is the only species with apparently absent uropods, but in several species the uropods are smaller than in other genera of the family, e. g. *H. ornatus* Menzies, 1962. A close investigation of *H. vitjazi* revealed that in this species the uropods are minute and un conspicuous, yet definitely present.

3.2 Biodiversity and zoogeography

Some of the graphics in this chapter are modified from the publication by Brandt, Brökeland, Brix and Malyutina, in press.

The total number of Isopods sorted from the samples of 21 epibenthic sledge stations was 5525. They belonged to at least 312 species.

98% of all isopods belonged to the suborder Asellota (Fig. 3.100). Apart from 2 specimens from the family Stenetriidae all asellotes were members of the superfamily Janiroidea, the dominant isopod taxon in the deep sea.

The most abundant isopod family was the family Munnopsididae with 61% of all isopod specimens, 118 species and 28 genera were discriminated.

Second most abundant was the family Haploniscidae with 14% of the isopod specimens from 40 species and four genera. The 30 species from four genera of Ischnomesidae comprised 7% of all isopod specimens, while the 6% desmosomatid specimens belonged to 48 species from 10 genera. The family Munnidae was represented by 12 species and the family Paramunnidae by 10 species.

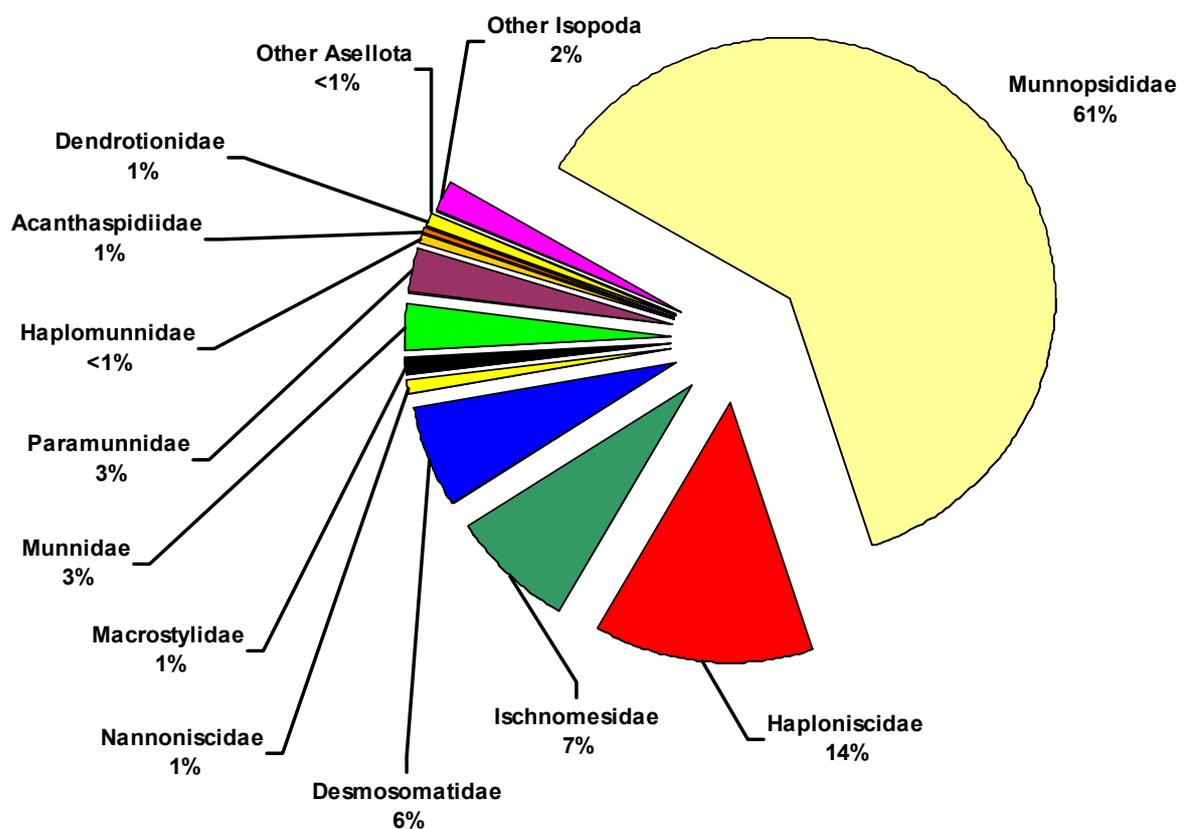


Figure 3.100: Relative abundance of the most important isopod families.

The families Nannoniscidae (15 species), Macrostylidae (7 species), Haplomunnidae (3 species), Acanthaspidiidae (5 species), Dendrotionidae (3 species), Mesosignidae (3 species), Janiridae (1 species), Janirellidae (1 species) and Joeropsidae (1 species) were rare or occurred only at some stations in higher numbers (Fig. 3.102). Isopods not belonging to the Asellota were Serolidae (3 species), Cirolanidae (1 species), Anthuridae (3 species), Gnathiidae (2 species) and species from the Valvifera (6 species), e.g. Antarcturidae, Pseudidotheidae.

The highest abundance was found at the relatively shallow station 133-3 in the Weddell Sea, while species richness was highest at station 131 at the lower continental slope east of the Antarctic Peninsula (Fig. 3.101, 3.102). A relatively high abundance and species richness (Fig. 3.101, 3.103) was also found at stations 46 and 42 near Elephant Island, but the species richness of station 135 is relatively low, while the abundance is almost as high as that of station 42. The lowest abundance and species richness were found at station 105 off the South Shetland Islands and at station 142 off the South Sandwich Islands.

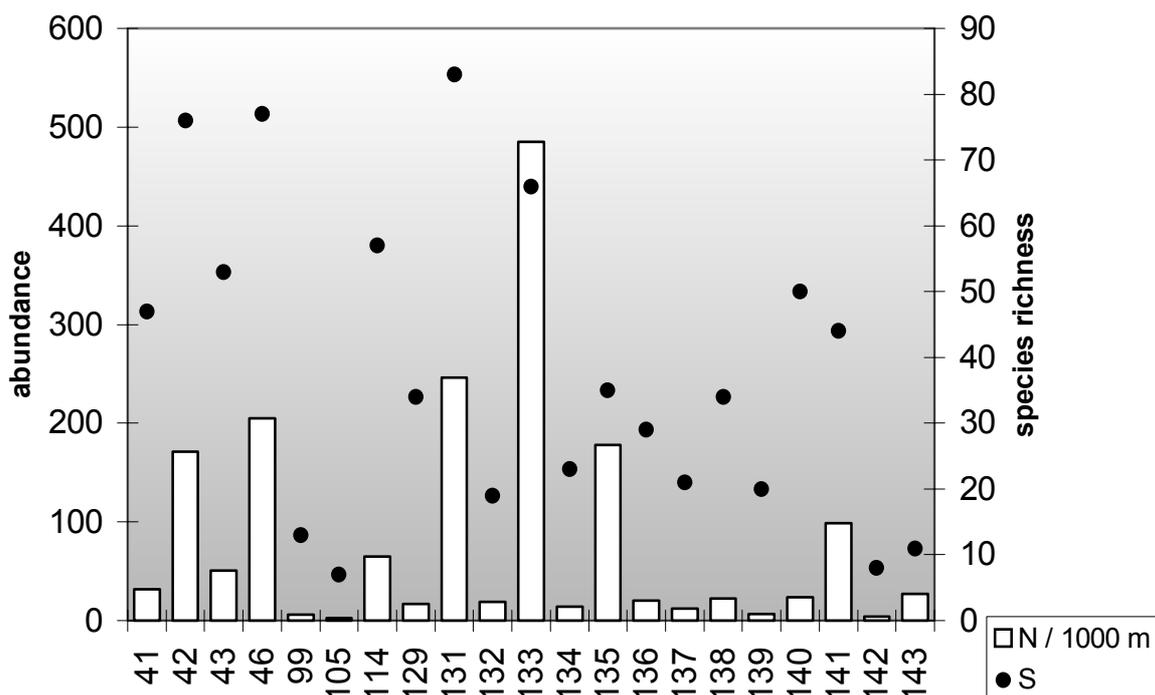


Figure 3.101: Species richness and abundance data combined (modified from Brandt *et al.*, in press).

Diversity was highest at station 140 near the South Sandwich Islands and at stations 42 and 43, while evenness was high at stations 105, 142 and 140 (Tab. 4).

Most of the ANDEEP isopod species were rare, 145 species occurred only at one and 80 species at two stations.

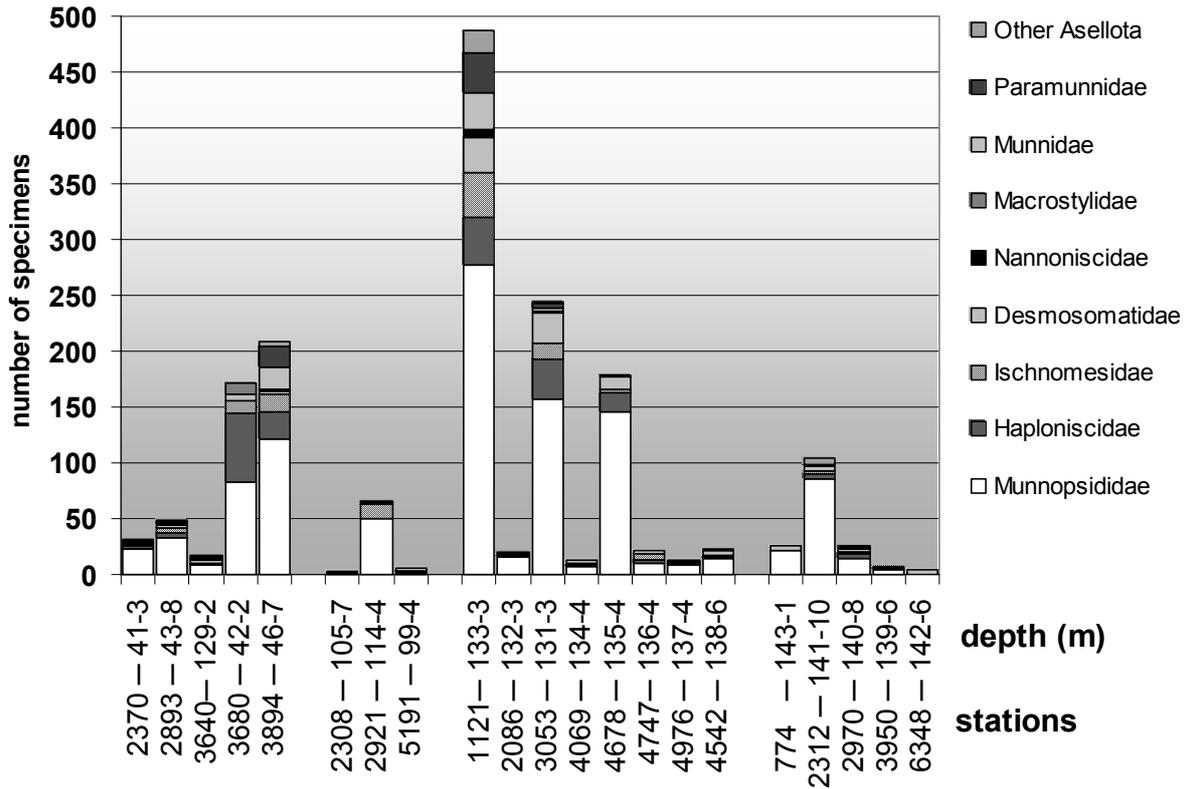


Figure 3.102: Abundance of the most important asellote families. Stations sorted after geographical region and depth.

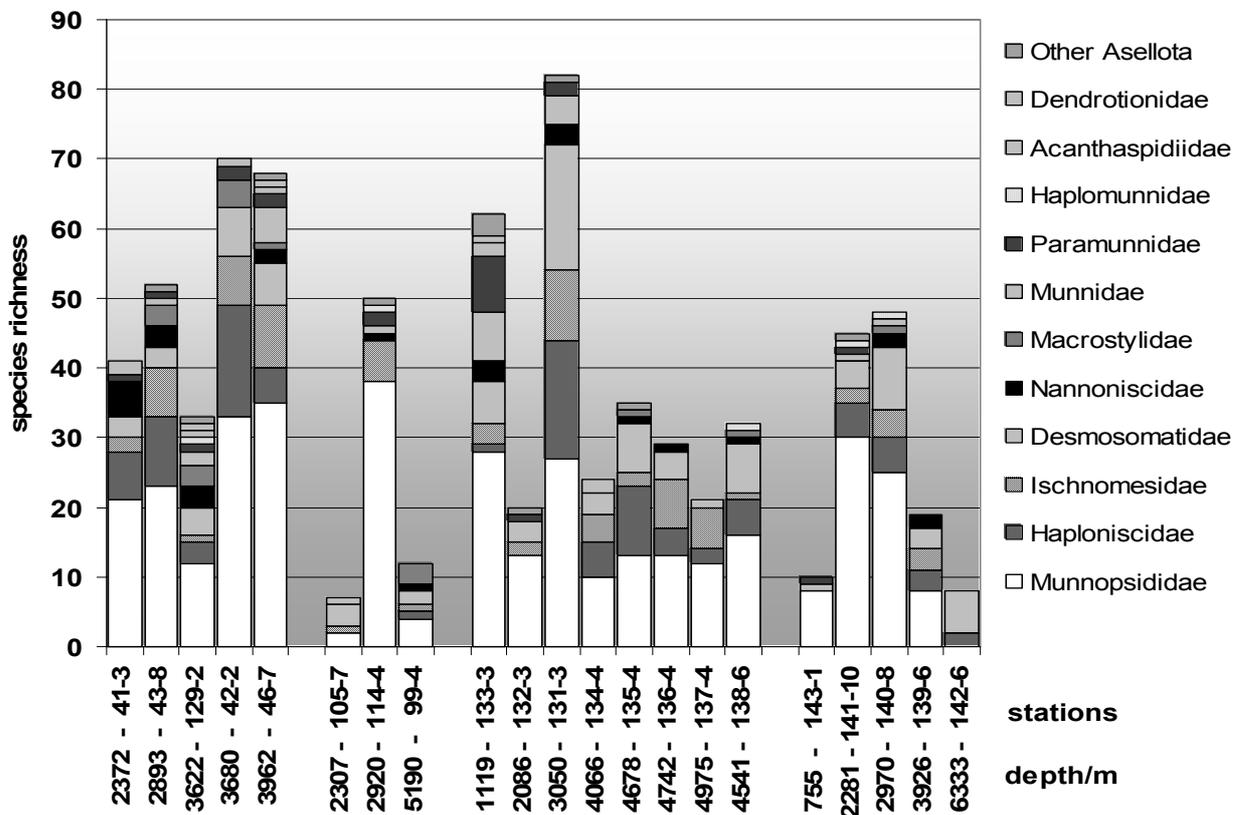


Figure 3.103: Species richness of the most important asellote families (modified from Brandt *et al.*, in press).

The cluster analysis with the program PRIMER using Bray-Curtis similarity (Fig. 3.104) revealed no significant differences in the isopod community structure between stations with regard to geographic area. Slight similarities can be found for the stations in the Weddell Sea and those in the Drake Passage and around Elephant Island (41-46, 129), while the stations from the South Shetland and the South Sandwich Island did not show much similarity. The dissimilarity of the shallowest (143) and the deepest (142) station is obvious. The depth relation of the community patterns were confirmed by a “bioENV” analysis (Tab. 5). The table shows the relation coefficients for some of the environmental parameters tested. The highest rank correlation was found with the parameter depth and the combination of depth and proportion of sand in the sediment.

Table 4: Depth, haul length, abundance(N), abundance per 1000m trawling distance, species richness (S), evenness (J') and diversity (H') (modified from Brandt *et al.*, 2004).

station	depth (m)	haul length (m)	N	N / 1000 m	S	J'	H'
41-3	2370	4928	157	32	47	0,78	2,98
42-2	3689	4766	816	171	76	0,78	3,39
43-8	3962	4782	245	51	53	0,85	3,37
46-7	3894	5639	859	152	77	0,74	3,23
99-4	5191	5336	32	6	13	0,83	2,13
105-7	2308	2881	10	3	7	0,94	1,83
114-4	2921	4482	289	65	57	0,82	3,29
129-2	3640	4076	69	17	34	0,91	3,21
131-3	3053	3553	873	246	83	0,75	3,3
132-2	2086	2523	47	19	19	0,82	2,4
133-3	1121	1314	636	485	66	0,79	3,29
134-3	4069	4553	64	14	23	0,87	2,72
135-4	4678	2773	494	178	35	0,48	1,72
136-4	4747	5306	107	20	29	0,88	2,96
137-4	4976	4581	56	12	21	0,83	2,54
138-6	4542	4147	91	22	34	0,87	3,08
139-6	3950	6464	48	7	20	0,85	2,54
140-8	2970	4183	102	24	50	0,93	3,62
141-10	2312	3094	306	99	44	0,71	2,68
142-6	6348	4221	18	4	8	0,93	1,94
143-1	774	1441	39	27	11	0,87	2,08

The graph of the species area plot (Fig. 3.105) would flatten towards the total number of species found, if the samples were sufficient to obtain the almost full number of species inhabiting the area. This is not the case for the 21 stations sampled during ANDEEP I and II,

therefore it can be concluded that the 312 species found are only a fraction of the species inhabiting the whole sampled area.

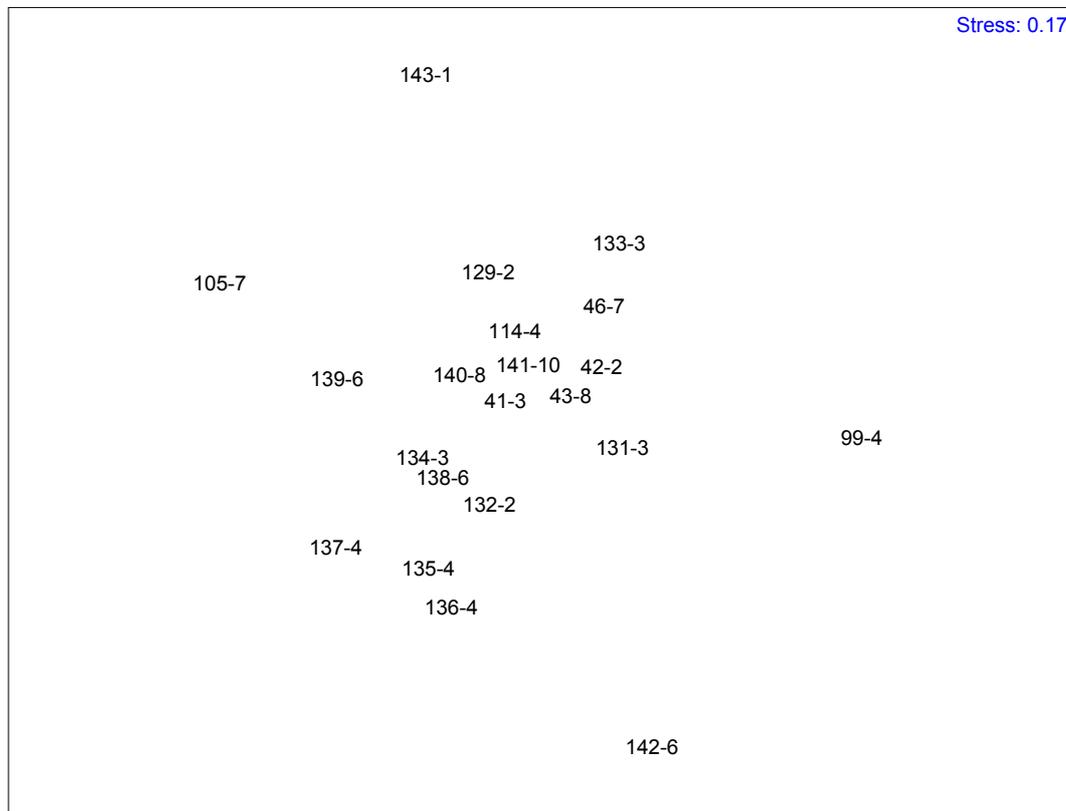


Figure 3.104: MDS plot of ANDEEP I and II station according to isopod community patterns (modified from Brandt *et al.*, in press).

Table 5: Rank correlation between isopod communities and environmental factors in the Antarctic deep sea for some of the tested variables (calculated with the bioENV module of PRIMER).

Number of factors	factor	value
1	depth	0.62
	sand	0.49
2	depth and sand	0.63
	depth and salinity	0.44
	depth and steepness	0.44

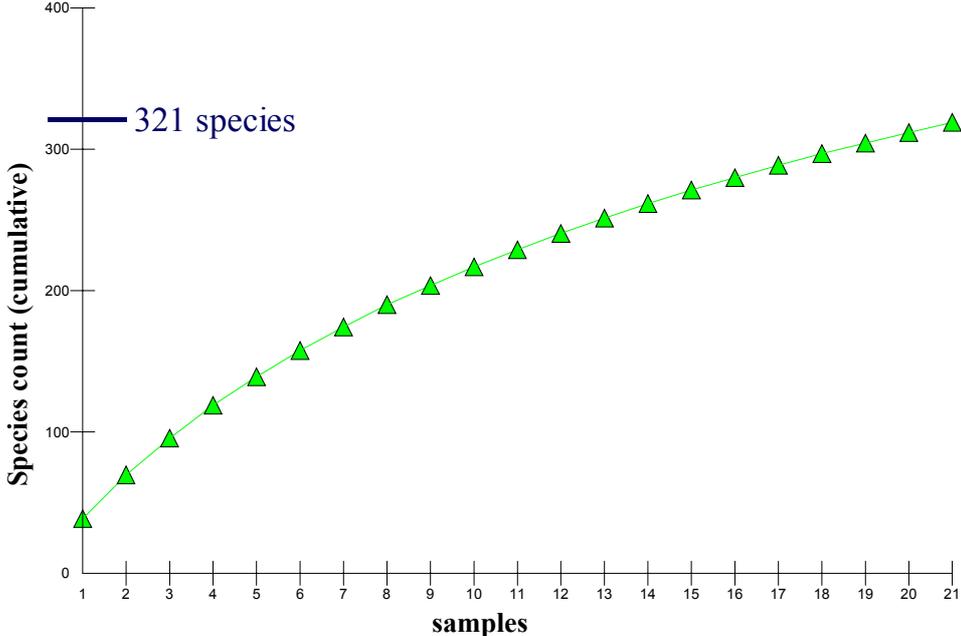


Figure 3.105: Species area plot for Isopoda of 21 EBS stations (modified from Brandt *et al.*, in press).

