

**Evolution, Systematics and Distribution of  
Desmosomatidae (Isopoda, Peracarida, Crustacea)  
in the deep sea**

**Dissertation**

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

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A handwritten signature in black ink, appearing to read "Arno Frühwald".

Professor Dr. Arno Frühwald  
Dekan

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### Summary

The present thesis deals with one deep-sea family of Isopoda: Desmosomatidae Sars, 1897. It contains three major topics: 1) taxonomy, 2) biogeographic and distributional aspects (aspects of zoogeography) and 3) phylogeny. Based on morphological characters, a revision of the family Desmosomatidae Sars, 1897 is presented.

In the taxonomy part four new species, *Desmosoma renatae* sp. nov., *Eugerdella theodori* sp. nov., *Momedossa longipedis* sp. nov. and *Torwolia tinbienae* sp. nov. are described from material of the DIVA-1 expedition and *Eugerdella serrata* sp. nov. is described from material of the ANDEEP-expeditions. Eight new species are described from museum material (Museum Victoria, Melbourne) and eight incompletely described species are redescribed.

Furthermore, modified diagnoses are presented for all genera. The genera are discussed. One new genus is erected (*Pseudergella* gen. nov.). As result of the phylogenetic discussion, Nannoniscidae Hansen, 1916 are included in Desmosomatidae Sars, 1897. Five subfamilies of Desmosomatidae are defined and discussed (phylogeny part): Austroniscinae, Desmosomatinae, Eugerdellatinae, Pseudomesinae and Nannoniscinae.

As zoogeographic aspects, the results of the DIVA-1 and the ANDEEP expeditions I & II are presented for the family Desmosomatidae *sensu* Hessler (1970) and Wägele (1989) excluding the genus *Thaumastosoma*. The percentage of new species in the DIVA-1 samples is very high (93%) and only slightly lower when Nannoniscidae are included in the family (85,7 %). Desmosomatidae are next to Munnopsididae the second most dominant isopod family in the samples.

As for all Isopoda, the distribution of Desmosomatidae at the ANDEEP stations is found to be rather patchy and many species are rare. In the ANDEEP samples, Desmosomatidae (48 species) are more diverse than in the DIVA-1 samples (27 species). Their abundance in the deep Southern Ocean is lower than in the Angola Basin.

The percentage of potential endemics in the DIVA-1 samples is 33,3 %, in the ANDEEP samples 52 %. With the present knowledge it is not possible to decide whether a species is endemic or not, because the density of stations in the deep sea

is extremely low compared to the not sampled (unknown) area.

The existing system (Hessler 1970, Siebenhaller & Hessler 1977, 1981, Wägele 1989) is discussed and brought up to date in the phylogeny part. The question if Desmosomatidae are monophyletic and how closely Desmosomatidae Sars, 1897 are related to their sister family Nannoniscidae Hansen, 1916 is addressed and discussed based on morphological characters. The two families are not clearly separated by the existing autapomorphies. Together, Nannoniscidae and Desmosomatidae are regarded as a monophyletic group. Desmosomatidae were erected by Sars in 1897, Nannoniscidae by Hansen in 1916. Thus, the valid family name is Desmosomatidae. In total, 107 species of 31 genera are analysed. The characters of all species included into the analysis are discussed in detail.

The present knowledge does not completely resolve the relationship of all taxa. The consistency indices of the resulting trees are low. All three consensus trees support the five subfamilies (taxonomy part). Desmosomatinae can be regarded as a monophyletic group, while Eugerdelatinae are weakly supported and are only completely resolved as monophyletic group in the 50 percent majority rule tree. Pseudomesinae are a monophyletic group. The position of *P. atypicum* resolved in the 50 percent majority-rule tree, while in the 80 percent majority-rule tree and the strict consensus the position of *P. atypicum* is not resolved. Austroniscinae and Nannoniscinae are monophyla in all three trees.

Polytomy leaves the relationships of the genera somewhat uncertain. The systematic position of some genera could be clarified. For example, the genus *Torwolia* was treated as subfamily *incertae sedis*. The present study can show that this genus belongs to the subfamily Desmosomatinae and is closely related to *Desmosoma*, *Pseudogerda* and *Eugerda*.

### Abbreviations

The following abbreviations are used in the text and figures:

|        |                              |
|--------|------------------------------|
| ♂      | male                         |
| ♀      | female                       |
| A1     | first antenna; antennula     |
| A2     | second antenna; antenna      |
| Ceph   | cephalothorax (head)         |
| Lm     | lacinia mobilis              |
| MdL/R  | mandible left or right       |
| Mx1    | first maxilla, maxillula     |
| Mx2    | second maxilla, maxilla      |
| Mxp    | maxilliped                   |
| Op     | operculum (pleopod 2)        |
| PI-VII | pereopods I-VII              |
| Ip     | incisior process             |
| Plt    | pleotelson                   |
| PI1-5  | pleopods1-5                  |
| Pm     | pars molaris                 |
| Prn1-7 | pereonites 1–7               |
| Urp    | uropods                      |
| EBS    | Epibenthic Sledge            |
| ZMH    | Zoological Museum of Hamburg |
| MT     | Multitrawl                   |
| SBT    | Small bottom trawl           |
| SEM    | Scanning Electron Microscopy |



### **1 Introduction**

“Our generation is the first to fully appreciate the threats facing millions of species, and the last generation with the opportunity to explore, describe and classify life on earth so completely.” (Wheeler 2004:S. 571)

The reason for the wide range in estimations of the worldwide species number is the lack of information about deep-sea communities (endemic species, regional differences) with increasing depth (Thorson 1971, Groombridge 1992, Grassle & Maciolek 1992, Lamshead 1993). While the global diversity of Metazoa is estimated with 10 to 30 million species, only 1.8 million species are described (Wilson 1985, May 1992, Purvis & Hector 2000). Despite the fact that oceans cover over 70% of the earth's surface, they host only about 200.000 of the 1.8 million species described (Grassle 2001, Boltovskoy *et al.* 2005). In deep-sea study areas that are sampled for the first time, the fraction of species new to science ranges from 50 to 100 % (Wilson 1980, Poore *et al.* 1994, Park 2000, Brandt *et al.* 2004, Brenke & Wägele submitted).

#### **1.1 Deep-sea Isopoda**

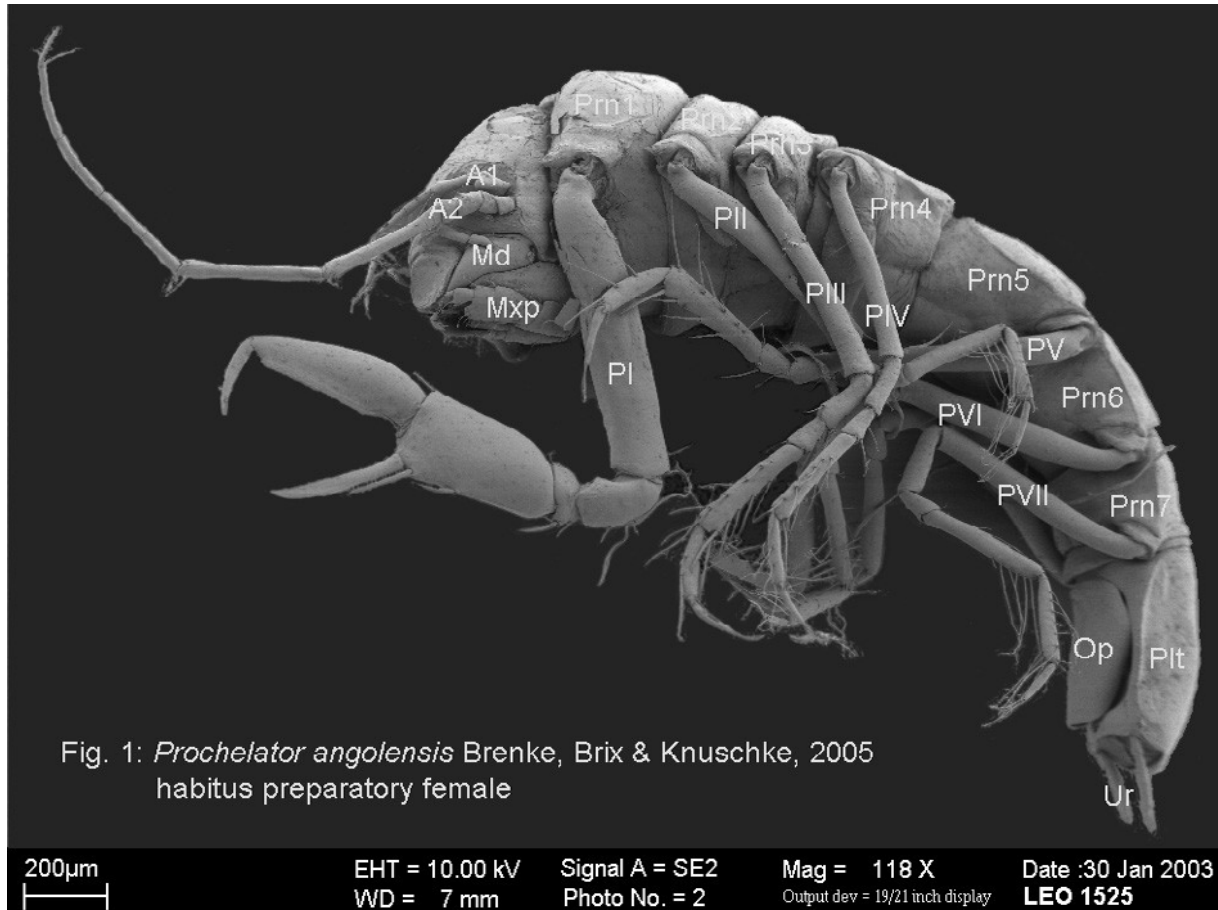
In marine habitats, crustaceans occupy a role which is as multi-faceted as that of insects on land; they are diverse, both in species numbers and range of morphologies and they are ubiquitous, both spatially and environmentally (Hessler 1982). In general, the species composition of abyssal deep-sea communities is poorly known in comparison with shelf and upper slope environments (Gage & Tyler 1991). It is also not known whether hot spots of species diversity exist, or how regional faunas can be delimited. Isopoda, especially the suborder Asellota Latreille, 1803 are characteristic faunal elements of the deep sea (Gage & Tyler 1991; Hessler *et al.* 1979; Hessler & Wilson 1987; Brandt *et al.* 2004, 2005).

#### **1.2 Desmosomatidae Sars, 1897**

The asellote family Desmosomatidae Sars, 1897 (Fig. 1) has a global distribution and a bathymetric range between 0 and 5500 meters (Kussakin 1973; Kussakin 1999). They are benthic macrofaunal isopods with a slender body (Hessler 1970; Svavarsson 1984, 1988a; Wägele 1989). At the beginning of the present study 115 species belonging to 18 genera were known worldwide, most of them from the North

Atlantic and polar regions. The family appears to be a very common group in deep-sea Isopoda (Malyutina & Kussakin 1996). They are widespread, especially in the North Atlantic Ocean (Hessler 1970; Svavarsson 1988a, b, 1993). They are also abundant in the South Atlantic Ocean (DIVA-1 and DIVA-2 samples from the Cape, Angola and Guinea Basins, see Brandt *et al.* 2005; Brenke & Wägele submitted, Brenke *et al.* submitted), the Southern Ocean (Brandt *et al.* 2004) and the equatorial Pacific (Park 2000), southeastern Australia (Poore *et al.* 1994) and New Zealand. 13 species are known from the Mediterranean area (Fresi & Schiecke 1969a, b).

The knowledge about the biology of deep-sea species is limited. Foraminifera were identified as important food source for some species (Gudmunssen *et al.* 2000; Svavarsson *et al.* 1993). Wolff (1962) documented the postmarsupial development of specimens of different age. Hessler (1970) described the postmarsupial development of *Desmosoma tetarta* (Hessler, 1970) in detail. A study of behavior of shallow-water species of different janiroidan (asellotan) families including Desmosomatidae Sars, 1897 was done by Hessler & Strömberg (1989). In the present study Desmosomatidae were frequently found in deep-sea samples and always one of the most abundant taxa (Brandt *et al.* 2004, 2005).





The most important work published about Desmosomatidae is the monograph written by Hessler (1970). He described 39 species from the North Atlantic, divided the family into two subfamilies (Eugerdellatinae Hessler, 1970 and Desmosomatinae Hessler, 1970) and erected nine new genera:

*Prochelator* Hessler, 1970; *Chelator* Hessler, 1970; *Disparella* Hessler, 1970; *Whoia* Hessler, 1970; *Oecidiobranchus*, Hessler, 1970; *Torwolia*, Hessler, 1970; *Thaumastosoma*, Hessler, 1970; *Mirabilicoxa* Hessler, 1970 and *Balbidocolon* Hessler, 1970.

Hessler's (1970) work followed Kussakin (1965) in the importance of the first pereopod (PI, Fig. 1) as main character. A summary of the history of the family until 1970 is presented by Hessler (1970). Since 1970 most papers dealing with Desmosomatidae Sars, 1897 are species descriptions including remarks about hypotheses of phylogenetic relationships: Menzies & George 1972; Paul & George 1975; Siebenhaller & Hessler 1977; Schultz 1979a; Just 1980; Siebenhaller & Hessler 1981; Svavarsson 1982, 1984, 1988; Mezhev 1986; Brandt 1992; Malyutina & Kussakin 1996; George 2001 or ecological studies: Brandt 1991; Poore *et al.* 1994; Svavarsson 1988b. Wägele (1989) presented an overview of the systematics of Isopoda and discusses the phylogenetic relationships of the families.

Including the results of the present study, the family now comprises 206 species belonging to 31 genera. However, the number of undescribed desmosomatids in museum collections worldwide is much higher. While doing this study over 200 species waiting for description were examined.

### 1.2.1 South Atlantic

#### DIVA (DIVERSity of the Atlantic benthos)

The series of DIVA-expeditions was designed to collect high quality data on the diversity and composition of deep-sea communities of the Atlantic Ocean (Brandt *et al.* 2005) and this study is a contribution to this objective. Before the DIVA expeditions the knowledge about benthic life the deep South Atlantic was poor. The Angola Basin was essentially unknown in terms of benthic biodiversity (Kröncke & Türkay 2003). Some details of the meiofauna were only known from coastal regions (Soltwedel & Thiel 1995, Soltwedel 1997). The diversity of all peracarid taxa is presented in Brandt *et al.* (2005). Peracarids are diverse at all stations, elements were Isopoda. Containing 104 species and 1741 individuals, they were the most

abundant and diverse. All known species were “cosmopolitans” or typical faunal elements of the deep North Atlantic. According to Brenke & Wägele (submitted), the Angola Basin contains only one homogeneous Isopod community and only five species of all Janiroidea in the DIVA-1 samples were also known from Antarctic Waters. The results of DIVA-1 indicate that the *Walvis Ridge* is an effective barrier in separating faunal elements in the deep South Atlantic from those in the deep Southern Ocean. (Brandt *et al.* 2005; Brenke & Wägele submitted).

The material from DIVA-1 contained 364 specimens belonging to Desmosomatidae Sars, 1897 and 85 specimens belonging to Nannoniscidae Hansen, 1916. 4 new species are described in the present study from this material. The preliminary sorting during DIVA-2 showed that species occurring in the Angola Basin are also present in the Guinea Basin. This leads to the hypothesis that the Guinea Basin and the Angola Basin contain a similar isopod community. According to Brenke & Wägele (submitted) the mean abundance in the sampling area of DIVA-1 is 48 isopods/m<sup>2</sup>, the portion of new species is approximately 45 to 55 %. For Desmosomatidae Sars, 1897 the percentage of new species is much higher (over 90%, chapter 3.3.1). Only 2 species are known, both from the North Atlantic.

### Oceanography

The eastern South Atlantic is divided into three deep sea basins: the Guinea Basin, the Angola Basin and the Cape Basin. The Guinea Basin lies on the equator and is separated from its southern neighbour the Angola Basin through the *Guinea Rise*. The Angola Basin ends at the *Walvis Ridge*, which separates it from the Cape Basin, the southernmost basin of the eastern South Atlantic. The Angola and Guinea basins are not separated as much as the western and eastern South Atlantic are by the *Midatlantic Ridge* or the Southern Ocean (Cape Basin) and the eastern South Atlantic (Angola Basin) are by the *Walvis Ridge*.

The *Guinea Rise* is not consistently high enough to be a barrier for benthic fauna and is not as high as the *Walvis Ridge*. The Guinea and Angola basins are both influenced by the southward moving North Atlantic Deep Water (NADW; Fig. 2) (Wefer *et al.* 1996; Reid 1996; Brandt *et al.* 2005). Results from DIVA-1 suggest that NADW influences the migration of species from north to south. Brandt *et al.* (2005) found that faunal elements of the Angola Basin also occur in the North Atlantic, but no faunal elements of the Southern Ocean could be found in the Angola Basin. The lack of a geographical barrier between the Guinea and Angola basins is probably the

reason for this pattern since the deep water can pass the *Guinea Rise* without problems (Fig. 2).

The *Angulhas Ridge* and the *Atlantic-Indic Ridge* form the southern boundary of the Cape Basin. The *Walvis Ridge* is the highest of all the ridges discussed. While the basins are 5000 m deep, the highest point of the *Walvis Ridge* reaches a depth of 1000m. In a depth of 4200 m lies the *Walvis Passage*, a limited pass way for deep water. Thus the *Walvis Ridge* is an effective barrier (Fig. 2) for northward flowing Antarctic Bottom Water (AABW; also known as Lower Circumpolar Deep Water: LCDPW), which enters the Cape Basin from the south (Bickert & Wefer 1996; Shannon & Nelson 1996).

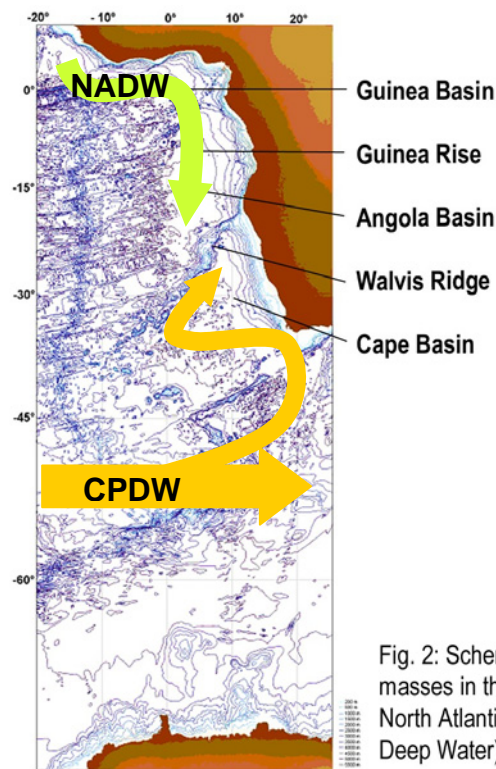
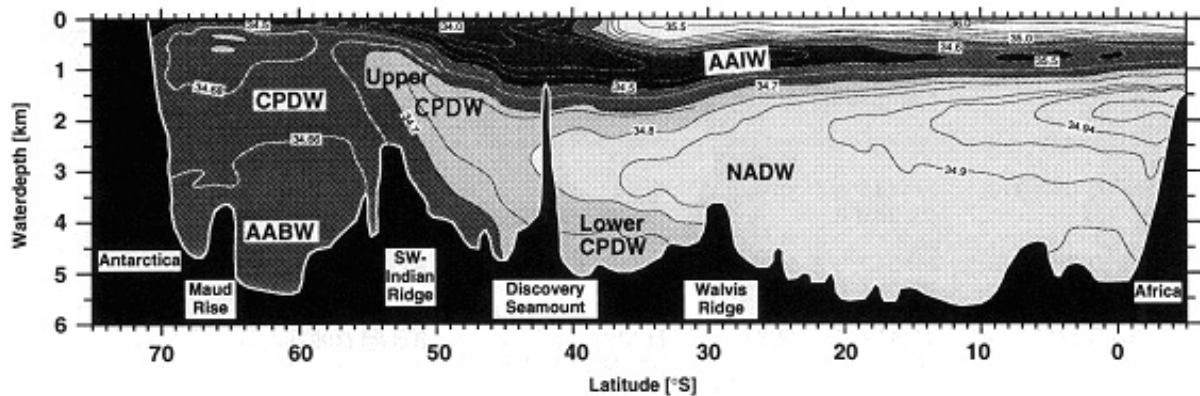


Fig. 2: Scheme of the flow of the deep water masses in the east South Atlantic Ocean (NADW: North Atlantic Deep Water, CPDW: Circumpolar Deep Water). Map created by W. Brökeland.

AABW enters the Cape Basin from east of the *Anghulas Ridge* and flows westward. The *Walvis Ridge* blocks the flow and directs the water mass towards the northeast. Upon reaching the south African continental slope, its flow is directed to the south and out of the Cape Basin (the flow is comparable to a loop) (Reid 1989). Only a very small portion of AABW reaches the Angola Basin from the south passing the *Walvis Passage* or flowing through the *Romanche Fracture Zone* entering the Angola Basin from the northwest (Bickert & Wefer 1996). The basins north of the *Walvis Ridge* are highly influenced by North Atlantic Deep Water (see above). NADW passes the *Walvis Ridge*, but AABW underlays NADW (Bickert & Wefer 1996). Thus, NADW

does not reach the bottom of the Cape Basin (Fig.3). North Atlantic Deep Water and AABW form layers due to differences in their physical properties: NADW is warmer and saltier than AABW (Gage & Tyler 1991).



**Fig. 3:** Layers in the water column (due to salinity) on a transect from North to South following the Greenwich-Meridian (Diekmann *et al.* 1996; AABW: Antarctic Bottom Water; CPDW: Circumpolar Deep Water; AAIW: Antarctic Interlay Water; NADW: North Atlantic Deep Water).

### 1.2.2 Southern Ocean

The Antarctic benthos includes over 3000-4000 recorded species (Arntz *et al.* 1997, Clarke & Johnston 2003, Boltovskoy *et al.* 2005) with estimates of up to 11.000-17.000 expected species from the continental shelf (Gutt *et al.* 2004). If benthic inventories are corrected for morphologically cryptic, so far undescribed species (Held & Wägele 2005), the number of described species will increase.

#### ANDEEP expeditions

Few desmosomatids were described from the deep sea of the Southern Ocean (Brandt 1991). *Eugerdella falklandica* Nordenstamm, 1933, *Desmosoma australis* Nordenstamm, 1933, *D. brevipes* Nordenstamm, 1933, *D. modestum* Nordenstamm, 1933, *D. latipes* (Hansen, 1916) and *Pseudogerda anversense* (Schultz, 1979) were collected in the Magellan region, the Scotia Arc and the Antarctic Peninsula at depths shallower than 200 m, while these species interestingly could not be found in shallow-water samples from the Beagle Channel (Doti *et al.* 2005). *Disparella longimana* (Schultz 1978) was sampled at the base of the continental shelf in 2735 m. Kussakin (1982) described *Desmosoma antarcticum* from the shelf region (25 m), Brandt (1992) *Reductosoma gunnera* from 3981 m depth. During ANDEEP I & II (ANT XIX3/4) (ANtarctic benthic DEEP-sea biodiversity, colonization history and recent community patterns) with RV *Polarstern* in spring 2002 samples were taken by means of an epibenthic sledge at 20 stations. The samples contained 365 specimens

of Desmosomatidae Sars, 1897 belonging to 48 species and 10 genera. Over 87% of these species are new to science. This high percentage shows how much is unknown in the deep sea.

### Oceanography

Extended deep-sea areas surround the Antarctic continent. Most areas are under the influence of AABW, the deepest water mass of the world (Gage & Tyler 1991). AABW contributes most to the formation of the Circumpolar Deep Water and flows into the Atlantic and the Indian and the Pacific oceans (Gage & Tyler 1991). Much of AABW is formed in the Weddell Sea (Pudsey *et al.* 1988, Foldvik & Gammelsrød 1988). AABW forms when extremely cold ( $-1.9^{\circ}\text{C}$ ) hypersaline water on the shelf, becomes dense by interaction with ice (temperature subsides to  $-2.3^{\circ}\text{C}$ ) and consequently sinks on the continental slope (Foldvik *et al.* 2004). This water mixes with Weddell Sea Deep Water, decreases in salinity, and becomes AABW. Thus, there is no permanent thermocline in this area, which favours the exchange of faunal elements between the shelf and the deep sea (Hessler *et al.* 1979, Gallardo 1987). The geography of the sampling area is presented in Brandt *et al.* (2004).

### **1.2.3 Systematic problems**

The relationship of Desmosomatidae Sars, 1897 and Nannoniscidae Hansen, 1916 is one of the most discussed questions in the literature about both families, especially the affiliation of *Pseudomesus* Hansen, 1916 (chapter 4.2.1.5.2) and *Thaumastosoma* Hessler, 1970 (chapter 4.2.1.3.11) are discussed more than once by several authors. Hessler's (1970) idea about phylogenetic relationships based on typological arguments. The same is true for the subfamilies Desmosomatinae Hessler, 1970 and Euerdellatinae Hessler, 1970. In the literature Desmosomatinae Hessler, 1970 have since been regarded as paraphyletic, while Euerdellatinae Hessler, 1970 are accepted as a monophyletic group. The systematic status of the genus *Torwolia* Hessler, 1970 (subfamily *incertae sedis*) is not solved in the literature. Furthermore, most genera are questioned to be para- or polyphyletic e.g., *Euerdella* Kussakin, 1965 (chapter 4.2.1.3.5) and *Desmosoma* Sars, 1864 (chapter 4.2.1.2.2). *Desmosoma*, the oldest genus (type genus) of the family, seems to be a collection of species not fitting into any of the newly erected genera. Thus, many species have been transferred to other genera. The remaining species are very

similar to species of the genus *Eugerdia*; both genera are not clearly distinguishable through their apomorphies. Distinguishing *Prochelator* and *Chelator* (chapter 4.2.1.3.9) is also a problem. The generic diagnoses of most genera of Desmosomatidae Sars, 1897 are not clear enough to define autapomorphies and have to be revised following the concept of phylogenetic systematics *sensu* Hennig (1966, 1982).

### 1.3 Phylogenetic cladistics

With as many as 90% of the earth's species undescribed, the vision of a resolved phylogeny of life may be compromised unless there is an ambitious effort to advance descriptive taxonomy as the base of phylogenetic systematics (Wheeler 2004). Taxonomic expertise is the foundation for a detailed discussion of characters and hypotheses of homology.

Taxonomy as the study of characters of living organisms is part of systematics and one of the oldest sciences in biology (Hennig 1982). Darwin's (1859) arguments for the importance of mechanisms of inheritance for natural selection and for the reconstruction of phylogeny led the way to the development of phylogenetic systematics. A century passed by before the theories were developed for a scientific method to deal with morphological characters, the hennigian method. Hennig (1966) understood that shared patterns (pattern replaces the word character) of common ancestry were the only thread binding species and introduced a phylogenetic systematic theory (Wheeler 2004). Ax (1984, 1987, 1988) explained the score of Hennig's method and included in his work a description of *a priori* outgroup comparison, a discussion of the importance of the estimation of the probability that characters are homologous, and the principle of parsimony to find the shortest tree. Computer programs replace only one of the several steps of phylogenetic analysis: the cladistic step as a purely deductive procedure that leads from a data matrix to one or more selected dendrograms (Wägele 2004).

With the development of computer software, new methods became available that were unknown to Hennig. Wägele (2001, 2004) presented a modern version of Hennig's method and named his analytical methodology phylogenetic cladistics to stress the difference to pure cladism. Phylogenetic cladistics is a synthesis of Hennig's method and numerical cladistics. When comparing Hennig's original method with modern applications of phylogenetic systematics, some steps of

phylogenetic analysis and theoretical arguments have been added to the hennigian method (Wägele 2004), such as

- numerical *a priori* character weighting and its theoretical justification
- the search for the shortest tree in space and the use of the cladistic version of the principle of parsimony, as implemented in computer programs
- and the cladistic outgroup comparison.