3.3 Phylogeny of the Haploniscidae

3.3.1 Taxa used in the analysis

Including the above described species, the family Haploniscidae now contains 118 species. Unfortunately most of these species are described inadequately and the type material was either not available or badly preserved. Therefore this analysis concentrates on those species that were described in detail or could be borrowed from museum collections.

Apart from the ANDEEP material, the species described by Lincoln (1985a, b), Park (2000), *Antennuloniscus dimeroceras* Barnard, 1920, *Disparella neomana* (Menzies and George, 1972), material from the DIVA-I expedition to the Angola Basin, the expedition ANT XXI/2 to the Southern Ocean and from the collection at the Zoological Museum Hamburg was used.

In total 48 ingroup and five outgroup taxa were chosen (Tab.6). The origin of the family Haploniscidae and its relationships to other families are unknown (Wägele, 1987), but *Neojaera* was recognized as the direct sistergroup of the Haploniscidae in the 16S rRNA based phylogeny of Michael Raupach (pers. com.). *Acanthaspidia drygalskii* Vanhöffen, 1914 (Acanthaspidiidae), *Disparella neomana* (Desmosomatidae) and *Haplomesus corniculatus* n. sp. (Ischnomesidae) were used as further representatives of the superfamily Janiroidea. *Stenetrium weddellense* (Schultz, 1978) was chosen as representative of another asellotan superfamily (Stenetrioidea). Unfortunately the types of the two monospecific genera *Abyssoniscus* and *Aspidoniscus* were not available; therefore these genera are not included in the analysis.

Table 6: Species and material used for the phylogenetic analysis.

taxon	author	material/data studied	males	females known
<i>Antennuloniscus sp. 1</i>	Würzberg and Brökeland, submitted	ANDEEP material	stage V	yes
<i>Antennuloniscus armatus</i>	Menzies, 1962	ANDEEP material	stage V	yes
<i>Antennuloniscus dimeroceras</i>	Barnard, 1920	SAM types	adult	yes
<i>Antennuloniscus diversus</i>	Lincoln, 1985b	BMNH types	adult	yes
<i>Antennuloniscus ornatus</i>	Menzies, 1962	ANDEEP material	adult	yes
<i>Antennuloniscus simplex</i>	Lincoln, 1985b	BMNH types	adult	yes
<i>Antennuloniscus latoperculus</i>	n. sp.	ANDEEP material	no males	yes
<i>Chauliodoniscus armadilloides</i>	(Hansen, 1916)	BMNH	adult	yes
<i>Chauliodoniscus coronatus</i>	Leese and Brenke, in press	ZMH types	adult	yes
<i>Chauliodoniscus tasmanicus</i>	Lincoln, 1985a	BMNH & NIWA types	adult	yes
<i>Chauliodoniscus sp.1</i>	undescribed	ANDEEP material	stage V	yes
<i>Haploniscus ampliatus</i>	Lincoln, 1985b	BMNH types	adult	yes
<i>Haploniscus angustus</i>	Lincoln, 1985b	BMNH types	adult	yes
<i>Haploniscus bicuspis</i>	(Sars, 1877)	ZMH DIVA material	stage V	yes
<i>Haploniscus bicuspis</i>	(Sars, 1877)	Data from Lincoln, 1985b	adult	yes
<i>Haploniscus borealis</i>	Lincoln, 1985b	BMNH types	adult	yes
<i>Haploniscus foresti</i>	Chardy, 1974	Data from Lincoln, 1985b	adult	yes
<i>Haploniscus hamatus</i>	Lincoln, 1985b	BMNH types	adult	yes
<i>Haploniscus ingolffi</i>	Wolff, 1962	BMNH Lincoln material	adult	yes
<i>Haploniscus miccus</i>	Lincoln, 1985a	BMNH & NIWA types	adult	yes
<i>Haploniscus nondescriptus</i>	Menzies, 1962	ZMH types	stage V	no
<i>Haploniscus piestus</i>	Lincoln, 1985a	BMNH & NIWA types	adult	yes
<i>Haploniscus rostratus</i>	(Menzies, 1962)	DIVA material (N. Brenke)	adult	yes
<i>Haploniscus saphos</i>	Lincoln, 1985a	BMNH & NIWA types	adult	yes
<i>Haploniscus silus</i>	Lincoln, 1985a	BMNH & NIWA types	adult	yes
<i>Haploniscus spinifer</i>	Hansen, 1916	ZMH & DIVA material	adult	yes
<i>Haploniscus tangaroae</i>	Lincoln, 1985a	BMNH & NIWA types	adult	yes
<i>Haploniscus cucullus</i>	n. sp.	ANDEEP material	stage V	yes
<i>Haploniscus cassilatus</i>	n. sp.	ANDEEP material	adult	yes
<i>Haploniscus weddellensis</i>	n. sp.	ANDEEP material	adult	yes
<i>Haploniscus procerus</i>	n. sp.	ANDEEP material	no males	yes

Table 6: Species and material used for the phylogenetic analysis (continued).

taxon	author	material studied	males	females known
<i>Haploniscus kyrbasius</i>	n. sp.	ANDEEP material	adult	no
<i>Haploniscus</i> sp.4	undescribed	ANDEEP material	adult	yes
<i>Haploniscus nudifrons</i>	n. sp.	ANDEEP material	no males	yes
<i>Haploniscus microkorys</i>	n. sp.	ANDEEP material	adult	no
<i>Haploniscus</i> sp. 12	undescribed	ANDEEP material	adult	yes
<i>Hydroniscus lobocephalus</i>	Lincoln, 1985a	BMNH & NIWA types	adult	yes
<i>Hydroniscus vitjazi</i>	Birstein, 1963a	ZMMU type	adult	no
<i>Mastigoniscus elegans</i>	Park, 2000	ZMB types	adult	yes
<i>Mastigoniscus gratissimus</i>	(Menzies & George, 1972)	ZMB	adult	yes
<i>Mastigoniscus pistus</i>	Lincoln, 1985°	NIWA types	adult	no
<i>Mastigoniscus platovatus</i>	Park, 2000	ZMB types	adult	yes
<i>Mastigoniscus stenocephalus</i>	Park, 2000	ZMB types	adult	yes
<i>Mastigoniscus andeepi</i>	n. sp.	ANDEEP material	adult	yes
<i>Mastigoniscus polygomphios</i>	n. sp.	ANDEEP material	adult	yes
<i>Mastigoniscus pseudoelegans</i>	n. sp.	ANDEEP material	adult	no
<i>Mastigoniscus</i> sp. A	undescribed	ANDEEP material	stage IV	no
<i>Mastigoniscus</i> sp. B	undescribed	ANDEEP material	no males	yes
<i>Neojaera</i> sp.	undescribed	ANT XXI/2 material	adult	yes
<i>Acanthaspidia drygalskii</i>	Vanhöffen, 1914	ANDEEP material	adult	yes
<i>Stenetrium weddellense</i>	(Schultz, 1978)	ZMH	adult	yes
<i>Disparella neomana</i>	(Menzies and George, 1972)	Data from S. Brix (pers. com.)	adult	yes
<i>Haplomesus corniculatus</i>	n. sp.	ANDEEP material	adult	no

3.3.2 Characters used in the analysis

The detailed description of characters is part of the discussion (4.4.1).

The data matrix contains 96 characters, 85 of these are parsimony informative; the remaining 11 characters distinguish the ingroup from the outgroup or some outgroup taxa from the other taxa. 83 characters are binary coded and 13 characters have three states. A weight of four was assigned to nine characters, a weight of two to one character; the remaining characters have weight one (Tab. 7).

Table 7: Characters, character states, *a priori* assigned weights and consistency indices of the characters used in the phylogenetic analysis.

characters	character states	weight	ci	
			acstran/deltran	unweighted
1. head frontal margin	1. concave; 2. straight; 3. convex	1	0.154/0.154	0.154/0.167
2. head frontal margin/	1. without deep indentation; 2. with deep indentation at antennal insertion	1	0.5/0.5	0.5/0.5
3. head rostrum	1. without rostrum; 2. with rostrum	1	0.091/0.091	0.091/0.091
4. rostrum	1. with ventral indentation between vertex and rostrum; 2. without ventral indentation	1	0.25/0.25	0.25/0.25
5. clypeus	1. not prolonged; 2. prolonged, adjacent to vertex, pointing dorsally; 3. prolonged, separated from vertex, pointing anteriorly	1	1.0/1.0	1.0/1.0
6. eyes	1. present; 2. absent	1	1.0/1.0	0.5/0.5
7. tergites	1. not expanded, coxae visible from dorsal; 2. laterally expanded covering coxae from above	1	0.5/0.5	0.5/0.5
8. anterior margins of pereonites 2-4 (male)	1. without prolonged angles; 2. with prolonged angles (directed anteriorly)	1	0.5/0.5	0.5/0.5
9. width of pereonites	1. all pereonites of subequal width; 2. pereonites 3-6 broadest; 3. pereonite 4 or 5 broadest	1	0.2/0.2	0.2/0.2
10. length of pereonite 7	1. as long as or slightly smaller than pereonite 6; 2. reduced, distinctly smaller than pereonite 6 (especially in males)	1	0.5/0.5	0.5/0.5
11. reduction of pereonite 7	1. still visible dorsally; 2. not discernible in dorsal view	1	1.0/1.0	1.0/1.0
12. fusion of pereonite 7	1. freely articulating with pleotelson; 2. fused to pleotelson	1	1.0/1.0	1.0/1.0
13. fusion of pereonite 6	1. freely articulating with pereonite 7; 2. fused to pereonite 7 and pleotelson	1	1.0/1.0	1.0/1.0
14. fusion of pereonite 5	1. freely articulating with pereonite 6; 2. fused with pereonites 6 and 7 and pleotelson	1	0.5/0.5	0.5/0.5
15. posterior part of body (prn 5-7 and pleotelson)	1. as long as or shorter than anterior part; 2. longer than anterior part	1	0.143/0.143	0.143/0.143
16. pleotelson posterolateral processes	1. absent; 2. present	1	1.0/1.0	1.0/1.0
17. pleotelson posterolateral processes (male)	1. not reaching terminal margin; 2. exceeding terminal margin slightly (<0.3 times as long as pleotelson); 3. more than 0.3 times as long as pleotelson	1	0.154/0.167	0.167/0.167
18. pleotelson dorsal surface	1. dorsal surface smooth; 2. dorsal surface with two rounded longitudinal ridges; 3. dorsal surface with two sharp longitudinal keels	1	0.2/0.2	0.2/0.2
19. pleotelson ventral surface	1. with bulge around branchial chamber tapering close to anus; 2. without such bulge	1	0.25/0.25	0.25/0.25
20. pleotelson ventral grooves	1. without grooves; 2. with two deep grooves between branchial chamber and tips of processes	4	0.5/0.5	1.0/0.5
21. enrollment	1. not possible; 2. with rostrum close to terminal margin; 3. with frontal margin close to branchial chamber	4	1.0/1.0	1.0/1.0

Table 7: Characters, character states, *a priori* assigned weights and consistency indices of the characters used in the phylogenetic analysis (continued).

characters	character states	weight	ci	
			actran/deltran ci (unweighted)	ci (weighted)
22. direction of antenna 1 and 2	1. anteriorly; 2. ventrally	1	1.0/1.0	1.0/1.0
23. antenna 1 article 2 length	1. longer than article 1; 2. shorter or as long as article 1	1	0.111/0.111	0.1/0.1
24. antenna 1 article 2 width	1. distinctly narrower than article 1; 2. almost as wide than article 1	1	0.167/0.167	0.167/0.2
25. antenna 2 article 1	1. larger and visible from ventral view; 2. small and concealed by article 2	1	0.5/0.5	0.5/0.5
26. antenna 2 article 3 length	1. shorter than article 6; 2. as long or longer than article 6	1	1.0/1.0	1.0/1.0
27. antenna 2 article 3 ornamentation	1. without scale or tooth; 2. with lateral scale; 3. with dorsal tooth	1	1.0/1.0	1.0/1.0
28. antenna 2 article 3 dorsal tooth	1. less than half as long as article width; 2. more than half as long as article width, but not as long as article width; 3. as long or longer than article width	1	0.4/0.4	0.4/0.4
29. antenna 2 article 3 dorsal tooth margins	1. margins smooth; 2. with jagged margin	1	0.25/0.25	0.25/0.25
30. antenna 2 articles 5 and 6	1. freely articulating; 2. fused	1	1.0/1.0	1.0/1.0
31. antenna 2 article 5	1. cylindrical; 2. inflated	1	1.0/1.0	1.0/1.0
32. antenna 2 article 6	1. without apical tooth; 2. with apical tooth	1	0.25/0.25	0.25/0.25
33. antenna 2 flagellum	1. inserting apically; 2. inserting subapically	1	1.0/1.0	1.0/1.0
34. antenna 2 number of flagellar articles	1. more than 8; 2. 8 or less than 8	1	0.25/0.25	0.25/0.25
35. mandibular palp article 3 spine-like setae	1. more than 7; 2. 4-7	1	0.5/0.5	0.5/0.5
36. molar process	1. reduced; 2. with tooth row; 3. with two cuticular ledges instead of tooth row	1	1.0/1.0	1.0/1.0
37. maxilla 1 inner lobe serrated setae	1. less than 2; 2. 2; 3. more than 2	1	0.667/0.667	0.667/0.667
38. maxilliped endite	1. not expanded; 2. distolaterally expanded	1	1.0/1.0	1.0/1.0
39. maxilliped coupling hooks	1. 2; 2. 3; 3.; 4 or more	1	0.25/0.25	0.25/0.25
40. pereopod 1	1. prehensile; 2. ambulatory	1	0.333/0.333	0.333/0.333
41. pereopods basis ventral setae	1. same number on P1-7 or varying between all pereopods; 2. different number of setae on anterior and posterior pereopods	1	0.167/0.167	0.167/0.167
42. pereopods 5-7 ischium ventral setae	1. 2; 2. more than 2	1	0.333/0.333	0.333/0.333
43. pereopods 1-4 merus medioventral seta	1. absent; 2. present	1	0.143/0.143	0.143/0.143

Table 7: Characters, character states, *a priori* assigned weights and consistency indices of the characters used in the phylogenetic analysis (continued).

characters	character states	weight	ci	
			acctran/ unweighted)	deltran (weighted)
44. pereopods 5-7 merus medioventral seta	1. absent; 2. present	1	0.143/0.143	0.143/0.143
45. pereopods merus	1. identical types of ventral apical setae on P1-7; 2. different types of ventral apical setae on P1-4 and P5-7	1	0.2/0.2	0.2/0.2
46. pereopods 5-7 merus ventral apical seta	1. simple or spine-like; 2. flagellate spine-like	1	0.25/0.25	0.25/0.25
47. pereopods carpus setae	1. identical types of setae on P1-7 (2-6); 2. different types of setae on P1-4 (2-4) and P5-7 (P5-6)	1	0.25/0.25	0.25/0.25
48. pereopod 5 carpus dorsal apical spine-like flagellate seta	1. absent; 2. present	1	0.2/0.2	0.2/0.2
49. pereopod 6 carpus dorsal apical spine-like flagellate seta	1. absent; 2. present	1	0.2/0.2	0.2/0.2
50. pereopod 7 carpus dorsal apical spine-like flagellate seta	1. absent; 2. present	1	0.125/0.125	0.125/0.125
51. pereopods carpus ventral simple setae	1. absent; 2. present	1	0.5/0.5	0.5/0.5
52. pereopods carpus ventral simple setae	1. more than half as long as width of carpus; 2. less than half as long as width of carpus	1	0.5/0.5	0.5/0.333
53. pereopod 1 carpus ventral flagellate setae	1. present; 2. absent	1	0.167/0.167	0.167/0.167
54. pereopods 2-4 carpus ventral flagellate setae	1. present; 2. absent	1	0.333/0.333	0.333/0.333
55. pereopods 5-6 carpus ventral flagellate setae	1. present; 2. absent	1	0.25/0.25	0.25/0.25
56. pereopod 7 carpus ventral flagellate setae	1. present; 2. absent	1	0.2/0.2	0.2/0.2
57. pereopod 1 carpus apical comb	1. absent; 2. present	1	1.0/1.0	1.0/1.0
58. pereopods 2-7 carpus apical combs	1. absent; 2. present	1	0.5/0.5	0.5/0.5
59. pereopods 2-5 carpus apical dorsal comb	1. absent; 2. present	1	0.167/0.143	0.143/0.143
60. pereopods 3-5 carpus apical lateral combs	1. spinose and setose; 2. both combs spinose; 3. both combs setose	1	0.286/0.286	0.286/0.286

Table 7: Characters, character states, *a priori* assigned weights and consistency indices of the characters used in the phylogenetic analysis (continued).

characters	character states	weight	ci	
			acctran/deltran ci (unweighted)	ci (weighted)
61. pereopods 1-4 carpus and propodus ventral combs	1. inconspicuous; 2. conspicuous	1	0.5/0.5	0.5/0.5
62. pereopods 1-4 propodus ventral combs	1. apical comb not extended; 2. apical comb distinctly extended	1	0.5/0.5	0.5/0.5
63. pereopods 1-4 propodus ventral flagellate setae	1. present; 2. absent	1	0.5/0.5	0.667/0.5
64. pereopods 5-7 propodus ventral flagellate setae	1. present; 2. absent	1	0.25/0.25	0.25/0.25
65. pereopods 2-4 propodus mediodorsal setae	1. absent; 2. present	1	0.125/0.125	0.125/0.125
66. pereopods 5-7 propodus mediodorsal setae	1. absent; 2. present	1	0.5/0.5	0.5/0.5
67. pereopods dactylus dorsal claw	1. one third of dactylus length or longer; 2. less than one third of dactylus length	1	0.5/0.5	0.5/0.5
68. pereopods 1-7 dactylus ventral claw	1. about as long as dorsal claw; 2. distinctly smaller than dorsal claw	1	1.0/1.0	1.0/1.0
69. pleopod 1 male rami	1. separated; 2. completely fused	4	1.0/1.0	1.0/1.0
70. pleopod 1 male length	1. less than half as long as pleotelson; 2. more than half as long as pleotelson	4	1.0/1.0	1.0/1.0
71. pleopod 1 and 2	1. covering most of ventral pleotelson; 2. smaller	1	0.333/0.333	0.333/0.333
72. pleopod 1 male distal part	1. proximally broader than distally; 2. distally broader than proximally	1	1.0/1.0	1.0/1.0
73. pleopod 1 subapical processes	1. absent; 2. present	1	0.125/0.125	0.125/0.125
74. pleopod 1 shape	1. lateral margins convex; 2. lateral margins concave	1	0.125/0.125	0.125/0.125
75. pleopod 1 apical margin	1. with apical indentation between sympods; 2. sympods with a continuous distal margin	1	0.143/0.143	0.134/0.143
76. pleopod 1 proximal	1. narrowing in the proximal part; 2. proximal part broadest	1	0.2/0.2	0.2/0.2
77. pleopod 2 male size	1. concealed by pleopod 1; 2. forming an operculum together with pleopod 1	4	1.0/1.0	1.0/1.0
78. pleopod 2 basipod setae	1. on whole lateral margin; 2. only in the distal part (sometimes a single seta laterally)	1	0.091/0.091	0.083/0.083
79. pleopod 2 endopod	1. endopod with open sperm groove; 2. with closed sperm duct	4	1.0/1.0	1.0/1.0
80. pleopod 2 endopod length	1. about as long as or slightly longer than basipod; 2. at least 2 times as long as basipod	2	0.333/0.333	0.333/0.333
81. pleopod 2 endopod article 1	1. directed medioproximally; 2. directed laterally	4	1.0/1.0	1.0/1.0

Table 7: Characters, character states, *a priori* assigned weights and consistency indices of the characters used in the phylogenetic analysis (continued).

characters	character states	weight	ci	
			acctran/deltran	
			ci (unweighted)	ci (weighted)
82. pleopod 2 female	1. less than half as long as pleotelson; 2. forming an operculum that covers the branchial chamber	4	1.0/1.0	1.0/1.0
83. pleopod 3 endopod plumose setae	1. 4 or more; 2. 3	1	1.0/1.0	1.0/1.0
84. pleopod 3 exopod size	1. two articles, as long as or longer than endopod; 2. one article, shorter than endopod	1	1.0/1.0	1.0/1.0
85. pleopod 3 exopod bristles	1. without fringe of bristles; 2. with fringe of fine bristles on lateral margin	1	0.5/0.5	0.5/0.5
86. pleopod 4 exopod	1. present; 2. absent	1	1.0/1.0	1.0/1.0
87. pleopod 4 exopod articles	1. with two articles; 2. with one article	1	0.5/0.5	1.0/1.0
88. pleopod 4 exopod bristles	1. without fringe of setae; 2. with fringe of fine setae at lateral margin	1	0.5/0.5	0.5/0.5
89. pleopod 4 exopod plumose setae	1. with several plumose setae; 2. with one plumose seta; 3. without plumose setae	1	0.5/0.5	1.0/1.0
90. pleopod 4 exopod size	1. not reaching terminal margin of endopod; 2. reaching or exceeding terminal margin of basipod	1	0.333/0.333	0.333/0.25
91. pleopod 5	1. present; 2. absent	1	1.0/1.0	1.0/1.0
92. pleopod 5 plumose setae	1. with plumose setae; 2. without plumose setae	1	1.0/1.0	/1.0
93. uropod	1. with two rami; 2. with one ramus	1	1.0/1.0	0.5/0.5
94. penes	1. well separated between coxae and midline of pereonite 7; 2. adjacent posteromedially on pereonite 7	4	1.0/1.0	1.0/1.0
95. sexual dimorphism	1. only antennae and pleopods sexually dimorph; 2. other characters sexually dimorph	1	0.25/0.25	0.25/0.25
96. sexual dimorphic characters	1. pleotelsonic processes sexually dimorphic; 2. pereonites sexually dimorphic; 3. shape of pleotelson sexually dimorphic	1	1.0/1.0	1.0/1.0

3.3.3 Parsimony analysis

96 equally parsimonious trees of length 344 were found in the analysis using unweighted characters; the consistency index (CI) is 0.32 (0.29 excluding uninformative characters) and the retention index (RI) 0.71. The strict consensus (Fig. 3.106) and the 50% majority-rule consensus trees were identical.

The analysis with weighted characters produced 1344 equally parsimonious trees of length 378, with a consistency index of 0.37 (0.32 excluding uninformative characters) and a retention index of 0.73. In the analysis with weighted characters the 50% majority-rule consensus tree (Fig. 3.108) was slightly more resolved than the strict consensus (Fig. 3.107).

The comparison of the two strict consensus trees shows that the unweighted tree has a better resolution in clade 26, which is equivalent to *Mastigoniscus*.