### 1.4 Aims and Questions

Based on morphological characters a revision of the family Desmosomatidae Sars, 1897 is presented, eight incompletely described species are redescribed and transferred to existing genera and a new genus (*Pseudergella* gen. nov.), *Eugerdella serrata* sp. nov. is described from the ANDEEP-expeditions and four new species from the DIVA-1 expedition as well as eight new species from museum material. Furthermore, the systematics of Desmosomatidae Sars, 1897 and Nannoniscidae Hansen, 1916 are discussed in detail. The genera are discussed and their phylogenetic relationships are studied. The question of the monophyly of Desmosomatidae is discussed based on morphological characters and how closely Desmosomatidae Sars, 1897 are related to their sister family Nannoniscidae Hansen, 1916 is addressed. The existing system (Hessler 1970, Siebenhaller & Hessler 1977, 1981, Wägele 1989) is discussed and brought up to date in the phylogeny part.

The following questions are addressed in the present study:

- Are Desmosomatidae monophyletic?
- Can Desmosomatidae and Nannoniscidae clearly be separated by their existing apomorphies?
- Do the genera represent monophyletic groups?
- How abundant and diverse are Desmosomatidae in the samples of the DIVA-1 expedition and the expeditions ANDEEP I and II?
- How many species are endemic?



## 2 Material and methods

### 2.1 Sampling

The material analysed in this study was collected on the cruise of RV *Meteor* (Fig. 4) in the southeast Atlantic Ocean (M48/1 in 2000 from July 06 to August 02 (DIVA-1)) and the cruises (ANT XIX3/4) of RV *Polarstern* (Fig. 4) in the Southern Ocean from January to April 2002 (ANDEEP I & II). (To generate the maps, the software PANMAP (pangea.de) and GEBCO (IOC *et.al.* 2003) were used.)

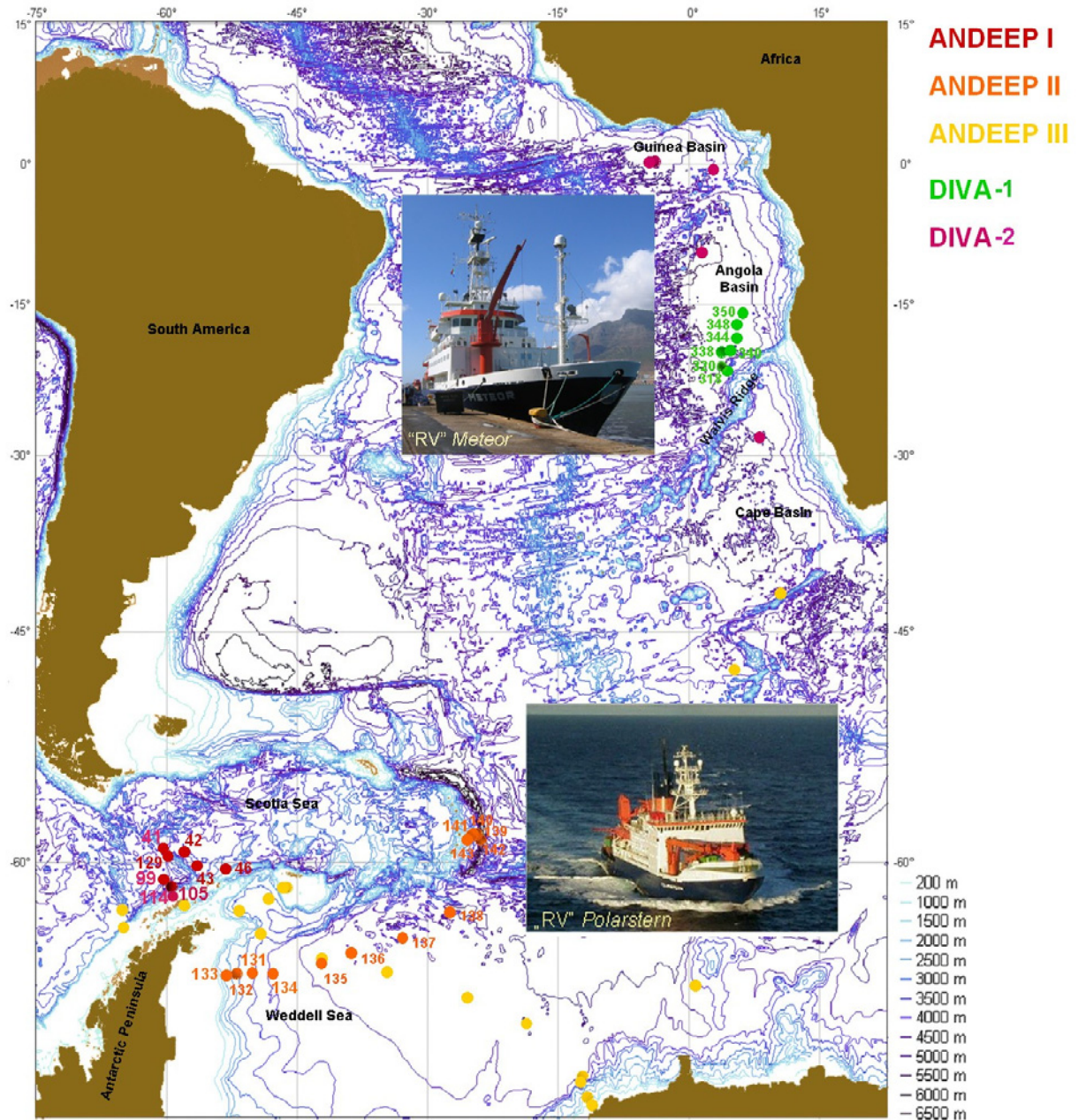


Fig.4: Stations of expeditions



## 2. Material and methods

During the expeditions the samples were obtained by means of an epibenthic sledge as described by Brenke (2005, modified after Brandt & Barthel 1995). The epibenthic



**Fig.5:** Epibenthic Sledge (EBS) at start of a haul in the water (picture taken during DIVA-2)

sledge (EBS) is a proven gear for sampling small benthic macrofauna. The sledge (Fig. 5) is equipped with an epinet (below) and a supranet (above). The mesh size of the nets is 500  $\mu\text{m}$ . The cod ends are equipped with net-buckets containing a 300  $\mu\text{m}$  mesh window (Brenke 2005). During DIVA-1 EBS samples were taken at seven stations (Table 1) along a north-south orientated transect of about 700 km length in depth between 5125 m and 5452 m. During the ANDEEP expeditions EBS samples were taken at 20 stations (Table 2) in the Scotia Sea (ANDEEP I) and the Weddell Sea (ANDEEP II).

**Table 1:** EBS stations of DIVA-1

| EBS stations | date     | Position start           | depth [m] | Position end             | depth [m] | trawled distance [m] |
|--------------|----------|--------------------------|-----------|--------------------------|-----------|----------------------|
| 318          | 09.07.00 | 22° 20,0' S 003° 18,3' E | 5125      | 22° 20,2' S 003° 18,4' E | 5144      | 3146.9               |
| 320          | 10.07.00 | 22° 19,9' S 003° 17,8' E | 5127      | 22° 20,0' S 003° 17,9' E | 5126      | 2445.9               |
| 338          | 22.07.00 | 18° 19,4' S 004° 39,7' E | 5397      | 18° 20,8' S 004° 38,6' E | 5398      | 5781.5               |
| 340          | 22.07.00 | 18° 18,3' S 004° 41,3' E | 5395      | 18° 19,4' S 004° 41,9' E | 5395      | 3984.6               |
| 344          | 25.07.00 | 17° 06,2' S 004° 41,7' E | 5415      | 17° 07,5' S 004° 42,3' E | 5415      | 5372.9               |
| 348          | 28.07.00 | 16° 18,1' S 005° 27,2' E | 5390      | 16° 19,3' S 005° 27,2' E | 5387      | 4261.5               |
| 350          | 29.07.00 | 16° 14,3' S 005° 26,8' E | 5389      | 16° 14,9' S 005° 26,7' E | 5389      | 2769.6               |

During DIVA-1 no cooling system at the sledge during heaving through the water column whether a cooling container on board was used, the material was fixed in precooled 96% ethanol in the laboratory at room temperature and kept cool at least for 48 hours for later DNA extraction for taxonomic and genetic research. The experience during molecular work with the DIVA-1 material showed, that temperature increase in the water column during sampling and fixation on board highly influenced

## 2. Material and methods

the quality of DNA. Temperature increase was the main factor in denaturation the DNA. Due to denaturation molecular studies using the DIVA-1 isopods were not possible.

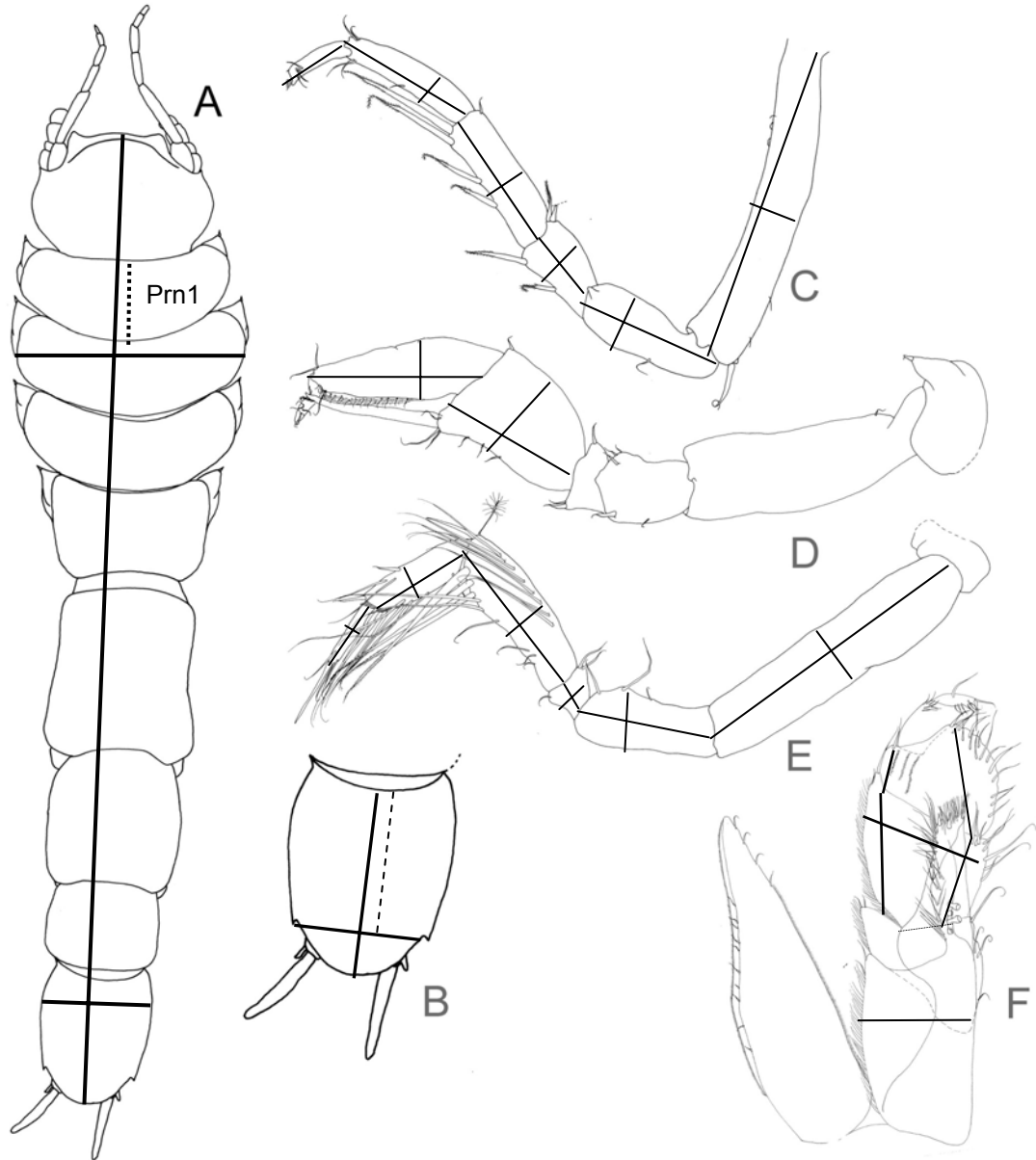
**Table 2:** EBS stations of ANDEEP I (stations 41-129) and ANDEEP II (stations 131-143).

|        | date     | depth (m) | lat°                  | long°                 | haul<br>length<br>(m) | N   | N / 1000 m | S  | J'   | H'(log) |
|--------|----------|-----------|-----------------------|-----------------------|-----------------------|-----|------------|----|------|---------|
| 41-3   | 26.01.02 | 2370      | 59°22.24 S-59°22.57 S | 60°04.06 W-60°04.05 W | 4928                  | 157 | 32         | 45 | 0,77 | 2,91    |
| 42-2   | 27.01.02 | 3689      | 59°40.30 S-59°40.32 S | 57°35.42 W-57°35.64 W | 4766                  | 816 | 157        | 74 | 0,79 | 3,38    |
| 43-8   | 03.02.02 | 3962      | 60°27.13 S-60°27.19 S | 56°05.12 W-56°04.81 W | 4782                  | 245 | 51         | 50 | 0,85 | 3,23    |
| 46-7   | 30.01.02 | 3894      | 60°38.33 S-60°38.06 S | 53°57.38 W-53°57.51 W | 5639                  | 859 | 153        | 77 | 0,75 | 3,35    |
| 99-4   | 12.02.02 | 5191      | 61°06.40 S-61°06.40 S | 59°16.57 W-59°17.61 W | 5336                  | 32  | 5          | 12 | 0,81 | 2,01    |
| 105-7  | 12.02.02 | 2308      | 61°24.16 S-61°24.25 S | 58°51.56 W-58°51.56 W | 2881                  | 10  | 3          | 7  | 0,94 | 1,83    |
| 114-4  | 17.02.02 | 2921      | 61°43.54 S-61°43.51 S | 60°44.21 W-60°44.43 W | 4482                  | 289 | 64         | 56 | 0,82 | 3,29    |
| 129-2  | 22.02.02 | 3640      | 59°52.21 S-59°52.20 S | 59°58.75 W-59°58.63 W | 4076                  | 69  | 17         | 35 | 0,91 | 3,24    |
| 131-3  | 05.03.02 | 3053      | 65°19.83 S-65°19.99 S | 51°31.61 W-51°31.23 W | 3553                  | 873 | 248        | 83 | 0,75 | 3,32    |
| 132-2  | 06.03.02 | 2086      | 65°17.75 S-65°17.62 S | 53°22.81 W-53°22.86 W | 2523                  | 47  | 19         | 19 | 0,82 | 2,4     |
| 133-3  | 07.02.02 | 1121      | 65°20.17 S-65°20.08 S | 54°14.30 W-54°14.34 W | 1314                  | 636 | 498        | 66 | 0,79 | 3,35    |
| 134-3  | 09.03.02 | 4069      | 65°19.20 S-65°19.05 S | 48°03.77 W-48°02.92 W | 4553                  | 64  | 14         | 23 | 0,86 | 2,69    |
| 135-4  | 10.03.02 | 4678      | 65°00.05 S-65°59.97 S | 43°03.02 W-43°00.82 W | 2773                  | 494 | 178        | 34 | 0,49 | 1,71    |
| 136-4  | 12.03.02 | 4747      | 64°01.54 S-64°01.51 S | 39°06.88 W-39°06.88 W | 5306                  | 107 | 20         | 28 | 0,88 | 2,92    |
| 137-4  | 14.03.02 | 4976      | 63°44.98 S-63°44.74 S | 38°47.75 W-38°48.23 W | 4581                  | 56  | 12         | 20 | 0,83 | 2,49    |
| 138-6  | 17.03.02 | 4542      | 62°58.08 S-62°57.99 S | 27°54.10 W-27°54.28 W | 4147                  | 91  | 22         | 34 | 0,87 | 3,08    |
| 139-6  | 20.03.02 | 3950      | 58°14.10 S-58°14.15 S | 24°21.20 W-24°21.21 W | 6464                  | 48  | 7          | 20 | 0,85 | 2,54    |
| 140-8  | 21.03.02 | 2970      | 58°15.98 S-58°16.28 S | 24°53.73 W-24°54.09 W | 4183                  | 102 | 24         | 50 | 0,93 | 3,62    |
| 141-10 | 23.03.02 | 2312      | 58°25.07 S-58°24.63 S | 24°00.78 W-24°00.74 W | 3094                  | 306 | 100        | 45 | 0,71 | 2,70    |
| 142-6  | 24.03.02 | 6348      | 58°50.78 S-58°50.44 S | 23°57.75 W-23°57.59 W | 4221                  | 18  | 4          | 7  | 0,94 | 1,82    |
| 143-1  | 25.03.02 | 774       | 58°44.69 S-58°44.45 S | 25°10.28 W-25°10.66 W | 1441                  | 39  | 27         | 11 | 0,87 | 2,08    |

### 2.2 Taxonomic methods

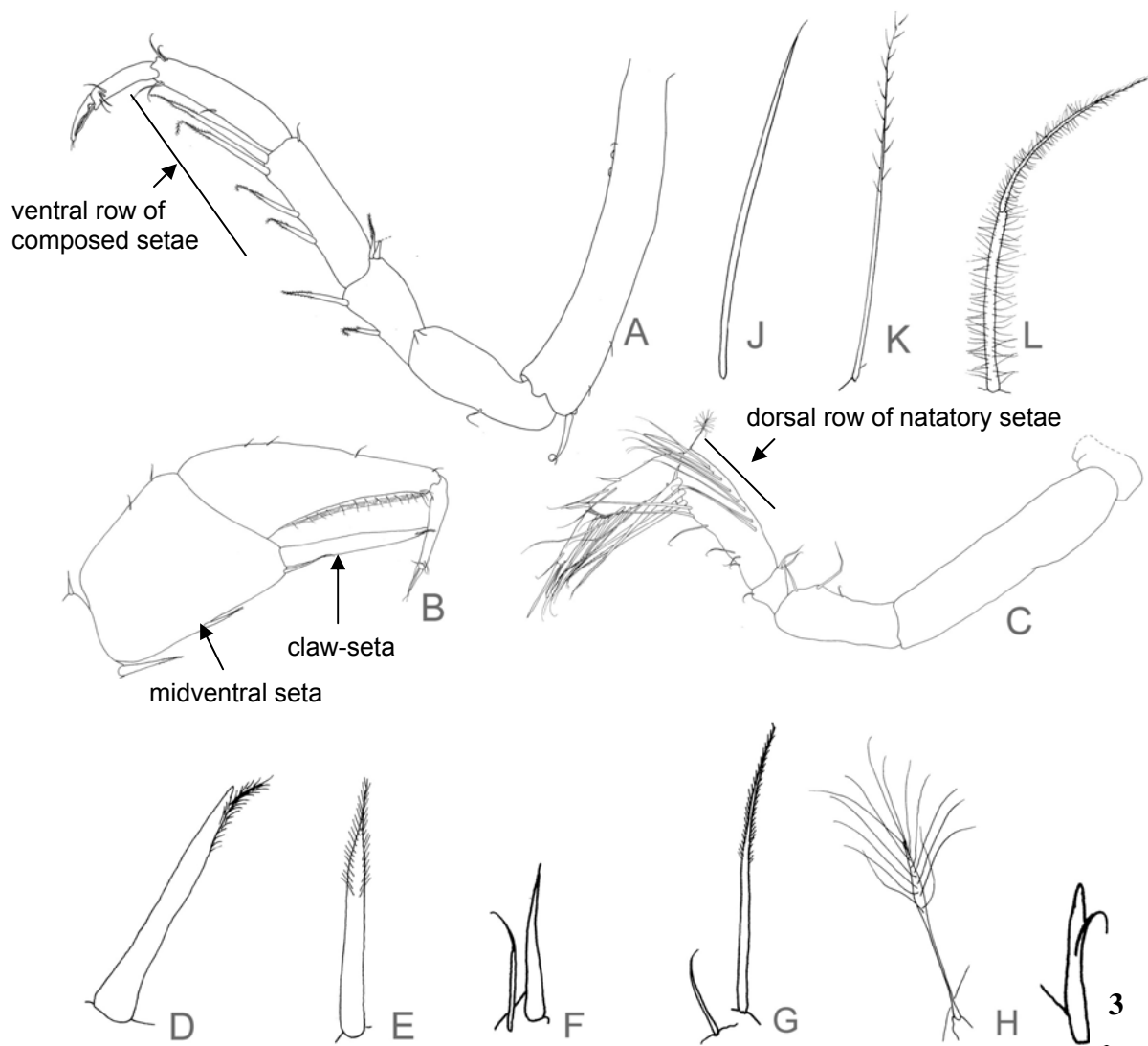
The DIVA-1 samples were sorted on family level and fixed at the Ruhr-University of Bochum, Germany, the ANDEEP I & II samples at the Zoological Museum of the University of Hamburg. After the sorting on family level, Desmosomatidae Sars, 1897 were identified on species level. For determination and taxonomic investigations standard methods were used. Species were identified using diagnostic keys and original descriptions. Since species names are known only for a very small number of individuals, species were provisionally numbered and characterized until complete description. Specimens in description were compared with type material.

Species were identified using a Wild dissecting microscope and illustrated using different compound microscopes. Total body length was measured in dorsal and lateral view from the anterior edge of the head to the posterior medial tip of the pleotelson (Fig. 6). In general, the length to width ratios refer to the greatest length and width of the limb article or segment (Fig. 6).



**Fig. 6:** Measuring of proportions according to Hessler (1970), the black lines indicate the measuring lines for length to width ratios. A: body length (dotted line: midsagittal length of pereonite 1; *Momedossa longipedis* sp. nov.), B: pleotelson length and position of posterolateral spines, C: articles of pereopod I (*Mirabilicoxa acuta* (Menzies & George, 1972)), D: carpus and propodus of an enlarged chelate pereopod I (*Chelator chelatum* (Stephensen, 1915)), E: articles of pereopod VI (*Chelator chelatum* (Stephensen, 1915)), F: endite and palp articles 2 and 3 of the maxilliped (*Disparella funalis* (Menzies & George, 1972))

The present study follows Wolff (1962) and Hessler (1970) in using roman numerals to refer to pereopods and arabic numerals for body segments and articles of appendages. Figure 7 illustrates the most important setal types along with the terminology used in this study (Hessler 1970, Watling 1989, Garm 2004).



**Fig. 7:** Types of setae (D, E, G (right), K and L are composed setae of different types).

A: pereopod I showing a row of seta ventrally on the carpus (*Mirabilicoxa acuta* (Menzies & George, 1972)); B: enlarged carpus and propodus of pereopod I with claw-seta (*Prochelator maorii* sp. nov.); C: pereopod VI with rows of natatory setae on carpus and propodus (*Chelator chelatum* (Stephensen, 1915)); D, E: unequally bifid distally setulate seta; F: slender simple (left) and robust simple seta (right); G: simple seta (left) and long distally setulate seta (right); H: broom seta; I: unequally bifid seta; J: long slender seta; K: long slender distally hairy seta; L: distally slender plumose seta (occurring in *Paradesmosoma* only)

For the drawings different microscopes, 'Leitz MI 85' compound microscope (ZMH, Hamburg), Olympus BH2, Wild M20 and Olympus BX 20 with a *camera lucida* were used. The dorsal and lateral habitus drawings were made with the holotype or the paratype kept in glycerine stained with methylene green. All appendages that are necessary for further taxonomic research (antennula, antenna, mouthparts, pereopods and pleopods) were dissected from a paratype (if there was no paratype from the holotype) and deposited in water-free glycerin jelly, stained and finally

sealed. The species description, the measuring of the dimensions and the nomenclature for setae and anatomical characters follows Hessler (1970), Watling (1989) and Garm (2004). The discussion of the newly described species is presented in chapter 3 (results) instead in chapter 4 (discussion) as it would be placed in a publication.

### 2.3 Collection Material

Type material from different collections was studied. The types of species described in this study from material collected during DIVA-1 and ANDEEP I & II are deposited in the crustacean collection of the Zoological Museum of the University of Hamburg (ZMH K- 40998 to ZMH K-401015).

#### 2.3.1 University of Hamburg: Zoological Museum

|                        |  |
|------------------------|--|
| ZMH K-40113            | <i>Chelator</i> sp. nov. A, holotype female                                    |
| ZMH K-40114            | <i>Chelator</i> sp. nov. A, allotype male                                      |
| ZMH K-40115            | <i>Chelator</i> sp. nov. A, paratypes  |
| ZMH K-40998            | <i>Eugerdella renatae</i> sp. nov., holotype female                            |
| ZMH K-40999            | <i>Eugerdella renatae</i> sp. nov., allotype male                              |
| ZMH K-40100            | <i>Eugerdella renatae</i> sp. nov., paratypes                                  |
| ZMH K-40101            | <i>Eugerdella theodori</i> sp. nov., holotype female                           |
| ZMH K-40102            | <i>Eugerdella theodori</i> sp. nov., allotype male                             |
| ZMH K-40103            | <i>Eugerdella theodori</i> sp. nov., paratypes                                 |
| ZMH K-40104            | <i>Eugerdella serrata</i> sp. nov., holotype female                            |
| ZMH K-40105            | <i>Eugerdella serrata</i> sp. nov., allotype male                              |
| ZMH K-40106            | <i>Eugerdella serrata</i> sp. nov., paratypes                                  |
| ZMH K-40674            | <i>Disparella maiuscula</i> Kaiser & Brix, 2005, holotype female               |
| ZMH K-40676            | <i>Disparella maiuscula</i> Kaiser & Brix, 2005, allotype male                 |
| ZMH K-40675 to K 40682 | <i>Disparella maiuscula</i> Kaiser & Brix, 2005, paratypes                     |
| ZMH K-40107            | <i>Momedossa longipedis</i> sp. nov., holotype female                          |
| ZMH K-40108            | <i>Momedossa longipedis</i> sp. nov., allotype male                            |
| ZMH K-40109            | <i>Momedossa longipedis</i> sp. nov., paratypes                                |
| ZMH K-40331 A – K      | <i>Prochelator angolensis</i> Brenke, Brix und Knuschke, 2005, holotype female |

|                        |   |
|------------------------|---|
| ZMH K-40322 to K-40323 | <i>Prochelator angolensis</i> Brenke, Brix und Knuschke, 2005, paratypes female |
| ZMH K-40110            | <i>Torwolia tinbienae</i> sp. nov., holotype female                             |
| ZMH K-40111            | <i>Torwolia tinbienae</i> sp. nov., paratype female                             |
| ZMH K-40112            | <i>Torwolia tinbienae</i> sp. nov., paratype female                             |
| ZMH K-40104            | <i>Regabellator abyssi</i> Brandt, 2002, holotype female                        |
| ZMH K-40106            | <i>Saetoniscus meteori</i> Brandt, 2002, holotype female                        |
| ZMH K-40108            | <i>Rapaniscus multisetosus</i> Brandt, 2002, holotype female                    |
| ZMH K-40110            | <i>Nannoniscus antennaspinis</i> Brandt, 2002, holotype female                  |
| ZMH K-40276            | <i>Macrostylis robusta</i> Brandt, 2004, holotype female                        |
| ZMH K-40278            | <i>Macrostylis longipedis</i> Brandt, 2004, holotype female                     |
| ZMH K-40280            | <i>Macrostylis angolensis</i> Brandt, 2004, holotype female                     |
| ZMH K-40282            | <i>Macrostylis meteorae</i> Brandt, 2004, holotype female                       |
| ZMH K-40284            | <i>Macrostylis abyssalis</i> Brandt, 2004, holotype female                      |
| ZMH K-40286            | <i>Macrostylis longispinis</i> Brandt, 2004, holotype female                    |

### 2.3.2 Smithonian Institution:

#### Natural Museum of Natural History (Washington D.C., U.S.A.)

|             |  |
|-------------|--|
| USNM 125088 | <i>Balbidocolon atlanticum</i> Hessler, 1970, holotype female        |
| USNM 125089 | <i>Chelator verecundus</i> Hessler, 1970, holotype female            |
| USNM 125090 | <i>Chelator vulgaris</i> Hessler, 1970, holotype female              |
| USNM 125091 | <i>Disparella pachythrinx</i> Hessler, 1970, holotype female         |
| USNM 125092 | <i>Disparella valida</i> Hessler, 1970, holotype female              |
| USNM 125101 | <i>Mirabilicoxa exopodata</i> Hessler, 1970, holotype female         |
| USNM 125106 | <i>Momedossa profunda</i> Hessler, 1970, holotype female             |
| USNM 125107 | <i>Prochelator abyssalis</i> Hessler, 1970, holotype female          |
| USNM 125108 | <i>Prochelator hampsoni</i> Hessler, 1970, holotype female           |
| USNM 125109 | <i>Prochelator incomitatus</i> Hessler, 1970, holotype female        |
| USNM 120963 | <i>Chelator brevicaudus</i> (Menzies & George, 1972), holotype male* |
| USNM 120971 | <i>Disparella neomana</i> (Menzies & George, 1972), holotype male*   |
| USNM 120972 | <i>Disparella neomana</i> (Menzies & George, 1972), allotype female* |

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\* Types are deposited as *Desmosoma*.

## 2. Material and methods

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|             |  |
|-------------|--|
| USNM 120973 | <i>Disparella neomana</i> (Menzies & George, 1972), 4 paratypes*         |
| USNM 120968 | <i>Disparella funalis</i> (Menzies & George, 1972), holotype female*     |
| USNM 120969 | <i>Disparella funalis</i> (Menzies & George, 1972), 3 paratypes female*  |
| USNM 120975 | <i>Eugerdella rotunda</i> (Menzies & George, 1972), holotype female*     |
| USNM 120966 | <i>Desmosoma dolosa</i> (Menzies & George, 1972), holotype male          |
| USNM 120967 | <i>Desmosoma dolosa</i> (Menzies & George, 1972), 1 female               |
| USNM 120962 | <i>Mirabilicoxa acuta</i> (Menzies & George, 1972), holotype female*     |
| USNM 121711 | <i>Mirabilicoxa similipes</i> (Menzies & George, 1972), holotype male*   |
| USNM 121712 | <i>Mirabilicoxa similipes</i> (Menzies & George, 1972), allotype female* |
| USNM 121750 | <i>Mirabilicoxa similipes</i> (Menzies & George, 1972), other material*  |
| USNM 171426 | <i>Desmosoma anversense</i> (Schultz, 1969), holotype sex undetermined   |
| USNM 138732 | <i>Mirabilicoxa hessleri</i> George 2001, holotype male                  |
| USNM 138733 | <i>Mirabilicoxa alberti</i> (George, 2001), holotype female              |
| USNM 138731 | <i>Prochelator sarsi</i> (George, 2001), holotype female                 |
| USNM 120964 | <i>Rapaniscus coalescum</i> (Menzies & George, 1972), holotype*          |
| USNM 143607 | <i>Mirabilicoxa fletcheri</i> (Paul & George, 1975) holotype female      |

### 2.3.3 American Museum of Natural History (New York, U.S.A.)

|            |  |
|------------|--|
| AMNH 12112 | <i>Mirabilicoxa birsteini</i> (Menzies, 1962), holotype*   |
| AMNH 12119 | <i>Mirabilicoxa magnispina</i> (Menzies, 1962), holotype * |
| AMNH 12121 | <i>Chelator striatus</i> (Menzies, 1962), holotype *       |

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Remark: Unfortunately, the typematerial of these three species is in a very bad condition. Identification of species is not possible even after study of the holotype due to the damage.

---

### 2.3.4 Museum Victoria (Melbourne, Australia)

|         |   |
|---------|---|
| J 18597 | <i>Pseudomesus satanus</i> sp. nov., holotype female      |
| J 18608 | <i>Paradesmomsoma australis</i> sp. nov., holotype female |
| J 18606 | <i>Oecidiobranchus slopei</i> sp. nov., holotype male     |

|         |   |
|---------|---|
| J 18605 | <i>Disparella kensleyi</i> sp. nov., holotype female        |
| J 18600 | <i>Echinopleura cephalomagna</i> sp. nov., holotype female  |
| J 18601 | <i>Echinopleura cephalomagna</i> sp. nov., paratype female  |
| J 53074 | <i>Echinopleura cephalomagna</i> sp. nov. , paratype female |
| J 18598 | <i>Whoia victoriensis</i> sp. nov., holotype female         |
| J 18599 | <i>Whoia victoriensis</i> sp. nov., paratype female         |
| J 18612 | gen. nov. sp. nov. 7 specimens (3 females, 4 males)         |

### 2.3.5 Australian Museum (Sydney, Australia)

|         |   |
|---------|---|
| J 53075 | Det. J. Just / AM4 2400-2500. <i>Whoia victoriensis</i> sp. nov., paratype female; vial plus 3 slides |
|---------|---|

-----  
Remark: The paratypes and allotypes of species which Hessler (1970) described in his monograph are deposited in the Australian Museum in Sydney.  
-----

|           |   |
|-----------|---|
| AM P59160 | <i>Chelator vulgaris</i> Hessler, 1970, paratype female     |
| AM P58856 | <i>Chelator insignis</i> Hessler, 1970, paratype female     |
| AM P59082 | <i>Prochelator litus</i> Hessler, 1970, paratype female     |
| AM P59075 | <i>Prochelator abyssalis</i> Hessler, 1970, paratype female |
| AM P59197 | <i>Prochelator hampsoni</i> Hessler, 970, paratype female   |
| AM P58781 | <i>Prochelator lateralis</i> (Sars, 1897)                   |

### 2.3.6 New Zealand Institution of Oceanographic and Atmospheric Research (NIWA) (Wellington, New Zealand)

“Lincoln material”

|       |   |
|-------|---|
| F 753 | <i>Prochelator maorii</i> sp. nov., paratype  |
| F 755 | <i>Prochelator maorii</i> sp. nov., paratype  |
| S 147 | <i>Prochelator maorii</i> sp. nov., holotype preparatory female, allotype copulatory male, 4 paratypes female |

### 2.3.7 Zoologisk Museum Kopenhagen (Kopenhagen, Danmark)

|              |   |
|--------------|---|
| ZMUC CRU-510 | <i>Chelator chelatum</i> (Stephensen, 1915), holotype* female |
|--------------|---|



ZMUC CRU            plus 14 specimens deposited as „other material” (nontype Isopoda, blue label, no number) det. E. Fresi as *Desmosoma chelatum*, Ischia, Italy, 110 m, 16 May 1968

ZMUC CRU            *Prochelator serratum* (Fresi & Schiecke, 1969)\*, nontype Isopoda (blue label, no number), det. E. Fresi, Ischia N., Italy 80-110 m, May 1968

ZMUC CRU-7027 *Prochelator lateralis* (Sars, 1897)\*, types

ZMUC CRU-514 *Eugerdella globiceps* Meinert, 1890, types

ZMUC CRU-515 *Eugerdella globiceps* Meinert, 1890, types

ZMUC CRU-516 *Eugerdella globiceps* Meinert, 1890, types

ZMUC CRU-517 *Eugerdella globiceps* Meinert, 1890, types

ZMUC CRU-518 *Eugerdella globiceps* Meinert, 1890, types

ZMUC CRU-9206 *Eugerdella globiceps* Meinert, 1890, types

ZMUC CRU-588 *Chelator insignis* (Hansen, 1916)\*, lectotype

ZMUC CRU-589 *Chelator insignis* (Hansen, 1916)\*, paralectotype

ZMUC CRU-7500 *Eugerdella natator* (Hansen, 1916)\*, holotype

ZMUC CRU-7810 *Oecidiobranchus plebejum* (Hansen, 1916)\*, lectotype

ZMUC CRU-7828 *Eugerdella polita* (Hansen, 1916)\*, syntype

ZMUC CRU-9170 *Mirabilicoxa similis* (Hansen, 1916)\*, lectotype

### 2.4            SEM: handling of species used for pictures

Specimens of *Eugerdella serrata* sp. nov., *Eugerdella theodori* sp. nov., *Chelator* sp. nov. A and *Prochelator angolensis* Brenke, Brix & Knuschke, 2005 were used for SEM pictures. The specimens were cleaned in an ultrasonic bath for 10 seconds and dehydrated in a series of ethanol concentrations, transferred to 100% acetone and critical point dried. After drying they were sputter coated with gold. The specimens were viewed in a Leo 1525 scanning microscope. The resulting digital images were taken using the PC-SEM and manipulated with Photoshop 7.0.

### 2.5            Phylogenetic Methods

For the morphological analysis the 8 steps of a complete phylogenetic analysis presented by Wägele (2004) were followed.

1. Search for similarities that occur among Desmosomatidae, Nannoniscidae and Macrostylidae (organisms of interest).
2. Perform a character analysis for the selected similarities and determine characters of high probability of homology and weight these characters higher than those of low probability.
3. Compare the character states of the selected characters with the closest related ones (i.e. the groundpattern of Janiroidea) and define the states occurring only in species or subgroups of the ingroup (Desmosomatidae, Nannoniscidae and Macrostylidae) as apomorphic states.
4. Describe explicitly all arguments used in the character analysis and enter the results into a data matrix.
5. Use hypotheses about apomorphic characters to support hypotheses of monophyly; putative synapomorphies support sister-group relationships.
6. Test the compatibility of hypotheses of monophyly: thus, the final tree with the largest number of well-supported monophyla should be the most parsimonious one.
7. Check data not used for tree construction to see if the result is plausible. Above all describe the fit with additional information (ecology, physiology and biogeography).
8. Explain contradictions that occur in step 7 and reexamine all previous steps to discover possible sources of error. Discuss the latter.

Step 5 and 6 are the cladistic steps. For these steps computerprograms are used. 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. 1999) and NEXUSEditor (version 0.5.0 2001 © Roderic D.M. Page, University of Glasgow). PAUP was used to conduct the analysis ( $\beta$ -test version 4.0b10 for Windows, Swofford 1998) after converting the DELTA matrix into a nexus file. The DELTA matrix contains 107 taxa, 129 characters and 12 characters are distinguishing the outgroup from the ingroup.

A heuristic search was conducted with randomised addition of taxa (addseq=random) using tree bisection-reconnection (TBR) as swapping algorithm. 1000 replicates were performed (nchuck=3 chuckscore=1 nreps=1000 randomize=trees). Both accelerated transformation (Acctran) as well as delayed transformation (Deltran) was

tested as character state optimisation criteria. Consensus trees were calculated and drawn with TreeView (version 1.6.6, © Roderic D. M. Page, 2001, Page 1996).

### 2.6 List of species used for phylogenetic analysis

In the following list, species are listed with the names that are the result of the present study. These names are also used in the trees (chapter 3.2.2 to 3.2.4). The genera and their composition are discussed in chapter 4.2.1.

1. *Macrostylis robusta* Brandt, 2004
2. *Macrostylis angolensis* Brandt, 2004
3. *Macrostylis meteorae* Brandt, 2004
4. *Austroniscus chelus* Kaiser, submitted
5. *Austroniscus obscurus* Kaiser, submitted
6. *Austroniscus ovalis* Vanhöffen, 1914
7. *Chelator chelatum* (Stephensen, 1915)
8. *Chelator insignis* (Hansen, 1916)
9. *Chelator verecundus* Hessler, 1970
10. *Chelator vulgaris* Hessler, 1970
11. *Chelator* sp. nov. A (ANDEEP)
12. *Cryodesma agnari* Svavarsson, 1988
13. *Cryodesma cryoabyssale* Malyutina & Kussakin, 1996
14. *Cryodesma polare* (Malyutina & Kussakin, 1996)
15. *Desmosoma arctica* (Svavarsson, 1988)
16. *Desmosoma hesslera* Brandt, 1992
17. *Desmosoma lobipes* Kussakin, 1965
18. *Desmosoma lineare* Sars, 1864
19. *Desmosoma latipes* (Hansen, 1916)
20. *Desmosoma gigantea* (Park, 1999)
21. *Desmosoma ochotense* Kussakin, 1965
22. *Desmosoma strombergi* Svavarsson, 1988
23. *Desmosoma renatae* sp. nov. (DIVA-1)
24. *Desmosoma thoracicum* Fresi & Schiecke, 1969
25. *Desmosoma tetarta* (Hessler, 1970)
26. *Disparella funalis* (Menzies & George, 1972)

27. *Disparella pachythrix* Hessler, 1970
28. *Disparella valida* Hessler, 1970
29. *Disparella maiuscula* Kaiser & Brix, 2005
30. *Disparella neomana* (Menzies & George, 1972)
31. *Disparella kensleyi* sp. nov. (Australia)
32. *Echinopleura aculeata* Sars, 1864
33. *Echinopleura cephalomagna* sp. nov. (Australia)
34. *Eugerdella tenuimana* Sars 1868
35. *Eugerdella reticulata* Gurjanova, 1946
36. *Eugerdella natator* (Hansen, 1916)
37. *Eugerdella nonfunalis* sp. nov.
38. *Eugerdella pugilator* Hessler, 1970
39. *Eugerdella serrata* sp. nov. (ANDEEP I & II)
40. *Eugerdella theodori* sp. nov. (DIVA-1)
41. *Exiliniscus clipeatus* Siebenhaller & Hessler, 1981
42. *Exiliniscus aculeatus* Siebenhaller & Hessler, 1981
43. *Hebefustis vafer* Siebenhaller & Hessler, 1977
44. *Hebefustis mollicellus* Siebenhaller & Hessler, 1977
45. *Hebefustis allenii* Siebenhaller & Hessler, 1977
46. *Mirabilicoxa alberti* (George, 2001)
47. *Mirabilicoxa atlanticum* (Hessler, 1970)
48. *Mirabilicoxa cornuta* (Hessler, 1970)
49. *Mirabilicoxa acuminata* Hessler, 1970
50. *Mirabilicoxa acuta* (Menzies & George, 1972)
51. *Mirabilicoxa gracilipes* (Hansen, 1916)
52. *Mirabilicoxa plana* Hessler, 1970
53. *Mirabilicoxa similis* (Hansen, 1916)
54. *Mirabilicoxa similipes* (Menzies & George, 1972)
55. *Momedossa longipedis* sp. nov. (DIVA-1)
56. *Momedossa profunda* Hessler, 1970
57. *Nannoniscoides biscutatus* Siebenhaller & Hessler, 1977
58. *Nannoniscoides coronarius* Siebenhaller & Hessler, 1977
59. *Nannoniscoides gigas* Siebenhaller & Hessler, 1977
60. *Nannoniscoides latediffusus* Siebenhaller & Hessler, 1977

61. *Nannonisconus latipleonus* Schultz, 1966
62. *Nannonisconus carinatus* Mezhov, 1986
63. *Nannoniscus bidens* (Vanhöffen, 1914)
64. *Nannoniscus teres* Siebenhaller & Hessler, 1981
65. genus novum *fletcheri* (Paul & George, 1975)
66. *Oecidiobanchus nansenii* Just, 1980
67. *Oecidiobanchus plebejum* (Hansen, 1916)
68. *Panetela wolffi* Siebenhaller & Hessler, 1981
69. *Panetela tenella* (Birstein, 1963)
70. *Paradesmosoma conforme* Kussakin, 1965
71. *Paradesmosoma orientale* Kussakin, 1965
72. *Paradesmosoma australis* sp. nov. (Australia)
73. *Prochelator angolensis* Brenke, Brix & Knuschke, 2005
74. *Prochelator abyssalis* Hessler, 1970
75. *Prochelator hampsoni* Hessler, 1970
76. *Prochelator incomitatus* Hessler, 1970
77. *Prochelator lateralis* Sars, 1897
78. *Prochelator litus* Hessler, 1970
79. *Prochelator uncatus* Hessler, 1970
80. *Prochelator maorii* sp. nov. (New Zealand)
81. *Pseudergella atypicum* (Fresi & Schiecke, 1969)
82. *Pseudergella hessleri* Just, 1980
83. *Pseudergella ischnomesoides* Hessler, 1970
84. *Pseudogerda anversense* (Schultz, 1969)
85. *Pseudogerda elegans* (Kussakin, 1965)
86. *Pseudogerda intermedia* (Hult, 1936)
87. *Pseudogerda kamchatica* (Kussakin, 1965)
88. *Pseudomesus satanus* sp. nov. (Australia)
89. *Pseudomesus pitombo* Kaiser, 2005
90. *Pseudomesus brevicornis* (Hansen, 1916)
91. *Rapaniscus dewdneyi* Siebenhaller & Hessler, 1981
92. *Rapaniscus crassipes* (Hansen, 1916)
93. *Rapaniscus multisetosus* Brandt, 2002
94. *Rapaniscus* sp. nov. A (ANDEEP II)

95. *Reductosoma gunnera* Brandt, 1992
96. *Regabellator profugus* Siebenhaller & Hessler, 1981
97. *Regabellator abyssi* Brandt, 2002
98. *Saetoniscus meteori* Brandt, 2002
99. *Thaumastosoma platycarpus* Hessler, 1970
100. *Thaumastosoma tenue* Hessler, 1970
101. *Torwolia creper* Hessler, 1970
102. *Torwolia subchelatus* Hessler, 1970
103. *Torwolia tinbienae* sp. nov. (DIVA-1)
104. *Whoia angusta* (Sars, 1899)
105. *Whoia dumbshafensis* Svavarsson, 1988
106. *Whoia variabilis* Hessler, 1970
107. *Whoia victoriensis* sp. nov. (Australia)

### 2.7 Characters used in phylogenetic analysis

The character matrix concentrates on highly complex characters, which are hypothesized to be phylogenetically informative. Macrostylidae are defined as outgroup. Characters of Nannoniscidae and Desmosomatidae are treated equally analysing the two families as one group. Characters of sexual dimorphism are not used within the phylogenetic analysis because not for all species males and females are known. For the phylogeny, only species that adult or preparatory females are described in detail or that could be borrowed from museum collections are used. A list of all characters and their *a priori* weighting *sensu* Wägele (2004) is presented in Table 4 (chapter 3.2.1).

### 3 Results

#### 3.0 Zoogeographic aspects

The following results are dealing with Desmosomatidae *sensu* Hessler (1970), Wägele (1989) and Brandt (1992), excluding the genus *Thaumastosoma*. Therefore, species previously assigned to Nannoniscidae are excluded from zoogeographic data. Additionally, for the analysis of the species composition at the seven EBS stations only individuals which were not damaged and could be identified on species level are included. For most genera, missing pereopods cause an important loss of information that makes determination to species level (mostly even to genus level) impossible. Only for few desmosomatid genera, other diagnostic characters, e.g. characters of the body, are enough for determination.

##### 3.0.1 Desmosomatidae of DIVA-1

In total, Desmosomatidae are represented with 360 individuals, 10 genera (Fig. 8) and over 22 species. Of an estimated total of 27 species (including up to seven species in the *Mirabilicoxa* complex), four species occurred with a single specimen and at one station only (*Chelator* sp.3, *Chelator* sp. 4, cf. *Disparella* sp. 2 and *Oecidiobanchus* sp.1). Most species (93 %) are new to science (Table 1).

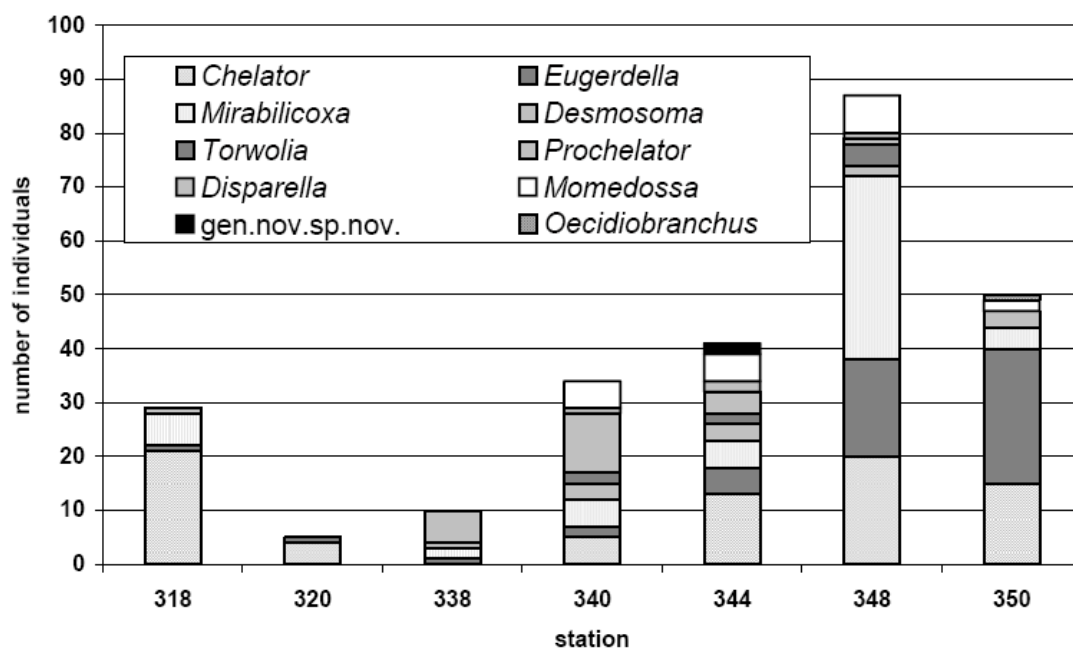


Fig. 8: Genera of Desmosomatidae per station

Only two desmosomatid species (*Mirabilicoxa exopodata* Hessler, 1970 and *M. acuminata* Hessler, 1970) found during DIVA-1 were previously described, both from the North Atlantic. These individuals are males. Most likely, some females which are assigned to the *Mirabilicoxa* complex (which needs further and detailed study) belong to these males. Of the remaining species new to science, *Prochelator angolensis* Brenke, Brix & Knuschke 2005 was recently described and four species are described in this thesis (*Eugerdella theodori* sp. nov., *Desmosoma renatae* sp. nov. *Torwolia tinbienae* sp. nov. and *Momedossa longipedis* sp. nov.). The seven stations show differences in diversity and abundance. At station 348 Desmosomatidae are most diverse, the diversity is lowest at station 320. *E. theodori* sp. nov. is the most abundant species at the northern stations of the DIVA-1 transect. *T. tinbienae* sp. nov. occurs only with few individual (stations 320, 340 and 344) and the presence of *M. longipedis* sp. nov. is limited to the northern stations (340, 344, 348 and 350). *D. renatae* sp. nov. occurs at six of the seven stations (except station 320) with one or two individuals at each station.

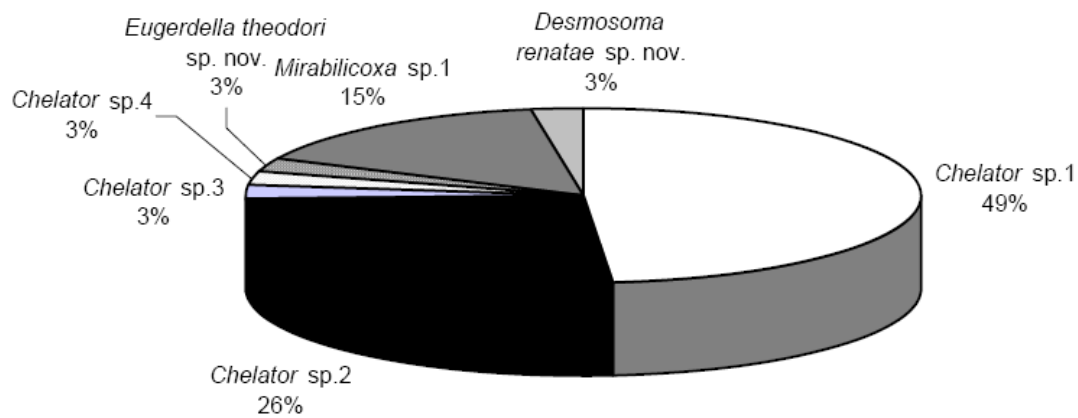
#### 3.0.2 Species composition at the seven EBS stations of DIVA-1

**Table 1:** List of species found at the seven sledge stations during DIVA-1

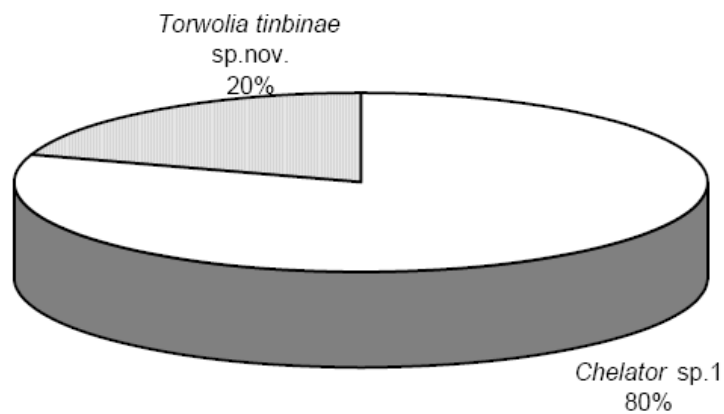
| species                                  | station   |          |           |           |           |           |           |
|--|-----------|----------|-----------|-----------|-----------|-----------|-----------|
|  | 318       | 320      | 338       | 340       | 344       | 348       | 350       |
| <i>Chelator</i> sp.1                     | 19        | 4        | 0         | 5         | 13        | 17        | 15        |
| <i>Chelator</i> sp.2                     | 10        | 0        | 0         | 0         | 0         | 3         | 0         |
| <i>Chelator</i> sp.3                     | 1         | 0        | 0         | 0         | 0         | 0         | 0         |
| <i>Chelator</i> sp.4                     | 1         | 0        | 0         | 0         | 0         | 0         | 0         |
| <i>Eugerdella</i> sp.2                   | 0         | 0        | 0         | 2         | 2         | 7         | 0         |
| <i>Eugerdella theodori</i> sp. nov.      | 1         | 0        | 1         | 0         | 3         | 11        | 25        |
| <i>Mirabilicoxa</i> sp.1                 | 6         | 0        | 2         | 2         | 5         | 0         | 0         |
| <i>Mirabilicoxa</i> sp.2                 | 0         | 0        | 0         | 3         | 0         | 0         | 0         |
| <i>Mirabilicoxa</i> sp.3                 | 0         | 0        | 0         | 0         | 0         | 1         | 3         |
| <i>Mirabilicoxa</i> cf. <i>exopodata</i> | 0         | 0        | 0         | 0         | 0         | 5         | 1         |
| <i>Mirabilicoxa</i> cf. <i>acuminata</i> | 0         | 0        | 0         | 0         | 0         | 9         | 0         |
| <i>Mirabilicoxa</i> sp. female complex   | 0         | 0        | 0         | 0         | 0         | 20        | 0         |
| <i>Torwolia tinbienae</i> sp. nov.       | 0         | 1        | 0         | 1         | 2         | 0         | 0         |
| <i>Torwolia</i> sp. nov. 2               | 0         | 0        | 0         | 1         | 0         | 4         | 0         |
| <i>Prochelator angolensis</i>            | 0         | 0        | 6         | 11        | 3         | 1         | 0         |
| cf. <i>Disparella</i> sp. nov.           | 0         | 0        | 0         | 1         | 0         | 0         | 0         |
| <i>Disparella</i> sp. nov. 1             | 0         | 0        | 0         | 0         | 2         | 1         | 0         |
| <i>Desmosoma</i> sp. nov.1               | 0         | 0        | 0         | 1         | 1         | 0         | 0         |
| <i>Desmosoma renatae</i> sp. nov.        | 1         | 0        | 1         | 2         | 2         | 2         | 3         |
| <i>Momedossa longipedis</i> sp. nov.     | 0         | 0        | 0         | 5         | 5         | 7         | 2         |
| gen. nov. sp. nov.                       | 0         | 0        | 0         | 0         | 2         | 0         | 0         |
| <i>Oecidiobranchus</i> sp.               | 0         | 0        | 0         | 0         | 0         | 0         | 1         |
| <b>individuals per station</b>           | <b>39</b> | <b>5</b> | <b>10</b> | <b>34</b> | <b>40</b> | <b>88</b> | <b>50</b> |