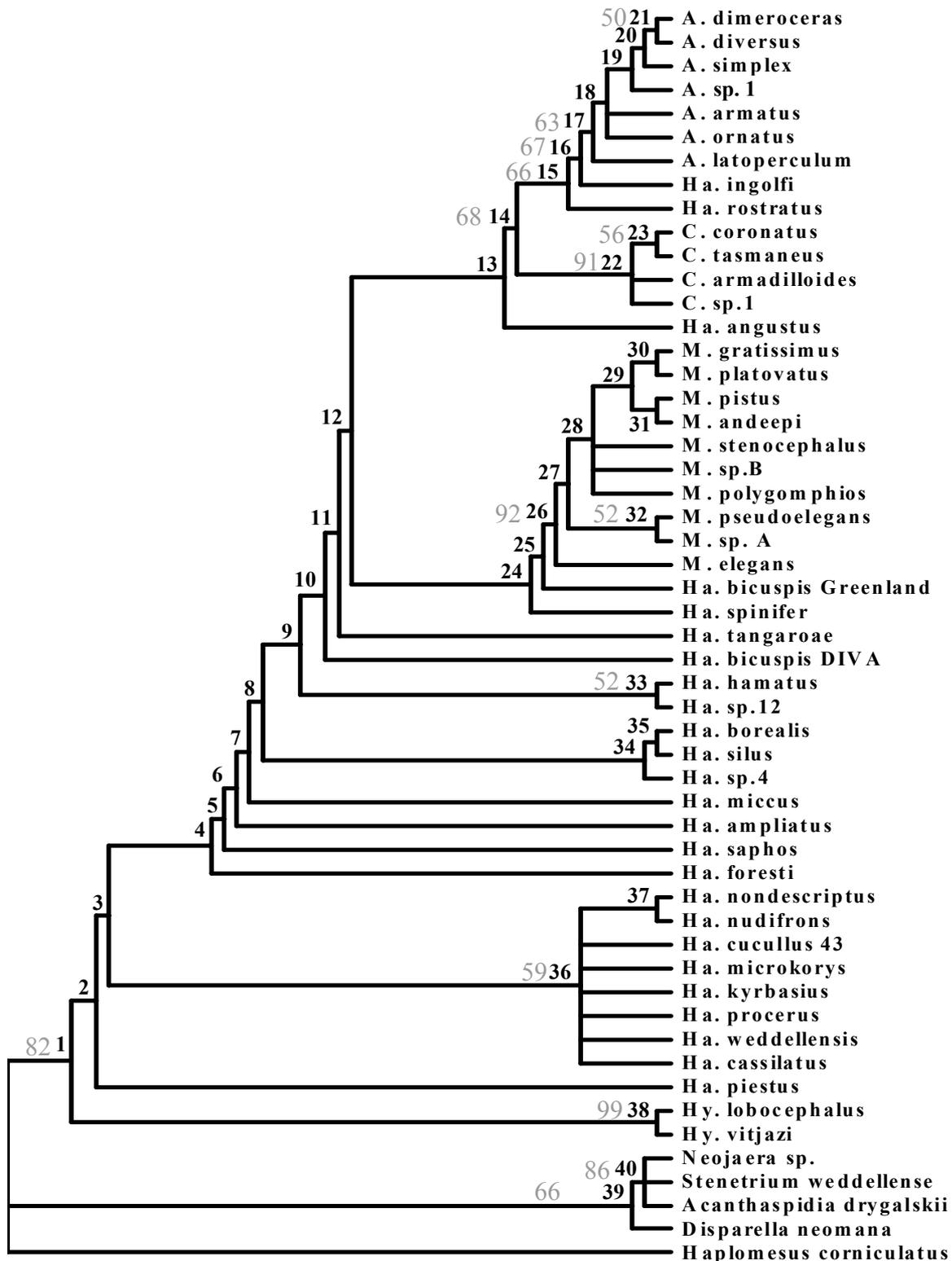


Figure 3.106: Strict consensus of 96 trees, all characters have equal weight. Numbers in black refer to clades, numbers in grey refer to bootstrap values of clades present in the bootstrap 50% majority rule tree (100 replicates).

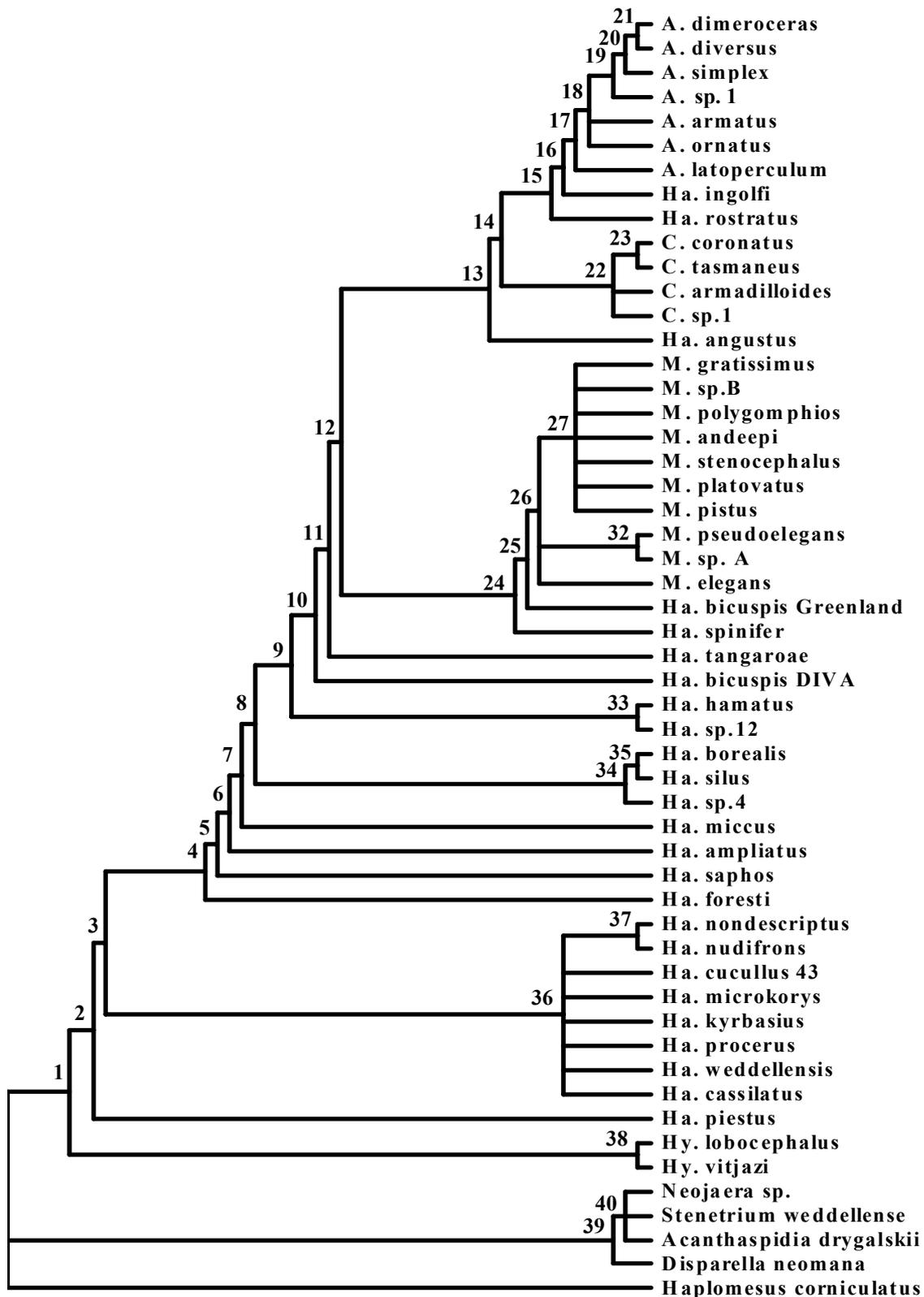


Figure 3.107: Strict consensus of 1344 trees, characters have weights from 1-4. Numbers refer to clades.

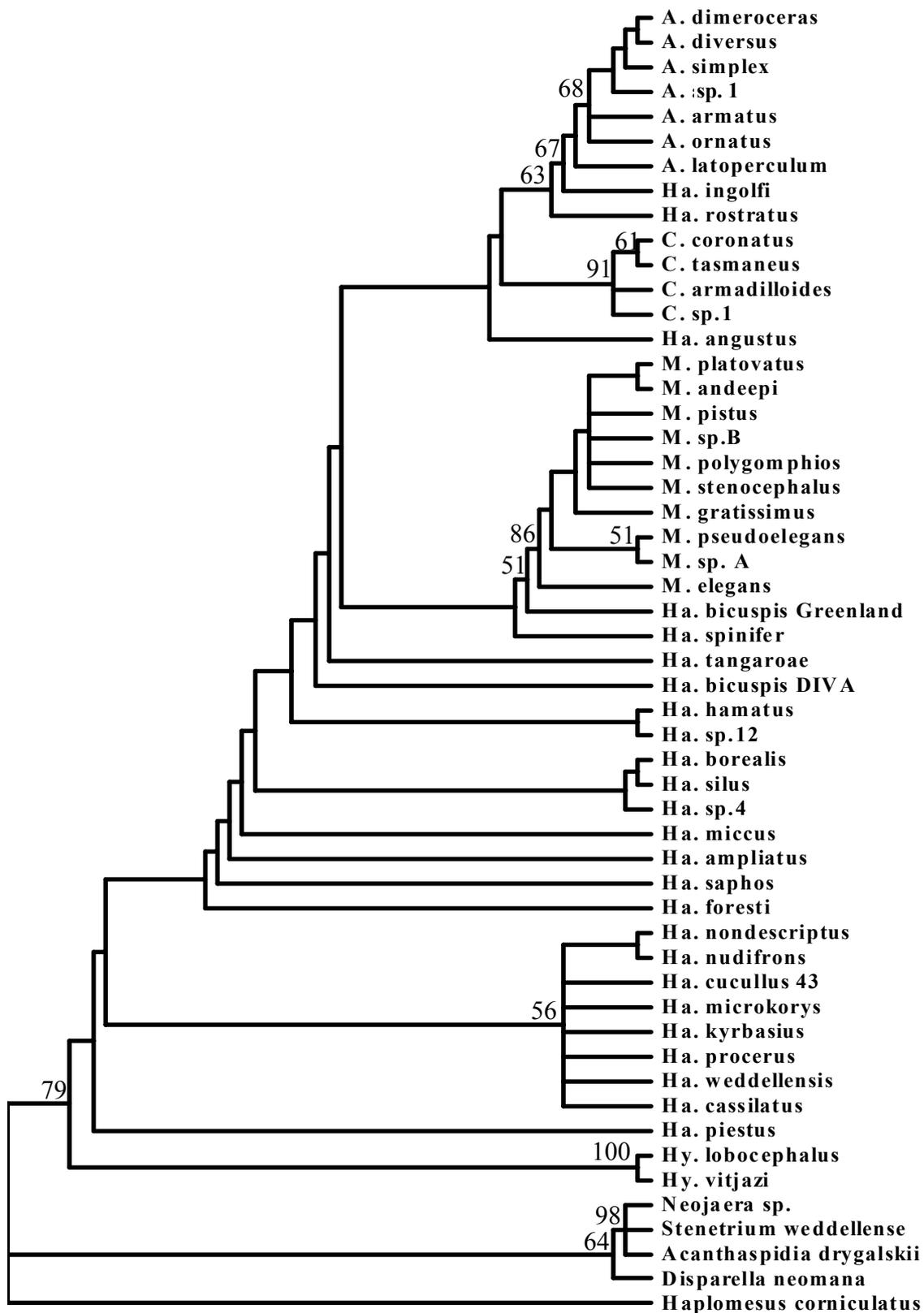


Figure 3.108: 50% majority rule consensus of 1344 trees, characters have weights from 1-4. Numbers refer to Bootstrap values of clades present in the bootstrap 50% majority rule tree (100 replicates).

Table 8: Taxa and synapomorphy list for unweighted and weighted consensus using delayed transformation as character optimization criterion; grey cells: clade does not exist in the weighted consensus tree; arrows indicate differences between weighted and unweighted analysis.

clade	taxa	synapomorphies unweighted	synapomorphies weighted
1	Haploniscidae	3(1>2), 9(1>2), 15(2>1), 17(1>2), 38(1>2), 40(1>2), 49(1>2), 51(1>2), 61(1>2), 66(2>1), 74(1>2)	3(1>2), 9(1>2), 15(2>1), 17(1>2), 38(1>2), 40(1>2), 49(1>2), 51(1>2), 61(1>2), 66(2>1), 74(1>2)
2	clade 1 without <i>Hydrioniscus</i>	4(2>1), 18(1>3), 27(1>3), 46(1>2), 63(1>2), 75(1>2)	4(2>1), 18(1>3), 27(1>3), 46(1>2), 63(1>2), 75(1>2)
3	clade 2 without <i>H. piestus</i>	19(2>1)	19(2>1)
4	clade 3 without <i>Haploniscus cucullus</i> complex and <i>H. nondescriptus</i>	9(2>3), 35(1>2), 42(2>1), 64(1>2)	9(2>3), 35(1>2), 42(2>1), 64(1>2)
5	clade 4 without <i>H. foresti</i>	45(2>1), 46(2>1)	45(2>1), 46(2>1)
6	clade 5 without <i>H. saphos</i>	75(2>1)	75(2>1)
7	clade 6 without <i>H. ampliatus</i>	9(3>2)	9(3>2)
8	clade 7 without <i>H. miccus</i>	28(2>3), 56(1>2)	28(2>3), 56(1>2)
9	clade 8 without <i>H. borealis</i> , <i>H. silus</i> , <i>H. sp.4</i>	43(2>1), 55(1>2)	43(2>1), 55(1>2)
10	clade 9 without <i>H. hamatus</i> , <i>H. sp.1</i>	4(1>2)	4(1>2)
11	clade 10 without <i>H. bicuspis</i> DIVA	1(1>2), 53(1>2), 65 (2>1)	53(1>2), 65 (2>1), 1(1>2)
12	clade 11 without <i>H. tangaroae</i>	3(2>1), 15(1>2), 19(1>2), 60(2>3)	3(2>1), 15(1>2), 19(1>2), 60(2>3)
13	clade 12 without <i>Mastigoniscus</i> , <i>H. spinifer</i> , <i>H. bicuspis</i> Greenland	9(2>1), 18(3>1), 54(1>2)	17(2>1), 18(3>1), 54(1>2)
14	clade 13 without <i>H. angustus</i>	39(2>1), 49(2>1), 78(1>2)	39(2>1), 49(2>1), 78(1>2),
15	clade 14 without <i>Chauliodoniscus</i>	1(2>3), 26(1>2), 28(3>2), 32(1>2), 33(1>2), 62(1>2)	1(2>3), 26(1>2), 28(3>2), 32(1>2), 33(1>2), 62(1>2)
16	<i>Antennuloniscus</i> , <i>H. ingolfi</i>	34(1>2), 50(1>2), 60(3>1)	34(1>2), 50(1>2), 60(3>1)
17	<i>Antennuloniscus</i>	5(1>3), 25(1>2), 30(1>2)	5(1>3), 25(1>2), 30(1>2)
18	clade 17 without <i>A. latoperculus</i>	18(1>2), 23(1>2), 28(2>1), 41(1>2), 43(1>2), 95(1>2),	18(1>2), 23(1>2), 28(2>1), 41(1>2), 43(1>2), 95(1>2),
19	clade 18 without <i>A. armatus</i> , <i>A. ornatus</i>	17(1>2)	17(1>2)
20	<i>A. simplex</i> , <i>A. diversus</i> , <i>A. dimeroceras</i>		
21	<i>A. diversus</i> , <i>A. dimeroceras</i>		
22	<i>Chauliodoniscus</i>	8(1>2), 14(2>1), 15(2>1), 21(1>3), 31(1>2), 75(1>2), 95(1>2), 96(3>2)	8(1>2), 14(2>1), 15(2>1), 21(1>3), 31(1>2), 41(1>2), 75(1>2), 96(3>2)
23	<i>C. coronatus</i> , <i>C. tasmanus</i>		
24	<i>Mastigoniscus</i> , <i>H. spinifer</i> , <i>H. bicuspis</i> Greenland	28(3>2), 80(1>2), 95(1>2), 96(3>1)	28(3>2), 80(1>2), 95(1>2)
25	<i>Mastigoniscus</i> , <i>H. bicuspis</i> Greenland	29(1>2), 73(1>2), 74(2>1), 81(1>2)	29(1>2), 73(1>2), 74(2>1), 81(1>2)
26	<i>Mastigoniscus</i>	10(1>2), 44(2>1), 54(1>2), 59(1>2), 71(2>1)	10(1>2), 44(2>1), 54(1>2), 59(1>2), 71(2>1)
27	clade 26 without <i>M. elegans</i>	41(1>2)	41(1>2)
28	clade 27 without <i>M. pseudoelegans</i> , <i>M. sp. A</i>	18(3>1)	
29	<i>M. andeepi</i> , <i>M. pistus</i> , <i>M. platovatus</i> , <i>M. gratissimus</i>		

Table 8: Taxa and synapomorphy list for unweighted and weighted consensus using delayed transformation as character optimization criterion; grey cells: clade does not exist in the weighted consensus tree; arrows indicate differences between weighted and unweighted analysis (continued).

clade	taxa	synapomorphies unweighted	synapomorphies weighted
30	<i>M. platovatus</i> , <i>M. gratissimus</i>	78(1>2)	
31	<i>M. andeepi</i> , <i>M. pistus</i>	52(1>2)	
32	<i>M. pseudoelegans</i> , <i>M. sp. A</i>	60(3>1)	60(3>1)
33	<i>H. hamatus</i> , <i>H. sp. 12</i>	44(2>1), 72(1>2), 73(1>2)	44(2>1), 72(1>2), 73(1>2)
34	<i>H. sp. 4</i> , <i>H. silus</i> , <i>H. borealis</i>	1(1>2), 60(2>1)	1(1>2), 60(2>1)
35	<i>H. silus</i> , <i>H. borealis</i>	23(1>2), 75(1>2)	23(1>2), 75(1>2)
36	<i>Haplونiscus cucullus complex</i> , <i>H. nondescriptus</i>	28(2>1)	28(2>1)
37	<i>H. nondescriptus</i> , <i>H. nudifrons</i>	3(2>1)	3(2>1)
38	<i>Hydroniscus</i>	2(1>2), 10(1>2), 11(1>2), 21(1>2), 22(1>2), 23(1>2), 52(1>2), 65(2>1), 67(1>2)	2(1>2), 10(1>2), 11(1>2), 21(1>2), 22(1>2), 23(1>2), 52(1>2), 65(2>1), 67(1>2)
39	<i>Neojaera sp.</i> , <i>Stenotrium weddellense</i> , <i>Acanthaspida drygalskii</i> , <i>Disparella neomana</i>	12(2>1), 13(2>1), 14(2>1), 36(2>1), 44(2>1), 58(2>1)	12(2>1), 13(2>1), 14(2>1), 36(2>1), 44(2>1), 58(2>1)
40	<i>Neojaera sp.</i> , <i>Stenotrium weddellense</i> , <i>Acanthaspida drygalskii</i>	27(1>2), 43(1>2), 45(1>2), 57(1>2), 68(1>2), 84(1>2)	27(1>2), 43(1>2), 45(1>2), 57(1>2), 68(1>2), 84(1>2)

In both analyses the genera *Antennuloniscus*, *Chauliodoniscus*, *Mastigoniscus* and *Hydroniscus* were found to be monophyletic, while *Haplونiscus* proved to be polyphyletic. Several *Haplونiscus* species are found as direct sistergroups or closely related to *Mastigoniscus* or *Antennuloniscus*.

In the following, the major clades of the ingroup found in the analysis are described. Accelerated transformation (ACCTRAN) as well as delayed transformation (DELTRAN) was tested as character state optimization methods; DELTRAN produced a more convincing synapomorphy pattern for those characters known as synapomorphy for the genera or the family, therefore these results are shown (see Tab. 8). Numbers in square brackets refer to the characters.

Clade 15 consists of *Antennuloniscus*, *Haplونiscus ingolfi* Wolff, 1962 and *H. rostratus* and is defined by the following synapomorphies: the convex frontal margin [1], although it is straight in some terminal taxa, the elongated article 3 of antenna 2 [26], the tooth on article 3 is more than half as long but not as long as the width of the article [28], article 6 of antenna 2 with apical tooth [32], the flagellum of antenna 2 inserts subapically [33] and the apical ventral comb is extended on pereopods 1-4 [62].

Clade 16 comprises *Antennuloniscus* and *H. ingolfi* and is defined by eight flagellar

articles in antenna 2 (6 in *A. simplex*) [34], an apical dorsal flagellate setae on carpus of pereopod 7 [50], and the apical carpus combs, which comprise a spinose and a setose comb [60].

Antennuloniscus (Clade 17) is characterized by three synapomorphies: clypeus prolonged anteriorly [5], first article of antenna 2 reduced [25] and articles 5 and 6 of antenna 2 fused [30].

Clade 14 is formed by *Chauliodoniscus* and clade 15, based on four characters: maxilliped with two coupling hooks [39], the apical dorsal flagellate seta on carpus of pereopod 6 absent [49], only distal margin of basipod of pleopod 2 with setae [78], pleotelson without bulge around branchial chamber [19].

Haploniscus angustus Lincoln, 1985b is the sistergroup to clade 14. Synapomorphies are: pereonites of subequal width [9], ventral flagellate setae absent from carpus of pereopods 2-4 [54] and dorsal surface of pleotelson smooth [18].

Clade 13 comprises clade 15, *Chauliodoniscus* and *H. angustus*. It is defined by pereonites of subequal width [9], pleotelson with a smooth dorsal surface [18], and the absence of flagellate setae from carpus of pereopods 2-4 [54].

Chauliodoniscus (clade 22) is characterized by prolonged anterior angles of one or more of pereonites 2-4 at least in males [8], pereonite 5 freely articulating with pereonite 6 [14], posterior part of body as long or shorter than anterior part [15], conglobating with frontal margin close to branchial chamber [21], article 5 of antenna 2 inflated, with convex lateral margins [31], sexually dimorphic [95] in the shape of the pereonites [96].

The following synapomorphies define clade 24, which comprises *Mastigoniscus*, *Haploniscus bicuspis* and *H. spinifer* Hansen, 1916 (Lincoln's specimens from Greenland): Tooth on article 3 of antenna 2 more than half as long but not as long as width of article [28], endopod of pleopod 2 elongated [80] and sexual dimorphism [95].

The sistergroup relationship between *H. bicuspis* and *Mastigoniscus* (clade 25) is defined by the jagged margins of the dorsal tooth on article 3 of antenna 2 [29], the lack of subapical processes on pleopod 1 [73], the shape of pleopod 1 that is broadening more distally [74] and the laterally directed first article of the endopod of pleopod 2 [81].

Mastigoniscus (clade 26) is characterized by the following synapomorphies: pereonite 7 reduced [10], merus of pereopods 5-7 lacks medioventral setae [44], pereopods 2-4 without ventral flagellate setae on carpus [54], carpus of pereopods 2-5 with apical dorsal combs [59], pleopods 1 and 2 of the male enlarged, covering most of the pleotelson [71], pleotelsonic processes sexually dimorphic [96].

Clade 36 contains the species of the *Haploniscus cucullus* complex and *Haploniscus nondescriptus* and is defined by only one synapomorphy: dorsal tooth on article 3 of antenna 2 is more than half as long but not as long as width of article [28]. The sistergroup relationship of *H. nudifrons* and *H. nondescriptus* is based on the absence of the rostrum [3].

Hydrioniscus (clade 38) was found to be the most basal genus of the Haploniscidae; it is characterized by numerous synapomorphies: Frontal margin with two deep indentations [2], pereonite 7 reduced [10], not visible dorsally [11], conglobating with frontal margin close to terminal margin [21], antennae directed ventrally [22], article 2 of antenna 1 shorter than article 1 [23], ventral simple setae on carpus less than half as long as carpus [52], mediodorsal setae on propodus of pereopods 2-4 absent [65], claw less than one third of dactylus length [67].

Haploniscus piestus Lincoln, 1985a was found to be the sistergroup of all remaining Haploniscidae, except *Hydrioniscus* (clade 3). Synapomorphy of clade 3 is the bulge around branchial chamber [19].

Within the remaining *Haploniscus* species two small clades were found. Clade 33 consists of *H. hamatus* and the undescribed species *H. sp. 12*; both were characterized by the unusual, distally extended pleopod 1 [72] that lacked distolateral processes [73], and by the absence of medioventral setae on propodus of pereopods 5-7 [44]. Clade 34 comprises *H. borealis* Lincoln, 1985b, *H. silus* Lincoln, 1985a and the undescribed species *H. sp. 4*, and is based on the straight frontal margin [1] and the apical carpus combs, which are setose and spinose [60].

H. foresti Lincoln, 1985b, *H. saphos* Lincoln, 1985a, *H. ampliatus* and *H. miccus* Lincoln, 1985a are branching off between clades 36 and 34. Clade 4 is defined by the following synapomorphies: pereonite 4 and 5 broadest [9], mandibular palp article 3 with 4-7 setae [35], ischium of pereopods 5-7 with 2 ventral setae [42] and propodus of pereopods 5-7 without ventral flagellate setae [64]. Clade 5 is characterized by identical types of ventral apical setae on the merus of posterior and anterior pereopods [45] and the absence of flagellate setae from the merus of pereopods 5-7 [46]; clade 6 by the apically indented margin of pleopod 1 [75]. The only synapomorphy for clade 7 is the body shape, with pereonites 3-6 being broadest.

Clade 8 consists of clade 34 and clade 9. It is defined by the tooth of article 3 of antenna 2, which is as long or longer than the width of the article [28] and the absence of flagellate setae from the ventral carpus of pereopod 7 [56].

The absence of medial setae from the ventral merus of pereopods 1-4 [43] and the absence of flagellate setae from the ventral carpus of pereopods 5 and 6 [55] define clade 9, which includes clades 10 and 33

Clade 10 comprises clade 11 and *H. bicuspis* from the Angola Basin; it is defined by the shape of the rostrum that lacks a ventral indentation [4]. Clade 11 includes clade 12 and *H. tangaroae* and is defined by the absence of flagellate setae from the ventral carpus of pereopod 1 [53], the absence of mediodorsal setae from the dorsal propodus of pereopods 2-4 [65], and the straight margin of the head [1].

The sistergroup relationship of clades 13 and 24 (clade 12), which contain the genera *Mastigoniscus*, *Chauliodoniscus* and *Antennuloniscus* as well as several *Haploniscus* species is supported by the absence of a rostrum [3], the longer posterior part of the body [15], the absence of a bulge around the branchial chamber [19] and setose apical carpus combs [60].

The ingroup (clade 1, Haploniscidae) is defined by numerous synapomorphies: rostrum present [3], pereonites 3-6 broadest [9], posterior part of body shorter or as long as anterior part [15], posterolateral processes of pleotelson exceeding terminal margin slightly [17], maxilliped endite distolaterally expanded [38], pereopod 1 ambulatory [40], flagellate seta present on dorsal apical carpus of pereopod 6 [49], carpus with simple setae [51], ventral combs on carpus and propodus of anterior pereopods conspicuous [61], propodus of pereopods 5-7 without mediodorsal setae [66], pleopod 1 broadening more proximally, lateral margins concave [74].

For clades 20, 21 and 29 no synapomorphies were found in both of the two most distant trees compared. Clade 20 and 21 are subgroups of *Antennuloniscus*, while clade 29 belongs to *Mastigoniscus* and is found only in the tree obtained with unweighted characters.

Differences between the analysis with weighted and unweighted characters were found in clades 13 and 22. By character weighting an additional synapomorphy was found in both clades: pleotelsonic processes not reaching terminal margin [17] for clade 13 and different number of ventral setae on basis of anterior and posterior pereopods [41] for clade 22.

4 Discussion

4.1 Taxonomy

In order to avoid confusion the remarks about the species and genera described within this thesis were included in the results chapter and are not repeated here.

4.1.1 Family Ischnomesidae

4.1.1.1 Neoteny in the family Ischnomesidae

Neoteny is defined as the retention of juvenile characters in adult specimens. Postmarsupial stages of isopods usually lack the seventh pereonite and its pair of pereopods. During postmarsupial development pereonite 7 usually develops from manca I to manca II stage. The seventh pair of pereopods appears in the third stage after leaving the marsupium (Wolff 1962: 20), but is still smaller than the other pereopods. The lack of pereopod 7 in the two species described above, is a juvenile character that persists in adults, even when sexual maturity is reached, recognizable by the fully developed marsupium in *Stylomesus hexapodus* and the fully developed male pleopods in *Haplomesus corniculatus*.

Haplomesus tenuispinis Hansen, 1916, *H. angustus* Hansen, 1916 and *Ischnomesus curtispinis* Brandt, 1992 are described with six pairs of pereopods as well. While *H. tenuispinis* and *I. curtispinis* might be described from juvenile specimens, the well developed pleopod 1 of the illustrated specimen of *H. angustus* indicates, that this species also is neotenic.

4.1.2 Family Haploniscidae

4.1.2.1 General remarks

Contrary to most taxa of the Asellota, which are rather fragile and often lack essential parts of their limbs, the Haploniscidae are usually found complete and relatively undamaged in the samples, which is probably due to their rather compact morphology. The family is rather conservative (Wägele, 1987), the interspecific variation is low. Interspecific differences are mostly subtle and need careful observation.

Important diagnostic characters are the shape of the pleotelson with its posterolateral processes, although these might be hardly visible dorsally, and certainly the compact more or less oval body outline, resembling terrestrial oniscidean isopods, which is due to the lateral extension of the pereonites

The pereopods and especially their setation have been only marginally described in the literature about Haploniscidae. Only Lincoln (1985a) covered these limbs in more detail in his family description. According to proportions and setation the pereopods can be divided into two, respectively four groups. Pereopods 1-4 are more similar to each other than to pereopods 5-7. However, pereopod 1 differs also considerably from pereopods 2-4 and the same applies to pereopod 7 and pereopods 5-6. The degree of these differences varies between species. Lincoln (1985a) already noticed, that the insertion of posterior and anterior pereopods differs; while the anterior pairs are more remote from each other and located near the anterior margins of the pereonites, the posterior pereopods are inserting more closely to each other at the posterior margins of the appertaining pereonites. Lincoln (1985a) also described the fact that the anterior pereopods tend to have slender simple setae, while the posterior pereopods often have spine-like setae. This is true for many species, especially for those without flagellate setae; spine-like or at least more robust setae in the posterior pereopods can be found on the ischium, the merus, the carpus and propodus. A different pattern may be observed in species with flagellate setae; here the difference between anterior and posterior pereopods is often less obvious on the carpus, where flagellate setae may be present in all pereopods, even if they are sometimes more numerous in the posterior pereopods; however, in most of these species, the propodus of the anterior pereopods does not have flagellate setae in contrast to that of the posterior pereopods. In some species, pereopod 1 and/or pereopod 7 lack ventral flagellate setae despite of them being present in the rest of the pereopods. Another difference between pereopod 1 and the remaining legs is the apical comb of the carpus; usually pereopod 1 has only one comb, while the other pereopods have two combs. Pereopod 1 also lacks the broom

setae of the basis, which are present in all other pereopods. Two different types of ventral combs on carpus and propodus could be determined; in most species the combs are spiky with a prominent first spine followed by more slender spines of decreasing length (Fig. 3.12); SEM investigations of an *Antennuloniscus* species revealed a different type (Fig. 3.12); here the combs are less spiky, almost hair-like and lack a differentiated first spine; besides, the studied species had two rows of combs, while most species of the Haploniscidae possess only one row. Additionally, the propodus may be covered all over with small scale rows, which are hardly visible when studied with the compound microscope, but obvious when viewed under the SEM. Lincoln also noticed the flagellate spine-like seta dorsally on the carpus of pereopod 6 in some species. Such a seta may be found also on pereopods 5 or 7 in some species.

The uropods show slight interspecific variation according to their proportions, but the setae are often broken off and cannot be used for species comparison.

The family comprises seven genera: *Haploniscus*, *Hydroniscus*, *Aspidoniscus*, *Abyssoniscus*, *Antennuloniscus*, *Chauliodoniscus* and *Mastigoniscus*. Recently George (2004) described the genus *Chandraniscus*, based on questionable characters: the nonfused pereonites 5-7, the lack of a dorsal spine on article 2 of antenna and uropods with single segment. The lack of fusion of pereonites 5-7 has to be doubted, because no haploniscid species apart from the aberrant species *Abyssoniscus ovalis* has freely articulating pereonites 6 and 7, and the Lincoln species included by George in the new genus (*Haploniscus tangaroae* Lincoln, 1985a, *H. silus* Lincoln, 1985a, *H. miccus* Lincoln, 1985a, *H. piustus* Lincoln, 1985a, *H. saphos*) have definitely fused pereonites, although the suture line between the segments may be still visible, as clearly stated in most of Lincoln's (1985a) descriptions. No haploniscid species has a spine on the second article of antenna 2. It is highly doubtful that the species of the new genus described by George (2004) possess single-articulated uropods; instead the suture between basipod and ramus was probably overlooked by George, as it is often inconspicuous. At least the Lincoln species possess the typical haploniscid uropod with basipod and ramus.

The type specimens of the two monospecific genera *Abyssoniscus* and *Aspidoniscus* were not available and unfortunately the descriptions of both species are not detailed enough for further analyses. Therefore these genera were not included in the taxonomy and phylogeny chapters.

4.1.2.2 Intraspecific variability

Intraspecific variability has to be regarded when choosing characters for diagnostic and phylogenetic purposes. Three types of intraspecific variability can be distinguished: Sexual dimorphism, ontogenetic variability, and normal variability, which is not related to sex and age.

4.1.2.2.1 Variability without relation to sex or age

Numerical characters are often variable, such as the number of flagellar articles of antenna 2, the number of teeth in the molar of the mandible or the number of certain setae in the mouthparts and the pleopods. The number of setae of the pereopods is variable within species of *Haploniscus*, for example the *Haploniscus cucullus complex*, but seems to be more conserved in species of *Mastigoniscus* and probably also *Antennuloniscus* and *Chauliodoniscus*, where the number of some setae, especially the spine-like setae of carpus and propodus of P5-7, seems to be constant for the whole genus.

4.1.2.2.2 Sexual dimorphism

Sexual dimorphism is a common phenomenon within the Haploniscidae. Besides pleopod 1 and 2 it usually includes the antennae and sometimes also the body shape. Variation of antenna 1 includes the number of flagellar articles, which is common in the genus *Antennuloniscus* and the number of aesthetascs. While the aesthetasc formula is constant between specimens of the same sex and age it varies between adult females and males as well as between males of different stages. Adult males of most species possess more aesthetascs than females. The second antenna of males is in most species more robust than that of females and the number of setae of the flagellar articles is increased. In some species also the number of setae on the peduncular articles 5 and 6 is higher. This difference in the number of aesthetascs indicates that the chemical sense plays an important role for males in mate finding (Wägele, 1992). Interestingly the number of aesthetascs does not vary between males and females of *Haploniscus cassilatus* and *H. weddellensis*, while the number of setae on antenna 2 is higher in males and the question arises whether mate finding in these species depends on the aesthetascs. Sexual dimorphism of the body shape may concern the head, the pereonites or the pleon. Variation of the head can be observed in most species of *Mastigoniscus*, while variation in the shape of the pereonites 2-4 is typically for the genus *Chauliodoniscus*.

The shape of the pleon is subject of sexual dimorphism in *Antennuloniscus* and *Mastigoniscus*. While species of *Mastigoniscus* show the greatest variation mainly in the length of the pleotelsonic processes, is the whole pleon of *Antennuloniscus* males broader than that of females.

Due to sexual dimorphism the allocation of males and females to the same species is sometimes extremely difficult. This concerns especially species of *Mastigoniscus* where species identification of the females is sometimes only possible by regarding the context, e. g. the presence of only one type of males at this station. The difference in the prolongation of the angles of the anterior pereonites in *Chauliodoniscus* may result in similar problems.

4.1.2.2.3 Ontogenetic variability

Wolff (1962) has already described most of the different stages of *Haploniscus bicuspis*, *H. spinifer*, *H. antarcticus* and *H. helgei*.

In the present study, fully mature, premature and stage IV specimens are included. These are the last three ontogenetic stages that can be distinguished within the Haploniscidae. In all three stages pereonite 7 and the appertaining pair of pereopods are already fully developed, although pereopod 7 may be somewhat smaller than pereopod 6 in stage IV. Maturity is reached after the fifth molt (stage VI) after leaving the marsupium.

Stage IV is the first stage in the ontogeny of Haploniscidae that allows distinguishing between males and females; in this stage pleopod 2 of both sexes forms a subcircular operculum, in males pleopod 1 is already present, but forms a small undifferentiated, triangular and apically bifid plate; pleopod 2 shows the beginning separation on the dorsal side by the appearing endopod and exopod.

Stage V males (subadult males) possess already separated pleopods 2, between the left and right pleopods 2 lies the almost fully developed pleopod 1; pleopod 1 has a continuous distal margin, without ornamentation like lateral processes or a prolonged medial part; it still lacks the transversal grooves in the distal part; the endopod of pleopod 2 is often shorter than in adult males and always lacks the sperm duct.

Lincoln (1985a) stated that the presence of the penes serves to confirm sexual maturity. This assumption is called into question by the presence of penes in the stage V holotype male of *H. cucullus* (see above, Fig. 3.72). Instead, sexual maturity of males can be confirmed by the presence of distinct dorsal transversal grooves in the distal part of pleopod 1, which form a support for the endopod of Pleopod 2 during copulation, and by the presence of the sperm

duct inside the endopod of pleopod 2. In most species of the Haploniscidae the adult males possess some kind of ornamentation in the distal part of pleopod 1, like lateral processes or a prolonged medial part and a characteristic arrangement of setae. Species of the *Haploniscus cucullus complex* lack this kind of differentiation; therefore distinguishing of stage V and VI males depends on the dissection of pleopod 1.

Stage IV females differ from males of the same age in lacking pleopod 1 and the developing appendages of pleopod 2, sometimes females may possess more setae on the margins of pleopod 2.

Stage V females do not possess developing oostegites, which can be found in preparatory females of other families, e. g. Desmosomatidae and Ischnomesidae. The complete oostegites appear after the fifth molt into adult stage VI females. Ovigerous females usually possess a somewhat broader bodyshape than other stages and the males. Often they are also bigger than these. The pereon is somewhat enlarged in comparison to the pleotelson, increasing the size of the marsupium as much as possible.

Apart from the pleopods the body shape and the antennae may vary between different stages. Stage IV and V males of *Antennuloniscus* possess a more slender pleotelson, than adult males and resemble females in that respect. At least within the genus *Mastigoniscus* antenna 1 gains an additional article from stage IV to stage V. As mentioned above, the number of aesthetascs changes also during ontogeny; stage V males usually have the same or a similar aesthetasc formula as females, the full number of aesthetascs appears after the fifth molt. The same applies to the setae of the flagellar articles of antenna 2.

Stage VI females are usually slightly broader than other stages, increasing the volume of the marsupium by this change of body shape.

Wolff (1962) has described signs of hermaphroditism in specimens of *H. bicuspis* and *H. helgei*. Such intermediate specimens were not observed in the ANDEEP material. The *Antennuloniscus subellipticus* specimen described by Menzies and Schultz (1968) seems to be a normal stage IV male and so is the *Chandraniscus negoescuae* specimen described by George (2004).

4.2 Biodiversity and Zoogeography

4.2.1. Isopod diversity and community patterns

The results revealed a high species richness of Isopoda in the Southern Ocean deep sea. This coincides with results from the Angola Basin (Nils Brenke, pers. com.) and other deep sea studies (Gage and Tyler, 1991, Hessler and Thistle 1975, Menzies, 1962).

An important factor for diversity is the age of the environment (Gaston and Chown 1999, Webb and Gaston 2000), i. e. the evolutionary time in which species can develop. This might be the reason why species richness is often higher in the Southern Ocean deep sea than in the European Northern deep sea.

The species richness was found to be higher than in samples from the European Northern Seas (Brandt, 1995, 1997; Svavarsson, 1997), while the abundance was lower. According to Grassle and Maciolek (1992) the deep-sea might be inhabited by 10 million species of macrofauna. Poore and Just (1994) have shown an unexpectedly high diversity of isopods at the south eastern Australian slope. The results of the ANDEEP expeditions with the huge number of new species fit well into this pattern and hint at a high species diversity in the Southern Ocean deep sea. As the species area plot shows, the high number of species found during ANDEEP seems to represent only a part of the actual number of isopod species inhabiting the sampled area.

Rex *et al.* (1993) have documented latitudinal gradients for Isopoda especially in the northern hemisphere, but Brey *et al.* (1994) showed that the results (from these authors) are due to sample bias as most samples came from the North Atlantic and no samples were analyzed south of 40°S, and that in fact species diversity in the Southern Ocean Isopoda is high. This could be confirmed by the ANDEEP data.

Most studies of Southern Ocean benthos included only shelf data and from the 371 isopod species known from the Southern Ocean only 22 were found in abyssal depth. The ANDEEP expeditions have increased the number of isopod species known from Southern Ocean waters to at least 666 and probably more, due to sibling species.

The isopods of abyssal depth of the North Atlantic belong mainly to the suborder Asellota and the superfamily Janiroidea (Svavarsson *et al.*, 1990, Svarsson *et al.*, 1993), while in samples from the South Atlantic a significant number from other isopod suborders was present (Wilson, 1998). Also the ANDEEP material contained a small fraction (2%) of species from other suborders. Serolidae and Antarcturidae are most speciose on the Antarctic shelf, but a number of asellote species was reported from there as well. The high proportion of

asellote isopods among the ANDEEP material (98%) shows that the pattern in the deep Scotia and Weddell Seas is similar to that of other deep-sea basins. Also the high proportion of Munnopsididae in the samples is comparable to that known from the North Atlantic. Several asellote species are known to feed on Foraminifera, which are usually highly abundant in deep sea sites and also in the ANDEEP samples (Cornelius and Gooday, in press). This might be another reason for the success of this suborder in the deep sea.

Desmosomatidae are usually highly speciose and abundant in the deep ocean (Brandt *et al.* submitted), but their abundance in the deep Southern Ocean was lower than if compared with the Angola Basin, for example (Saskia Brix, pers. com.), while they were the secondmost speciose family. Instead the Haplonsiscidae, frequently found in deep sea samples around the world, were the secondmost abundant family.

Serolidae and Antarcturidae, the dominant Antarctic shelf taxa were extremely rare in the deep Southern Ocean. Wilson (1998) believes that the low diversity of these taxa in the deep sea is due to the fact that this faunal component is evolutionarily further derived than the Asellota and therefore invaded the deep sea later.

The cluster analysis (Fig. 3.104) as well as the similarity analysis (Tab. 4) shows that the pattern of species composition and distribution observed for the ANDEEP stations is patchy. The stations from the South Shetland Islands and those from the South Sandwich Islands are quite different from each other, while the stations from the Weddell Sea show at least slight similarities, but with higher diversity at stations 131 and 133 and highest abundances at station 133. In total the distribution of Isopods in the Southern Ocean deep sea was found to be rather patchy and many species were rare. This can be observed in other deep sea areas as well and Snelgrove and Smith (2002) stated that considerable variability in diversity is found in deep-sea systems.

The “bioENV” analysis has hinted at the fact that beside depth the sediment grain size might play an important role for the isopod community structure. It is known that heterogeneity in grain size enhances diversity (Etter and Grassle 1992). The data from Howe *et al.* (in press) and Diaz (in press) show that sediment types and composition varied strongly between ANDEEP stations and even between the relatively similar Weddell Sea stations. Strong variations in the sediment types were observed at the South Sandwich stations which differed considerably from each other in the community pattern, but these stations also had the widest depth range of all ANDEEP stations, containing the shallowest (774 m) and the deepest (6348 m) station.

4.2.2. Zoogeography

From the few isopod species identified so far most were known from the Atlantic, several from the Pacific and only one species from the Indian Ocean, a pattern likely due to the fact that the Atlantic sector of the Southern Ocean was sampled during ANDEEP. Species from the families Ischnomesidae and Haploniscidae were compared with the material of the DIVA-I expedition (Nils Brenke, pers. com.) and only one or two common species were found. *A. armatus*, redescribed from ANDEEP material above (3.1.2.2.2), was found during the Vema Expedition near the Walvis Ridge in the South Atlantic (Menzies, 1962). However it is uncertain, whether the specimens were really the same species or belong to different and very similar species (see under 4.2.2.1).

The bathymetric ranges of species from several isopod families in the Southern Ocean are relatively large and support the theory of enhanced eurybathy of Southern Ocean taxa. Though it has to be considered that this seemingly extended depth range might be due to sibling species as shown by Held (2003) for the Serolidae and as found in the *Haploniscus cucullus* complex (Michael Raupach, pers. com.).

Hessler and Thistle (1975) already pointed out that families with deep sea origin are likely to lack eyes completely, while in those families where only few species have invaded the deep sea, at least the shelf species possess well developed eyes.