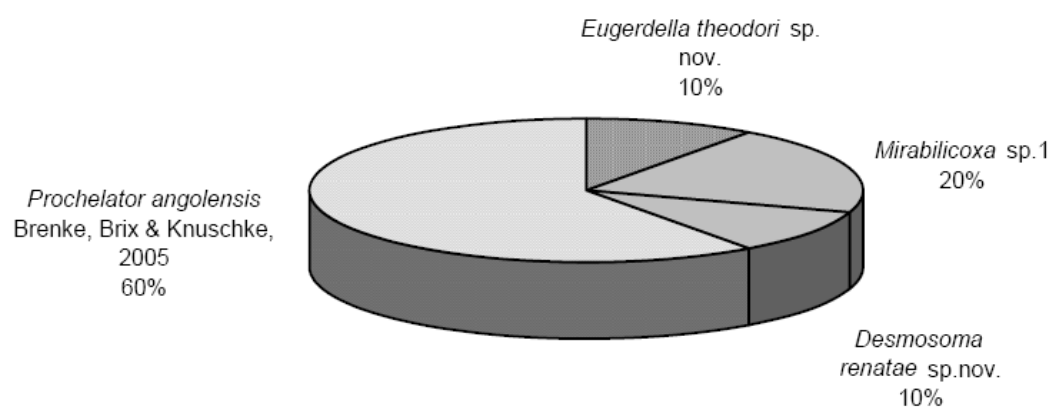
### 3. Results



**Fig. 9:** Species composition at station 318

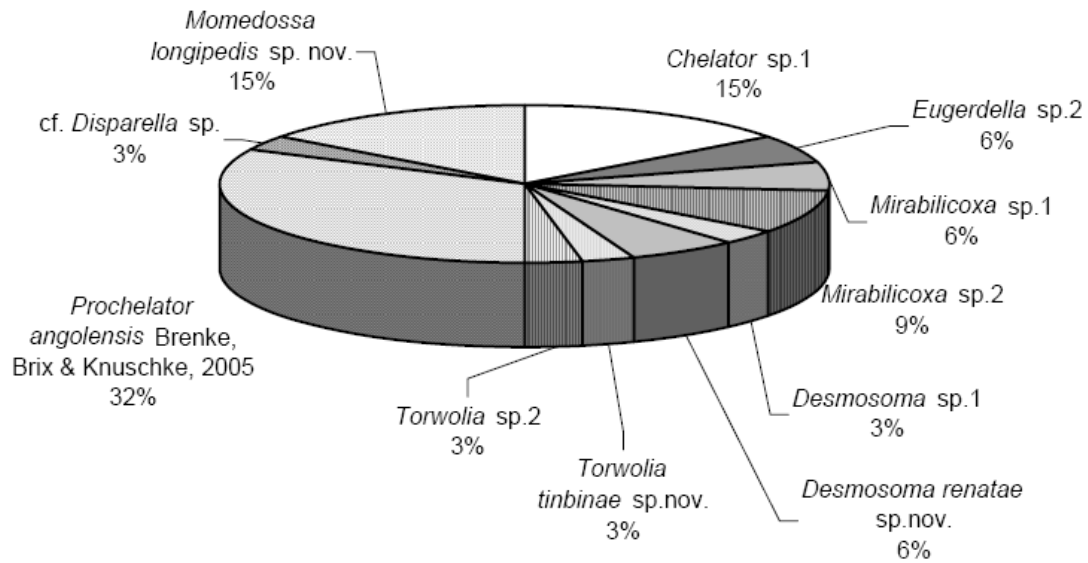


**Fig. 10:** Species composition at station 320

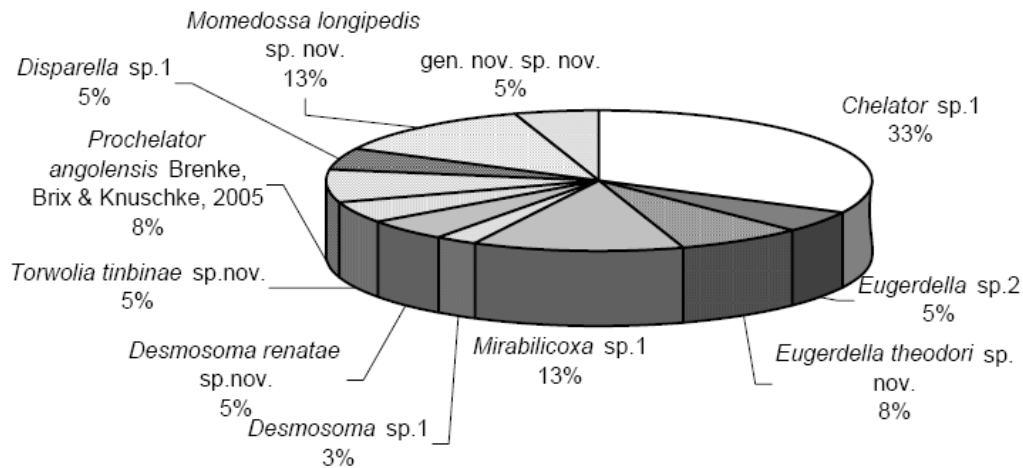


**Fig. 11:** Species composition at station 338

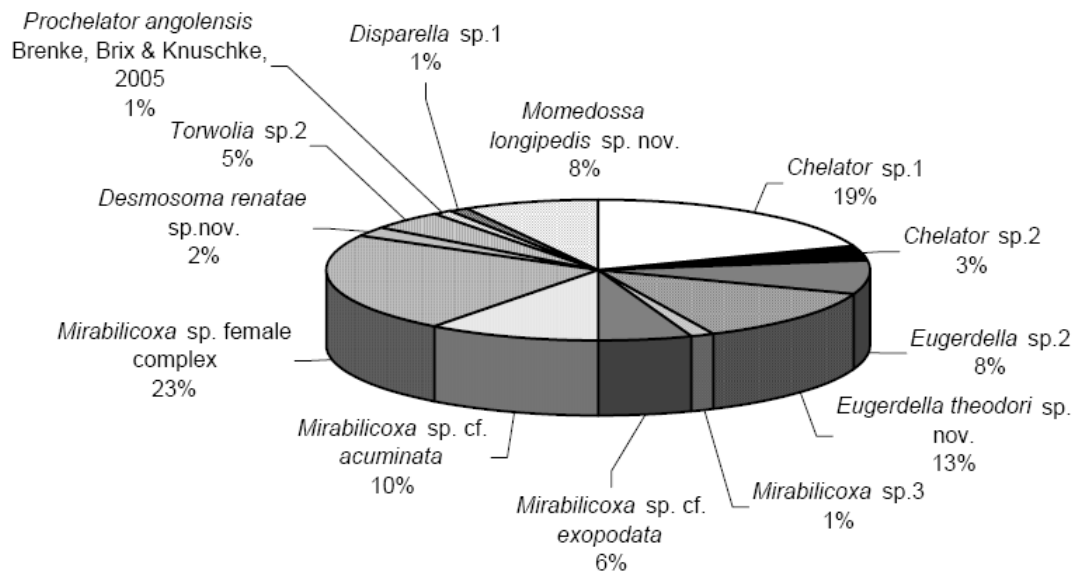
### 3. Results



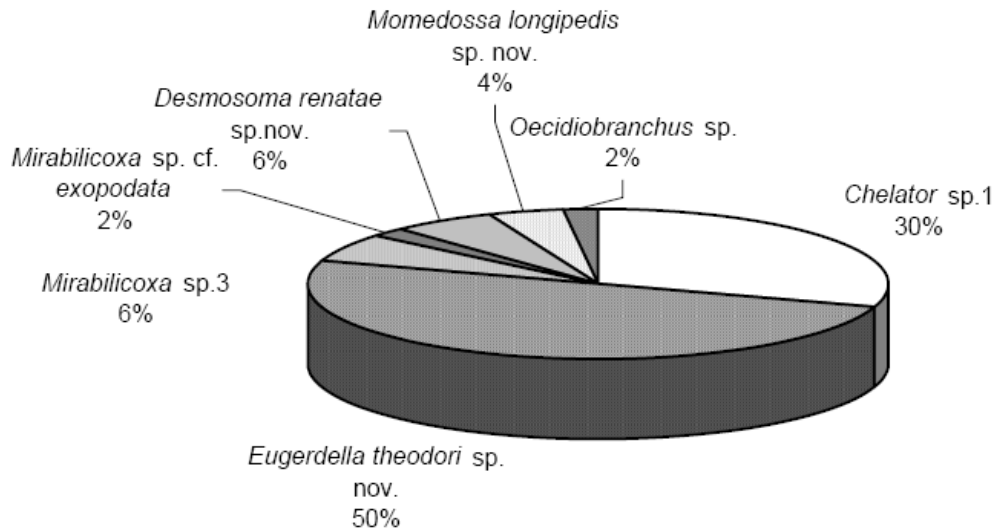
**Fig. 12:** Species composition at station 340



**Fig. 13:** Species composition at station 344



**Fig. 14:** Species composition at station 348

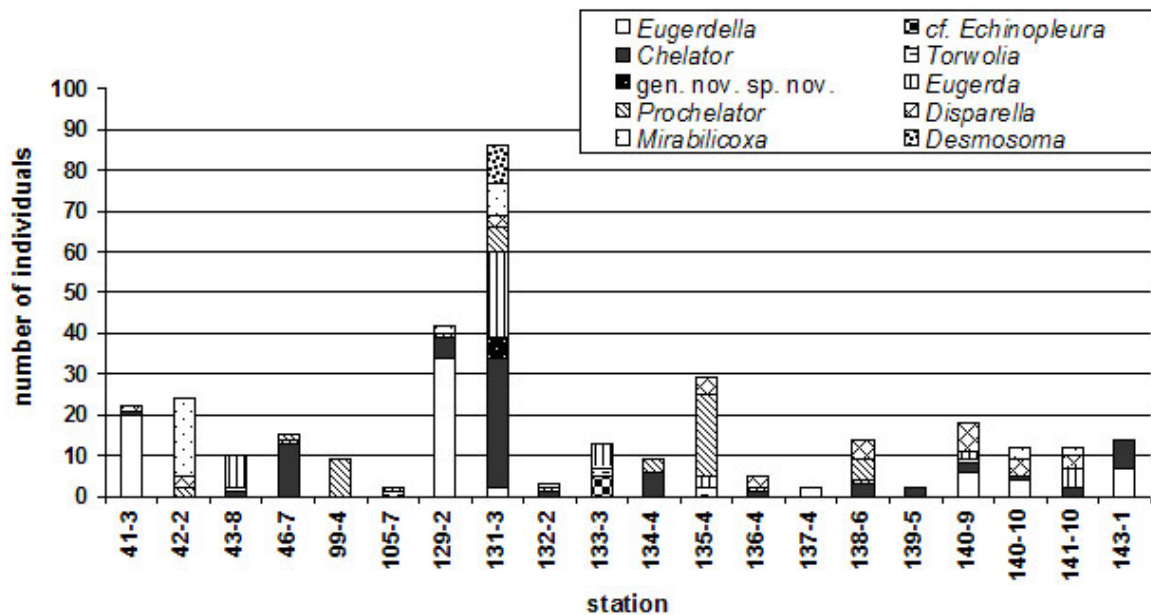


**Fig. 15:** Species composition at station 350

#### 3.0.3 Desmosomatidae of ANDEEP I & II

With 365 specimens belonging to 48 species and 10 genera, Desmosomatidae are one of the most diverse isopod families in the samples (compare Brandt *et al.* 2004, Brökeland 2004). In ANDEEP I all stations are very diverse. No station resembles another in regard to the species composition. This is the same for all stations of ANDEEP II, each station is highly diverse. Some species are very abundant and occur at every station, while 25 species occur with only one individual at one station only.

In total, 11 of 21 stations from both expeditions contain a species occurring at that station only and only with a single individual. Only 13 of a total of 48 species occur at stations of both cruises and 42 of the 48 species are new to science (87.5 %). For example, *Disparella maiuscula* Kaiser & Brix, 2005 and *Eugerdella serrata* sp. nov. are two of the four most abundant species within the samples of ANDEEP II. These species do not occur in samples of ANDEEP I.



**Fig. 16:** Composition of the genera of Desmosomatidae at the stations of ANDEEP I (41-3, 42-2, 43-8, 46-7, 99-4, 105-7 and 129-2) and ANDEEP II (131-3, 132-2, 133-3, 134-4, 135-4, 136-4, 137-4, 138-6, 139-5, 140-9, 140-10, 141-10 and 143-1)

### 3.0.4 Species composition at the ANDEEP stations

Species occurring in the Scotia Sea (ANDEEP I) and in the Weddell Sea (ANDEEP II) are: *Egerda* sp. 6, *Egerda* sp. 5, *Egerda* sp. 2, *Egerda* sp. 1, *Disparella* sp. 2, *Prochelator* sp. 5, *Prochelator* sp. 4, *Prochelator* sp. 3, *Torwolia* sp.1, *Chelator* sp. 3, *Chelator* sp. 2, *Chelator antarcticus* sp. nov. and *Egerdella* sp. 7.

Species found only during ANDEEP I are: *Mirabilicoxa* sp. 4, *Mirabilicoxa* sp. 3, *Mirabilicoxa* sp. 2, *Prochelator* sp. 1, *Egerdella* sp. 10, *Egerdella* sp. 9 and *Egerdella* sp.8. Of these species, *Egerdella* sp. 8 (station 105-10), *Prochelator* sp. 1 (station 46-7) and *Mirabilicoxa* sp. 4 (station 42-2) occur with a single individual only.

Species found only during ANDEEP II are: *Egerdella serrata* sp. nov., *Egerdella* sp. 11, *Egerdella* sp. 6, *Egerdella* sp. 5, *Egerdella* sp. 4, *Egerdella* sp. 3, *Egerdella* sp. 1, *cf. Echinopleura* sp., *Chelator* sp. 4, gen. nov. sp. nov., *Egerda* sp. 3, *Egerda* sp. 4, *Egerda* sp. 7, *Egerda* sp. 8, *Prochelator* sp. 2, *Prochelator* sp. 6, *Disparella maiuscula* sp. nov., *Disparella* sp. 3, *Disparella* sp. 4, *Mirabilicoxa* sp. 5, *Mirabilicoxa* sp. 6, *Mirabilicoxa* sp. 7, *Mirabilicoxa* sp. 8, *Mirabilicoxa* sp. 9, *Desmosoma* sp. 1 and *Desmosoma* sp. 2. Of these species, *Egerda* sp. 4 (station 138-6) and *Mirabilicoxa* sp. 7 (station 131-3) occur with a single individual only.

### 3. Results

**Table 2:** List of all desmosomatid species found during ANDEEP I & II

| species                     | stations of ANDEEP I |      |      |      |      |       |       |       | stations of ANDEEP II |       |       |       |       |       |       |       |       |       |        |        |       |
|-----------------------------|----------------------|------|------|------|------|-------|-------|-------|-----------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--------|--------|-------|
|                             | 41-3                 | 42-2 | 43-8 | 46-7 | 99-4 | 105-7 | 114-4 | 129-2 | 131-3                 | 132-2 | 133-3 | 134-4 | 135-4 | 136-4 | 137-4 | 138-6 | 139-5 | 140-9 | 140-10 | 141-10 | 143-1 |
| <i>Eugerdella serrata</i>   | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 29    | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 1     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 4      | 0     |
| <i>Eugerdella</i> sp. 2     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 4     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 3     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 7     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 4     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 7     |
| <i>Eugerdella</i> sp. 5     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 2     | 1     | 1     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 6     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 2     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 7     | 0                    | 0    | 0    | 0    | 1    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 2      | 0      | 0     |
| <i>Eugerdella</i> sp. 8     | 0                    | 0    | 0    | 0    | 0    | 1     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 9     | 2                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 10    | 0                    | 3    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| cf. <i>Echinopleura</i>     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 5     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 11    | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 11                    | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Chelator</i> sp. nov. A  | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 1     | 30                    | 0     | 0     | 5     | 0     | 0     | 0     | 0     | 0     | 1     | 0      | 0      | 0     |
| <i>Chelator</i> sp. 2       | 1                    | 0    | 0    | 13   | 0    | 0     | 0     | 4     | 1                     | 1     | 0     | 1     | 0     | 1     | 0     | 3     | 1     | 1     | 0      | 2      | 0     |
| <i>Chelator</i> sp. 3       | 0                    | 0    | 1    | 0    | 0    | 0     | 0     | 0     | 1                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Chelator</i> sp. 4       | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 1     | 0     | 1      | 0      | 0     |
| <i>Torwolia</i> sp. 1       | 0                    | 0    | 1    | 0    | 0    | 1     | 0     | 0     | 0                     | 0     | 2     | 0     | 2     | 0     | 0     | 0     | 0     | 1     | 0      | 0      | 0     |
| genus nov. sp. nov.         | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 5                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 1     | 0                    | 0    | 1    | 0    | 0    | 0     | 0     | 0     | 12                    | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 2     | 0                    | 0    | 4    | 0    | 0    | 0     | 0     | 0     | 2                     | 0     | 2     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 1      | 0     |
| <i>Eugerdella</i> sp. 3     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 4      | 0     |
| <i>Eugerdella</i> sp. 4     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 1     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 5     | 0                    | 0    | 1    | 1    | 0    | 0     | 0     | 0     | 0                     | 0     | 2     | 0     | 3     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 6     | 0                    | 0    | 2    | 0    | 0    | 0     | 0     | 0     | 4                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 2     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 7     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 3                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Eugerdella</i> sp. 8     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 2     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Prochelator</i> sp. 1    | 0                    | 0    | 0    | 1    | 9    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Prochelator</i> sp. 2    | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 1     | 1     | 0     | 3     | 0     | 0     | 0      | 0      | 0     |
| <i>Prochelator</i> sp. 3    | 0                    | 2    | 0    | 0    | 0    | 0     | 0     | 0     | 2                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Prochelator</i> sp. 4    | 0                    | 0    | 0    | 0    | 0    | 1     | 0     | 0     | 0                     | 0     | 0     | 0     | 8     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Prochelator</i> sp. 5    | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 1     | 4                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Prochelator</i> sp. 6    | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 3     | 11    | 0     | 0     | 2     | 0     | 0     | 0      | 0      | 0     |
| <i>Disparella maiuscula</i> | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 3                     | 1     | 0     | 0     | 4     | 3     | 0     | 3     | 0     | 2     | 4      | 3      | 0     |
| <i>Disparella</i> sp. 2     | 1                    | 3    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 2     | 0      | 0      | 0     |
| <i>Disparella</i> sp. 3     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 2     | 0      | 0      | 0     |
| <i>Disparella</i> sp. 4     | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 2     | 0     | 1     | 0      | 0      | 0     |
| <i>Mirabilicoxa</i> sp. 1   | 0                    | 2    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Mirabilicoxa</i> sp. 2   | 0                    | 12   | 0    | 0    | 0    | 0     | 0     | 2     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Mirabilicoxa</i> sp. 3   | 0                    | 4    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Mirabilicoxa</i> sp. 4   | 0                    | 1    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Mirabilicoxa</i> sp. 5   | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 0                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 3      | 2      | 0     |
| <i>Mirabilicoxa</i> sp. 6   | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 3                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Mirabilicoxa</i> sp. 7   | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 1                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Mirabilicoxa</i> sp. 8   | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 2                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Mirabilicoxa</i> sp. 9   | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 2                     | 1     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Desmosoma</i> sp. 1      | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 2                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| <i>Desmosoma</i> sp. 2      | 0                    | 0    | 0    | 0    | 0    | 0     | 0     | 0     | 7                     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0     | 0      | 0      | 0     |
| individuals per station     | 4                    | 27   | 10   | 15   | 10   | 3     | 0     | 8     | 95                    | 3     | 42    | 9     | 33    | 12    | 2     | 15    | 3     | 14    | 10     | 16     | 7     |

### 3. Results

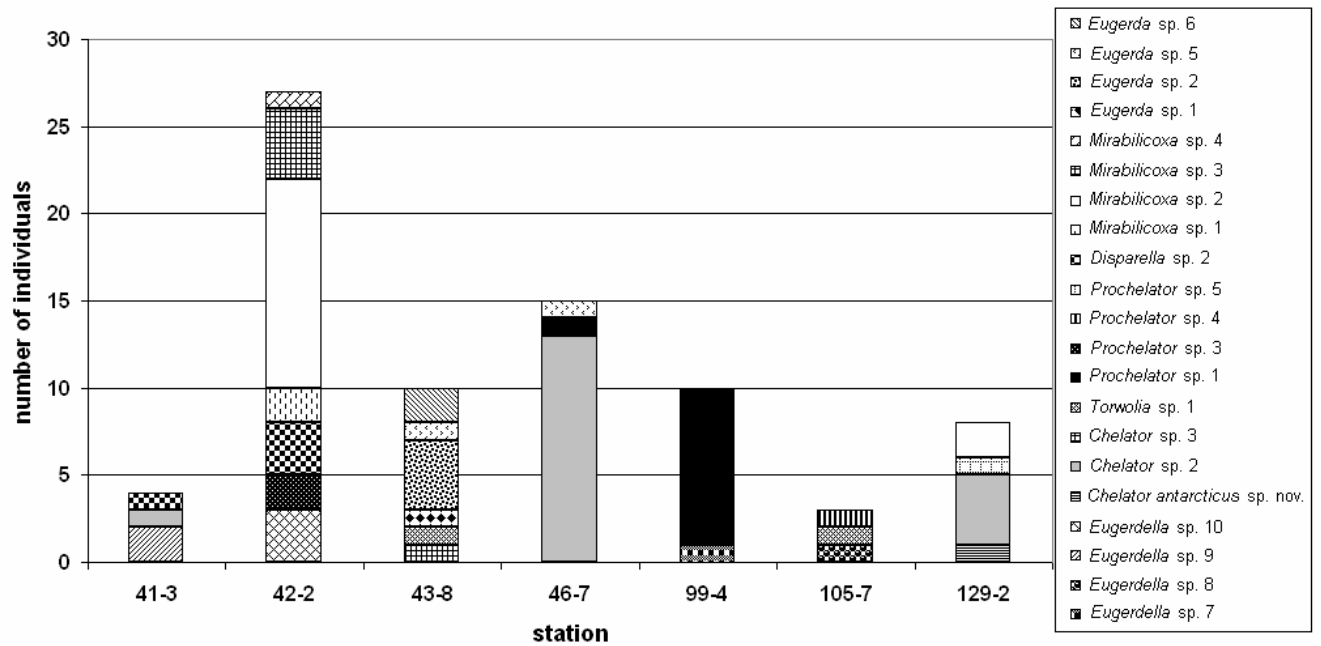


Fig. 17: Species composition at the ANDEEP I stations

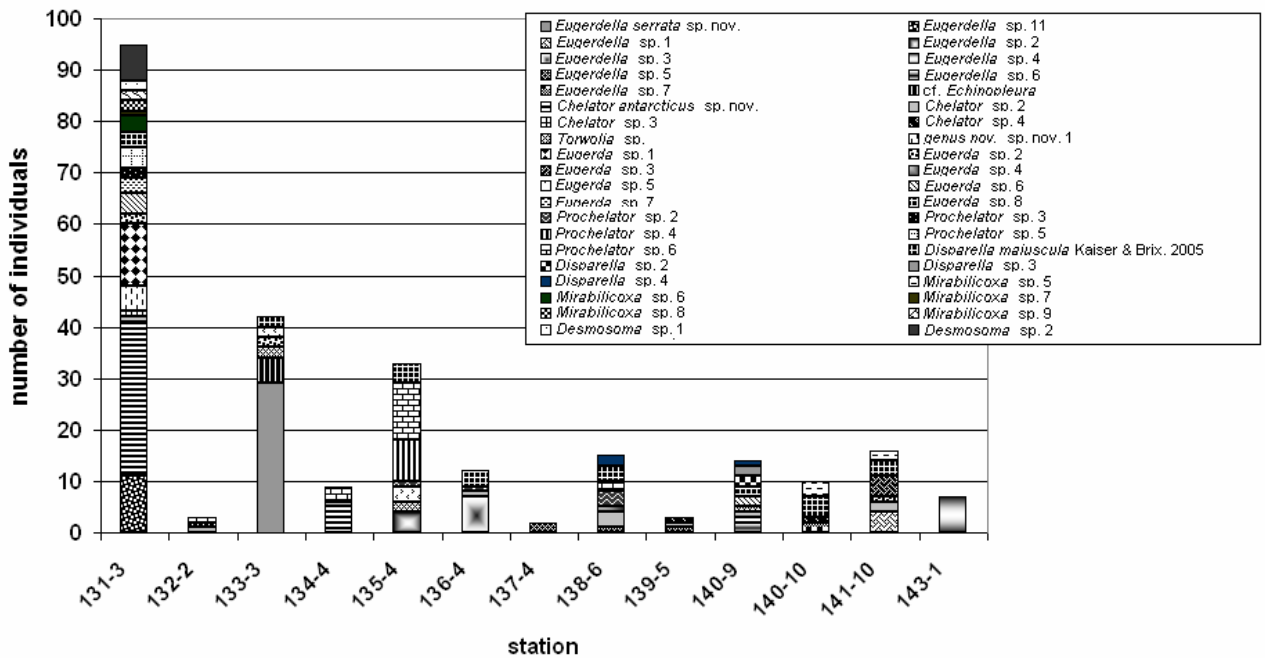


Fig. 18: Species composition at the ANDEEP II stations

### 3.0.5 Distribution of the family Desmosomatidae

The following list includes all species that are assigned to Desmosomatidae in the present study (chapter 3.1.4; as discussed in chapter 4.1.1).