The Antarcturidae are known to occur down to >7200 m (Kussakin and Vasina 1993, 1995) and the fact that they are far more abundant and speciose on the shelf and that shelf species possess well developed eyes leads to the conclusion that the deep-sea species have submerged and have shelf ancestors. The same was supposed for the asellote families Acanthaspidiidae, Munnidae and Paramunnidae (Brandt 1991; Hessler and Thistle, 1975) and for the Serolidae (Held 2000). The family Munnidae, whilst having 19 known species present on the Antarctic shelf was found only at few ANDEEP stations (at the relatively shallow station 133 and also at the two deeper stations 46 and 131) in higher numbers, but nevertheless with 12 species. In contrast to the 20 known shelf species of Acanthaspidiidae, which mostly possess eyes, only five species of this family were found during ANDEEP.

For other families of the Asellota, such as Munnopsididae, Haploniscidae, Desmosomatidae, Nannoniscidae and Ischnomesidae, polar emergence has been postulated (Brandt 1991; Wilson, 1998; Hessler and Thistle, 1975). This hypothesis is supported by the ANDEEP results. While on the shelf 45 species of Munnopsididae, eight species of Desmosomatidae and six species of Haploniscidae were known, the ANDEEP samples contained 118 species of Munnopsididae, 48 species of Desmosomatidae and 40 species of

Haploniscidae. All species of these families are known to be eyeless. Brandt (1991) explained that both, sub- and emergence can be observed simultaneously. The evolution of many shelf taxa is closely associated with that of their deep-sea relatives and cannot be studied independently.

The degree of endemism on the Antarctic shelf is high (Brandt, 1991; Crame, 2000b). Because many species from the ANDEEP material are still not identified and because our knowledge about the distribution of deep-sea species is deficient due to lack of sampling effort, it is difficult to make a statement about the degree of endemism in the Southern Ocean deep sea or the role the Southern Ocean deep-water production plays for the spreading of isopod taxa in the world's oceans. But from the findings in the *Haploniscus cucullus* complex it may be concluded that the degree of endemism in the deep sea is high. The *Haploniscus cucullus* complex also hints at the fact that in the abyss of the Southern Ocean the evolution of Isopoda has taken place simultaneously and separately from that of the shelf taxa. Yet it is still not known whether the importance of the Southern Ocean deep sea as a centre for evolution equals that of the Antarctic shelf.

4.2.2.1 Distribution patterns within the family Haploniscidae

Most genera of the Haploniscidae are distributed worldwide. The two monospecific genera *Abyssoniscus* and *Aspidoniscus* are known only from single specimens, making assumptions about their actual distribution impossible.

The genus *Mastigoniscus* was recorded only from the Pacific until now. Seven species *M. concavus*, *M. gratus* Menzies and George, 1972, *M. gratissimus* Menzies and George, 1972, *M. generalis*, *M. elegans*, *M. platovatus* and *M. stenocephalus*, are known from the Peru-Chile Trench and the Peru Basin, *M. latus* (Birstein, 1971) was found in the Kurilen-Kamchatka Trench and *M. microcephalus* (Gamo, 1989) in the Okinawa Trench. The type species of the genus, *M. pistus* Lincoln, 1985a, was described from the Tasman Sea. Park (2000) proposed a possible radiation center of the genus in the Southern Pacific. The *Mastigoniscus* species described above (3.1.2.3) represent the first record for the genus in the Atlantic sector of the Southern Ocean. The three species *M. polygomphios*, *M. andeepi* and *M. pseudoelegans* were found in the Scotia Sea, while the two juvenile specimens from *M. sp. A* and *M. sp. B* were found at stations in the Weddell Sea. Apart from these two species a third species was found with a single juvenile male at station PS61-135-4 (65°00.05-59.97'S 43°3.02-43°00.82'W) in the Weddell Sea. It was damaged and therefore not illustrated above,

but clearly belonged to a different species than the above described. In addition another species of the genus was found during the DIVA-I expedition in the Angola Basin, South Atlantic (St. 338: 18°19,4'S 4°39,7'E and St. 340: 18°18,3'S 4°41,3'E, N. Brenke, pers.com.). This leads to the conclusion that the hitherto known restricted distribution of the genus is the result of a sampling artifact rather than a reflection of the real situation. Yet it is an interesting fact that the genus was apparently absent from the extensive haploniscid material of the Danish Ingolf Expedition (Hansen, 1916; Wolff, 1962) in the North Atlantic as well as from the material found during the Vema Expeditions (Menzius, 1962) in the Atlantic Ocean.

Contrary to Gaston and Chown's (1999) statement that high latitude species can have broad ranges because of their ability to survive a broad range of conditions the ANDEEP results suggest that on the species level the distribution pattern seems to be different.

Corresponding to the findings of Wilson (1983a, 1985) in the *Eurycope complanata* complex and the *Eurycope longiflagranta* complex, the species of the *Haploniscus cucullus* complex show a rather restricted distribution. Except for *H. cucullus*, which was found on two neighboring stations, all species were found only at a single station. Wilson (1985) found a depth correlated variation in populations of *Eurycope iphtima*. A reduced vertical gene flow was less expected in the Southern Ocean, because no thermocline exists; yet the molecular data from the *Haploniscus cucullus* complex indicate that speciation in this group is also depth related. (Michael Raupach, pers. com.). Similar restricted distributions can be expected within other genera of the Haploniscidae. The apparently vast distribution of some species, e.g. *Haploniscus bicuspis* is probably due to sibling species, which are difficult to identify by morphological means.

4.2.3 Problems affecting the quantitative analysis of epibenthic-sledge samples

The precise quantitative analysis of EBS samples depends on the comparability of the samples. Comparability depends on several factors, one of which is the correct calculation of trawling distances for the standardizing of the hauls.

Trawling distance can be calculated on the basis of the GPS-derived positions of the ship at the start of the haul to the time when the sledge leaves the ground (Brattegard, 1991) using the following formula (Brandt, 1995):

$$\text{haul length } s = \sqrt{\Delta lat^2 + (\cos \bar{lat} \times \Delta long)^2}$$

Δlat = difference latitude at start position – latitude at end position

\bar{lat} = arithmetic mean of latitude at start position and end position

$\Delta long$ = difference longitude at start position – longitude at end position

This calculation neglects the distance that is trawled by the winch alone during heaving. As the cable length equals 1.5 times of the depth at the station the error caused by neglecting the distance trawled by the winch alone increases with depth and may be more than one third of the actual trawling distance. This is less problematic for shallower stations on the shelf, where the error might in fact be neglectable, but would certainly have an effect for the deep ANDEEP stations. Therefore the method described in the material and methods chapter of the present thesis, which uses velocity and trawling time of the ship and the winch, was chosen to achieve a more realistic calculation for the deep-sea samples.

However, this method also holds sources of errors. For this calculation it had to be assumed that the ships velocity did not change during trawling or heaving. Because of the currents influencing the ships movements this assumption is hardly realistic.

Another problem with both methods is the detection of the precise moment when the trawling starts and when the sledge leaves the ground. Both can be confirmed by the tensionmeter of the winch; however this becomes difficult with increasing depth, because of the weight of the cable, which surpasses that of the sledge several times at deeper stations and outweighs the signal of the tensionmeter.

Other factors influencing the quantitative accuracy of epibenthic sledge data are bottom currents and the sediment type. The current may have a strong influence on the amount of material that is collected by the samplers; a frontal current may increase the sample size, while a lateral current may result in a decreased sample size. The amount of sediment in suspension and collected by the samplers depends on the sediment type and the sediment penetration of the sledge.

All these sources of error affect the accuracy of the quantitative results and therefore these have to be treated carefully and with awareness of the inaccuracy, which is common for trawled gear and increases with depth.

Nevertheless the epibenthic sledge is an important gear to access the benthic diversity of an area, because it samples large areas in relatively short times and accumulates the specimens in the codends. Compared to the more quantitative sampling gears like the giant box corer or the multicorer it provides a much more detailed insight into the species

assortment in the deep sea and supplies extensive material for taxonomic and phylogenetic studies.

4.3 Phylogeny

4.3.1 Characters and taxa used in the analysis

4.3.1.1 Characters

The Haploniscidae represent a relatively homogenous family of the Asellota; the interspecific variability is low; therefore the definition of characters and character states, which are useful for the investigation of the phylogeny, proved to be difficult. Few assumptions have been made about trends and patterns of morphological characters within this family. Most extensive studies of the Haploniscidae dealt with the diagnostic use of characters, solely Lincoln (1985a) presented some more careful considerations about several characters within the family. However, until now the only phylogenetic analysis of the Haploniscidae was done by Chardy (1977); it will be discussed below (4.3.3).

After careful examinations of the interspecific variability characters were checked for their intraspecific variability, which revealed numerous characters as useless for phylogenetic purposes. Finally, 96 characters were defined as potentially phylogenetic informative and coded for the data matrix. Considerations about these are presented below. Numbers in square brackets refer to the character numbers.

Body

The habitus of Haploniscidae is subject to a high degree of inter- and intraspecific variation, but also holds several important diagnostic characters. However, the phylogenetic use of habitus characters may be limited, due to the fact that these characters are mostly continuous or the phylogenetic information content is low. Nevertheless, 21 characters related to the body were defined. Five of these are parsimony uninformative, and serve to separate either the ingroup from the outgroup taxa or some outgroup taxa from the other taxa.

Head

The frontal margin of the head [1] may be straight, convex or concave, due to the extension of the lateral margins, the presumably more basal outgroup taxa *Neojaera sp.* and *Acanthaspidia drygalskii* as well as *Stenetrium weddellense* possess extended lateral margins and hence a concave frontal margin of the head. Where the frontal margin is convex, it has to be decided whether this can be interpreted as the presence of a rostrum or not. However, if a rostrum is present, it is usually distinct. In the genus *Hydroniscus* the frontal margin has two

deep indentations [2], a character that is functionally related with the compact subcylindrical body shape and is an apomorphy of the genus.

It is not clear whether the rostrum [3] is part of the groundpattern of the family and was reduced several times or if it is a convergent development in several clades of the family. Within the Asellota various groups have developed a rostrum; nevertheless the character was maintained because the absence or presence of a rostrum seems to be a common feature within some genera. While species of *Chauliodoniscus* and *Mastigoniscus* generally lack a rostrum, it is always present in species of *Hydroniscus*; in the genera *Haploniscus* and *Antennuloniscus* species with and without rostrum are known.

Species of the *Haploniscus cucullus* complex possess a rostrum which is separated from the frontal margin of the head by a deep ventral notch visible in lateral view [4] (Fig. 3.99). The same can be found in *H. rostratus*, but the rostrum of this species is much longer and more slender than in the *Haploniscus cucullus* complex.

Hessler and Thistle (1975) already proposed the deep-sea origin of the family; the absence of eyes [6] is typically for the whole family and can be regarded as part of the haploniscid groundpattern, while the sistergroup *Neojaera sp.* and *Stenetrium weddellense*, with a probable shallow water origin, possess well developed eyes.

An anteriorly prolonged clypeus [5] (Fig. 3.13, 4.4) could be observed only for species of the genus *Antennuloniscus*. The prolonged clypeus of *Stenetrium weddellense* is directed more dorsally and directly adjacent to the vertex, and therefore is probably an analogous structure and the character can be considered as apomorphic for *Antennuloniscus*.

Pereon

Fusion of the posterior pereonites is common within the Asellota. Within the Haploniscidae pereonites 5-7 are usually fused with each other and the pleotelson [12-14], although the suture lines may be still present. Only in the genus *Chauliodoniscus* pereonite five is completely free and movable against pereonite 6. It is not clear whether this is the plesiomorphic character state or if it is an apomorphy of the genus that is associated with the ability to conglobate.

Another possible apomorphy of the genus *Chauliodoniscus* is the prolongation of the posterior angles of the pereonites 2-4 and is mostly expressed in males [8] (Fig. 4.2). A slight elongation of these angles was also observed in *Stenetrium weddellense*, but is probably another analogy. Various kinds of spines and lobes of the pereonites can be observed within

the Asellota. But within the Haploniscidae this variation from the normally compact and smooth body outline is most uncommon.

The pereon may be almost rectangular, slightly oval or broadly oval; although this is a somewhat continuous character, it was tried to define the character states by the relative width of the single pereonites [9].

The length of pereonite 7 is greatly reduced in the genus *Mastigoniscus* (e. g. Fig. 3.32), whereas it is completely reduced dorsally in the species of *Hydrioniscus* [10-11]; the appertaining pereopod is fully developed in both genera, unlike in other taxa of the Asellota, where pereopod 7 is reduced (see 4.1.1.1). The reduction of pereonite 7 in *Mastigoniscus* might be related to the enlargement of the pleotelson compared to other genera, while a correlation with the high degree of fusion of the posterior pereonites (highest within the Haploniscidae, the dorsal suture lines are completely absent) and the conglobating ability in *Hydrioniscus* can be suspected. Therefore the reduction of pereonite 7 probably happened two times in the evolution of the Haploniscidae.

The lateral expansion of the tergites [7] is the main reason for the compact and broad habitus of the Haploniscidae that resembles terrestrial isopods. As a result the insertion of the pereopods is not visible from above, being covered by the tergites. The coxae are reduced to small circular sclerites (Fig. 3.12) fused to the ventral surface of the body. These characters can be considered as autapomorphies of the Haploniscidae and part of their groundpattern.

Pleotelson

The posterior part of the body (pereonites 5-7 and pleotelson) is longer than the anterior part, mainly due to an enlargement of the pleotelson, in several of the species studied [15]. This feature is striking within the genus *Mastigoniscus*, where the strongly enlarged pleotelson is possibly an apomorphy.

The posterolateral processes of the pleotelson are important diagnostic characters. Such processes are present in many taxa of the Asellota and can be found in most of the outgroup taxa as well, although the position may be somewhat different due to the modified form of the terminal margin of the pleotelson [16]. Extraordinary long processes are mainly found within the genus *Mastigoniscus*, while they are usually short in species of *Hydrioniscus*, *Chauliodoniscus* and *Antennuloniscus* as well as in the species of the *Haploniscus cucullus* complex [17]. In species of *Mastigoniscus* they are subject to a pronounced sexual dimorphism and maybe a correlation with the extraordinary long endopod of pleopod 2 can be assumed, because many species also possess deep grooves extending from the branchial

chamber along the posterolateral processes of the pleotelson (e.g. Fig. 3.11, 3.33). These grooves form receptions for the endopods of pleopod 2 and are therefore found in males only [20].

In many species of the Haploniscidae the dorsal surface of the pleotelson [18] is structured by two sharp longitudinal keels, which are absent in all outgroup taxa. They might represent another character of the haploniscid groundpattern, being present in many species of *Haploniscus* and *Mastigoniscus*. Their absence in the genera *Chauliodoniscus* and *Hydroniscus* might be related to the subcylindrical body shape combined with a rather short and compact pleotelson; while the two rounded bulges of *Antennuloniscus* species are unique and probably apomorphic for the genus. The ventral surface of the pleotelson [20] is usually smooth, but may exhibit a bulge around the branchial chamber tapering towards the anus (Fig.3.11), which is typical for many *Haploniscus* species, but absent in the outgroup taxa.

Enrollment

The ability to enroll into a ball [21] is shared by species of *Chauliodoniscus* and *Hydroniscus* as well as some *Haploniscus* species (Fig. 4.2). While the *Hydroniscus* and *Haploniscus* species usually enroll with the frons close to the terminal margin, the *Chauliodoniscus* species conglobate with the frons close to the branchial chamber. Therefore it seems likely that this ability was developed at least twice in the evolution of the family. Nevertheless it is an important character, as it requires several adaptations, e. g. in the shape of the tergites and the articulation membranes.

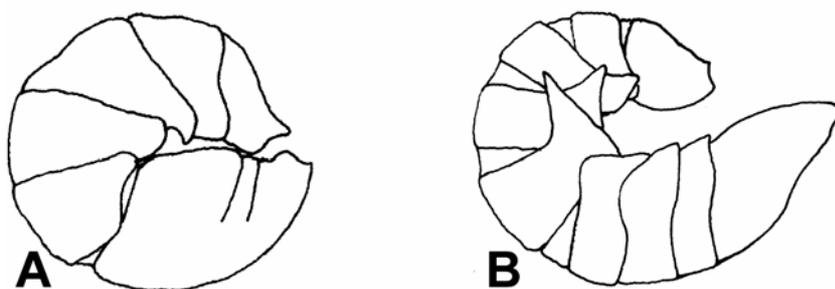


Figure 4.2: Enrollment: A *Hydroniscus*; B *Chauliodoniscus*. (modified from Chardy, 1975 and Lincoln, 1985a).

Appendages

The suitability of the different appendages for phylogenetic purposes varies. While the mouthparts proved to be phylogenetically uninformative, the pereopods and pleopods 1 and 2

of the male hold a number of potentially informative characters. Characters of the pleopods 3-5 are mainly used for the distinction between outgroup taxa and ingroup.

Antennae

Usually the antennae are directed anteriorly, but in species of *Hydroniscus* they are directed more ventrally and often not visible from dorsal view; therefore they are well protected inside when the specimen enrolls into a ball [22]. This is an apomorphic character state of *Hydroniscus*.

Length and width of the articles of antenna 1 vary considerably between species of the Haploniscidae. Yet the first article is usually short and broad, often almost globular, while the second article is longer and more slender. However, in some species this is different; in the genus *Antennuloniscus* the second article is mostly shorter than or as long as the first article, while there is a certain tendency in the genus *Mastigoniscus* towards a broader second article. Because proportional characters are often continuous, discrete character states were defined by comparison of the two articles [23-24].

The praecoxa, the first article of antenna 2 is well developed in most Haploniscidae as well as in many other Asellota; therefore its reduction in the genus *Antennuloniscus* (Fig. 4.4) represents the apomorphic situation [25].

Article 3 of antenna 2 is short in most species of the Asellota and this is also true for most haploniscid species, but it is elongated in the species of *Antennuloniscus* (e.g. Fig. 3.16, 4.4) as well as in *Haploniscus rostratus*. To define two discrete character states, the length of article 3 was compared with that of article six [26]. Even in species of *Antennuloniscus*, where articles 5 and 6 are fused, the suture line between both articles is present and the length of article 6 can be determined. This fusion of articles 5 and 6 [30] (e.g. Fig. 3.16, 4.4) is another apomorphy of *Antennuloniscus*.

The dorsal tooth on article 3 of antenna 2 is typical for most species of the Haploniscidae. Within the outgroup species this article usually has a lateral scale [27]. *Hydroniscus* species lack the tooth as well as the scale, and it is probably reduced secondarily. The length of the tooth [28] is another continuous character; character states were defined by the comparison with the width of article 3. The tooth is short in most species of *Antennuloniscus* and elongated in species of *Chauliodoniscus*.

Usually some setae are found on the tooth and in several species the margins are jagged [29], especially within the genus *Mastigoniscus* (e.g. Fig. 3.40).

In species with unfused articles 5 and 6 (all haploniscids except *Antennuloniscus* species), article 5 is usually cylindrical and longer than wide, but in *Chauliodoniscus* species it is inflated, almost globular; an apomorphy of the genus [31].

Within the genus *Antennuloniscus* article 6 always terminates with a strong apical tooth (e.g. Fig. 3.16), presumably the apomorphic character state. A tooth was also observed in some species of *Mastigoniscus* (e.g. Fig.3.34), in *Haploniscus rostratus* and *Haploniscus spinifer* [32].

The flagellum of antenna 2 is small and inserts subapically in all species of *Antennuloniscus*, while it is distinctly larger in most of the other species of the family [33].

The number of flagellar articles [34] is subject to intraspecific variation; the fact that it was chosen despite this variability is due to the observation that most *Antennuloniscus* species possess only eight flagellar articles in antenna 2 and that this number seems to be constant in the species concerned; most species possess distinctly more articles.

Mandible

The molar process of the mandible [36] typically has a tooth row and a cuticular ledge framing the subcircular surface; only in *Haploniscus ampliatus* two cuticular ledges were found. Within the outgroup taxa the molar process is often acute and reduced. Apart from the molar, only features of the mandibular palp (Fig. 4.4) proved to be phylogenetically informative. The number of stout serrated setae on the third article of the palp was used as character [35]. This character is subject to intraspecific variation, too. However it could be observed, that most haploniscid species possess not more than seven setae on this article, while all outgroup taxa and some species of *Haploniscus*, especially the *Haploniscus cucullus* complex, possess eight or more setae, the presumed plesiomorphic state.

Maxillae

Neither maxilla 1 nor maxilla 2 provided any parsimony informative characters, because characters, which are not constant throughout the family or all Asellota, showed a high degree of intraspecific variation. The number of serrated setae on the inner lobe of maxilla 2 is two for all Haploniscidae, but differs in the outgroup taxa [37].

Maxilliped

The maxilliped endite is characteristically expanded distally within the family compared to the outgroup taxa, a synapomorphy of the family [38].

The number of retinacula [39] seems to be constant within species, but varies between two to four within the family. Characteristic for *Chauliodoniscus* species are two retinacula, but also some other species possess only two hooks.

Pereopods

By far the most characters were defined for the pereopods. These limbs have been hardly studied and are often left out in the description of new species, probably due to the assumption that they hold little or no variation. The careful observation of the various features of Haploniscid legs carried out for this study revealed that this is not true. Considerable variation between pereopods 1-7 as well as interspecific variation was found.

Two different trends can be observed within the Haploniscidae: Species with high intraspecific variation in the number of setae, and species or even genera with a conserved number of setae, especially within *Antennuloniscus* and *Mastigoniscus*. The different articles of the legs were coded separately according to their armature. In many characters a difference between pereopod 1-4 and 5-7 can be observed, but pereopod 1 and pereopod 7 may also differ from the rest of the legs, and in some characters, e. g. the number of ventral setae on the basis pereopod 4 has the same character state as the pereopods 5-7 in some species.

Pereopod 1 is typically ambulatory within the Haploniscidae, while most species of other asellotan families possess a prehensile pereopod 1, which is often sexually dimorphic [40]. Yet the presumed sistergroup of the family, *Neojaera* sp.; possess an ambulatory pereopod 1 as well; this might represent a synapomorphy of both taxa, regarding the prehensile pereopod 1 as part of the groundpattern of the Asellota or Janiroidea (Wägele, 1987).

Mastigoniscus and most *Antennuloniscus* species possess a single ventral seta on the basis of P1-3 and two ventral setae on the basis of P4-7, while in the outgroup taxa and most species of *Haploniscus* this number is higher and might vary between pereopods 1-7 [41].

A similar pattern can be observed for the ventral setae of the ischium [42]; most species of *Antennuloniscus* and *Mastigoniscus* possess constantly two setae, while in several *Haploniscus* species and some outgroup taxa this number is higher and less conserved. Because the setae are usually stouter on the posterior pereopods and therefore easier to detect, only these were coded in the datamatrix.