**Table 3:** Distribution of species (206)

| Taxon  | Distribution                     | Depth (m)        |
|--|----------------------------------|------------------|
| <b><i>Austroniscus</i> Vanhoeffen, 1914 (10 species)</b> |                                  |                  |
| <i>A. acutus</i> Birstein, 1970                          | Japan                            | 5005-6135        |
| <i>A. chelus</i> Kaiser & Brandt, submitted              | W. Antarctic                     | 910-899          |
| <i>A. coronatus</i> Schiecke & Modigh Tota, 1976         | Mediterranean                    | 55-200           |
| <i>A. groenlandicus</i> Hansen, 1916                     | W. Greenland                     | 10-132           |
| <b><i>A. karamani</i> Birstein, 1962</b>                 | <b>East- Japan, N.W.-Pacific</b> | <b>5005-5495</b> |
| <i>A. norbi</i> Svavarsson, 1982                         | Greenland                        | 3595             |
| <i>A. obscurus</i> Kaiser & Brandt, submitted            | West-Antartica                   | 910-899          |
| <i>A. ovalis</i> (Vanhoeffen, 1914)                      | E. Antarctica                    | 70-385           |
| <i>A. rotundatus</i> Vanhoeffen, 1914                    | E. Antarctica                    | 70-385           |
| <i>A. vinogradovi</i> Gurjanova, 1950                    | Kamchatka Trench                 | 125              |
| <b><i>Chelator</i> Hessler, 1970 (8 species)</b>         |                                  |                  |
| <i>C. brevicaudus</i> (Menzies & George, 1972)           | Peru-Chile Trench                | 1238             |
| <i>C. chelatum</i> (Stephensen, 1915)                    | Mediterranean                    | planktonnet      |
| <i>C. insignis</i> (Hansen, 1916)                        | Davis Strait                     | 1065-2702        |
| <i>C. stellae</i> Malyutina & Kussakin, 1996             | Polar Sea                        | 230              |
| <i>C. striatus</i> (Menzies, 1962)                       | N. Atlantic                      | 126              |
| <i>C. verecundus</i> Hessler, 1970                       | N. Atlantic                      | 1150-2500        |
| <i>C. vulgaris</i> Hessler, 1970                         | N. Atlantic                      | 2496-4833        |
| <i>C. sp. nov. A</i>                                     | Antarctica                       | 2500             |
| <b><i>Cryodesma</i> Svavarsson, 1988 (3 species)</b>     |                                  |                  |
| <i>C. agnari</i> Svavarsson, 1988                        | Norwegian Sea                    | 970-3642         |
| <i>C. cryoabyssale</i> Malyutina & Kussakin, 1996        | Polar Sea                        | 3290             |
| <i>C. polare</i> Malyutina & Kussakin 1996               | Polar Sea                        | 3550             |
| <b><i>Desmosoma</i> Sars, 1864 (22 species)</b>          |                                  |                  |
| <i>D. affine</i> Fresi & Schiecke, 1969                  | Off Italy                        | 110              |
| <i>D. australis</i> Nordenstam, 1933                     | South Georgia                    | 64-148           |
| <i>D. brevipes</i> Nordenstam, 1933                      | South Georgia                    | 64-148           |
| <i>D. dolosa</i> (Menzies & George, 1972)                | Peru-Chile Trench                | 4506-4609        |
| <i>D. elegans</i> Fresi & Schiecke, 1969                 | Mediterranean                    | 500              |
| <i>D. elongatum</i> Bonnier, 1896                        | Bay of Biscay                    | 950              |
| <i>D. gigantea</i> Park, 1999                            | S. Pacific                       | 4162             |
| <i>D. hessleri</i> Brandt, 1992                          | Antarctic                        | 4335             |
| <i>D. imbricata</i> Hessler, 1970                        | N. Atlantic                      | 4800-4825        |
| <i>D. latipes</i> (Hansen, 1916)                         | Davis Strait                     | 200-1102         |
| <i>D. lineare</i> Sars, 1864                             | N. Atlantic                      | 17-699           |
| <i>D. lobipes</i> Kussakin, 1965                         | Okhotsk Sea                      | 220              |
| <i>D. modestum</i> Nordenstam, 1933                      | South Georgia                    | 125-250          |
| <i>D. ochotense</i> Kussakin, 1965                       | Okhotsk Sea                      | 220              |
| <i>D. pannosa</i> Hessler, 1970                          | N. Atlantic                      | 3742-4800        |
| <i>D. puritanum</i> Fresi & Schiecke, 1969               | Mediterranean                    | 500              |
| <i>D. renatae</i> sp. nov.                               | S. Atlantic (Angola Basin)       | 5126-5415        |
| <i>D. stroembergi</i> Svavarsson, 1988                   | Norwegian Sea                    | 794-1288         |
| <i>D. tetarta</i> Hessler, 1970                          | N. Atlantic                      | 530-2496         |
| <i>D. thoracicum</i> Fresi & Schiecke 1969               | Off Italy                        | 100              |
| <i>D. tyrrhenicum</i> Fresi & Schiecke, 1969             | Off Italy                        | 105              |
| <i>D. zenkewitschi</i> (Gurjanova, 1946)                 | N. Polar Sea                     | 65               |

### 3. Results

#### ***Disparella* Hessler, 1970 (7 species)**

|  |                   |           |
|--|-------------------|-----------|
| <i>D. funalis</i> (Menzies & George, 1972) | Peru-Chile Trench | 3909-4609 |
| <i>D. longimana</i> (Vanhoeffen, 1914)     | Indian Ocean      | 2200-2735 |
| <i>D. pachytrix</i> Hessler, 1970          | N. Atlantic       | 4680      |
| <i>D. valida</i> Hessler, 1970             | N. Atlantic       | 3459-3806 |
| <i>D. maiuscula</i> Kaiser & Brix, 2005    | Weddell Sea       | 5400      |
| <i>D. neomana</i> (Menzies & George, 1972) | Peru-Chile Trench | 4526-4609 |
| <i>D. kensleyi</i> sp. nov.                | S. Australia      | 2690      |

#### ***Echinopleura* Sars, 1899 (2 species)**

|                                 |              |        |
|---------------------------------|--------------|--------|
| <i>E. aculeata</i> (Sars, 1864) | N. Norway    | 15-681 |
| <i>E. cephalomagna</i> sp. nov. | S. Australia | 400    |

#### ***Eugerdella* Meinert, 1890 (7 species)**

|   |                |          |
|---|----------------|----------|
| <i>E. tenuimana</i> (Sars, 1868)                | N. Atlantic    | 4698     |
| <i>E. fulcimandibulata</i> Hessler, 1970        | N. Atlantic    | 587-4833 |
| <i>E. reticulata</i> (Gurjanova, 1946)          | N. Polar Sea   | 2500     |
| <i>E. dubia</i> Malyutina & Kussakin 1996       | Polar Sea      | 230      |
| <i>E. gurjanova</i> Malyutina & Kussakin 1996   | Polar Sea      | 230      |
| <i>E. mandibulata</i> Malyutina & Kussakin 1996 | Polar Sea      | 230-340  |
| <i>E. svavarssoni</i> George, 2001              | Carolina Slope | 620      |

#### ***Eugerdella* Kussakin, 1965 (12 species)**

|  |                            |           |
|--|----------------------------|-----------|
| <i>E. armata</i> (Sars, 1864)              | Greenland                  | 50-478    |
| <i>E. coarctata</i> (Sars, 1899)           | Skagerrak                  | 24-2702   |
| <i>E. falklandica</i> (Nordenstam, 1933)   | Falkland Is.               |           |
| <i>E. minutula</i> Mezhev, 1986            | N. Pacific                 | 3240-3300 |
| <i>E. natator</i> (Hansen, 1916)           | Davis Strait               | 2626-4833 |
| <i>E. nonfunalis</i> sp. nov.              | Peru-Chile Trench          | 4526-4609 |
| <i>E. ordinaria</i> Mezhev, 1986           | N. Pacific                 | 1550      |
| <i>E. polita</i> (Hansen, 1916)            | Iceland                    | 1070-1505 |
| <i>E. pugilator</i> Hessler, 1970          | N. Atlantic                | 2864-2886 |
| <i>E. rotunda</i> (Menzies & George, 1972) | Peru-Chile Trench          | 4526-4609 |
| <i>E. theodori</i> sp. nov.                | S. Atlantic (Angola Basin) | 5387-5415 |
| <i>E. serrata</i> sp. nov.                 | Antarctic                  | 4000-6000 |

#### ***Exilinisca* Siebenhaller & Hessler, 1981 (4 species)**

|  |               |           |
|--|---------------|-----------|
| <i>E. aculeatus</i> Siebenhaller & Hessler, 1981 | S.E. Atlantic | 1964-2031 |
| <i>E. chandravoli</i> George, 2001               | N. Atlantic   | 3620      |
| <i>E. clipeatus</i> Siebenhaller & Hessler, 1981 | N. Atlantic   | 3834-5023 |
| <i>E. hansenii</i> Just, 1970                    | Greenland     | 80-1288   |

#### **genus novum (monotypic) \***

|  |            |      |
|--|------------|------|
| gen. nov. <i>fletcheri</i> (Paul & George, 1975) | Arctic Sea | 1740 |
|--|------------|------|

#### ***Hebefustis* Siebenhaller & Hessler, 1977 (10 species)**

|  |                    |           |
|--|--------------------|-----------|
| <i>H. allenii</i> Siebenhaller & Hessler, 1977     | Biskaya & Atlantic | 1623-1796 |
| <i>H. cornutus</i> Siebenhaller & Hessler, 1977    | N. Atlantic        | 3806      |
| <i>H. dispar</i> Siebenhaller & Hessler, 1977      | S Atlantic         | 5208-5223 |
| <i>H. hirsutus</i> Menzies, 1962                   | S Atlantic         | 5024      |
| <i>H. mollicellus</i> Siebenhaller & Hessler, 1977 | S. Atlantic        | 943-1007  |
| <i>H. par</i> Siebenhaller & Hessler, 1977         | Atlantic           | 4426-4435 |
| <i>H. primitivus</i> Menzies, 1962                 | Caribbean Sea      | 2868-2875 |
| <i>H. robustus</i> Birstein, 1963                  | N.W. Pacific       | 5461-5690 |
| <i>H. vafer</i> Siebenhaller & Hessler, 1977       | S. Atlantic        | 587       |
| <i>H. vitjazi</i> Mezhev, 1986                     | Golf of Alaska     | 1550      |

\* The genus name is not presented in this study, because the new genus is part of the results of the diploma thesis of Stefanie Kaiser and the paper in preparation with a redescription of *Mirablikcoxa fletcheri* and the erection of the new genus is in preparation and not published yet.



### 3. Results

#### **Micromesus** Birstein, 1963 (monotypic)

*M. nannoniscoides* Birstein, 1963 N.W.- Pacific 4001-4150

#### **Mirabilicoxa** Hessler, 1970 (19 species)

*M. alberti* George, 2001 North Carolina, USA 3010  
*M. atlanticum* Hessler, 1970 N. Atlantic 4436-4749  
*M. cornuta* (Hessler, 1970) N. Atlantic 3834  
*M. acuminata* Hessler, 1970 N. Atlantic 3834-4800  
*M. acuta* (Menzies & George, 1972) Peru-Chile Trench 3909-3970  
*M. birsteini* (Menzies, 1962) N. Atlantic, Bermuda 5166  
*M. coxalis* (Birstein, 1963) N.W. Pacific 5461-5495  
*M. curticoxalis* Pasternak, 1982 Mediterranean 1376  
*M. exopodata* Hessler, 1970 N. Atlantic 3834  
*M. hessleri* George, 2001 North Carolina, USA 2700  
*M. gracilipes* (Hansen, 1916) Davis Strait 2194-2702  
*M. longispina* (Hansen, 1916) Davis Strait 2496-5321  
*M. magnispina* (Menzies, 1962) Bay of Panama 1800-1906  
*M. minuta* Hessler, 1970 N. Atlantic 4800  
*M. palpata* Hessler, 1970 N. Atlantic 3834  
*M. plana* Hessler, 1970 N. Atlantic 3834  
*M. richardsoni* Mezhev, 1986 N. Pacific 3240-3300  
*M. similis* (Hansen, 1916) Davis Strait 530-2194  
*M. similipes* (Menzies & George, 1972) Peru-Chile Trench 3909-6134  
*M. tenuipes* (Birstein, 1970) 44°48'156°33' 5005-5045

#### **Momedossa** Hessler, 1970 (2 species)

*M. profunda* Hessler, 1970 N. Atlantic 4680-4833  
*M. longipedis* sp. nov. S. Atlantic (Angola Basin) 5126-5415

#### **Nannoniscoides** Hansen, 1916 (7 species)

*N. angulatus* Hansen, 1916 N. Atlantic 74-1322  
*N. biscutatus* Siebenhaller & Hessler, 1977 Atlantic 3459  
*N. coronarius* Siebenhaller & Hessler, 1977 S. Atlantic 1493  
*N. excavatifrons* Birstein, 1970 Kurile-Kamchatka-Trench 1440-1450  
*N. gigas* Siebenhaller & Hessler, 1977 S.- Atlantic 3906-3917  
*N. latediffusus* Siebenhaller & Hessler, 1977 N. Atlantic 587  
*N. laticontractus* Mezhev, 1986 Golf of Alaska, USA 1550

#### **Nannonisconus** Schultz, 1966 (2 species)

*N. carinatus* Mezhev, 1986 Golf of Alaska 1040  
*N. latipleonus* Schultz, 1966 Redondo Canyon, CA 465

#### **Nannoniscus** Sars, 1870 (29 species)

*N. acanthurus* Birstein, 1963 N.W. Pacific 3941-5495  
*N. aequiremus* Hansen, 1916 Off Jan Mayen 885  
*N. affinis* Hansen, 1916 S.W. Iceland 1505  
*N. analis* Hansen, 1916 Davis Strait 2258  
*N. antennaspinis* Brandt, 2001 Angola Basin 5389-5415  
*N. arcticus* Hansen, 1916 Off Jan Mayen 75-699  
*N. arctoabyssalis* Just, 1980 Polar Sea 3970  
*N. australis* Vanhoeffen, 1914 E. Antarctica 385  
*N. bidens* Vanhoeffen, 1914 E. Antarctica 191- 385  
*N. camayae* Menzies, 1962 Caribbean Panama 1714  
*N. caspius* Sars, 1899 Caspian Sea  
*N. cristatus* Mezhev, 1986 Golf of Alaska, USA 3200  
*N. detrimentus* Menzies & George, 1972 Peru- Chile- Trench 3909-3970  
*N. inermis* Hansen, 1916 Davis Strait 2258  
*N. intermedius* Siebenhaller & Hessler, 1981 W. Atlantic 508- 523  
*N. laevis* Menzies, 1962 S.E. Atlantic 4885  
*N. laticeps* Hansen, 1916 N. Iceland 552  
*N. menziesi* Mezhev, 1986 Golf von Alaska, USA 4800

### 3. Results

|   |                            |            |
|---|----------------------------|------------|
| <i>N. minutus</i> Hansen, 1916                                      | Davis Strait               | 1096       |
| <i>N. muscarius</i> Menzies & George, 1972                          | Peru- Chile- Trench        | 3909- 3970 |
| <i>N. oblongus</i> Sars, 1870                                       | Lofoten, Iceland           | 219- 5843  |
| <i>N. ovatus</i> Menzies & George, 1972                             | Peru- Chile- Trench        | 6321- 6328 |
| <i>N. perunis</i> Menzies & George, 1972                            | Peru- Chile- Trench        | 4823- 6281 |
| <i>N. plebejus</i> Hansen, 1916                                     | S.W.-Iceland               | 1505       |
| <i>N. profundus</i> Svavarsson, 1982                                | Norwegian Sea, Greenland   | 2475- 2502 |
| <i>N. reticulatus</i> Hansen, 1916                                  | N. Iceland                 | 80-1020    |
| <i>N. simplex</i> Hansen, 1916                                      | W.- Iceland                | 1070-1505  |
| <i>N. spinicornis</i> Hansen, 1916                                  | Off Jan Mayen, N. Atlantic | 2465       |
| <i>N. teres</i> Siebenhaller & Hessler, 1981                        | N.E. Atlantic              | 4426- 4435 |
| <b><i>Oecidiobranchus</i> Hessler, 1970 (5 species)</b>             |                            |            |
| <i>O. glacialis</i> Malyutina & Kussakin, 1996                      | Polar Sea                  | 260        |
| <i>O. nansenii</i> Just, 1980                                       | Arctic Sea                 | 794-3920   |
| <i>O. plebejum</i> (Hansen, 1916)                                   | Iceland                    | 80-1666    |
| <i>O. polare</i> (Gurjanova, 1946)                                  | N. Polar Sea               | 40-510     |
| <i>O. slopei</i> sp. nov.   | Australia, New South Wales | 2500       |
| <b><i>Panetela</i> Siebenhaller &amp; Hessler, 1981 (3 species)</b> |                            |            |
| <i>P. compacta</i> Malyutina & Kussakin, 1996                       | Arctic Sea, W.-Kanada      | 3230       |
| <i>P. tenella</i> Birstein, 1963                                    | N.W. Pacific               | 5461-5495  |
| <i>P. wolffi</i> Siebenhaller & Hessler, 1981                       | S.E. Atlantic              | 1964-2031  |
| <b><i>Paradesmosoma</i> Kussakin, 1965 (3 species)</b>              |                            |            |
| <i>P. conforme</i> Kussakin, 1965                                   | Okhotsk Sea                | 105-237    |
| <i>P. orientale</i> Kussakin, 1965                                  | Sea of Japan               | 95-111     |
| <i>P. australis</i> sp. nov.  | Australia, Victoria        | 400        |
| <b><i>Prochelator</i> Hessler, 1970 (11 species)</b>                |                            |            |
| <i>P. angolensis</i> Brenke, Brix & Knuschke, 2005                  | S. Atlantic (Angola Basin) | 5430 m     |
| <i>P. abyssalis</i> Hessler, 1970                                   | N. Atlantic                | 3459-4833  |
| <i>P. hampsoni</i> Hessler, 1970                                    | N. Atlantic                | 4680-4758  |
| <i>P. incomitatus</i> Hessler, 1970                                 | N. Atlantic                | 5100       |
| <i>P. lateralis</i> (Sars, 1899)                                    | Skagerrak                  | 50-2021    |
| <i>P. litus</i> Hessler, 1970                                       | N. Atlantic                | 4680-4800  |
| <i>P. sarsi</i> George, 2001  | Off North Carolina, USA    | 5350       |
| <i>P. uncatus</i> Hessler, 1970                                     | N. Atlantic                | 119-300    |
| <i>P. kussakini</i> Mezhev, 1986                                    | Off Kurile Islands         |            |
| <i>P. serratum</i> (Fresi & Schiecke, 1969)                         | Mediterranean              | 100        |
| <i>P. maorii</i> sp. nov.   | Off New Zealand            | 1200       |
| <b><i>Pseudogorda</i> (Kussakin, 1965) (7 species)</b>              |                            |            |
| <i>P. anversense</i> (Schultz, 1979)                                | Antarctic                  | 109-137    |
| <i>P. arctica</i> Svavarsson, 1988                                  | Norwegian Sea              | 2400-2630  |
| <i>P. elegans</i> Kussakin, 1965                                    | Okhotsk Sea                | 105        |
| <i>P. fragilis</i> Kussakin, 1965                                   | Okhotsk Sea                | 32-327     |
| <i>P. globiceps</i> Meinert, 1890                                   | N. Atlantic                | 34-1300    |
| <i>P. intermedia</i> (Hult, 1936)                                   | Norway                     | 30-2258    |
| <i>P. kamtschatica</i> Kussakin, 1965                               | Okhotsk Sea                | 87-220     |
| <b><i>Pseudergella</i> gen. nov. (4 species)</b>                    |                            |            |
| <i>P. atypicum</i> Schiecke & Fresi, 1969                           | Mediterranean              | 80         |
| <i>P. bispinosus</i> Chardy, 1974                                   | Westl. Mediterranean       | 2827       |
| <i>P. hessleri</i> Just, 1980                                       | N. Polar Sea               | 800-3620   |
| <i>P. ischnomesoides</i> Hessler, 1970                              | N. Atlantic                | 1150-4833  |
| <b><i>Pseudomesus</i> Hansen, 1916 (4 species)</b>                  |                            |            |
| <i>P. brevicornis</i> Hansen, 1916                                  | Iceland                    | 80-2105    |
| <i>P. pitombo</i> Brix & Kaiser, submitted                          | Angola Basin               | 5415-5387  |
| <i>P. satanus</i> sp. nov.  | Australia                  | 1277       |
| <i>P. similis</i> Birstein, 1963                                    | N. W. Pacific              | 5441       |

### 3. Results

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***Rapaniscus* Siebenhaller & Hessler, 1981 (5 species)**

|   |                          |           |
|---|--------------------------|-----------|
| <i>R. crassipes</i> Hansen, 1916                | N. Norway, N.W. Atlantic | 219-2754  |
| <i>R. dewdneyi</i> Siebenhaller & Hessler, 1981 | N.W. Atlantic            | 1501-1693 |
| <i>R. multisetosus</i> Brandt, 2002             | Angola- Basin            | 5389-5415 |
| <i>R. coalescus</i> (Menzies & George, 1972)    | Peru- Chile- Trench      | 4823-4925 |
| <i>R. sp. nov. A</i>                            | Weddell Sea              | 5400      |

***Reductosoma* Brandt, 1992 (monotypic)**

|                                |            |      |
|--------------------------------|------------|------|
| <i>R. gunnera</i> Brandt, 1992 | Antarctica | 3981 |
|--------------------------------|------------|------|

***Regabellator* Siebenhaller & Hessler, 1981 (3 species)**

|   |                 |           |
|---|-----------------|-----------|
| <i>R. abyssi</i> Brandt 2002                    | Angola- Basin   | 5389-5415 |
| <i>R. armatus</i> Hansen, 1916                  | S. Davis Strait | 3521      |
| <i>R. profugus</i> Siebenhaller & Hessler, 1981 | S.E. Atlantic   | 1964-2031 |

***Saetoniscus* Brandt 2002 (monotypic)**

|                               |              |      |
|-------------------------------|--------------|------|
| <i>S. meteori</i> Brandt 2002 | Angola Basin | 5389 |
|-------------------------------|--------------|------|

***Thaumastosoma* Hessler, 1970 (4 species)**

|                                     |               |           |
|-------------------------------------|---------------|-----------|
| <i>T. distinctum</i> Birstein, 1963 | N.W. Pacific  | 5680-5690 |
| <i>T. jebamoni</i> George, 2001     | N.W. Atlantic | 5325      |
| <i>T. platycarpus</i> Hessler, 1970 | N. Atlantic   | 2886-3753 |
| <i>T. tenue</i> Hessler, 1970       | N. Atlantic   | 2886-3753 |

***Torwolia* Hessler, 1970 (3 species)**

|                                     |                            |           |
|-------------------------------------|----------------------------|-----------|
| <i>T. creper</i> Hessler, 1970      | Atlantic                   | 3753-5100 |
| <i>T. subchelatus</i> Hessler, 1970 | N. Atlantic                | 2000-5100 |
| <i>T. tinbienae</i> sp. nov.        | S. Atlantic (Angola Basin) | 5126-5415 |

***Whoia* Hessler, 1970 (4 species)**

|  |                     |           |
|--|---------------------|-----------|
| <i>W. angusta</i> (Sars, 1899)           | Skagerrak           | 50-2500   |
| <i>W. dumbshafensis</i> Svavarsson, 1988 | Northern Sea        | 1279-2024 |
| <i>W. variabilis</i> Hessler, 1970       | N. Atlantic         | 3753-4892 |
| <i>W. victoriensis</i> sp. nov.          | Australia, Victoria | 1277-1119 |

**genus *incertae sedis***

|   |            |      |
|---|------------|------|
| gen. <i>incertae sedis canaliculatus</i> Mezhev, 1986 | N. Pacific | 1190 |
|---|------------|------|

#### 3.1 Taxonomy

##### 3.1.1 Systematic overview

Order Isopoda Latreille, 1817 (11 suborders)

Suborder Asellota Latreille, 1803 (4 superfamilies, 27 families)

Superfamily Janiroidea Sars, 1897 (21 families)

Family Desmosomatidae Sars, 1897

Subfamily Austroniscinae subfam. nov.

Desmosomatinae Hessler, 1970

Eugerdellatinae Hessler, 1970

Nannoniscinae (Hansen, 1916)<sup>1</sup>

Pseudomesinae (Hansen, 1916)

Macrostylidae Hansen, 1916

Munnopsididae Lilljeborg, 1866

##### 3.1.2 Groundpattern of Janiroidea (modified after Ax 1999; Gruner 1965; Hessler, Wilson & Thistle 1979; Wilson 1987 and Wägele 1989)<sup>2</sup>

Body broad and flattened, pereonites of same height, secondarily variable, slender and elongated. Cephalothorax with eyes dorsolaterally. Antennula primarily with peduncle of 3 articles and flagellum of 4 articles; flagellum shortened. Antenna with six peduncular articles, article 3 with rudimentary exopodite; flagellum long with numerous articles. Mouthparts formed for biting. Originally with 7 free pereonites. Anterior 3 pereonites shorter than following 4 pereonites. Usually 2 short pleonites visible. Remaining pleonites fused to pleotelson. Anus and uropods terminal. Pereopod I originally propodosubchelate, secondarily carposubchelate or slender; carpus elongated, not triangular, anticipating in forming the subchela. Coxa present at all pereopods, not produced, coxal plates absent. Dactylus slender, secondarily elongated with two terminal claws. Pleopods not used for swimming, pleopods 1 and 2 sexually dimorphic. In female pleopod 1 missing, pleopods 2 fused forming the operculum. In male pleopods 1 fused building sexual organ together with pleopod 2.

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<sup>1</sup> The subfamilies Conusinae, Leutzinae and Nannoniscinae erected by George (2001) are not accepted in agreement with Kaiser (2005).

<sup>2</sup> The apomorphies for the groundpattern of Isopods are taken from Ax 1999 and Wägele 1989 as basis, the apomorphies of the Asellota from Wägele 1989 and the autapomorphies for the Janiroidea from Wägele 1989, Gruner 1965, Hessler, Wilson & Thistle 1979 as well as from Wilson 1987.

Pleopod 2 formed to *gonopodium*. *Gonopodium* bended, basal part medially upright. Pleopods 1 and 2 forming together the male operculum. Uropods styliform.

#### **3.1.3 Characters of Desmosomatidae referring to the groundpattern of Janiroidea**

For Desmosomatidae the most complex character is pereopod I, which was already used by Hansen (1916) to separate his two sections of the genus *Desmosoma*. Additional “classical” characters of Desmosomatidae according to previous authors (Sars 1897, Hansen 1916, Gurjanova 1946, Kussakin 1965, Hessler 1970, Svavarsson 1988a) are the mandibular palp, the uropodal exopod, pereonite 1, pereopod IV, the pleotelson, details of the sexual dimorphism and the face of the cephalon. The characters used for the phylogenetic analysis are discussed separately (chapter 4.2.2). In this chapter a general overview of the characters of Desmosomatidae is presented.

##### **3.1.3.1 Body**

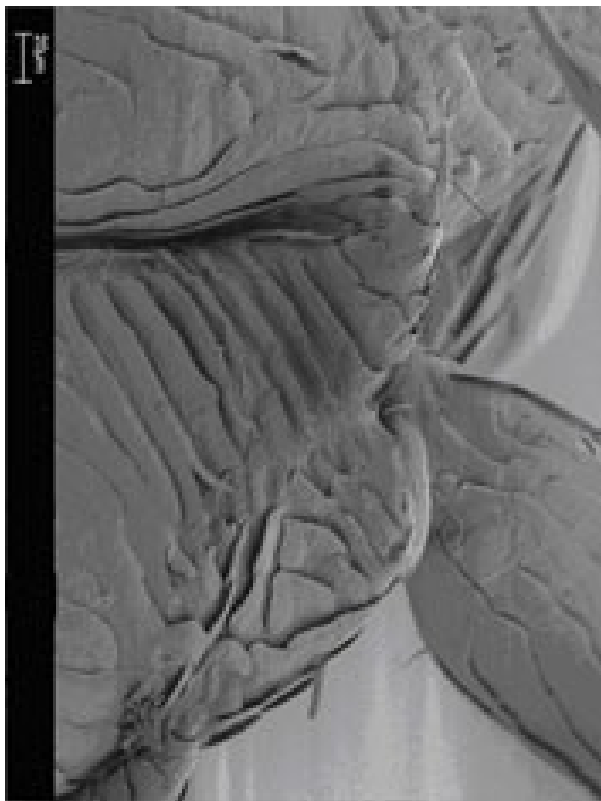
Wägele (1989) hypothesizes the oval body shape as the plesiomorphic body form. In regard to the fact, that the habitus is strongly correlated with the lifestyle, it is most possible, that habitus evolved convergently more than once in species living on similar environments. The body form of Desmosomatids is not oval. All species originally described in the family are clearly (over 3.5 times) longer than broad (Wägele 1989). This is the same in Macrostylidae. Exceptions are the genera of Austroniscinae subfam. nov. and some species of Nannoniscinae. In Desmosomatids usually pereonites 5-7 are more flattened than pereonites 1-4. Pereonites 1-4 are increasing in the flattening and therefore are decreasing in size, except for species of the genus *Austroniscus*. This is hypothesized for a “desmosomatid groundpattern” as an apomorphy of the family while pereonites 1-4 of Macrostylidae are more quadrangular and not flattening. In Munnopsididae one may see high diversity of the body shape, but the groundpattern is: pereonites 1-4 short and pereonites 5-7 enlarged, fused.