The merus has a varying number of apical setae ventrally and dorsally in all species of the Haploniscidae, but in some species different types of setae can be found on anterior and posterior pereopods [45], e.g. in the *Haploniscus cucullus* complex, where the posterior pereopods have only simple setae and the posterior pairs possess additional flagellate setae

[46]. Medioventral setae may be present on the merus or not and again in some species a difference can be observed between posterior and anterior pereopods, therefore these groups of legs were coded separately [43-44].

Differences between anterior and posterior pereopods can also be found for the carpus of several species, but the pattern is not necessarily identical with that of the merus or the propodus [47].

An important character is the presence of ventral flagellate setae (Fig. 3.11) on merus, carpus and propodus; this type of setae is present in many peracarids (Wägele, 1992, Brandt, 1988) and was found to be present in all outgroup taxa, except for *Stenetrium weddellense*, and in the species of the *Haploniscus cucullus* complex as well as some other *Haploniscus* and the *Hydroniscus* species; yet it is absent in all species of *Mastigoniscus*, *Antennuloniscus* and *Chauliodoniscus*, which is most probably the apomorphic character state. The presence pattern of the ventral flagellate setae on the carpus is quite different between pereopods 1, 2-4, 5-6 and 7 and was therefore coded separately for the four groups of legs [53-56]. In all but the *Hydroniscus* species ventral flagellate setae are absent on the propodus of the anterior pereopods [63], whereas they are present on the propodus of the posterior pereopods in several *Haploniscus* species as well [64].

Dorsal flagellate setae on the carpus are absent in all outgroup taxa, but they are known from species of the Santiidae and some species of the Munnidae, for example; within the Haploniscidae these setae may be present on pereopod 5, 6 or 7 [48-50], sometimes on all three legs; while *Haploniscus* and *Mastigoniscus* usually possess a dorsal flagellate seta on pereopod 6, this is absent in *Antennuloniscus* and *Chauliodoniscus* species, but several *Antennuloniscus* species possess a dorsal flagellate seta on pereopod 7; such a seta on pereopod 5 is found in the *Haploniscus cucullus* complex.

In some of the outgroup taxa ventral simple setae are completely absent from the carpus, while all ingroup species possess such setae [51]; these are extremely short in the *Hydroniscus* species, while most other species possess longer setae; to code this character the length of the setae was compared with the width of the carpus [52].

Ventral cuticular combs on carpus and propodus are common within the Isopoda and they are present in the outgroup taxa as well; however they are more distinct in species of the Haploniscidae and are in this appearance part of the groundpattern [61]. Unfortunately the difference between the two different types of ventral combs (see 3.1.2, fig. , 3.12, 4.3) is less obvious, when studied with a compound microscope, which was the only possibility to study most of the species. Yet, *Antennuloniscus* species are also characterized by an extended apical

ventral comb on the propodus and a less distinctly extended one on the carpus as well, and this feature is fairly discernable with the compound microscope [62].



Figure 4.3: Apical ventral combs of propodus (schematic): A *Antennuloniscus*; B *Haploniscus*

The lateral apical combs of the carpus (Fig. 3.12) are typical for the family, although they are present in some other taxa of the Asellota as well, e. g. *Ischnomesidae* [57-58]. To distinguish between the different types of combs the terms “spinose” and “setose” were chosen, although they are not comprised of real setae, but are extensions of the cuticle. Usually pereopod 1 has just one comb that is setose, while pereopods 2-7 may have two setose respectively spinose combs or one setose and one spinose comb [60]; spinose combs, the presumed plesiomorphic character state, were found in species of the *Haploniscus cucullus* complex and in *Haplomesus*, the only outgroup with apical carpus combs; the comb types were determined for pereopod 3-5 only, because the combs are usually biggest on these legs; only *Hydroniscus vitjazi* lacked both types of combs. In *Mastigoniscus* and several other species additional dorsal apical combs could be observed [59].

Apart from apical dorsal setae, which are present in all species of the Haploniscidae the propodus of some species has additional mediodorsal setae, which is true for all outgroup taxa as well; again the pattern for anterior and posterior pereopods may differ [65-66].

The ventral claw of the dactylus is reduced in all species of the family and forms a small, often bifid blade that was called “accessory tooth” by Lincoln (1985a). This character state is part of the groundpattern of the Haploniscidae [68]. The dorsal claw is often almost as long as the dactylus itself, but in species of *Hydroniscus* it is rather short and comprises less than one third of the dactylus length [67].

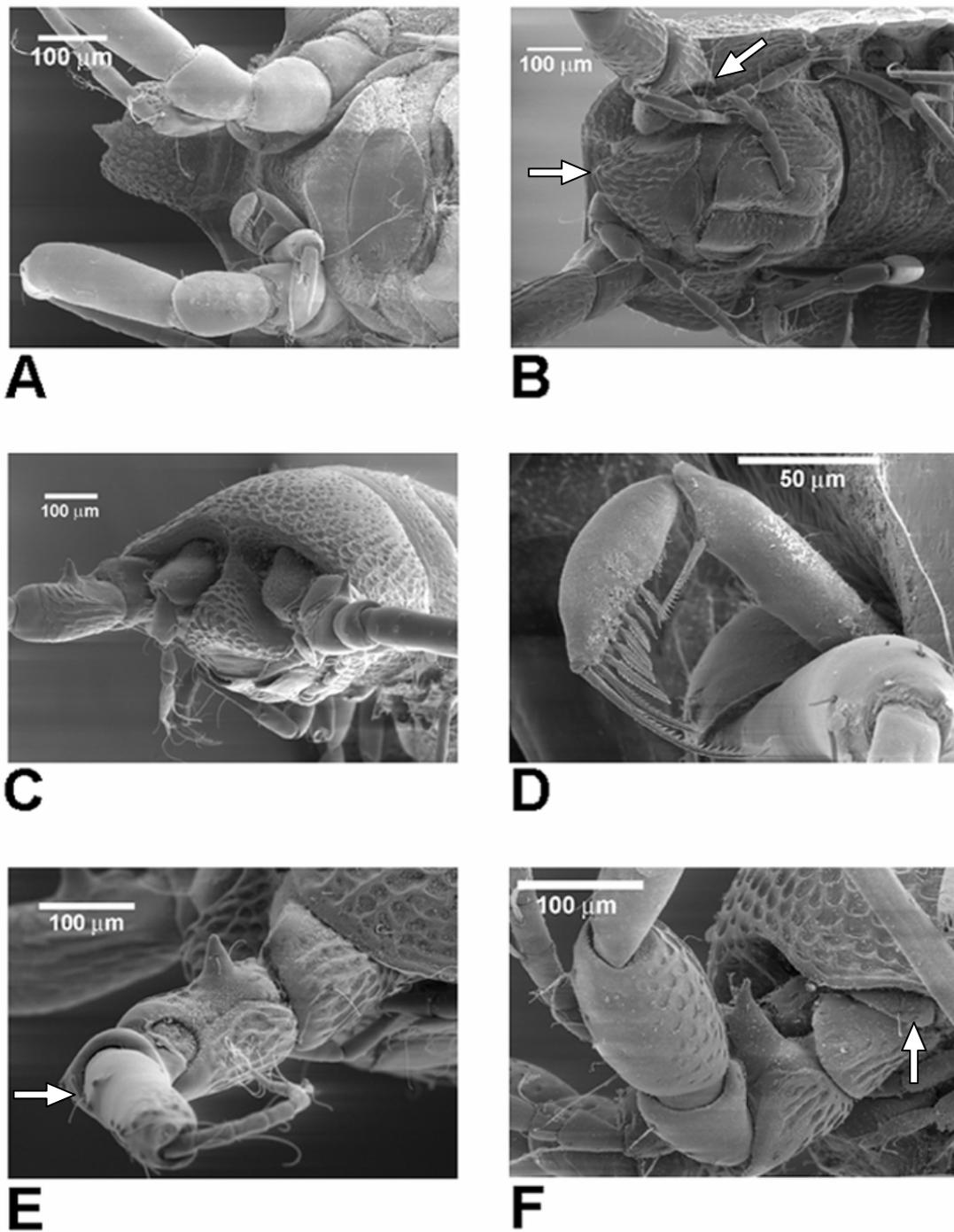


Figure 4.4: A *Haploniscus cucullus* n. sp., ventral view of head; B *Antennuloniscus* sp. 1, ventral view of head, arrows: clypeus and antenna 2, article 2; C *Antennuloniscus* sp. 1, anterior view of head; D *Haploniscus cucullus* n. sp., mandibular palp; E *Antennuloniscus* sp. 1, female, antenna 2, arrow: fused articles 5 and 6; F *Mastigoniscus andeepi* n. sp., male, antenna 2, arrow: article 1.

Pleopods

The rami of pleopod 1 of the males are fused in all Janiroidea, while they are separated in *Stenetrium weddellense* [69]; besides the pleopod is considerably larger in the Janiroidea [70]. By far the largest male pleopods 1 and 2 are found in species of *Mastigoniscus*; presumably apomorphic the pleotelson together with the pleopods is enlarged within this genus, pleopod 1 is more than half as long as the posterior body [71] (Fig. 3.11); in females this enlargement is hardly apparent.

In two species, *Haploniscus hamatus* and the undescribed *Haploniscus* sp. 12, pleopod 1 was remarkably similar and distally broader than proximally [72], although otherwise a few differences were found between these species.

A number of species possess laterodistal processes on pleopod 1 [73] (e.g. Fig. 3.42), which usually form a prolongation of the dorsal transversal grooves and support the endopod of pleopod 2; they are particularly common in the genus *Mastigoniscus* although they are missing in *M. gratissimus*.

A typical character of *Mastigoniscus* species is the shape of pleopod 1 [74] that is broadening more distally (e.g. Fig. 3.42); therefore the lateral margins are convex rather than concave. This is most probably an apomorphy of the genus, while in the groundpattern of the Haploniscidae the pleopod has typically concave lateral margins with the broadest part more basally.

The most basal part of pleopod 1 is usually tapering towards the insertion, but in some species pleopod 1 has a more triangular shape with the frontal margin being the broadest part of the limb [76], presumably the apomorphic situation.

The distal margin of pleopod 1 has either a deep notch, due to the prolongation of the most distal part of the rami, or, as in the *Haploniscus cucullus* complex, a nearly continuous margin [75].

Pleopod 2 of the male and female is short in *Stenetrium weddellense*, but a great deal larger in the Janiroidea, where it forms an operculum that covers the branchial chamber, in males together with pleopod 1 [77, 82].

The basipod of pleopod 2 has a very similar shape in most species of the family, but while the setae on the lateral margin are restricted to the distal part in some species, they are present along the whole lateral margin in other species [78].

Another character, which is typical for the Janiroidea and their modified method of spermatophore transport, is the closed sperm duct of the male pleopod 2 (Wilson, 1991), in

contrast to the situation in *Stenetrium weddellense* males, where the sperm duct forms an open groove [79].

The length of the endopod of pleopod 2 [80] varies strongly within several families of the Asellota, but Wägele (1987) proposed that the plesiomorphic state is a short endopod; therefore the extremely elongated endopod of *Mastigoniscus* as well as some *Haploniscus* species can be regarded as apomorphic; likewise, the lateral direction of the first article of the endopod in *Mastigoniscus* species can be considered as apomorphic [81](e.g. Fig. 3.33).

The length of the exopod of pleopod 4 in relation to the endopod [90] is the only parsimony informative character that could be defined for the posterior pleopods (3-5); it is usually elongated in species of *Mastigoniscus*, but exceeds the endopod only in *M. gratissimus*, *M. pistus*, *M. platovatus* and *M. andeepi*, as well as in *Acanthaspidia drygalskii* and *Stenetrium weddellense*.

The number of articles and setae, the absence or presence of the exopod or the whole pleopod 5 [83-89, 91-92] are characters that are parsimony uninformative and distinguish the ingroup from the outgroup taxa or some outgroup taxa from the rest of the taxa.

Uropods

The Haploniscid uropod is small and has only one ramus, another groundpattern character of the Haploniscidae [93].

Penes

These are adjacent to the midline of pereonite 7 and close to pleopod 1 in all taxa except *Stenetrium weddellense*, where they are located between the coxae and the midline of pereonite 7 [94]; the latter is thought to be the plesiomorphic state (Wilson, 1991).

Sexual dimorphism

Sexual dimorphism apart from differences in the pleopods and the proportions and setation of the antennae is known from numerous taxa of the Asellota, but is not expressed in the presumed sistergroup *Neojaera* as well as in *Stenetrium weddellense* and *Acanthaspidia drygalskii*. Interestingly the *Haploniscus cucullus* complex has apparently not even sexually dimorphic antennae, while this dimorphism is typical for most Haploniscidae. In several groups of the Haploniscidae an increased level of sexual dimorphism can be observed [95]; the prolongation of the anterior angles of pereonites 2-4 is usually much stronger in *Chauliodoniscus* males, while differences in the pleotelson are typically found in

Antennuloniscus and *Mastigoniscus*; this concerns mainly the shape of the pleotelson in *Antennuloniscus* species, where it is much broader in males and the shape of the posterolateral processes in species of *Mastigoniscus* [96]. This increased sexual dimorphism is probably the apomorphic character state and due to the different structures concerned it probably evolved more than once within the family.

4.3.1.1.1 Character weighting, coding and polarity

The *a priori* weighting of characters in a phylogenetic analysis is difficult. While it seems clear that some characters have a higher probability of homology than others, due to the more extensive change on the genetic level required, and cannot be entered with the same weights, the assignment of concrete numerical weights remains difficult, because our knowledge about the genetic information behind phenetic differences is insufficient. Therefore two analyses, with unweighted and with weighted characters were conducted, and only three weights, 1, 2 and 4, were assigned to the characters, which means a doubling of the character weight with increasing probability of homology. Besides, weights are also assigned indirectly to some structures, by coding all details within a frame homology. For example, the pereopods have a high weight in the present analysis, because so many characters of the legs are coded. The same is true for the pleopods 1 and 2 and antenna 2.

86 characters were given the weight 1, because it is assumed that changes in these characters require less complex changes on a molecular level than those in the remaining characters and consequently the probability of homology is lower.

The length of the male stylet [80] is probably correlated with a corresponding change in the female sexual organs and changes in the behavior during mating. This indicates a high probability of a common origin. Nevertheless an elongated copulatory filament is present in numerous species of the Janiroidea and is clearly an analogous development on this higher taxonomic level. Therefore a weight of two was assigned to this character.

The remaining nine characters were given a weight of four:

The presence of deep grooves on the ventral surface of the pleotelson [20] is a synapomorphy of several *Mastigoniscus* species, which is probably correlated with the elongated copulatory filament (3.1.2.3). However the correlation of both characters is not obligate, proved by those species, which do possess the elongated endopod of pleopod 2 but not the grooves.

The direction of the first endopodal article of pleopod 2 [81] distinguishes *Mastigoniscus* from the rest of the Haploniscidae as well as from most Janiroidea. Again, a change requires probably corresponding adaptations in the mating behavior. That the elongation of the endopod is not necessarily combined with the aberrant lateral direction of the first article is proven by *Haploniscus spinifer* and *H. sp. 12*.

The possession of a closed sperm duct [79], which distinguishes the Janiroidea from the Stenetrioidea (*Stenetrium weddellense*), is part of the complex system of spermatophore transport within the Janiroidea and therefore the probability of homology is high.

Similar applies to pleopod 1 with its separated rami in *Stenetrium weddellense* [69] and its size [70], as well as to the position of the penes [94].

The large pleopods 1 [70] and 2 [77] of the male and pleopod 2 of the female [82] Janiroidea form a protective cover for the delicate posterior pereopods; in contrast pleopod 1 and 2 are small in *Stenetrium weddellense*, which has certainly an effect on the posterior pleopods.

The ability to enroll into a ball [21] requires a number of mechanical adaptations of the body, such as the broad articulating membranes of the pereonites or changes in the muscular system.

For a number of characters the polarity was determined *a priori*. Entering these ancestral states for the PAUP* analysis had little influence on the resulting topologies; in the present analysis some inconsistencies are found in characters interpreted *a priori* as synapomorphy of the ingroup; for these the presumed plesiomorphic state was identified as apomorphy of the outgroup, e. g. the fusion of pereonites 5-7 with each other and pleotelson.

Most characters were coded binary, but for some characters a convergent development of two apomorphic states was assumed; therefore these were coded with three states, e.g. enrollment.

4.3.1.2 Taxa and missing data

The subset of species used for the analysis was small, because most species descriptions are insufficient and type material was not available. The analysis includes only those species, which could be studied using own material or the type material or those, which were well described. Despite this fact the data matrix contains several gaps, because ontogenetic and sexually dimorphic characters were included and adult males were not always available or

because important characters, e.g. of antenna 2 were missing. Besides the matrix contains several characters that are controlled by others; as consequence the matrix contains further gaps in those places where the controlled character is made inapplicable by the controlling character. The treatment of missing data is discussed controversially in the literature (Rieppel, 1999), but to maintain a dataset that is as extensive as possible according to both the number of characters as well as the number of species, characters respectively species with missing data were nevertheless included into the analysis.

4.3.2 Topology and tree data

The consistency indices of the trees found in both analyses are low; consequently the homoplasy indices are high. However, the retention index, which is thought not to be distorted by autapomorphies and symplesiomorphies (Wägele, 2000), is distinctly higher, 0.71 respectively 0.73. Nevertheless, 32 apomorphies were found only once in the trees, while the rest occurred more than once.

The most interesting results are the relationships between the genera, the polyphyly of *Haploniscus* and the close proximity of certain *Haploniscus* species to *Antennuloniscus* (clade 15) or *Mastigoniscus* (clade 24).

The resolution in the bootstrap tree is low. Clades 2-14, which are important for the relationships between genera, and some terminal clades are not found. Bootstrap values for the remaining clades are mostly low, indicating that the resulting trees do not reproduce the data in a satisfying way. This is probably due to the fact that the number of characters used was relatively low compared to the number of terminal taxa and the occurrence of many homoplasies in the trees.

4.3.3 Previous phylogenetic studies of the Haploniscidae

In his phylogenetic analysis Chardy (1977) compared mostly the genera; only within *Haploniscus* he defined three different groups. On closer inspection the groups *Haploniscus* A and B correspond to the later described genera *Chauliodoniscus* and *Mastigoniscus*. The remaining *Haploniscus* species (C and D) were treated as terminal taxon, although Chardy realized that this group cannot be regarded as monophylum.

In his analysis two major clades were identified; one comprises *Abyssoniscus* and *Aspidoniscus*, the other one comprises *Antennuloniscus*, *Hydrioniscus*, *Haploniscus*, *Chauliodoniscus* (*Haploniscus* A) and *Mastigoniscus* (*Haploniscus* B). Within the second

clade, *Antennuloniscus* is found as the most basal genus, while *Hydroniscus* is the sistergroup of the remaining genera, whose relationships to each other remain unresolved.

Chardy defined eight character states with phylogenetic relevance for his analysis, all of which he interpreted as novelty developed within the Haploniscidae:

1. Appearance and development of the posterolateral processes of the pleotelson: A close look at other families of the Asellota reveals that similar structures are in fact present in a number of taxa outside the Haploniscidae; the only difference is the less produced terminal margin of the latter, which causes the more caudal position of the processes within the Haploniscidae.

2. Reduction and modification of the uropods: The clubshaped uropods of *Aspidoniscus* are indeed unusual. However they represent an autapomorphy of the only species of the genus and therefore are without phylogenetic relevance for the relationships of the genera. The reduction of uropods within *Hydroniscus* has a meaning only for the phylogenetic relationships within *Hydroniscus*. As this feature is not homogeneous within *Hydroniscus*, it can not be used in a phylogeny that treats the genus as terminal taxon. Additionally this character combines two different features in one. This makes no sense for a phylogenetic analysis.

3. and 4. Fusion of pereonites 5-7 with the pleotelson: This character is often misinterpreted due to faint sutures present between the segments (e. g. in George, 2004). In fact, most Haploniscidae have the pereonites 6 and 7 fused with each other and the pleotelson. Only *Chauliodoniscus* species possess a freely articulating pereonite 5. Concerning the situation in *Abyssoniscus* and *Aspidoniscus*, one has to regard that the described specimen of *Aspidoniscus* was apparently badly damaged and that it might well be a juvenile specimen. The description by Menzies and Schultz (1968) is inadequate, highly doubtful and useless for phylogenetic purposes. Birstein (1971) described his new genus *Abyssoniscus* with freely articulating posterior pereonites; pereonite 7 seems to be slightly reduced within this genus. Unfortunately, neither the holotype of *Aspidoniscus perplexus* nor that of *Abyssoniscus ovalis* was available to confirm the interpretations from the species descriptions.

5. Transformation of the lateral margins (respectively the anterior angles) of pereonites 2-4: This character confirms the monophyly of the genus *Chauliodoniscus*. It has no relevance for the relationships between genera.

6. Fusion of article 5 and 6 of antenna 2: Again this character provides no information about the relationships between genera, as it represents an autapomorphy of the genus *Antennuloniscus*.

7. Reduction of the dorsal tooth of antenna 2 article 3 or its modification into a robust cone and reduction of the peduncular articles of antenna 2: The only reduction of the peduncular articles is found in *Antennuloniscus* and few species of *Haploniscus* (*H. rostratus*, *H. ingolfti*), where the praecoxa is distinctly reduced. The situation in *Aspidoniscus* remains uncertain in the description by Menzies and Schultz (1968), where articles 1 and 2 of antenna 2 are not figured; the meaning of the statement “first and second peduncular articles do not show” (Menzies and Schultz, 1986) is not clear; it might mean that these articles are absent, were lost during dissection or are not visible in dorsal view, a character often used by Menzies and other authors (Menzies, 1962, Menzies and Schultz, 1986, Chardy, 1977). The modification of the dorsal tooth on article 3 concerns mainly the length of this structure, which may vary greatly between different species of the family. Ornamentation and setation were not noticed by Chardy. The complete absence of this tooth in *Hydroniscus* may be due to secondary reduction and be an autapomorphy of this genus. Again this character definition combines at least two (if the complete reduction of the dorsal antennal tooth is interpreted as extreme modification of its length) completely different features.

8. Development of a rostrum: This was not considered in Chardy’s analysis, because he was not able to determine the derived state for this character.

As demonstrated, most characters used in Chardy’s phylogenetic analysis are not appropriate for a phylogenetic analysis on genus level. Two of the characters (2 and 7) are dubiously coded, as they combine more than one character. The use of a non-monophyletic group as terminal taxon (*Haploniscus* C and D) may also distort the result. Therefore the phylogenetic analysis of the Haploniscidae as presented by Chardy has to be regarded as inadequate, and the results have to be questioned.