Desmosomatidae possess one free pleonite remaining between pereonite 7 and the pleotelson. In Austroniscinae and Nannoniscinae pereonite 7 and the remaining pleonite may be fused with the pleotelson. In Macrostylidae no free pleonite is visible

and seems to be fused with the pleotelson. In Munnopsididae the remaining pleonite may be fused into the pleotelson.

Cuticular structures like spines and sensory organs may be very specific. In most Isopods the dorsum is smooth and without ornamentation or structures (Wägele 1989). This may be a plesiomorphy in Isopods. Sensory organs indicate the presence of a female by chemoreceptory use. Thus, the variability of structures may be explained by having evolved independently. On the other hand, it is probable, that most drawings of species descriptions are not detailed enough to present such structures, which are only clearly visible on SEM pictures.

In Austroniscinae and Nannoniscinae exists lateral spines frontally directed at pereonites 1-4, which were regarded as an autapomorphy of Nannoniscidae (Wägele 1989). For Desmosomatidae no special cuticular structures were known. Some new species from the ANDEEP expeditions possess cuticular structures.



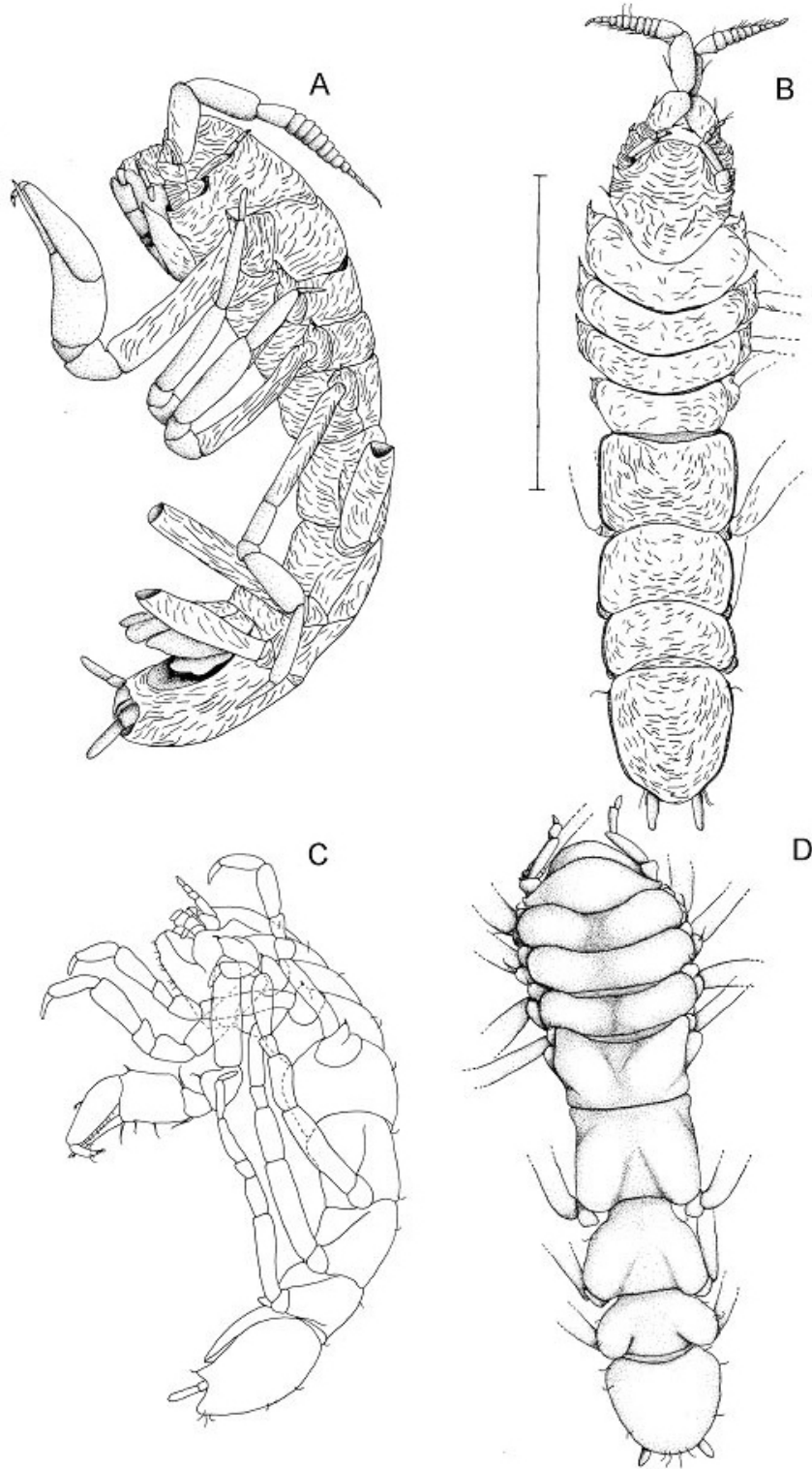
**Fig. 19:** SEM picture of *Chelator* sp. nov. A, male. Cuticular folds on pereonite 4 and pereopod IV (coxa, part of basis).



**Fig. 20:** SEM picture of *Eugerdella serrata* sp. nov., male. Part of dorsal surface of pleotelson.

The male individuals of *Chelator* sp. nov. A have deep cuticular folds (Fig. 19, 21) on the whole body including the bases of the pereonites and some parts of the pleopods. Males of *Eugerdella serrata* sp. nov. (chapter 3.1.5.2) possess an

ornamentation of triangular form (Fig. 20), the single triangles formed by the formation of small denticles (for definition see Garm 2004). These cuticular structures may be a sexual dimorphism, female individuals of these species possess no comparable structures or in initial stages only.



**Fig. 21:** *Chelator* sp. nov. A, habitus lateral (A) male (C) female, habitus dorsal (B) male (D) female, scale = 1 mm

#### **3.1.3.2 Anus**

The plesiomorphic position of the anus in the Janiroidea is ventral under the caudal tip/posterior margin of the pleotelson in a fold (Wägele 1989). This position of the anus is found in Desmosomatidae and the closely related families. The anus is not covered by the pleopods and is positioned external to the pleopodal cavity (Wilson 1987).

#### **3.1.3.3 Sexual dimorphism**

The sexual dimorphism can be regarded as plesiomorphic character of Janiroidea like for all other Isopoda (Wägele 1989). There is the marsupium and the position of the sexual openings in female near the coxae of the fifth pereopod. The position of the cuticular organ opening is distinctly associated with the opening of the oviduct or is located on the surface of the pereonite 5 (Wilson 1987). Wilson (1987) prefers the condition seen in *Asellus* as plesiomorphic state of the cuticular organ, because the dorsal cuticular organ of the Janiroidea has not been reported for Isopods outside of the Asellota.

The male pleopod 1 throughout the Janiroidea is similar: paired, uniramous and typically small limbs (Wilson 1987). Wilson (1987) describes the medial fusion of the male first pleopods and a cuticular tube for sperm conduction on the line of fusion as an apomorphy of the Janiroidea. Like all Janiroidea Desmosomatidae and Macrostylidae have the proximal end of the tube fused into a funnel, into which the penis fits. Its distal end opens on the dorsal side of the fused pleopods above the distal article of the endopod of pleopod 2. All other Asellota have unfused distal rami of the first pleopods (Wilson 1987).

Variations in the copulatory organs may be specific for a species. Often the copulatory organs have not always been described in detail. For example the position and number of the female oostegites may vary in different genera (Wägele 1989). There are neither variations known in Desmosomatidae nor in Macrostylidae. The female operculum is a single shield-like structure, which evolved out of a fusion of the female pleopods 2 (Wilson 1987).

Hessler (1970) bases his classification of Desmosomatidae as far as possible on adult females. In his opinion the degree of sexual dimorphism and the way it is expressed in males is significant in Desmosomatidae, but the use of these characters is limited because of the rarity of mature males. The cuticular structures expressed in



males of *Chelator antarctica* sp. nov. (fig. 8) and *Eugerdella serrata* sp. nov. (fig. 9) may be apomorphies containing useful phylogenetic information, but also the use of this character is limited, because not for all described species comparable males are known.

#### **3.1.3.4 Cephalic rostrum**

A cuticular projection on the cephalic frons between the antennulae, which is sometimes prominent is not known for the asellotan groundpattern, but occurs in the Janiroidea; thus it is regarded as apomorphy in the Janiroidea (Wilson 1987). Some nannoniscid taxa (for example species of the genus *Exciliniscus*) possess a rostrum. In Desmosomatidae some species (*Eugerdella pugilator* Hessler, 1970 and *Eugerdella serrata* sp. nov.) possess cephalic spines resembling a rostral structure. The nannoniscid rostrum and these cephalic spines are discussed in detail in chapter 4.2.2.2.

#### **3.1.3.5 Eyes**

In the Janiroidea eyes are located dorsolaterally on the cephalothorax (head) like in all Isopods except for the Chaetiliidae (*Glyptonotus*). About the size in the groundpattern nothing can be said; reductions of the eyes are a very common process for deep-sea taxa (Wägele 1989, Raupach *et. al.* 2004). In all desmosomatid species eyes are absent as well in Macrostylidae. According to Raupach *et. al.* (2004) Desmosomatidae belong to the clade of “munropsid radiation” and the reduction of eyes is regarded as a synapomorphy in this monophylum.

#### **3.1.3.6 Antennula**

In the groundpattern of Isopoda there exists a pair of antennulae, which does not have a character of a biramous pereopod. This is a very big difference to the antenna, which evolved out of a biramous appendage. In Malacostraca the antennula bears the following plesiomorphic characters: 3 peduncular articles and 3 flagella. The groundpattern of Isopoda shows 1 long flagellum. Reductions of the flagellar articles occur very often and it is very difficult to find homologies (Wägele 1989).

The antennula of Desmosomatidae consists out of 2 peduncular articles and a flagellum consisting of 3 or 4 articles. Peduncular article 2 is clearly longer than the peduncular article 1, which is described as autapomorphy of the family by Wägele

(1989). Notable is the position of broom setae on the distal end of the elongated peduncular article 2. According to Wägele (1989) 2 big broom setae inserting in opposite to each other are an autapomorphy of Desmosomatidae. 3 or 4 broom setae is regarded as a plesiomorphic character state according to Wägele (1989). However, most desmosomatid species own more than these 2 big broom setae on the distal end of peduncular article 2, which vary in size.

The flagellum is basally thicker than at its tip. In Nannoniscinae the peduncular articles bear very characteristic spines, which have a special function holding the following bulbous article (for a detailed discussion see chapter 4.2.2.2).

#### **3.1.3.7 Antenna**

This appendage evolved out of a biramous appendage of the early Malacostraca and the first 3 peduncular articles can be homologised as praecoxa, coxa and basis. In Asellota sometimes an exopodite is present at peduncular article 3. Praecoxa, coxa and basis and additionally the following three articles of the endopodite are named “peduncular articles”, because they do not belong to the flagellum. The antenna in the groundpattern bears 6 peduncular articles and a long flagellum consisting of numerous articles. Spines are described at the peduncular articles as specific variations by Wägele (1989). Some desmosomatid species have spines on the peduncular articles.

#### **3.1.3.8 Mandible**

The mandible contains a palp of 3 articles and an endite with pars incisiva, lacinia mobilis, a setal row and pars molaris in the plesiomorphic condition. They are somehow asymmetric and the laciniae and incisivae are variable in size and form. Macrostylidae and Desmosomatidae possess a triangular pars molaris without grinding plate, which is considered to be a synapomorphy of this group (Wägele 1989).

The incisivae usually are composed of three to five strong teeth. The mandibular palp may be reduced and is missing totally in some genera of Desmosomatidae, in Macrostylidae (Wägele 1989) and also in some species of Munnopsididae (*Acanthocope*, some Ilyarachninae).

According to Hessler (1970) the position and structure of the desmosomatid mandibular palp suggests, that it does not function for feeding, but may serve to

groom the face and the base of the antenna. Usually the palp of Desmosomatidae is composed of three articles, the terminal one fringed by several setae. It arises from the base of the mandible and extends dorsally along the face medial to the insertion of the antenna.

Hessler (1970) describes varying stages of reduction: for example *Prochelator lateralis* (Sars, 1899) or *Paradesmosoma conforme* Kussakin, 1965 show the earliest “stage”<sup>3</sup> of reduction; article 3 is weakly developed and bears only one or two distal setae. In more advanced reduction the third article is completely missing like in *Paradesmosoma australis* sp. nov. (chapter 3.1.5.3.4). The palp may be completely absent. A palp of only one article is not known.

Macrostylidae bear no mandibular palp. The absence of it is considered as an autapomorphy of the family by Wägele (1989). Following Hessler (1970) the presence or absence of the mandibular palp is a doubtful character on generic level. The presence or absence of the mandibular palp might be used as a diagnostic character, but is only of phylogenetic use, if the monophyly of the group is clearly defined by other phylogenetic informative characters.

The absence of the palp is a reduction character, which evolved convergently in different species, in different genera. Hessler (1970) concluded, viewing the family as a whole, that the palp must have been lost more than once and is a condition, which may separate closely related species only. For example only two of the species included in *Mirabilicoxa* by Hessler (1970) bear a palp (*M. longispina* (Hansen, 1916) and *M. palpata* Hessler, 1970).

#### **3.1.3.9 Maxillae**

According to Scheloske (1977) maxilla 1 has two basal sklerites and two endites (lobes), a palp is missing. The lateral lobe is longer than the medial one and possesses apically robust tipped setae, which are inserting broad and immovable. The setae of the medial lobe are more slender and more movable than those of the lateral lobe. The robust setae on the medial endite may be fused basally with the lobe, so that they become teeth (Wägele 1989). In Desmosomatidae the number is often reduced to three.

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<sup>3</sup> It is not possible to speak here of „stages“ of reduction. The species possessing the reductions are not so closely related to each other, that a „line of reduction“ can be hypothesized.

The desmosomatid maxilla 1 shows the plesiomorphic state of a longer lateral lobe and a shorter medial one. The lateral lobe bears distally 11 strong teeth standing in three rows, which may be fringed by several small simple setae. The number of 11 is consistent in Desmosomatidae, a conservative condition, for example also found in Munnopsididae. Characteristic are the rows of long simple seta inserting as pairs or groups of three on the upper and lower margin of the lateral lobe. The medial lobe may be extremely setose or contrary bear few setae only. Rows of long setae may also be found on the upper and lower margin of the medial lobe. No seta of the medial lobe is strong enough to be defined as tooth.

Maxilla 2 consists of a sympodite with 1 medial endite (lobe), which is not movable and 2 outer endites (lobes), which are movable independently. Distally the lobes bear many robust setae. The medial setal row on the lower side of the medial endite is rarely not developed, but is given here as a plesiomorphy of the Janiroidea (Wägele 1989). In Desmosomatidae the two outer lobes are similar to each other and bear 3 or 4 robust setae distally, which may be additionally described by structures like setules. The medial lobe is always broader and slightly shorter than the 2 outer lobes bearing the same number of robust setae distally as the outer lobes. A special condition is found in *Thaumastosoma* (chapter 4.2.1.3.11).

#### **3.1.3.10 Maxilliped**

The desmosomatid maxilliped is constructed in the same way as it is presented for the groundpattern of Janiroidea. The number of retinaculae on the endite varies between 2 and 4, also depending of the molting stage. The coxa is small, a strong basis (basipodite) carries mediodistally an endite with retinaculae; basally inserts an epipodite (scale), distally a palp out of 5 articles. The epipodite is of similar size as the basipodite and lies laterally of the basipodite. It covers the basal parts of the mouthparts (Wägele 1989).

Special adaptations are known with regard to the number of palp articles or form. Of the palpus of the Janiroidea the articles 2 and 3 are broadest, the distal articles are smallest. The palp is slightly longer than the basipodite. The setae of the maxilliped are mostly smooth, the endite setae are serrated or plumose (Wägele 1989).

#### **3.1.3.11 Face of cephalon**

Hessler (1970) described the features of the head. In most Desmosomatinae the surface of frons, clypeus and labrum forms a smooth curve in lateral view. In most Eugerdellatinae the frons is developed into a pronounced transverse ridge towards the anterior end. Between this ridge and the base of the clypeus the frons bends downwards. Thus frons and clypeus meet at the base of the transverse furrow. The slope of the clypeus is often straight, and may even be horizontal; the labrum bent straight downward to a vertical orientation. The result of these modifications is a flattened appearance of the face. These features vary between the species: the frons-clypeal furrow may be modestly present or neither furrow nor ridge is developed. Hessler (1970) noted, that these features may be useful for generic determination, but presented no details in the diagnosis of the genera or in his species descriptions.

#### **3.1.3.12 Coxae**

Proximally the pereopods bear a circular coxal plate, which is almost immovable and bears the female oostegites ventrally. Such coxae are the plesiomorphic condition (Wägele 1989). Desmosomatids have well developed coxae, which may produce anteriorly directed elongations tipped by setae, but no coxal plates. These elongations are very characteristic for some species like *Mirabilicoxa exopodata* Hessler, 1970. Their size depends on sex: in males the elongations are longer and more robust than in females.

#### **3.1.3.13 Pereonites**

Ventral elongation (spines) at the pereonites occur in Macrostylidae, Nannoniscidae and Desmosomatidae. In *Macrostylis longispinis* Brandt, 2004 ventral elongations occur on pereonite 6 and 7, *Macrostylis abyssalis* Brandt, 2004 on pereonites 5 and 6, *Macrostylis longipedis* Brandt, 2004 on the female operculum (may be not regarded as the same as a ventral elongation of the pereonites). The genus *Desmostylis* is without any ventral elongation at the pereonites.

In Nannoniscidae a spine on the female operculum is known (*Thaumastosoma*, *Rapaniscus*). Desmosomatids bear ventral elongations on the pereonites 1 to 5 (*Prochelator lateralis* (Sars, 1899) on 1 to 4, *Disparella kensleyi* sp. nov. on 5,

*Eugerdella serrata* sp. nov. on 1 to 5 (fig. 10) as well as *Eugerdella pugillator* Hessler, 1970).



**Fig. 22:** SEM picture *Eugerdella serrata* sp. nov., female. Ventral elongation at pereonite 3.

In some taxa in Munnopsididae comparable ventral elongations exist (*Acanthocope*, Storthyngurinae. Wägele (1989) considered the family Munnopsididae as next outgroup to the group of the families Macrostylidae, Desmosomatidae and Nannoniscidae. Using morphological characters the monophyly of this cluster is very probable (Brandt 2002a) although the phylogenetic relationships in the single families need further discussion (chapter 4.1.1). Ventral elongations are presented as a synapomorphy of Macrostylidae, Desmosomatidae and Nannoniscidae by Wägele (1989) differentiating this group from

Munnopsididae. Although such an ancestor is possible regarding these arguments, in this study an ancestor is hypothesized possessing any ventral elongation. Instead, the spine-like ventral elongations at the different pereonites may have evolved convergently. This is discussed in detail in the discussion of the characters used for phylogenetic analysis (chapter 4.2.2.2).

#### 3.1.3.14 Pereopods

The pereopods tend to taper towards the tip; the muscles are concentrated into two opposing bundles; the bulkiest muscles controlling the movement of the limb are located in the body, not in the limb (Hessler 1982). Thus, the mass of the limb is minimized and following the energy needed for movement. While the ability to walk is the plesiomorphic method of locomotion in the deep sea, there exists a wide range of families, some of which are both benthic and accomplished swimmers (Munnopsididae), while others like Desmosomatidae display an intermediate condition (Hessler 1982).

Similarity may result from phylogenetic relationships or functional necessity (convergent evolution). Pereopods are extremely important for desmosomatid generic taxonomy (Malyutina & Kussakin 1996). For Macrostylidae it is not obvious to conclude a swimming ability with regard to the morphologies of the anterior pereopods. In contrast to Desmosomatidae no natatory setae occur on carpus and propodus of the pereopods V to VII although long setae on the basis are present (Brandt 2004).

Desmosomatidae walk on the soft bottom or burrow anteriorly by means of pushing sediment aside with their anterior pereopods (Hult 1941, Hessler 1982, Hessler & Strömberg, 1989). In Desmosomatids the anterior pereopods are used as paddles: on the power stroke the coefficient of friction and the rotational distance through which the limb travels must be large, while on the recovery stroke they should be as small as possible to minimize their breaking effect (Hessler 1982). Desmosomatids are able to swim backwards. The backward stroke is swimming backwards using the last three pairs of pereopods. Marginal swimming setae are positioned on the margins of propodus and carpus in such a manner, that they can automatically fold down during the recovery stroke. All the skeletomuscular modifications are the reverse to those of animals swimming forwards: the corresponding pereonites are somewhat enlarged to accommodate the greater bulk of extrinsic muscles (Hessler 1982).

Therefore, the ability to swim must be very well in species of *Torwolia* and *Eugerdia*: these animals possess anterior pereopods with strong musculature, remarkably stronger and longer than the posterior pereopods (see chapters 4.2.1.2.4 and 4.2.1.2.8).

#### **3.1.3.14.1 Pereopod I**

The first pereopod consists of coxa, basis and the five articles of the endopodite: ischium, merus, carpus, propodus and dactylus. The first pereopod is hypothesized to be propodosubchelate in the groundpattern (Wägele 1989). In the Janiroidea the first pereopod resembles the more posterior walking limbs - a condition one would expect to be a plesiomorphic state, although similarities in non-asellota indicate that a first pereopod with grasping capability between the dactylus and the propodus is the plesiomorphic state and the walking form with grasping between the propodus and

the dactylus is the more derived state, opposing surfaces between the propodus and the dactylus allowing free articulation and large movement (Wilson 1987).

According to Wägele (1989) shape and setation are variable. Unusual is the presence of setae on the lower margin of the propodus. A slender first pereopod (Fig. 23) is regarded as apomorphic character (secondarily evolved). Some desmosomatid species (genus *Torwolia*) revert to grasping with the dactylus and the propodus (fig.13), the elongated propodus indicates a former walking condition of the limb (Wilson 1987). Elongation of the carpus is present in the Janiroidea. In most janiroid families the first pereopod is primarily carposubchelate. This character may be reduced secondarily to a slender first pereopod with a cylindrical carpus (Wägele 1989). Following previous authors, especially Kussakin (1965) and Hessler 1970) the most conspicuous differences between species of Desmosomatidae occur in the structure of the first pereopod. Five types can be defined for the morphology of this limb:

1. slender (Fig. 23): ischium, carpus and propodus elongated. Nearly devoid of setae, if setae present feebly developed

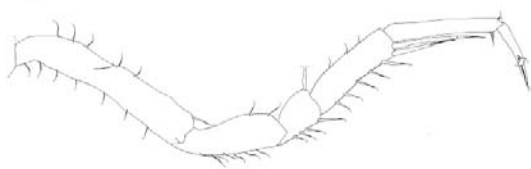


Fig. 23: Pereopod I of *Echinopleura cephalomagna* sp. nov. showing a slender condition with an elongation of the propodus.

2. chelate (Fig. 24): well-built large carpus bears one major seta, which forms a claw together with the propodus. The propodus tapers distally and the much smaller dactylus forms the movable claw



Fig. 24: Pereopod I of *Prochelator maorii* sp. nov. showing the typical carpo-euchela, a derived specialization of this limb.



3. subchelate (Fig. 25): the dactylus folds in opposite to the much enlarged propodus

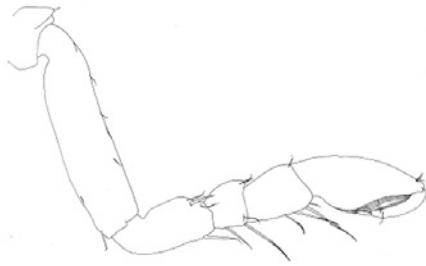


Fig. 25: Pereopod I of *Torwolia tinbinae* sp. nov. showing a subchelate condition that must have secondarily evolved. Thus, the subchela is a derived specialization.

4. robust (Fig 26, 27): the whole limb is enlarged, the carpus is massively built and carries a ventral row of long stout setae in a condition neither chelate nor subchelate, but intermediate



Fig. 26: Pereopod I of *Eugerdella serrata* sp. nov. showing the derived specialization of a robust limb.



Fig. 27: Pereopod I of *Whoia victorialis* sp. nov. showing a robust condition without further specialization.

5. not specialized (Fig. 28): the first pereopod is similar in size and form to the second and third pereopod

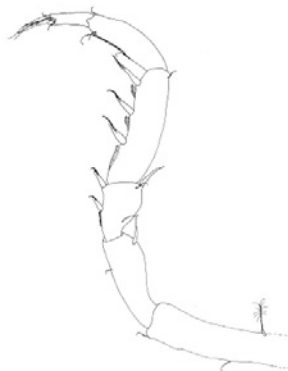


Fig. 28: Pereopod I of *Pseudomesus satanus* sp. nov. without further specialization and the typical composed robust setae ventrally on the carpus.

In Hessler's (1970) opinion the general relationship among all these types is well documented by a series of intermediate types, except for the condition found in *Torwolia*. He thought, that the condition shown in *Balbidocolon atlanticum* Hessler, 1970 (transferred to *Mirabilicoxa* in this study, chapter 4.2.1.2.1) is most primitive. His argumentation is typological, but may have true elements with regard to Wägele's (1989) arguments of the asellotan groundpattern. In fact, the plesiomorphic state of the pereopods should be, that they are similar to each other, any difference and specialization can be regarded as autapomorphy.

The main argument is that the characters of the first pereopod are the most sensitive indicators of phylogenetic relationships found in Desmosomatidae (Hessler 1970; Kussakin 1965). Although his arguments are valuable, the division of the subfamilies is typological (small PI – large PI).

The setation is different in Macrostylidae. While Desmosomatidae possess the synapomorphic rows of setae (fig. 15) according to Wägele (1989), Macrostylidae possess robust setae on propodus and carpus, but not standing in a row. Their setae are placed at the lower or dorsal margin of the articles, the distances between them are irregular. A row is defined here as 3 or more setae inserting in regular distances to each other. If the distances between the robust setae are not regular, the setae are not standing in a row.

#### **3.1.3.14.2 Pereopods II and III**

These pereopods are slender in nearly all asellota. The carpus is short and from lateral view it looks trapezoidal and triangular. Like pereopod I the specific variations of the setation can characterise single taxa. In Desmosomatidae the setae on the propodus of pereopod II are reduced (Wägele 1989). Pereopods II and III are more conservative than pereopod I, even with a high specialized pereopod I pereopod II still bears the row of ventral and dorsal setae given as synapomorphy of the family.

#### **3.1.3.14.3 Pereopods IV to VII**

In contrast to pereopods II and III the carpus of pereopods IV to VII is usually long and cylindrical (Wägele 1989). In Desmosomatidae pereopod IV resembles more pereopod II and III than pereopods V to VII. In Macrostylidae pereopod IV is shortest. In *Desmostylis* the limb is actually tapering towards the dactylus (Brandt 2004). In Nannoniscidae the posterior pereopods are in most species as slender as the anterior ones and used for walking.