4.3.4 Problematic characters and clades

The difference between the analysis with *a priori* assigned weights and the unweighted analysis is low when comparing the consensus trees, but the fact that the analysis with weighted characters produced more trees than that with unweighted characters, suggests that one or more of the characters with weight 1 have a strong effect on the resolution of the consensus trees in the unweighted analysis. This is diminished by assigning higher weights to other characters. Therefore the resolution within the clade (26) has to be treated with care.

The same applies to those clades, which are not supported by the same synapomorphies in the two most distant trees. A somewhat uncertain resolution in the terminal clades was

expected, because the interspecific variation within the Haploniscidae is rather low compared to other families of the Asellota, which causes difficulties in finding a sufficient number of phylogenetically informative characters. Also expected was the polytomy in the *Haploniscus cucullus* clade (36); the species of this clade are morphologically rather similar to each other and the relationships can probably not be solved by using morphological characters. The absence of the rostrum, which supports the sistergroup relationship between *H. nudifrons* and *H. nondescriptus*, is not a very convincing character, because it varies greatly within the whole family.

Some of the major clades are only weakly supported. Clade 3 is based on a single synapomorphy, the bulge on the ventral surface of the pleotelson, which is lost again in clade 12. This bulge might as well be part of the groundpattern of the family and be reduced in *Hydroniscus* and *H. piestus*. Besides it was also present in *H. bicuspis* and *H. rostratus*, members of clade 12, suggesting a convergent development or reduction of this structure.

The more derived position of clade 12, which comprises the genera *Antennuloniscus*, *Chauliodoniscus* and *Mastigoniscus*, is based on several characters with low consistency indices (see Tabs 7, 8). Important is the gradual reduction of the flagellate setae on the pereopods. But this trend is disturbed by some species: An increasing reduction of the flagellate setae of the ventral pereopods occurs on the way from the most basal taxa to the more derived genera. The basalmost genus *Hydroniscus* is the only one that possesses such setae on the ventral propodus of the anterior pereopods. In clade 36 (*Haploniscus cucullus* complex and *H. nondescriptus*) flagellate setae can be found on the ventral carpus of all pereopods, on the propodus of the posterior pereopods and on the merus.

In those species that are more derived than the *Haploniscus cucullus* complex, the propodus lacks flagellate setae. On the branch towards clade 12 (*Mastigoniscus*, *Chauliodoniscus*, *Antennuloniscus* and several *Haploniscus* species) the flagellate setae are successively reduced. Only the flagellate setae on pereopods 1-4 are present in clade 24 (*Mastigoniscus*, *H. spinifer*, *H. bicuspis*) namely in *H. bicuspis* (present on pereopods 1-4) and *H. spinifer* (present on pereopods 2-4), while they are absent in all *Mastigoniscus* species and in the sistergroup of clade 24. *H. piestus*, *H. tangaroae*, *H. bicuspis* and *H. spinifer* do not fit into the pattern of successive reduction of flagellate setae in the stem lineage of clade 12.

Apart from *Hydroniscus*, *H. piestus* is the basalmost taxon in the tree. This species lacks the flagellate setae on pereopod 1, while the species of the more derived *Haploniscus cucullus* complex possess these setae. These are lost only in clade 11.

The absence of flagellate setae from pereopod 1 supports the sistergroup relationship of *H. tangaroae* and clade 12, while by the presence of these setae on the carpus, propodus and merus of pereopods 5-7 in *H. tangaroae* a more basal position of this species is supported. Several other characters support the present position of *H. tangaroae*, but these are mostly characters with a low consistency index, such as the width of the pereonites or the length of the dorsal tooth of article 3 of antenna 2. Therefore the position of this species in the topology presented above has to be doubted somewhat.

Contrary the sistergroup relationships of *H. bicuspis* and *H. spinifer* are supported by some strong characters, to which higher weights were assigned *a priori*, such as the length of the endopod of pleopod 2, the sexually dimorphic processes of the pleotelson and the laterally directed first article of the endopod of pleopod 2.

Because of this inconsistency in the presence of flagellate setae the reliability of this character and its importance for the topology of the tree is somewhat diminished.

In addition, the presence of flagellate setae on the dorsal carpus follows a different pattern. Even in those clades where flagellate setae are completely absent from the ventral carpus, they may be found on the dorsal carpus, on pereopod 7 within *Antennuloniscus* and on pereopod 6 within *Mastigoniscus*. *Chauliodoniscus* is the only genus where flagellate setae are completely absent.

The absence of flagellate setae from the pereopods is a reduction; usually reductions are regarded as less informative, because they are supposed to require less change on a genetic level than the development or appearance of structures. Nevertheless, flagellate setae, which are known to be mechanical receptors (Brandt, 1988; Wägele, 1992), seem to be an important sensory structure for most isopods and their absence surely has implications for the perception of mechanical stimuli.

Besides the lack of flagellate setae the following trends could be observed in the derived genera *Antennuloniscus*, *Mastigoniscus* and *Chauliodoniscus*: the number of setae, especially of the spine-like or stout setae of the posterior pereopods seems to be more conserved in these genera than in the more basal groups of *Haploniscus*. Unfortunately this could not be confirmed for all species, because not enough specimens were available. The difference between posterior and anterior pereopods according to the size of the combs on the ventral carpus and propodus seems to be more obvious in these three genera, than in the more basal taxa. All three genera show a pronounced sexual dimorphism, but as different parts of the body are concerned by this, it seems likely, that this was developed convergently.

The sistergroup relationship of clade 15 and *Chauliodoniscus* is also supported by characters with mostly low consistency indices, which might have developed convergently. Interesting is again the lack of flagellate setae on the ventral carpus of pereopods 2-4 and the absence of a flagellate seta from the dorsal carpus of pereopod 6.

As mentioned above the sistergroup relationships in the terminal clades, namely in the genera *Antennuloniscus*, *Chauliodoniscus* and *Mastigoniscus* are somewhat doubtful, being supported by low-weight characters that are distributed all over the tree and have low consistency indices.

The relationships of *H. rostratus* and *H. ingolfi* to *Antennuloniscus*, and of *H. bicuspis* (Greenland) and *H. spinifer* to *Mastigoniscus* are distinctly better supported.

Some of the antennal characters that were attributed to *Antennuloniscus* are found in *H. rostratus* and *H. spinifer* and either the generic definition of *Antennuloniscus* has to be extended to include this two species or it has to be restricted to mainly three characters, which are the prolonged clypeus, the fusion of antennal articles 5 and 6 and the reduction of article 1 of antenna 2. The last character is somewhat problematic; in *A. simplex* this article seems to be larger than in other *Antennuloniscus* species; nevertheless it is distinctly smaller than in other genera of the family.

Park (2000) already stated that the elongated endopod of pleopod 2 is not exclusively found in *Mastigoniscus*. But it is an important character supporting the sistergroup relationships of *H. spinifer* and *H. bicuspis* (Greenland) to *Mastigoniscus*. An elongated endopod of pleopod 2 was also found in *H. sp. 12*, but here it was only about twice as long as the basipod, while it was distinctly longer in the species of clade 24. The lateral direction of the first article of the endopod can not be regarded as exclusive for *Mastigoniscus* as well, but seems to be a synapomorphy of *H. bicuspis* and *Mastigoniscus*. As important apomorphies for *Mastigoniscus* remain the reduction of pereonite 7 and the enlargement of pleotelson and pleopods, both in males.

The different position of the two species identified as *H. bicuspis*, can be partly explained by the fact that only subadult males were available of the DIVA species from the Angola Basin. Several characters separating the two species can be determined only in adult specimens, such as the length of the endopod of pleopod 2 and the sexual dimorphism. Nevertheless some differences between the two species exist. Some of the differing characters have only low consistency indices and low weights. Contrary the direction of the first article of the endopod of pleopod 2 has weight 4 and was found to differ between the two species. However, it is possible that the direction of the article undergoes a change during the last

molt. The same might be true for the shape of pleopod 1, which is another differing character. Nevertheless it has to be assumed, that two different species are present as mentioned above (4.2.2.1).

The only synapomorphy for clade 36 (*Haploniscus cucullus* complex and *H. nondescriptus*) is the short dorsal tooth on antennular article 3. This is not a very convincing character, as it might have developed convergently several times in the evolution of the family. Other characters shared by the species of this clade are the broad body shape, the keels on the dorsal pleotelson, the concave frontal margin, the simple shape of pleopod 1, the numerous setae on article 3 of the mandibular palp, maybe the missing sexual dimorphism of the antennae and of course the presence pattern of flagellate setae on the pereopods. Most of these characters were attributed to the groundpattern of the family or of clade 2.

As an alternative theory the short antennular tooth could be regarded as part of the groundpattern of clade 1 or 2 or as convergent development; then the species of clade 36 would belong to a paraphylum basally of clade 3. However, in a molecular phylogeny of the *Haploniscus cucullus* complex its monophyly is supported.

Unfortunately only two species from the genus *Hydroniscus* were available for this analysis. The characters supporting the sistergroup relationship of these two species cannot be equated to apomorphies of the whole genus without checking the other species of *Hydroniscus*. All species of the genus can enroll into a ball with the frontal margin close to the terminal margin, possess two deep indentations of the frontal margin, show a high degree of fusion of the posterior pereonites and seem to lack in fact any trace of pereonite 7 in dorsal view. To the contrary the length of the dorsal claw seems to be longer than one third of the dactylus length in *H. ornatus* Menzies, 1962, while the simple setae on the carpus of *H. vandeli* Chardy, 1974 are almost as long as the width of the carpus in Chardy's figure.

Despite the evidence from molecular studies (Michael Raupach, pers. com.), which supported *Neojaera* sp. as sistergroup of the Haploniscidae, *Disparella neomana* and *Haplomesus corniculatus* are found to be more closely related to the ingroup in this analysis. However, only few characters were used to resolve the relationships of the outgroup taxa, so this can be considered as an artifact.

4.4.3 Implications for the evolution of the Haploniscidae

Despite the problems discussed above, which affect the reliability of the resulting phylogeny, a general idea of the phylogeny of this problematic family was gained from the results and is presented below (Fig. 4.5). It shows the most important clades and the synapomorphies supporting these. Still it has to be regarded that these assumptions about the evolution within the family are not based on solely unambiguous results. The generic diagnoses of *Antennuloniscus*, *Chauliodoniscus* and *Mastigoniscus* have to be supplemented to include the absence of flagellate setae from the ventral margins of the pereopods.

Despite the close proximity of some *Haploniscus* species to *Antennuloniscus* respectively *Mastigoniscus*, these shall not be allocated to the two genera here, because both genera are still defined by easily recognized apomorphies (*Antennuloniscus* by the fused articles 5 and 6 and the small article 1 of antenna 2 and the prolonged clypeus; *Mastigoniscus* by the reduced pereonite 7) and because of the generally limited significance of the results.

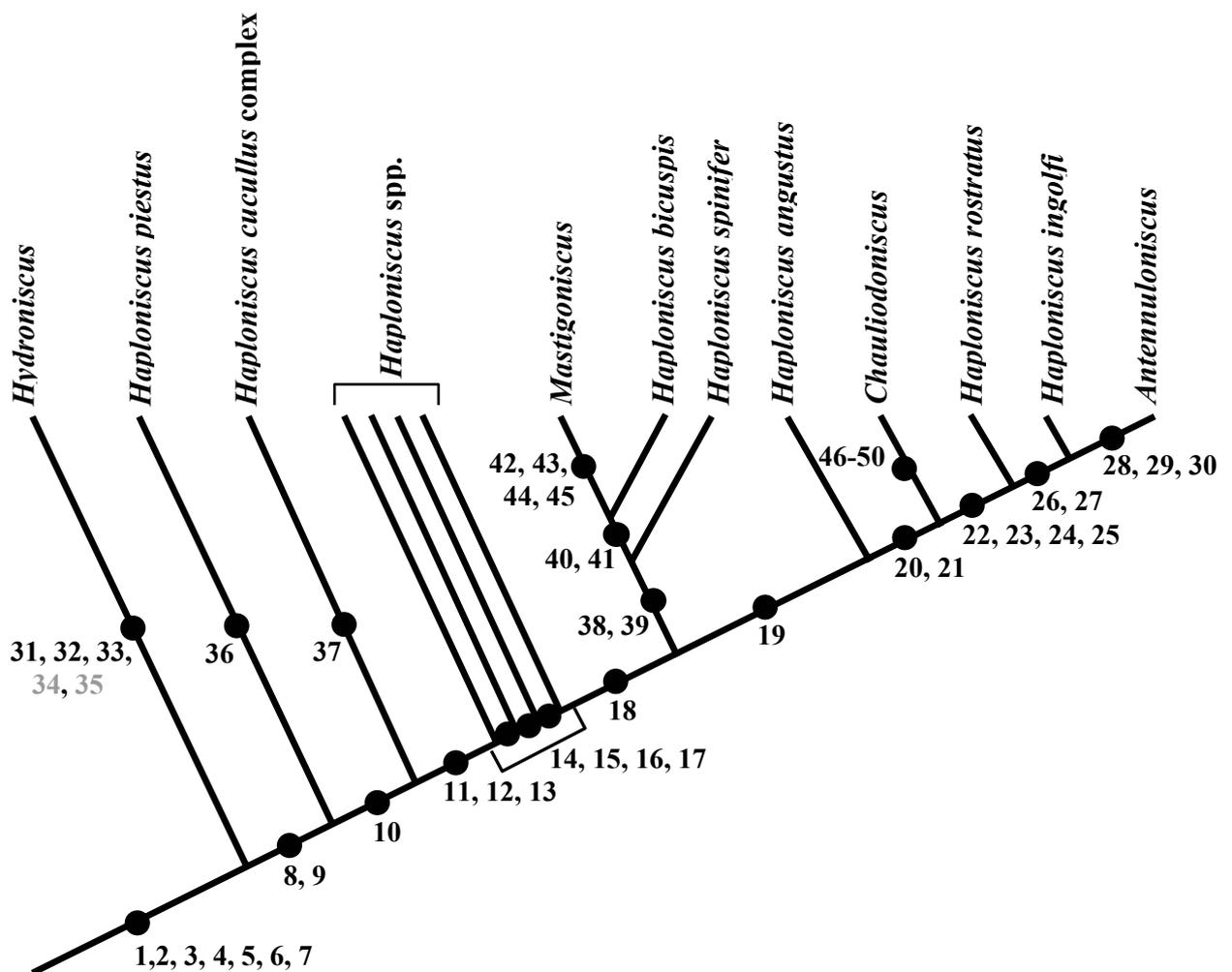


Figure 4.5: Phylogeny of the Haploniscidae with important synapomorphies (characters in grey can not be generalized for the whole genus, continued next page)

- 1: pereonites 5-7 fused middorsally with each other and pleotelson
- 2: antenna 2 article 3 with dorsal tooth
- 3: maxilliped endite distolaterally expanded
- 4: ventral combs on carpus and propodus well developed
- 5: carpus with distinct apical combs
- 6: ventral claw reduced
- 7: pleopod 3 with small triangular exopod
- 8: propodus of pereopods 1-4 without ventral flagellate setae
- 9: pleotelson with two sharp longitudinal keels
- 10: pleotelson with bulge around branchial chamber tapering towards anus
- 11: mandibular palp article 3 with no more than seven serrated setae
- 12: ischium of posterior pereopods with only two ventral setae
- 13: propodus of pereopods 5-7 without ventral flagellate setae
- 14: merus of pereopods 5-7 without flagellate setae
- 15: carpus of pereopod 7 without ventral flagellate setae
- 16: carpus of pereopods 5-6 without ventral setae
- 17: carpus of pereopod 1 without ventral flagellate seta
- 18: pleotelson without bulge around branchial chamber
- 19: carpus of pereopods 2-4 without ventral flagellate setae
- 20: maxilliped with 2 retinacula
- 21: without dorsal flagellate seta on carpus of pereopod 6
- 22: antenna 2 article 3 elongated, longer than article 6
- 23: antenna 2 article 6 with apical tooth
- 24: antenna 2 flagellum inserting subapically on article 6
- 25: apical ventral comb on propodus extended
- 26: antenna 2 flagellum with no more than eight articles
- 27: apical carpus of pereopod 7 with dorsal flagellate seta
- 28: clypeus prolonged anteriorly
- 29: antenna 2 praecoxa reduced, small
- 30: antenna 2 articles 5 and 6 fused
- 31: frontal margin with two deep indentations
- 32: pereonite 7 not visible dorsally

Figure 4.5: Phylogeny of the Haploniscidae with important synapomorphies (continued).

- 33:** conglobating with frontal margin close to terminal margin
- 34:** ventral simple setae on carpus short, less than half as long as carpus width
- 35:** dorsal claw less than one third of dactylus length
- 36:** pereopod 1 carpus without ventral flagellate setae
- 37:** dorsal tooth on article 3 of antenna 2 less than half as long as article
- 38:** endopod of pleopod 2 at least more than twice as long as basipod
- 39:** pleotelsonic processes sexually dimorph
- 40:** pleopod 1 broadening more distally, lateral margins more or less convex
- 41:** endopod of pleopod 2 with laterally directed first article
- 42:** males with reduced, short pereonite 7
- 43:** carpus of pereopods 2-4 without ventral flagellate setae
- 44:** carpus of pereopods 2-5 with apical dorsal combs
- 45:** pleopods 1 and 2 of males enlarged
- 46:** anterior angles of one or more of pereonites 2-4 prolonged
- 47:** pereonite 5 freely articulating with pereonite 6
- 48:** conglobating with frontal margin close to branchial chamber
- 49:** antenna 2 article 5 inflated, with convex lateral margins
- 50:** shape of anterior pereonites sexually dimorphic

Figure 4.5: Phylogeny of the Haploniscidae with important synapomorphies (continued).

5 Outlook

Every deep-sea expedition reveals numerous species that are new to science. At present we are still far from a complete assessment of the species inventory of the deep sea. As studies of ecology, phylogeny, biodiversity and evolution of the deep-sea fauna all depend on taxonomic knowledge, the description of these new species is the first important step towards an understanding of biological processes in the deep-sea. Although the description of new species is a time consuming work, its importance cannot be neglected. Many of the ANDEEP species still have to be described and the problem of sibling species will probably enhance the efforts necessary for a full account of species found in the samples.

Recently the problem of sibling species becomes more and more obvious (Wilson 1983 a, b, 1985; Held, 2003). What was thought to be a single species is found to represent in fact a number of very similar species. The *Haploniscus cucullus* complex is one example for such species complexes, but similar findings can be expected within other genera of the Haploniscidae and other families as well. Also in the ANDEEP material further species complexes might be present; there is some hint in the genus *Antennuloniscus*, for example. Therefore the detailed study of species complexes in the Haploniscidae and other families of the Janiroidea by both, morphological and molecular means, is an important task in deep-sea isopod research; the results might hint to the reasons for the development and maintaining of the astounding diversity of the deep-sea benthos.

Because the deep sea is difficult to access and expeditions devoted to the study of the deep sea require enormous financial and logistic efforts, sampling activities in the deep sea are scarce and our database about the distribution of many taxa is poor. The discovery of *Mastigoniscus* species in the South Atlantic suggests that our knowledge about zoogeography depends essentially on sampling activity. As the species area plot has shown, even the extensive ANDEEP material does contain only a fraction of the isopod species inhabiting the sampled area. During the ANDEEP III expedition, which is planned for January – April 2005, extensive samples will be taken in the eastern Weddell Sea, to gain a more detailed picture about the benthic life in the deep Weddell Sea.

The phylogenetic relationships within the Haploniscidae are still problematic. However, it has to be doubted that a considerably better resolution can be found by morphological means alone. Using molecular methods will probably be necessary to access a better understanding

of this enigmatic family. Yet, this depends on fresh material for DNA extraction. The phylogeny of many other families remains uncertain as well, and will require much efforts in future studies.