Hessler (1970) mentions the morphology of pereopod IV as “unusual” only in *Paradesmosoma*. In the species of this genus the fourth limb is resembling a paddle: propodus and carpus are folios and broadened. The type of setae surrounding the margins of propodus and dactylus occur not only on pereopod IV, as well on pereopods I to III, but their occurrence seems to be restricted on species of *Paradesmosoma*.

The “swimming setae” mentioned by Brandt (2004) at the basis of pereopod VII in Macrostylidae are not occurring in Desmosomatidae. Macrostylidae possess on propodus and carpus of this limb only robust setae while in Desmosomatidae rows of ventral and dorsal swimming setae are present (see above).

#### **3.1.3.15 Pleopods**

In the groundpattern the general shape of the five pairs of pleopods are very similar. The “rami” are longer than wide and folious in the plesiomorphic state. Exo- and endopodite are of similar size. The articles of the exopodite are fused. The pleopods are used for respiration and are protected in the breathing chamber, which is covered by the operculum. In the Janiroidea the exopodite of pleopods 3 to 5 is much smaller than the endopodite. Variations in size and shape of the pleopods may be due to function (Wägele 1989).

The sympodites of the first pleopods are basally fused in males, those of the second pleopods in females. The sexual dimorphism of the pleopods (see above) is similar in Desmosomatidae. Primarily, all pleopods bear swimming setae, which may be secondarily reduced. The constant number of three setae at the endopod of pleopod 3 in most families of the Janiroidea is interesting. The exopodite bears no setae in most species (Wilson 1987). In these families a variation of the setation may be regarded apomorphic (Wägele 1989).

In Desmosomatidae pleopod 3 is conservative in form and shape of the endopodite, but varies in form and setation of the reduced exopodite. The exopodite may bear a plumose seta and additionally numerous small setae, a single seta or may be fringed with fine hairs. The same aspects are to discuss for pleopod 4. As pleopod 3 it is conservative in form and shape of the endopodite, but may vary in the exopodite. Some species completely lost the exopodite. This often correlates with a total loss of pleopod 5, which is reduced in all desmosomatid species as well as in Nannoniscidae and Macrostylidae.

#### **3.1.3.16 Uropods**

In Asellota, the uropods primarily are inserting laterally at the terminal margin of the pleotelson. Originally, the sympodite is shorter than the “rami”, secondarily the sympodite may be elongated, reduced or totally absent. Uniramous and elongated uropods are known for Macrostylidae. Position and form of the uropods are very

characteristic and usually differ from the groundpattern, so there may be good synapomorphies (Wägele 1989).

In Desmosomatidae, the uropods are biramous in the plesiomorphic condition; the exopod is reduced and may be completely absent in half of the species described. If the exopod is well possessed it is usually nearly as large as the endopod and clearly articulated with the protopod. In Hessler's (1970) opinion, the species possessing a reduced exopod indicate how this structure might have got lost. The loss of the exopod cannot be regarded as transformation series, because the species with a reduced exopod are not related in a monophylum. The description of different „stages of reduction“ is at most possibly a description of different steps of convergent evolution. The phylogenetic information of these reductions is questioned, but the reduction may serve well as diagnostic characters. In Desmosomatidae the uropodal exopod does never reach the full length of the endopod. Like the mandibular palp the uropodal exopod must have disappeared more than once. The presence or absence of the exopod varies also in a single species and is therefore a weak character – e.g. *Mirabilicoxa exopodata* (Hessler 1970).

#### **3.1.3.17 Pleotelson**

The flattened and tongue-formed pleotelson, which is not or slightly concave ventrally is a plesiomorphy. Variations of this shape are regarded as apomorphies (Wägele 1989). The distal part of the (pleo)telson is reduced in Asellota; it is concave ventrally to allow space and protection of the pleopods. In Macrostylidae the statocysts in the pleotelson are an apomorphy. Also fusions of the pleonites are apomorphies (Wägele 1989). Hessler (1970) is the first author who used the morphology of the pleotelson as a character in defining desmosomatid genera, especially the presence or absence of posterolateral spines.

#### **3.1.4 Diagnoses**

##### **3.1.4.1 Desmosomatidae Sars, 1897**

Synonyms: Desmosomidae Sars 1899: 118; Menzies 1962: 162; Desmosomatini Hansen 1916: 105-106; Nordenstamm 1933: 254; Hult 1936: 1-2; Vanhöffen 1914; Desmosomatidae Gurjanova 1932: 57, 1946; Birstein 1963: 89; Kussakin 1965: 117-118; Kussakin 1999: 121-336; Hessler 1970: 20; Svavarsson 1984: 42-43, Mezhev 1986: 186; Svavarsson 1984: 37-44; Svavarsson 1988: 3-4; Wägele 1989; Malyutina

### 3. Results

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& Kussakin 1996; George 2001; Nannoniscini Hansen 1916: 83; Gurjanova 1932: 50; 1933: 413; Nordenstamm 1933: 251, Menzies 1962: 133; Wolff 1962: 31; Menzies & George 1972: 95; Nannoniscidae Siebenhaller & Hessler 1977: 17-43, 1981: 227-249; Kussakin 1999: 28-117; Pseudomesini Hansen 1916; Gurjanova 1946, Pseudomesidae Chardy 1974: 409-420 Svavarsson 1984: 37-44

Type genus: *Desmosoma* Sars, 1864

Composition:

Austroniscinae subfam. nov.

Type genus: *Austroniscus* Vanhöffen, 1914

Composition: *Austroniscus* Vanhöffen, 1914; *Nannoniscoides* Hansen, 1916

Desmosomatinae Hessler, 1970

Type genus: *Desmosoma* Sars, 1864

Composition: *Desmosoma* Sars, 1864; *Echinopleura* Sars, 1897; *Eugerdella* Meinert, 1890; *Mirabilicoxa* Hessler, 1970; *Momedossa* Hessler, 1970; *Pseudogerdella* Kussakin, 1965; *Torwolia* Hessler, 1970

Eugerdellatinae Hessler, 1970

Type genus: *Eugerdella* Kussakin, 1965

Composition: *Chelator* Hessler, 1970; *Cryodesma* Svavarsson, 1988; *Disparella* Hessler, 1970; *Eugerdella* Kussakin, 1965; *Oecidiobranchus* Hessler, 1970; *Paradesmosoma* Kussakin, 1965; *Prochelator* Hessler, 1970; *Reductosoma* Brandt, 1992; *Thaumastosoma* Hessler, 1970; *Whoia* Hessler, 1970

Nannoniscinae (Hansen, 1916)

Type genus: *Nannoniscus* Sars, 1870

Composition: *Exilinisca* Siebenhaller & Hessler 1981; *Hebefustis* Siebenhaller & Hessler 1977; *Micromesus* Birstein, 1963; *Nannonisconus* Schultz, 1966; *Nannoniscus* Sars, 1870; genus novum; *Panetela* Siebenhaller & Hessler 1981; *Rapaniscus* Siebenhaller & Hessler 1981; *Saetoniscus* Brandt, 2002b

Pseudomesinae (Hansen, 1916)

Type genus: *Pseudomesus* Hansen, 1916

Composition: *Pseudergella* gen. nov.; *Pseudomesus* Hansen, 1916

**Diagnosis of the family Desmosomatidae Sars, 1897** modified after Hansen (1916), Hessler (1970), Kussakin (1965), Sars (1864) and Siebenhaller & Hessler (1977, 1981):

Body slender, (broad and flattened in Austroniscinae and some species of *Nannoniscus*), ventral elongation of pereonites robust. Cephalothorax free. Antennula short, located dorsally, peduncle comprising 2 articles: article 2 elongated (about twice as long as article 1), distally with 3-4 articulated broom setae, last article with 1 terminal aesthetasc. Flagellum of antenna basally swollen in males and richly supplied with sensory setae. Antenna inserting dorsally, long (reaching more than one quarter of body length). Mandible with well-developed incisor, lacinia mobilis and strong row of saw bristles; molar process triangular, distally fringed with slender setae. Palp of maxilliped with second and third article of same general width as basis; fourth and fifth article much smaller. Pereonites 1-4 shorter than pereonites 5-7. Pereonites 5-7 more depressed than pereonites 1-4. Marginal flanges at pereonites 5-7 in male more conspicuously developed than in female. Pereopods I-IV directed anteriorly, usually fringed with strong, stout setae ventrally. Pereopod I diversely specialized. Pereopods V-VII directed posteriorly, similar to one another, carpus and propodus with long setae. Coxae of pereopods I-IV angular or anteriorly produced, in males more produced than in females. Uropods inserting ventrally; endopod well developed, consisting of a single article; exopod smaller or absent.

#### **3.1.4.2 Diagnoses of the subfamilies**

##### **3.1.4.2.1 Austroniscinae subfam. nov.**

Body broad and depressed (length about 2.5 times of width of pereonite 2), tergites laterally expanded into flat flanges. Flagellum of antennula with 5-7 articles. Lateral corners of tergites 1-4 anteriorly with small sensory spine. Anterior part of body as broad as pleotelson. Pereopod I carpus and propodus with composed setae, not lined-up in rows. All pereopods slender, posterior pereopods not modified for

swimming. Uropods biramous, protopod nearly quadrangular, exopod slightly smaller than endopod.

#### **3.1.4.2.2    *Desmosomatinae* Hessler, 1970**

Pereonite 1 not larger than pereonite 2. Coxae of pereopods I to IV anteriorly produced, with small stout seta. Pereopod I more slender than pereopod II, setal rows absent on propodus, propodus elongated (more than 3.5 times longer than wide). Pereopods II-IV with dorsal and ventral rows of setae on carpus and propodus. Pereopods V-VII modified for swimming.

#### **3.1.4.2.3    *Eugerdellatinae* Hessler, 1970**

Body anteriorly compact. Pereonite 1 (in midsagittal length) longer than pereonite 2. Coxae of pereopods I-IV anteriorly produced, with small stout seta. Pereopod I robust or enlarged, carpus and propodus specialized, acting as grasping structure, carpus with large composed setae ventrally. Pereopod II not enlarged, similar to pereopod III, with dorsal and ventral rows of setae on carpus and propodus. Pereopods V-VII modified for swimming.

#### **3.1.4.2.4    *Nannoniscinae* (Hansen, 1916)**

Corners of tergites of pereonites 1-4 tipped with small stout setae. Pereonites 5-7 not enlarged. Pereonites 6 and 7 often fused. Antennula with 5 articles, first flagellar article smallest article of flagellum, second flagellar article with elongation holding the distal article, distal article bulbous and ball-shaped. Carpus of pereopod I usually without rows of robust composed setae. Uropods inserting ventrally close to the anus and partly overlapping anus valves.

#### **3.1.4.2.5    *Pseudomesinae* (Hansen, 1916)**

Body elongated (5-6 times longer than width of pereonite 2). Pereonite 1 not as long as pereonite 2. Coxae of pereopods I to IV anteriorly produced, with small stout seta. Pereopod I carpus ventrally with minimum of 3 robust composed setae standing in a row, dorsal row of simple seta absent, propodus lacking rows of setae. Pereopods V-VII modified for swimming. Pleotelson enlarged, dorsally inflated. Uropods uniramous.

#### 3.1.4.3 Diagnoses of the genera

##### 3.1.4.3.1 *Austroniscus* Vanhöffen, 1914

Synonyms: *Austroniscus* Vanhöffen, 1914; *Nannoniscella* Hansen, 1916

Type species: *A. ovalis* (Vanhöffen, 1914)

Composition: *A. acutus* Birstein, 1970; *A. chelus* Kaiser, 2005; *A. coronatus* Schiecke & Modigh Tota, 1976; *A. groenlandicus* Hansen, 1916; *A. karamani* Birstein, 1962; *A. norbi* Svavarsson, 1982; *A. obscurus* Kaiser, 2005; *A. ovalis* (Vanhöffen, 1914); *A. rotundatus* Vanhöffen, 1914; *A. vinogradovi* Gurjanova, 1950

Diagnosis modified after Hansen 1916 and Siebenhaller & Hessler, 1981: Body broad and flattened (length about 2.5 times of width of pereonite 2). Cephalon with bilateral rostral-like structure. Lateral margins of pereonites expanding laterally into flat flanges. Tergites of pereonites 1-4 expanding anterolaterally. Pereopods slender. Posterior pereopods not modified for swimming. Pereopod I slightly shorter than pereopods II-IV. Pleotelson without posterolateral spines. Branchial chamber and operculum in relation to size of pleotelson small, operculum of oval shape and posterior part broadest. Uropods biramous, endopod and exopod of nearly similar length.

##### 3.1.4.3.2 *Chelator* Hessler, 1970

Synonyms: *Desmosoma* Sars, 1864: 11 (part); *Chelator* Hessler, 1970: 28

Type species: *C. insignis* (Hansen, 1916)

Composition: *C. brevicauda* (Menzies & George, 1972); *C. chelatum* (Stephensen, 1915); *C. insignis* (Hansen, 1916); *C. stellae* Malyutina & Kussakin, 1996; *C. striatus* (Menzies, 1962); *C. verecundus* Hessler, 1970; *C. vulgaris* Hessler, 1970; *C. sp. nov.*

A

Diagnosis: Body anteriorly compact, from pereonite 5 to pleotelson of similar height. Pereopod I enlarged, chelate, propodus and claw-seta forming chela, lower margin of carpus behind claw-seta with small setae, carpus anteriorly produced. Pleotelson in females without posterolateral spines, small spines may be present in males (sexual dimorphism).

##### 3.1.4.3.3 *Cryodesma* Svavarsson, 1988

Synonyms: *Balbidocolon* Hessler, 1970: 23 (part); *Cryodesma* Svavarsson, 1988: 25



Type species: *C. agnari* Svavarsson, 1988

Composition: *C. agnari* Svavarsson, 1988; *C. cryoabyssale* Malyutina & Kussakin, 1996; *C. polare* Malyutina & Kussakin, 1996

Diagnosis: Pereonite 1 longer than pereonite 2. Pereopod I more strongly developed than pereopod II, propodus broad with convex ventral margin without composed setae, carpus with ventral row of long composed setae increasing in length towards propodus, most distal seta as long as penultimate one. Uropods uniramous.

#### **3.1.4.3.4     *Desmosoma* Sars, 1864**

Synonyms: Sars 1864: 11, 1899: 127 (part); Bonnier 1886: 605; Hansen 1916: 106-120 (part); Guranova 1932: 57-63 (part); Nordenstamm 1933: 154-164 (part); Hult 1936: 1-11 (part); Menzies 1962: 165 (part); Birstein 1963: 89 (part); Kussakin 1965: 165; Hessler 1970: 24; Park 1999: 1061-1067

Type species: *D. lineare* Sars, 1864

Composition: *D. affine* Fresi & Schiecke, 1969; *D. australis* Nordenstamm, 1933; *D. brevipes* Nordenstamm, 1933; *D. dolosa* (Menzies & George, 1972); *D. elegans* Fresi & Schiecke, 1969; *D. elongatum* Bonnier, 1896; *D. gigantea* Park, 1999; *D. hesslera* Brandt, 1992; *D. imbricata* Hessler, 1970; *D. latipes* (Hansen, 1916); *D. lineare* Sars, 1864; *D. lobipes* Kussakin, 1965; *D. modestum* Nordenstamm, 1933; *D. ochotense* Kussakin, 1965; *D. pannosa* Hessler, 1970; *D. puritanum* Fresi & Schiecke, 1969; *D. renatae* sp. nov.; *D. stroembergi* Svavarsson, 1988; *D. tetarta* Hessler, 1970; *D. thoracicum* Fresi & Schiecke 1969; *D. tyrrhenicum* Fresi & Schiecke, 1969; *D. zenkewitschi* (Gurjanova, 1946)

Diagnosis: Pereonite 1 smaller than pereonite 2. Pereopod I more slender and often distinctly shorter than pereopod II, propodus ventrally with few slender setae, ventral margin of carpus with row of unequally bifid or finely serrated thin and slender setae, in more robust forms, dorsal margin of carpus with row of slender setae. Pereonites 5-7 enlarged. Pereopods V-VII heavily built and modified for swimming, carpi and propodi broad, with rows of long natatory setae.

#### **3.1.4.3.5     *Disparella* Hessler, 1970**

Synonyms: *Desmosoma* Sars, 1964: 11 (part); *Disparella* Hessler, 1970: 28-29

Type species: *D. valida* Hessler, 1970

Composition: *D. funalis* (Menzies & George, 1972); *D. longimana* (Vanhöffen, 1914); *D. pachythrix* Hessler, 1970; *D. valida* Hessler, 1970; *D. maiuscula* Kaiser & Brix, 2005; *D. neomana* (Menzies & George, 1972); *D. kensleyi* sp. nov.

Diagnosis modified (after Hessler 1970 and Kaiser & Brix 2005): Cephalic spines lateral to antennae. Mandible incisor process with strong shelf-like tooth. Pereopod I chelate; propodus elongated (more than 3.5 times longer than wide), carpus not produced at base of robust seta, lacking composed setae except claw-seta, with row of small setae on ventral margin. Pereopod II carpus and propodus with numerous robust setulate setae (carpus > 20, propodus > 8 in adult, respectively). Pleotelson with posterolateral spines. Uropods reaching one third or more of pleotelson length; exopod present, clearly smaller than endopod, much longer than wide.

#### **3.1.4.3.6     *Echinopleura* Sars, 1899**

Synonyms: *Desmosoma* Sars, 1864: 13 (part); *Echinopleura* Sars, 1899: 130-131; Hessler 1970:25

Type species: *E. aculeata* (Sars, 1864)

Composition: *E. aculeata* (Sars, 1864); *E. cephalomagna* sp. nov.

Diagnosis (modified after Sars 1899 and Hessler 1970): Body slender, margins serrated. Pereonite 5 slender. Lacinia mobilis reduced to one (bulge-like) tooth, molar process reduced, incisor process simplified. Pereopod I propodus elongated with few simple setae distally, carpus ventrally with row of long composed setae. Uropods uniramous.

#### **3.1.4.3.7     *Eugerdia* Meinert, 1890**

Synonyms: *Desmosoma* Sars, 1868 (part); Hansen 1916 (part); Gurjanova 1946 (part); *Eugerdia* Meinert, 1890: 194; Sars 1899: 252-255; Kussakin 1965; 121, 1999: 193-194; Hessler 1970: 23-24 (part)

Type species: *E. tenuimana* (Sars, 1868)

Composition: *E. tenuimana* (Sars, 1868); *E. fulcimandibulata* Hessler, 1970; *E. reticulata* (Gurjanova, 1946)

Diagnosis modified: All pereonites of similar height, pereonite 1 slightly higher than following pereonites. Pereonite 1 about 0.6 times of size of pereonite 2. Pereonites 5-7 enlarged, with broad marginal flanges. Pereopod I strongly attenuated (propodus more than 15 times longer than wide, carpus more than 11 times longer than wide), setae absent on propodus and carpus. Pereopods V-VII heavily built, carpi and propodi broad, with rows of long natatory setae. Uropods biramous.

#### **3.1.4.3.8     *Eugerdella* Kussakin, 1965**

Synonyms: *Desmosoma* Sars, 1864 (part); *Eugerdella* Kussakin, 1965: 125-126; Hessler 1970: 26-27

Type species: *E. natator* (Hansen, 1916)

Composition: *E. armata* (Sars, 1864); *E. coarctata* (Sars, 1899); *E. falklandica* (Nordenstam, 1933); *E. minutula* Mezhov, 1986; *E. natator* (Hansen, 1916); *E. nonfunalis* sp. nov.; *E. ordinaria* Mezhov, 1986; *E. polita* (Hansen, 1916); *E. pugilator* Hessler, 1970; *E. rotunda* (Menzies & George, 1972); *E. theodori* sp. nov.; *E. serrata* sp. nov.

Diagnosis modified after Hessler (1970): Pereopod I raptorial, enlarged, carpus largest and broadest article. Carpus of pereopod II longer and not as broad as carpus of pereopod I. Ventral setal row on carpus of pereopod I consisting of large robust composed setae of irregular size.

#### **3.1.4.3.9     *Exilinisca* Siebenhaller & Hessler, 1981**

Synonyms: *Exilinisca* Siebenhaller & Hessler, 1981: 229

Type species: *E. clipeatus* Siebenhaller & Hessler, 1981

Composition: *E. aculeatus* Siebenhaller & Hessler, 1981; *E. chandravoli* George, 2001; *E. clipeatus* Siebenhaller & Hessler, 1981; *E. hansenii* Just, 1970

The diagnosis presented by Siebenhaller & Hessler (1981) is followed here.

#### **3.1.4.3.10    *Hebefustis* Siebenhaller & Hessler, 1977**

Synonyms: *Nannoniscus* Sars, 1870 (part); *Nannoniscoides* Hansen, 1916 (part); *Hebefustis* Siebenhaller & Hessler, 1977: 30

Type species: *Hebefustis vafer* Siebenhaller & Hessler, 1977

Composition: *H. alleni* Siebenhaller & Hessler, 1977; *H. cornutus* Siebenhaller & Hessler, 1977; *H. dispar* Siebenhaller & Hessler, 1977; *H. hirsutus* Menzies, 1962; *H. mollicellus* Siebenhaller & Hessler, 1977; *H. par* Siebenhaller & Hessler, 1977; *H. primitivus* Menzies, 1962; *H. robustus* Birstein, 1963; *H. vafer* Siebenhaller & Hessler, 1977; *H. vitjazi* Mezhev, 1986

The diagnosis presented by Siebenhaller & Hessler (1977) is followed here.

#### **3.1.4.3.11    *Micromesus* Birstein, 1963**

Synonyms: *Micromesus* Birstein, 1963

Type species: *M. nannoniscoides* Birstein, 1963

Composition: *M. nannoniscoides* Birstein, 1963

The diagnosis presented by Birstein (1963) is followed here.

#### **3.1.4.3.12    *Mirabilicoxa* Hessler, 1970**

Synonyms: Hessler 1970: 24-25; *Desmosoma* Sars, 1864 (part); *Mirabilicoxa* Hessler, 1970: 24

Type species: *M. gracilipes* (Hansen, 1916)

Composition: *M. alberti* George, 2001; *M. atlanticum* Hessler, 1970; *M. cornuta* (Hessler, 1970); *M. acuminata* Hessler, 1970; *M. acuta* (Menzies & George, 1972); *M. birsteini* (Menzies, 1962); *M. coxalis* (Birstein, 1963); *M. curticoxalis* Pasternak, 1982; *M. exopodata* Hessler, 1970; *M. hessleri* George, 2001; *M. gracilipes* (Hansen, 1916); *M. longispina* (Hansen, 1916); *M. magnispina* (Menzies, 1962); *M. minuta* Hessler, 1970; *M. palpata* Hessler, 1970; *M. plana* Hessler, 1970; *M. richardsoni* Mezhev, 1986; *M. similis* (Hansen, 1916); *M. similipes* (Menzies & George, 1972); *M. tenuipes* (Birstein, 1970)

Diagnosis modified (after Hessler 1970): Pereopod I and II of similar shape, pereopod I slightly more slender (except in *Mirabilicoxa coarctata*). Propodus of pereopod I without setae, carpus with ventral row of long composed setae increasing in length towards propodus, with few dorsal setae. Coxae of pereopods I-IV with anterolateral elongation, in copulatory males produced enormously.

#### **3.1.4.3.13    *Momedossa* Hessler, 1970**

Synonyms: *Momedossa* Hessler 1970: 23

Type species: *M. profunda* Hessler, 1970

Composition: *M. profunda* Hessler, 1970; *M. longipedis* sp. nov.

Diagnosis modified after Hessler (1970): incisor process large, shelf-like. Pereonites 1 and 2 subequal. Pereopods long in relation to the length of the animal compared to all other members of Desmosomatinae. Anterior pereopods setose (carpi with more than 15 setae in the ventral and dorsal rows). Pereopod I slender, carpus and propodus somewhat attenuated, propodus without setal rows, carpus with row of composed setae ventrally, setae in this row not reaching half of length of propodus. Pleotelson with posterolateral spines. Uropods biramous (exopod reaching less than one third of endopod length)

#### **3.1.4.3.14    *Nannoniscoides* Hansen, 1916**

Synonyms: *Nannoniscoides* Hansen, 1916; Siebenhaller & Hessler 1977: 21, 1981: 246

Type species: *N. angulatus* Hansen, 1916

Composition: *N. angulatus* Hansen, 1916; *N. excavatifrons* Birstein, 1970; *N. gigas* Siebenhaller & Hessler, 1977; *N. latediffusus* Siebenhaller & Hessler, 1977; *N. laticontractus* Mezhov, 1986

Diagnosis modified after Siebenhaller & Hessler (1977, 1981): Body broad (not more than 3 times longer than wide), depressed. Cephalon with cephalic keels (bilateral rostral-like structure). Antennula with 6 (rarely 7) articles, last article elongated (clearly longer than wide) and inflated (bulbous). Pereopod I with thin setae ventrally on carpus and propodus except 1 distal composed seta on the carpus. Pleotelson with posterolateral spines. Operculum elongated, with concavity and calcareous fringe at midline of distal edge. Uropods biramous, endopod and exopod of nearly similar length.

#### **3.1.4.3.15    *Nannonisconus* Schultz, 1966**

Synonyms: *Nannonisconus* Schultz, 1966

Type species: *N. latipleonus* Schultz, 1966

Composition: *N. carinatus* Mezhov, 1986, *N. latipleonus* Schultz, 1966

The diagnosis as presented by Siebenhaller & Hessler (1981) is followed here.

#### **3.1.4.3.16    *Nannoniscus* Sars, 1870**

Synonyms: *Nannoniscus* Sars, 1870, 1877; Hansen, 1916; Menzies 1962; Birstein 1970; Just 1970, 1980; Menzies & George 1972; Siebenhaller & Hessler 1977;

Svavarsson 1982; Mezhev 1986

Type species: *N. oblongus* Sars, 1870 (figured 1899)

Composition: *N. acanthurus* Birstein, 1963; *N. aequiremus* Hansen, 1916; *N. affinis* Hansen, 1916; *N. analis* Hansen, 1916; *N. antennaspinis* Brandt, 2001; *N. arcticus* Hansen, 1916; *N. arctoabyssalis* Just, 1980; *N. australis* Vanhöffen, 1914; *N. bidens* Vanhöffen, 1914; *N. camayae* Menzies, 1962; *N. caspius* Sars, 1899; *N. cristatus* Mezhev, 1986; *N. detrimentus* Menzies & George, 1972; *N. inermis* Hansen, 1916; *N. intermedius* Siebenhaller & Hessler, 1981; *N. laevis* Menzies, 1962; *N. laticeps* Hansen, 1916; *N. menziesi* Mezhev, 1986; *N. minutus* Hansen 1916; *N. muscarius* Menzies & George, 1972; *N. oblongus* Sars, 1870; *N. ovatus* Menzies & George, 1972; *N. perunis* Menzies & George, 1972; *N. plebejus* Hansen, 1916; *N. profundus* Svavarsson, 1982; *N. reticulatus* Hansen, 1916; *N. simplex* Hansen, 1916; *N. spinicornis* Hansen, 1916; *N. teres* Siebenhaller & Hessler, 1981

The diagnosis presented by Siebenhaller & Hessler (1981) is followed here.

#### **3.1.4.3.17    genus novum**

Synonyms: *Mirabilicoxa* Hessler, 1970 (part)

Type species: gen. nov. *fletcheri* (Paul & George, 1975)

Composition: gen. nov. *fletcheri* (Paul & George, 1975)

Diagnosis modified after Kaiser 2005: Body about 4 times longer than width of pereonite 2. Pereonites 6,7 and pleotelson dorsally fused. Cephalon anteriorly with a midsagittal fold, anterolateral corners tapering into triangular tips. Antennula consisting of 5 article, last article bulbous. Pereopod I more robust than pereopods II-VII. Posterior pereopods without natatory setae. Carpus and propodus of all pereopods ventrally with small robust setae and fringed with fine hairs in a cuticular membrane. Terminal margin of pleotelson triangular. Operculum rounded, fringed

with numerous small setae. Uropodal exopod extremely small, not reaching one quarter of endopod length.