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8 Appendix

Abbreviations

ANDEEP: Antarctic benthic deep-sea biodiversity

BMNH: British Museum of Natural History

DIVA I: Diversity of the Deep Atlantic Ocean I

EBS: epibenthic sledge

Md: mandible

NIWA: National Institute of Water and Atmospheric Research, New Zealand

P1-7: pereopods 1-7

pers. com.: personal communication

Plp1-5: pleopods 1-5

SAM: South African Museum

ZMB: Zoologische Sammlungen des Museums für Naturkunde, Berlin

ZMH: Zoologisches Museum Hamburg

ZMMU: Zoological Museum of Moscow University

Table 9: Character matrix of 53 taxa and 96 characters used in the phylogenetic analysis

Taxa	Characters									
	0	1	2	3	4	5	6	7	8	9
	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789
<i>A. alfi</i>	3-1-32212	1-22212222	1112122311	2-22222222	2212211111	2212222221	2222211122	221?2?1222	?122221222	1122223
<i>A. armatus</i>	2-2232212	1-22222222	1112122311	2-22222221	2212211111	2212222222	1222211122	221?2?1222	1122221222	1122223
<i>A. dimerocheras</i>	2-2232211	1-22222222	1112122311	2-22222221	2112211111	2212222221	2222221122	2211121212	1122221222	1122223
<i>A. diversus</i>	2-2?32211	1-22212322	1112122311	2-22222222	2122211111	1212222221	2222221122	2211111212	1122221222	1122223
<i>A. ornatus</i>	3-1-32211	1-22222122	1112122311	2-22222221	2212211111	2212222222	1222211122	2211211222	1122221222	1122223
<i>A. simplex</i>	2-1-32211	1-2221222?	1112112311	2-22222222	2211211111	1212222221	2222211122	2211221212	1122221222	1122223
<i>A. latoperculus</i>	112232211	1-22222112	1111122321	2-22222222	2111111111	2212222221	1222211122	2?1?????2?	?222221222	11222?-
<i>C. armadilloides</i>	111-12221	1-22112112	1311111331	1211122221	2211211111	1212222221	3212211122	2211122222	1122221222	1122222
<i>C. coronatus</i>	2-1-12221	1-22112332	1312111332	1211222221	2212211111	1212222222	3212211122	2212211222	1122221222	1122222
<i>C. tasmanus</i>	2-1-12221	1-22112212	1312111331	1211122221	2112211111	1212222222	3212211122	2211221222	1122221222	1122222
<i>C. sp.1</i>	2-1-12222	1-22112112	1311111331	1211222221	2211111111	1212222221	3212211122	221?2?1222	1122221222	11222?-
<i>Ha. ampliatus</i>	3-2112213	1-222122?1	1112111321	1111123222	2112211112	1211111221	1212221122	2211211222	1122221222	112221-
<i>Ha. angustus</i>	2-1-12211	1-2222211?	1111211331	1111122222	2111111112	2212222221	3212211122	2211112212	1122221222	112221-
<i>Ha. bicuspis_DIVA</i>	3-2212211	1-22212?31	1111111331	1111122222	2111211212	1211122221	2212221122	221?2?1222	?122221222	11222?-
<i>Ha. bicuspis_Greenland</i>	2-2212212	1-22222231	1111111322	1111122222	2111211212	1211122221	2212211122	2212111222	2222221222	1122221
<i>Ha. borealis</i>	3-2112212	1-2221221?	1112111331	1111122222	2112211112	2211111221	1212221122	2211121212	1122221222	112221-
<i>Ha. foresti</i>	111-12213	1-22?1221?	1111111321	111112?222	2112222111	1211111?22	?212211122	2211221212	1122221222	112221-
<i>Ha. hamatus</i>	2-2112212	1-2221223?	1111111331	1111122222	2111111212	1211122221	2212211122	2222211212	1122221222	112221-
<i>Ha. ingolfi</i>	3-1-12211	1-2221211?	1111112321	1122222221	2111211212	1212222222	1222211122	2211221222	1122221222	112221-
<i>Ha. miccus</i>	112212212	1-222122?1	1111111321	1111122222	2112211112	1211111221	2212211122	2211212212	1122221222	112221-
<i>Ha. nondescriptus</i>	111-12212	1-22212231	1111111311	1111122222	2122222112	2211111221	2212121122	221?2?1212	1122221222	11222?-
<i>Ha. piestus</i>	112112212	1-22212232	1111111321	1111122222	2122222122	1212111221	?212121122	2211221212	1122221222	112221-
<i>Ha. rostratus</i>	3-2112211	1-22222231	1112112321	1122122221	2111211111	1212222221	3222211122	2212211222	1122221222	112221-
<i>Ha. saphos</i>	112112213	1-22212231	111111?321	?????22222	2112211112	1211111221	2212222122	2211221212	1122221222	112221-
<i>Ha. silus</i>	2-2112212	1-22212131	1112111331	1111122222	2112211112	1212112221	1212211122	2211221122	1122221222	112221-
<i>Ha. spinifer</i>	2-1-12212	1-22222232	1111111321	1121122222	2112211112	1212122222	3222211122	2211211212	2122221222	1122221
<i>Ha. tangaroae</i>	2-2212212	1-22212231	1112111331	1111122222	2111222112	1212111221	2212111122	2211211212	1122221222	112221-
<i>Ha. cucullus</i>	112112212	1-22212131	1111111311	1111122222	2122222122	1211111221	2212121122	221?2?1222	1122221222	11222?-
<i>Ha. cassilatus</i>	112112212	1-22212131	1111111311	1111122223	2122222122	1211111221	2212121122	2211221212	1122221222	112221-
<i>Ha. weddellensis</i>	112112212	1-22212131	1111111311	1111122222	2122222112	1211111221	2212121122	2211221212	1122221222	112221-
<i>Ha. procerus</i>	112112212	1-22212231	1111111311	1111122222	2122222122	2211111221	2212111122	221?2?1222	?222221222	11222?-
<i>Ha. kyrbasius</i>	112112212	1-22212131	1111111311	1111122222	2122222121	2211111221	2212121122	2211221212	1122221222	11222?-
<i>Ha. sp.4</i>	2-1-12212	1-22212111	1111111332	1111122222	2112221112	1211112221	1212221122	2211211222	1122221222	11222?-
<i>Ha. nudifrons</i>	111-12212	1-22212231	111?1?3111	?????22222	2122222122	1211111221	2212121122	221?2?1222	?222221222	11222?-
<i>Ha. microkorys</i>	112112212	1-22212131	1111111311	1111122222	2122222122	1211111221	2212121122	2211221212	1122221222	11222?-
<i>Ha. sp.12</i>	112112212	1-22212231	1111111331	1111122222	2111111122	1211122221	2212221122	2222111222	2122221222	112221-
<i>Hy. lobocephalus</i>	122212212	2222212212	12222111--	1111122222	2121111122	2221111221	3211111222	2212211212	1122221222	112221-
<i>Hy. vijazi</i>	122212212	2222212212	12222111--	1111112?22	2122222112	122111121-	-211111222	2211211212	1122221222	11222?-
<i>M. elegans</i>	2-1-12212	212222232	1111111322	1111122222	2111111112	1212222222	3212211122	2112111212	2222221222	1122221
<i>M. gratissimus</i>	2-1-12212	212222312	1111111322	1111122222	?211111111	1212222222	3212211122	2111112222	2222221222	2122221
<i>M. pistus</i>	111-12213	212222312	2111111321	?????22222	?2?1??????	?2222?2222	?212?1?122	2112112212	2222221222	21222?-
<i>M. platovatus</i>	2-1-12212	212222312	2111211322	1111122222	2111111112	1212222222	3212211122	2112111222	2222221222	2122221
<i>M. stenocephalus</i>	111-12212	212222312	2111111322	?????22222	2211111112	1212222221	3212211122	2112111222	2222221222	1122221
<i>M. andeepi</i>	2-1-12211	212222332	2111211322	1111122222	2211111112	1222222222	3212211122	2111111212	2222221222	2122221
<i>M. polygomphios</i>	2-1-12212	212222312	2111111322	1121122222	2211111112	1212222222	3212211122	2112111212	2222221222	1122221
<i>M. pseudoelegans</i>	2-1-12212	212222232	1111211322	1111122222	2211111112	1212222222	1212211122	2112111212	2222221222	11222?-
<i>M. sp. A</i>	2-1-12212	212222?32	?111111322	1121122221	2211111112	1212222222	1212211122	211?2?2?2?	?222221222	11222?-
<i>M. sp.B</i>	2-1-12212	212222?12	?112111322	1111122222	2211111112	1212222222	3212211122	2?1?2?2?2?	?222221222	11222?-
<i>Neojaera sp.</i>	111-11111	1-11112112	11121112--	1111111211	2111111111	11-111111-	-111122112	2112111222	2122112222	112121-
<i>Acanthaspidia drygalskii</i>	112212211	1-11121-12	1112112--	1111211313	2121111111	11-111111-	-111122112	2211111222	1122121212	212221-
<i>Stenitrium weddellense</i>	111-21121	1-11122112	11121112--	111111?313	1121111111	11-222211-	-112222111	1-1----111	1111111111	211111-
<i>Disparella neomana</i>	121-12111	1-11122212	11111111--	1111211112	1122121211	121212221-	2112222222	2112112221	1222212122	1122223
<i>Haplomesus corniculatus</i>	2-1-12211	1-22222112	11111111--	11111?2312	1122221111	?1-111?221	2111112212	2111111212	1122212---	-2-?2?-

Table 10: Environmental parameters for BioEnV calculation.

environmental parameter	131-3	132-2	133-3	134-3	135-4	136-4	137-4	138-6	139-6	140-8	141-10
depth (m)	3053	2086	1121	4069	4678	4747	4976	4542	3950	2970	2312
CTD density	2,94	1,95	1,03	0,57	3,25	1,46	1,2	4,37	3,83	4,14	1,46
CTD temp	-0,85	-0,65	-0,71	-0,24	0,49	0,89	0,09	-0,43	-0,89	1,42	1,16
CTD sal	34,64	34,65	33,64	34,04	34,08	34,12	34,68	34,66	34,66	33,99	33,97
Tanaidacea	25	0	75	4	7	3	7	7	27	69	94
Amphipoda	419	32	321	21	30	5	18	74	19	91	228
Cumacea	65	3	547	15	10	5	5	15	8	53	29
Mysidacea	37	15	13	0	2	0	0	2	2	1	36
sand	10	35	70	5	5	5	5	1	25	15	30
silt	40	55	15	30	30	40	75	70	50	60	60
clay	50	10	15	65	65	55	20	19	25	25	10
steepness	2	1	0	3	2	2	2	2	5	10	46
Lat S	65,1983	65,1775	65,2017	65,1920	65,0005	64,0154	63,4498	62,5808	58,1410	58,1598	58,2507
Long E	51,3161	53,2281	54,1430	48,0377	43,0302	39,0688	38,4775	27,5410	24,2120	24,5373	24,0078

Table 11: Basic data for PRIMER analysis. ANDEEP I stations.

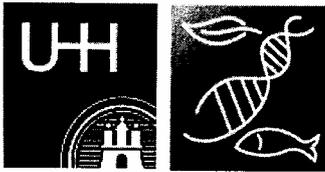
Stations	41-3	42-2	43-8	46-7	99-4	105-7	114-4	129-2
<i>Disconectes sp. 1 antarctica</i>	0,81	1,05	1,00	33,69	0,00	0,00	6,47	0,00
<i>Disconectes sp. 2 ovaloides</i>	0,00	0,00	0,00	0,18	0,00	0,00	0,45	0,00
<i>Disconectes sp. 3 ovalis</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Disconectes sp. 4</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Disconectes sp. 5</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Disconectes sp. 6</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Disconectes sp. 7</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Disconectes sp. 8</i>	0,00	0,00	0,00	0,89	0,00	0,00	0,67	0,00
<i>Disconectes sp. 9</i>	0,00	0,21	0,00	0,00	0,00	0,00	0,22	0,00
<i>Disconectes vanhoeffeni</i>	1,42	9,83	4,60	0,00	0,00	0,00	0,45	1,23
<i>Disconectes curta</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>near Disconectes / Lionectes</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Munnopsurus sp. 1</i>	0,00	0,00	0,21	0,00	0,00	0,00	0,45	0,00
<i>Munnopsurus sp. 2</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,22	0,00
<i>Munnopsurus sp. 3</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Munnopsurus australis = giganteus?</i>	0,20	0,84	0,00	1,60	0,00	0,00	0,67	0,25
<i>Munneurycope sp. 1</i>	0,20	0,21	0,00	0,35	0,00	0,00	2,90	1,96
<i>Munneurycope sp. 2</i>	0,00	0,21	0,00	0,00	0,00	0,00	0,00	0,00
<i>Munneurycope harrietae or antarctica</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Munneurycope crassa</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Munneurycope nodifrons</i>	0,20	0,00	0,00	0,00	0,00	0,00	1,12	0,00
<i>Munneurycope sp. 3</i>	0,00	2,30	0,21	1,95	0,00	0,00	3,57	0,74
<i>Munneurycope sp. 4</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Munneurycope sp. 5</i>	2,23	0,00	0,21	0,00	0,00	0,00	0,45	0,00
<i>Munneurycope menziesi</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,22	0,00
<i>Munneurycope moulted</i>	0,20	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Betamorpha fusiformis</i>	9,13	6,07	4,81	4,08	0,00	0,00	7,37	0,25
<i>Betamorpha africana</i>	2,23	1,26	0,84	0,00	0,00	0,00	0,89	0,00
<i>Betamorpha with setae</i>	0,41	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Betamorpha cf. indentifrons</i>	0,20	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Betamorpha cf. profunda</i>	0,20	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Betamorpha n. sp.</i>	0,00	0,00	0,21	0,00	0,00	0,00	0,00	0,00
<i>Ilyarachna sp. 1</i>	0,00	0,21	0,21	0,53	0,00	0,00	0,22	0,00
<i>Ilyarachna sp. 2</i>	1,01	2,09	0,00	0,00	0,00	0,00	0,45	0,00
<i>Ilyarachna sp. 3</i>	0,00	0,21	0,00	0,00	0,00	0,00	0,00	0,00
<i>Ilyarachna sp. 4</i>	0,20	0,21	0,00	4,79	0,00	0,00	0,00	0,00
<i>Ilyarachna sp. 5</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,22	0,00
<i>Ilyarachna sp. 6</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,67	0,00
<i>Ilyarachna/Hapsidohedra ?juv.</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,25
<i>Ilyarachna antarctica</i>	0,41	26,36	6,07	3,01	0,19	0,00	3,13	2,21
<i>Ilyarachna bicornis</i>	0,00	0,63	1,05	0,00	0,00	0,00	0,22	0,00
<i>Ilyarachna spinosissima</i>	0,00	0,00	0,00	0,18	0,00	0,00	0,00	0,00
<i>Ilyarachna triangular</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Ilyarachna nordenstami</i>	0,00	0,21	0,00	0,00	0,00	0,00	0,00	0,00
<i>Ilyarachna sp. nov? - spines</i>	0,00	0,00	0,21	0,00	0,00	0,00	0,00	0,00
<i>Aspidarachna/Hapsidohed./Ilyarachna</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Aspidarachna sp. 1</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Aspidarachna sp. 2</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Echinozone sp. 1 spinosa</i>	0,00	0,00	0,00	1,06	0,00	0,00	1,56	0,00
<i>Echinozone sp. 2 quadrispinosa</i>	0,00	0,00	0,00	0,18	0,00	0,00	0,67	0,00
<i>Echinozone magnifica</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope "complanata" sp. 1</i>	2,84	11,51	4,18	11,88	0,00	0,35	2,23	0,25
<i>Eurycope sp. 2 - rugose plt</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 3 - "galathea"</i>	0,20	1,67	2,51	1,42	0,00	0,69	4,02	0,00
<i>Eurycope glabra</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 4 - narrow plt</i>	0,20	0,63	1,26	0,00	0,00	0,00	2,01	0,49
<i>Eurycope "complanata" sp. 5</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 6 - sim Hapsidoh.</i>	0,00	0,42	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 7</i>	0,00	0,00	0,00	0,00	0,00	0,00	1,79	0,00
<i>Eurycope sp. 8 - sim dahli</i>	0,00	0,21	0,84	0,00	0,00	0,00	0,00	0,25
<i>Eurycope moulted - like gaussi</i>	0,00	0,21	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 9 "longiflagrata"</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 10</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 11</i>	0,00	0,00	0,00	0,18	0,00	0,00	0,00	0,00

Table 11: Basic data for PRIMER analysis. ANDEEP I stations (continued).

Stations	41-3	42-2	43-8	46-7	99-4	105-7	114-4	129-2
<i>Eurycope sp. 12</i>	0,00	0,00	0,42	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sarsi</i>	0,00	0,00	0,42	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 13</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 14</i>	0,00	1,46	1,05	0,18	0,00	0,00	3,57	0,00
<i>Eurycope sp. 15</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycope sp. 16</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,22	0,00
<i>Eurycope sp. 17</i>	0,00	0,21	1,05	0,00	0,00	0,00	0,00	0,00
<i>Belonectes sp. 1</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Belonectes sp. 2</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycopinae n.gen. cf. nodosa</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycopinae n. gen sp. 1</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Eurycopinae n. gen sp. 2</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Mimocopelates sp. 1 "longipes"</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,67	0,00
<i>Mimocopelates sp. 2</i>	0,00	0,00	0,00	0,71	0,00	0,00	0,22	0,00
<i>Mimocopelates sp. 3</i>	0,00	0,00	0,00	0,18	0,00	0,00	0,00	0,00
<i>Mimocopelates sp. 4</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,22	0,00
<i>Hapsidohedra sp. 1</i>	0,00	0,42	0,00	0,00	0,00	0,00	0,00	0,00
<i>Hapsidohedra sp. 2</i>	0,00	4,60	0,00	0,00	0,00	0,00	0,00	0,00
<i>Hapsidohedra or Aspidarachna</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Lipomera (Paralipomera) knorrae</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Lipomera (Tetracope)</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Coperonus nordenstami</i>	0,00	1,88	0,00	1,60	0,00	0,00	0,00	0,00
<i>Coperonus pinguis</i>	0,00	2,93	0,00	5,14	0,00	0,00	0,00	0,00
<i>Coperonus sp. 1</i>	0,00	0,21	0,42	4,43	0,00	0,00	0,22	0,00
<i>Coperonus sp. 2</i>	0,00	0,00	0,00	0,53	0,00	0,00	0,00	0,00
<i>Coperonus sp. 3</i>	0,00	0,00	0,63	0,53	0,00	0,00	0,00	0,00
<i>Coperonus sp. 4</i>	0,00	0,00	0,00	0,35	0,00	0,00	0,00	0,00
<i>Lionectes humicephalatus</i>	0,00	0,00	0,00	1,06	0,00	0,00	0,22	0,00
<i>Thythiscope gruneri</i>	0,00	0,21	0,00	0,18	0,00	0,00	0,00	0,00
<i>Syneurycope heezeni</i>	0,20	1,46	0,00	0,00	0,19	0,00	0,00	0,00
<i>Bellibos sp.</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Bellobos (Bemerria) monicae</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,45	0,00
<i>Paramunnopsis cf. "justi"</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Paramunnopsis sp.</i>	0,00	0,00	0,00	0,18	0,00	0,00	0,00	0,00
<i>Munnopsis australis</i>	0,00	0,00	0,00	0,18	0,37	0,00	0,22	0,00
<i>Munnopsis sp. 1</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Munnopsis sp.nov?</i>	0,00	0,00	0,00	0,89	0,00	0,00	0,00	0,00
<i>Storhyngura longispina</i>	0,00	0,00	0,00	0,35	0,00	0,00	0,00	0,00
<i>Storhyngura antarctica</i>	0,20	0,00	0,00	0,71	0,00	0,00	0,00	0,00
<i>Storhyngura elegans</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,49
<i>Storhyngura kussakini</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Storhyngurella andeepi</i>	0,00	0,00	0,00	0,18	0,00	0,00	0,00	0,00
<i>Storhyngurella triplispinosa</i>	0,20	1,26	1,46	1,42	0,00	0,00	1,12	0,25
<i>Storhyngurella menziesi</i>	0,00	0,00	0,00	0,00	0,19	0,00	0,00	0,00
<i>Storhyngurella hirsuta</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Sursumura kussakini</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Sursumura angulata</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Sursumura sp. 3 andeepi</i>	0,00	0,00	0,00	0,18	0,00	0,00	0,00	0,00
<i>Rectisura sp. nov.</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Vanhoeffenella scotia</i>	0,00	0,84	1,67	0,00	0,00	0,00	0,22	0,00
<i>Vanhoeffenella sp. (juv.)</i>	0,00	0,21	0,00	0,00	0,00	0,00	0,00	0,00
<i>Acanthocope sp. nov. 1</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,45	0,00
<i>Acanthocope annulata</i>	0,00	1,46	0,00	0,00	0,00	0,00	0,00	0,00
<i>Acanthocope galathea</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Cryptoniscidae	0,00	0,42	0,00	0,35	0,00	0,00	0,00	0,00
<i>Gnathia sp.</i>	0,00	0,00	0,00	0,18	0,00	0,00	0,22	0,00
<i>Gnathia n. sp.?</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,22	0,00
<i>cf. Euneognathia gigas</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Pseudomesus sp. nov.?</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Pseudomesus sp. 1</i>	0,00	0,00	0,00	0,35	0,00	0,00	0,00	0,00
<i>Macrostylis sp. 1</i>	0,00	0,21	0,00	0,00	0,19	0,00	0,00	0,25
<i>Macrostylis sp. 2</i>	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Macrostylis sp. 3</i>	0,00	0,21	0,00	0,00	0,00	0,00	0,00	0,25
<i>Macrostylis sp. 4</i>	0,00	1,46	0,00	0,35	0,00	0,00	0,00	0,25

Table 12: Source data for PRIMER analysis. ANDEEP II stations (continued).

Stations	131-3	132-2	133-3	134-3	135-4	136-4	137-4	138-6	139-6	140-8	141-10	142-6	143-1
Dendrotonidae sp. 1	0,00	0,00	11,45	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Dendrotonidae sp. 2	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Dendrotonidae sp. 3	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Dendrotonidae sp. 2/3	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Dendromunna n. sp. 1</i>	0,00	0,00	0,76	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Dendrotonidae ?	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Haplomunnidae sp. 1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,24	0,00	0,48	1,29	0,00	0,00
Haplomunnidae sp. 2	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,24	0,00	0,00	0,00	0,00	0,00
Haplomunnidae sp. 3	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	2,59	0,00	0,00
Janirellidae sp. 1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Joeropsidae	0,00	0,00	2,29	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Stenetriidae sp. 1	0,00	0,00	1,53	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 1	0,00	0,00	2,29	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 2	0,56	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 3	0,00	0,00	0,76	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 4	1,13	0,00	2,29	0,00	0,00	0,00	0,00	0,00	0,00	0,48	0,65	0,00	0,00
Munnidae Munna sp. 4/5	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 5	0,56	0,00	0,76	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 6	0,00	0,00	0,76	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 7	0,28	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 8	0,00	0,00	3,82	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 9	0,00	0,00	20,61	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae Munna sp. 11	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Munnidae ?	0,00	0,00	1,53	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 1	3,94	0,40	5,34	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 2	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 3	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 4	1,41	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 5	0,00	0,00	6,87	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 6	0,00	0,00	8,40	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 7	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,69
Paramunnidae sp. 8	0,00	0,00	3,05	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 9	0,00	0,00	7,63	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 10	0,00	0,00	0,76	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae sp. 11	0,00	0,00	3,05	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Paramunnidae ?	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Mesosignum cf. usheri</i>	1,13	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,65	0,00	0,00
<i>Mesosignum aff. aspersum</i>	0,56	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
<i>Mesosignum n. sp. weddellensis</i>	0,00	0,00	0,00	0,00	0,36	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Eugerdella sp.nov. 1	0,00	0,00	22,14	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Eugerdella sp.nov. 2	3,10	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Eugerdella sp. 1	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,95	0,00
Eugerdella sp. 2	0,00	0,00	0,00	0,00	1,44	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Eugerdella sp. 3	0,00	0,00	0,00	0,00	0,00	1,32	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Eugerdella sp. 4	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	4,86
Eugerdella sp. 5	0,00	0,00	0,00	0,00	0,00	0,00	0,44	0,24	0,15	0,00	0,00	0,00	0,00
Eugerdella sp. 6	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,48	0,00	0,00	0,00
Eugerdella sp. 7	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,65	0,00	0,00
Eugerdella sp. 8	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Eugerdella sp. 9	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Eugerdella sp. 10	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
genus Echinopleura?	0,00	0,00	3,82	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Chelator sp.nov. 1	8,45	0,00	0,00	1,10	0,00	0,00	0,00	0,00	0,00	0,24	0,00	0,00	0,00
Chelator sp.nov. 2	0,28	0,40	0,00	0,22	0,00	0,19	0,00	0,72	0,15	0,24	0,00	0,47	0,00
Chelator sp.nov. 3	0,28	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00
Chelator ? sp. nov.	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,00	0,15	0,00	0,32	0,00	0,00



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This is to certify that the quality of the English employed in PhD thesis submitted by the candidate Wiebke Brökeland entitled "Systematics, zoogeography, evolution and biodiversity of Antarctic deep-sea Isopoda (Crustacea:Malacostraca)" is of a standard sufficient to fulfill the language requirements of the University of Hamburg.

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