#### **3.1.4.3.18    *Oecidiobanchus* Hessler, 1970**

Synonyms: *Desmosoma* Sars, 1864 (part); *Oecidiobanchus* Hessler, 1970: 29

Type species: *O. plebejum* (Hansen, 1916)

Composition: *O. glacialis* Malyutina & Kussakin 1996; *O. nanseni* Just, 1980; *O. plebejum* (Hansen, 1916); *O. polare* (Gurjanova, 1946); *O. slopei* sp. nov.

Diagnosis modified: Pereopod I chelate, propodus enlarged, ventral margin of carpus without row of setae behind claw-seta. Pleotelson vaulted. Branchial chamber and operculum in comparison to pleotelson small and rounded.

#### **3.1.4.3.19    *Panetela* Siebenhaller & Hessler, 1981**

Synonyms: *Panetela* Siebenhaller & Hessler, 1981: 236

Type species: *Panetela wolffi* Siebenhaller & Hessler, 1981

Composition: *P. compacta* Malyutina & Kussakin, 1996; *P. tenella* Birstein, 1963; *P. wolffi* Siebenhaller & Hessler, 1981

The diagnosis presented by Siebenhaller & Hessler (1981) is followed here.

#### **3.1.4.3.20    *Paradesmosoma* Kussakin, 1965**

Synonyms: *Paradesmosoma* Kussakin, 1965: 131; Hessler 1970: 29-30

Type species: *P. conforme* Kussakin, 1965

Composition: *P. conforme* Kussakin, 1965; *P. orientale* Kussakin, 1965; *P. australis* sp. nov.

Diagnosis modified (after Kussakin 1965 and Hessler 1970): Pereopod I chelate, propodus more enlarged than carpus, setae in ventral row of irregular size, with single very slender setae distal to claw. Pereopod IV ventral margins of ischium, merus, carpus and propodus with dense row of setae with sturdy bases and abruptly narrowing in distal part (distally plumose setae), carpus and propodus broad (paddle-like). Ischium of pereopods II and III with same setal type as pereopod IV. Mandibular palp with 2 articles.

#### **3.1.4.3.21    *Prochelator* Hessler, 1970**

Synonyms: *Desmosoma* Sars, 1864 (part); *Prochelator* Hessler, 1970: 27-28

Type species: *P. lateralis* (Sars, 1899)

Composition: *P. angolensis* Brenke, Brix & Knuschke, 2005; *P. abyssalis* Hessler, 1970; *P. hampsoni* Hessler, 1970; *P. incomitatus* Hessler, 1970; *P. lateralis* (Sars, 1899); *P. litus* Hessler, 1970; *P. sarsi* George, 2001; *P. uncatus* Hessler, 1970; *P. kussakini* Mezhev, 1986; *P. serratum* (Fresi & Schiecke, 1969); *P. maorii* sp. nov.

Diagnosis modified after Hessler (1970) and Brenke, Brix & Knuschke (2005): Pereopod I large, carpo-euchelate. Dactylus and propodus forming movable counterpart to large flexible spine (claw-spine) on distal end of carpus. Lower margin of carpus of pereopod I with short, stout seta centrally and somewhat longer, slender seta distally proximal to claw-seta. Pleotelson with posterolateral spines.

#### **3.1.4.3.22    *Pseudogerda* Kussakin, 1965**

Synonyms: *Desmosoma* Sars, 1864 (part); *Eugerdella* Meinert, 1890: 194 (part.); *Pseudogerda*, Kussakin, 1965:165 (part)

Type species: *P. fragilis* Kussakin, 1965

Composition: *P. anversense* (Schultz, 1979); *P. arctica* Svavarsson, 1988; *P. elegans* Kussakin, 1965; *P. fragilis* Kussakin, 1965 *P. globiceps* Meinert, 1890; *P. intermedia* (Hult, 1936); *P. kamtschatica* Kussakin, 1965

Diagnosis: Pereopod I very slender, slightly attenuated (propodus about 6-9 times longer than wide, carpus about 5 times longer than wide), carpus and propodus ventrally and dorsally with few (up to 5) small setae.

#### **3.1.4.3.23    *Pseudergella* gen. nov.**

Synonyms: *Desmosoma* Sars, 1864 (part), *Eugerdella* Hessler, 1970 (part), *Pseudomesus* Hansen, 1916 (part)

Type species: *P. ischnomesoides* Hessler, 1970

Composition: *P. atypicum* Schiecke & Fresi, 1969; *P. bispinosus* Chardy, 1974; *P. hessleri* Just, 1980; *P. ischnomesoides* Hessler, 1970

Diagnosis: Body elongated (length about 6 times of width of pereonite 2). Pereonite 1 smaller than pereonite 2. Pereonite 5 elongated with convex inflated lateral margins. Pleotelson enlarged, slightly inflated dorsally. Pereopod I slightly stouter than



pereopod II, carpus with row of 3 or 4 robust composed setae ventrally, dorsally without setal row, propodus lacking setae. Ischium of posterior pereopods elongated (about 5 times longer than wide). Uropodal endopod longer than wide.

#### **3.1.4.3.24    *Pseudomesus* Hansen, 1916**

Synonyms: *Pseudomesus* Hansen, 1916; Chardy 1974; Birstein 1963; Svavarsson 1984

Type species: *P. brevicornis* Hansen, 1916

Composition: *P. brevicornis* Hansen, 1916; *P. pitombo* Kaiser, 2005; *P. satanus* sp. nov.; *P. similis* Birstein, 1963

Diagnosis modified: Body form elongated (more than 5.5 times longer than width of pereonite 2). Pleotelson enlarged, dorsally inflated. Uropods not extending beyond distal margin of pleotelson, inserting close to anus valves, endopod extremely short and nearly bulbous. Pleotelson with posterolateral spines. Ischium of posterior pereopods with anteriorly directed cuticular hook dorsally. Pereonites 5, 6 and 7 of nearly same size. Carpus of pereopod I ventrally with a minimum number of 3 composed setae standing in a row. Bilateral bulges on the cephalon occurring in males only.

#### **3.1.4.3.25    *Rapaniscus* Siebenhaller & Hessler, 1981**

Synonyms: *Rapaniscus* Siebenhaller & Hessler, 1981: 234

Type species: *R. dewdneyi* Siebenhaller & Hessler, 1981

Composition: *R. crassipes* Hansen, 1916; *R. dewdneyi* Siebenhaller & Hessler, 1981; *R. multisetosus* Brandt, 2002; *R. coalescus* (Menzies & George, 1972); *R. sp.A*

The diagnosis presented by Siebenhaller & Hessler (1981) is followed here.

#### **3.1.4.3.26    *Reductosoma* Brandt, 1992**

Synonyms: *Reductosoma* Brandt, 1992: 58

Type species: *R. gunnera* Brandt, 1992

Composition: *R. gunnera* Brandt, 1992

The diagnosis presented by Brandt (1992) is followed here.

#### **3.1.4.3.27    *Regabellator* Siebenhaller & Hessler, 1981**

Synonyms: *Regabellator* Siebenhaller & Hessler, 1981: 238

Type species: *R. profugus* Siebenhaller & Hessler, 1981

Composition: *R. abyssi* Brandt 2002; *R. armatus* Hansen, 1916; *R. profugus* Siebenhaller & Hessler, 1981

The diagnosis presented by Siebenhaller & Hessler (1981) is followed here.

#### **3.1.4.3.28    *Saetoniscus* Brandt 2002**

Synonyms: *Saetoniscus* Brandt 2002: 11

Type species: *S. meteori* Brandt 2002

Composition: *S. meteori* Brandt 2002

The diagnosis presented by Brandt (2002) is followed here.

#### **3.1.4.3.29    *Thaumastosoma* Hessler, 1970**

Synonyms: *Desmosoma* Sars, 1864 (part), *Leutziniscus* George, 2001: 1841; *Thaumastosoma* Hessler, 1970: 25

Type species: *Thaumasotosoma platycarpus* Hessler, 1970

Composition: *T. distinctum* Birstein, 1963; *T. jebamoni* (George, 2001); *T. platycarpus* Hessler, 1970; *T. tenue* Hessler, 1970

#### **3.1.4.3.30    *Torwolia* Hessler, 1970**

Synonyms: *Torwolia* Hessler, 1970: 30

Type species: *T. creper* Hessler, 1970

Composition: *T. creper* Hessler, 1970; *T. subchelatus* Hessler, 1970; *T. tinbienae* sp. nov.

Diagnosis modified after Hessler (1970): Pereopod I small, subchelate, carpus broad and short, propodus enlarged. Pereopod II enlarged. Pereonite 1 reduced. Pereonite 2 largest of the first four pereonites (enlargement corresponding to the enlarged pereopod II).

#### **3.1.4.3.31    *Whoia* Hessler, 1970**

Synonyms: Hessler 1970: 22-23; *Desmosoma* Sars, 1864 (part), *Desmosomella* Kussakin, 1965 (part)

### 3. Results

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Type species: *W. angusta* (Sars, 1899)

Composition: *W. angusta* (Sars, 1899); *W. dumbshafensis* Svavarsson, 1988; *W. variabilis* Hessler, 1970; *W. victoriensis* sp. nov.

Diagnosis modified after Hessler (1970): Body slender. Pereonites 1 and 2 of subequal size. Pereopods I and II of similar size and shape, with long robust composed setae, carpus with ventral and dorsal row of setae, propodus elongated, without dorsal setal row. Coxae not produced, slightly angular lobe with small seta. Lateral margins of pereonite 5 convex, inflated laterally.

#### 3.1.5 New species

##### 3.1.5.1 DIVA-1

##### 3.1.5.1.1 *Desmosoma renatae* sp. nov.

Holotype. – Female, preparatory, 9.1 mm; ZMH K-40998; type locality. – Angola Basin, start position: 16° 14,3' S 005° 26,8' E, end position: 16° 14,9' S 005° 26,7' E, depth 5389 m; RV *Meteor* M48/1; station 350; gear: EBS

##### Paratype

Allotype. – 1 male, adult, 8.4 mm; ZMH K-40999; locality. – Angola Basin, start position: 17° 06,2' S 004° 41,7' E, end position: 17° 07,5' S 004° 42,3' E, depth 5415 m; RV *Meteor* M48/1; station 344 ; gear: EBS

#### Etymology

The name refers to the author's mother Renate. *Renata* (lat. fem.) means “re-born”.

#### Diagnosis

Body length about 4 times longer than width of Prn2. A1 consisting of six articles. Lm of MdL with four teeth, ip with three strong teeth. Mxp with three retinaculae. From lateral view, anterior four Prns of similar height as posterior Prns. Prn1 0.42 times of midsagittal length of Prn2. Prn2 largest of anterior four Prns. Prn4 with quadrangular distal corners (marginal flanges). Prn5-7 enlarged, with broad marginal flanges. Coxae of P I-IV produced anteriorly and tipped with a stout sensory setae. P I slender, smaller than P II. Carpus elongated (5.8 times longer than wide), merus to propodus ventrally with rows of irregular simple slender and slender distally setulate setae. P V-VII enlarged, with broad carpi and propodi that bear rows of numerous natatory setae. Uropods biramous, exopod 0.4 times of endopod length, endopod distally setose (6 simple setae).

#### Description of holotype female

Habitus (Fig. 29): Body 9.1 mm long (measured without appendages), 3.98 times longer than width of Prn2. Cephalothorax free, as long as wide. Prn1 width 0.8 times cephalon width in dorsal view, without frons clypeal furrow or transverse ridge on frons. Prn1 length 0.42 Prn2 length, 0.82 Prn2 width. Prn4 length 0.76 Prn3 length,

### 3. Results

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0.95 Prn3 width. Anterior margin of Prn5 convave, lateral margins of Prn5 convex, marginal flanges with rounded anterior corners. Lateral margins of Prns 6 and 7 straight at marginal flanges. Coxae 1-4 produced, tipped with small stout setae. Pleotelson damaged (squeezed), length approximately 1.1 width, posterolateral spines absent. Lateral margins convex. Posterior margin slightly rounded.

Antennula (Fig. 30): 3.1 mm long, length 0.13 body length, with 6 articles. Article 1 with 4 small simple and 8 small broom setae. Article 2 length 6.3 width, 1.6 article 1 length; with 3 articulated broom setae. Article 3 with 3 slender setae, article 4 with 2 broom and 1 slender setae. Articles 2-5 length relative to article 1: 1.6: 1.2: 0.5: 0.42: 0.54.

Antenna: broken off

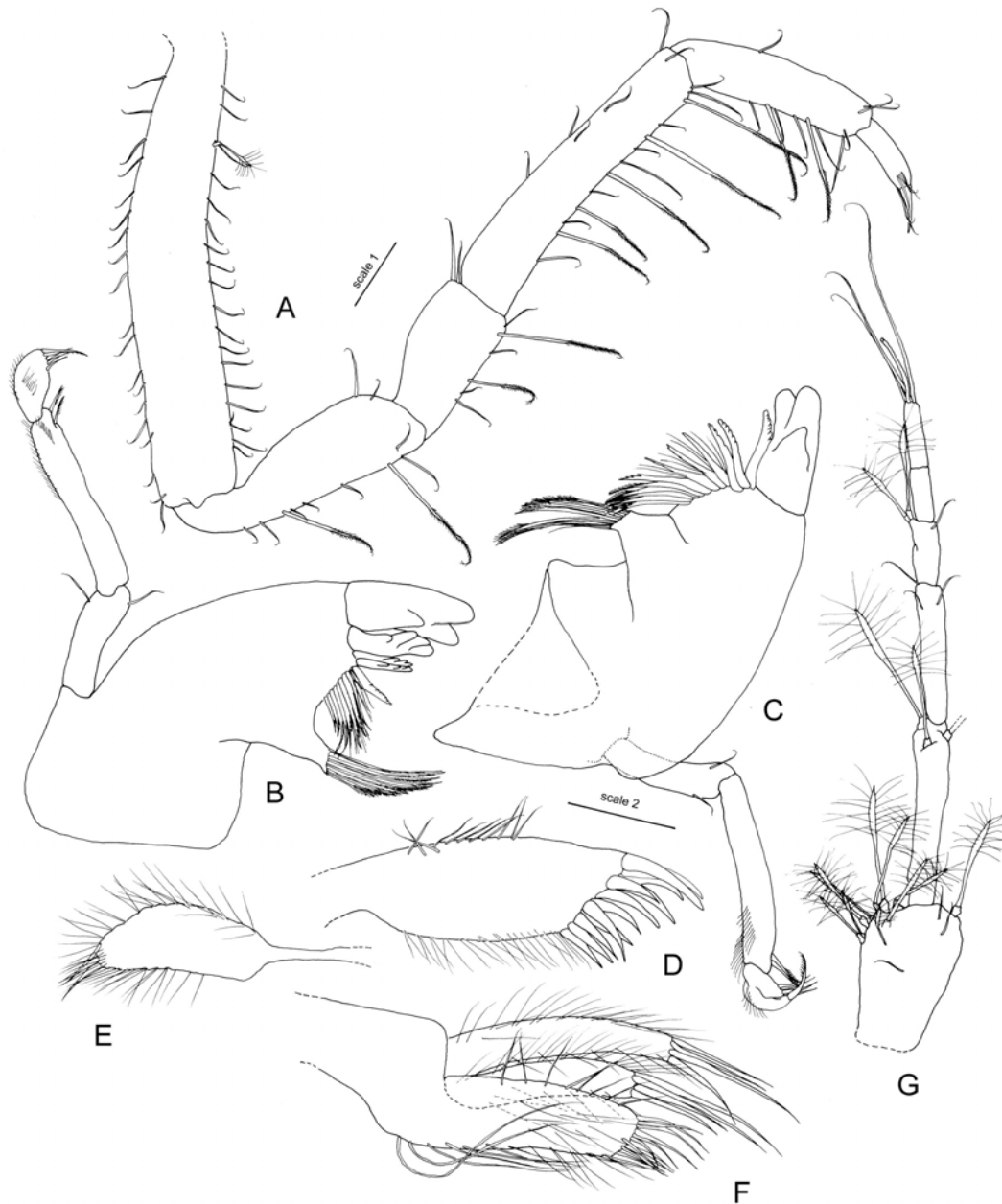
Mandible (Fig. 30): First article of palp distally with 2 simple setae, second article with 2 small setulate setae, apical article with 5 small setulate setae, distal seta longest. Ip with 3 lobes. Lm of MdL with 4 teeth, Lm-like structure of right mandible triangular, distal margin with 8 small teeth (serrated). Spine row containing 11 spines. Mp triangular, with 10 distally plumose slender setae.

Maxillula (Fig. 30): Inner lobe slightly smaller than outer lobe (0.82 of outer lobe length), surrounded by numerous fine setae, distally with 3 simple setae. Outer lobe 3.1 times longer than wide, ventrally with 12 pairs of fine setae and dorsally with 11 simple slender setae, terminally with 12 strong spines.

Maxilla (Fig. 30): Medial lobe 0.9 length, 1.9 width in comparison to other lobes, terminally with 12 simple setae, laterally with 7 long simple seta at base of lobe going over into 5 pairs of fine setae on ventral margin and 8 simple slender setae on dorsal margin. Outer lobe with 4 long distal setae, laterally with 12 pairs of fine setae on dorsal margin and 7 fine setae on ventral margin.



**Fig: 29:** *Desmosoma renatae* sp. nov., holotype female, habitus dorsal (A), habitus lateral (B), scale = 1 mm



**Fig. 30:** *Desmosoma renatae* sp. nov., holotype female, P I (A, scale 1), antennula (G, scale 2), mouthparts (B-F, scale 2): MdL (B), MdR (C), Mx1 (D), Mx2 (F)

**Maxilliped** (Fig. 31): Epipodite length 3.5 width, length 0.97 endite length. Endite with 3 coupling hooks, terminally with 2 star-shaped cuspidate setae and few simple setae, fringed by numerous fine setae. Distal edges of palp article 1 tipped with small setae, outer margin fringed with 6 setae. Inner margin of palp article 2 with 4, outer margin with 10 setae. Inner margin of palp article 3 with 11 setae inserting in marginal bulges, outer margin with single seta. Palp-article 4 with 4 setae, article 4 terminally with 4 setae. Article 1 length 0.56 width, article 2 length 0.89 width, article 3 length 0.96 width, article 4 length 2.64 width, article 5 length 4.0 width.



**Fig. 31:** *Desmosoma renatae* sp. nov.; holotype female, Mxp (H), scale = 0.1 mm

Pereopod I (Fig. 30): Basis length 6.0 width, with 1 small broom seta near to coxa and marginally with numerous (37) small simple setae. Ischium length 3.1 width, ventrally with 2 long slender distally setulate and 7 small slender setae, dorsally with 2 simple slender setae. Merus length 1.63 width, ventrally with 2 long slender distally setulate and 4 small simple slender setae, dorsally with 2 distal simple setae. Carpus length 5.81 width, ventrally with row of 13 setae: 5 long slender distally setulate and 8 simple slender setae, dorsally with 5 simple setae. Propodus length 3.8 width, ventrally with row of 3 long slender distally setulate and 4 small simple slender setae, dorsally with 1 slender seta midway and 2 simple slender setae distally. Dactylus length 3.5 width, with 3 simple setae next to claw. Claw of dactylus with 2 conate setae as well as 2 slender setae medially.

Pereopods II-VII: broken off.

Pleopod 2 (operculum) (Fig. 32): Length 0.96 width. Lateral margins slightly convex, distal margin rounded, with 32 slender setae.

Pleopod 3 (Fig. 32): Endopod length 1.4 width, distally 3 long plumose setae. Exopod length 0.56 of endopod length, outer margin hirsute, distally with 1 simple seta.

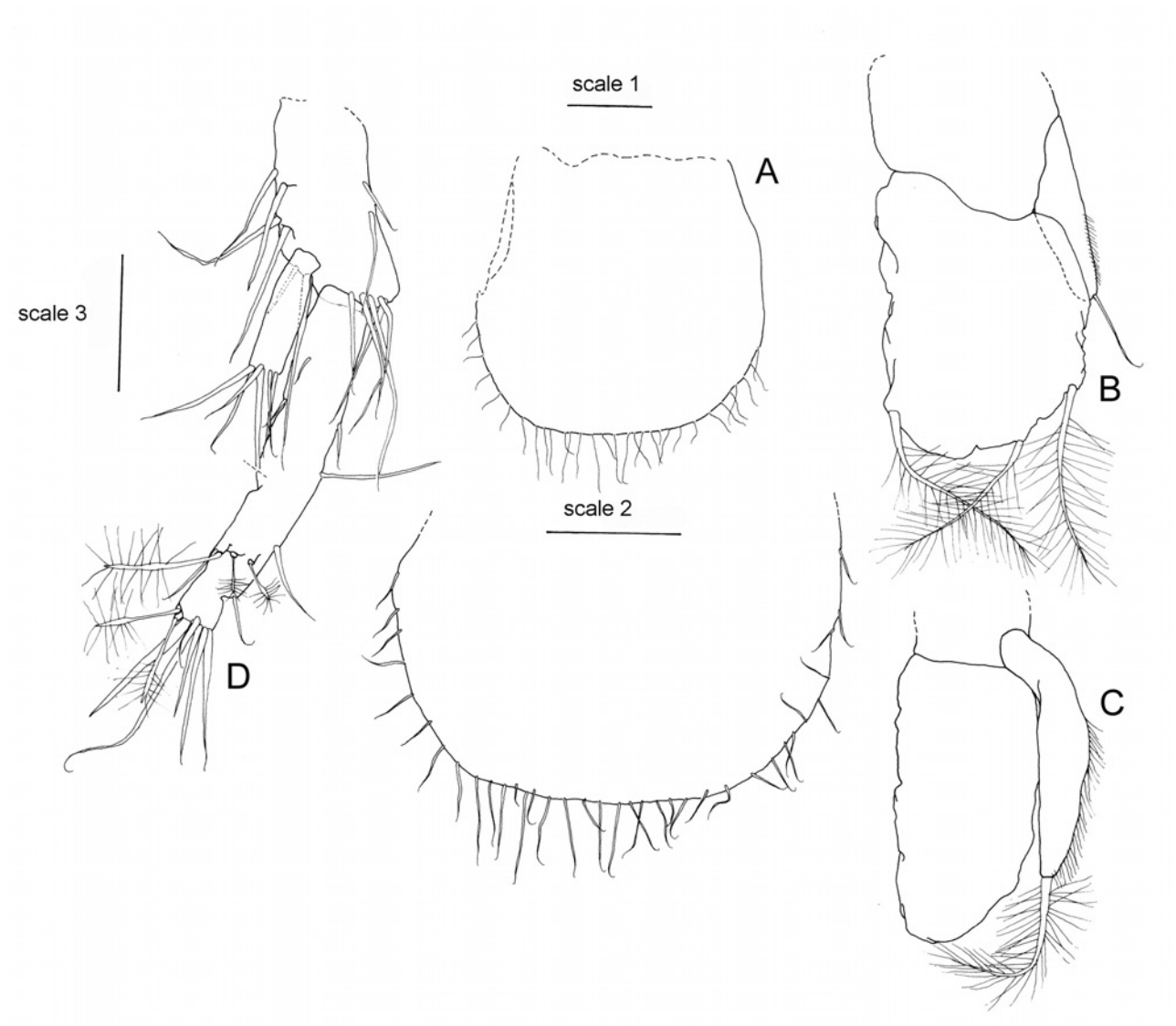
Pleopod 4 (Fig. 32): Endopod of oval shape, length 2.04 width. Exopod length 4.2 width, outer margin hirsute, distally 1 long plumose seta

Uropods (Fig. 32): biramous. Endopod length 1.9 protopod length, 5.5 times longer than wide, with five broom setae of different sizes, with 5 simple setae and 1 small



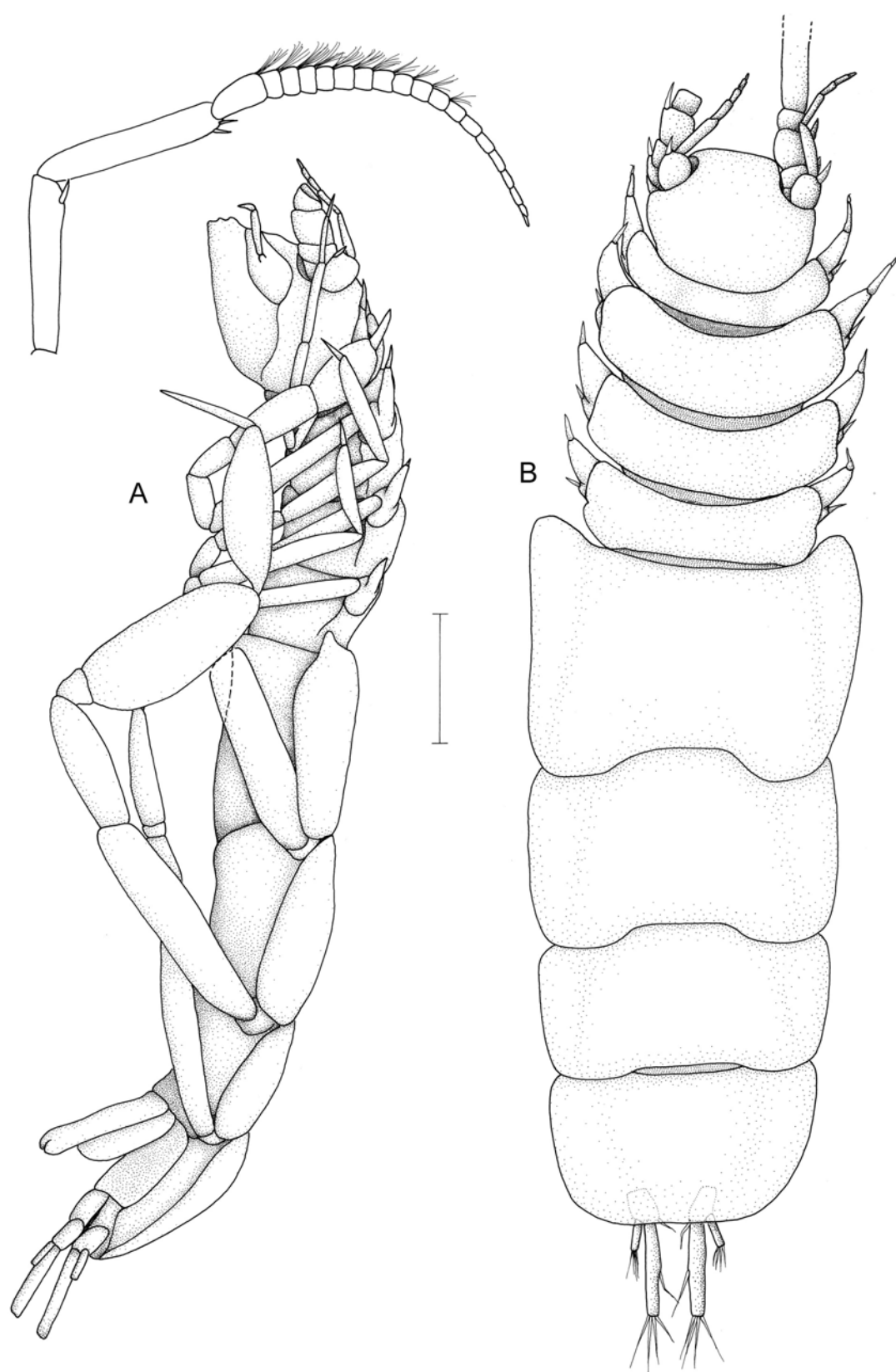
### 3. Results

seta distally, lateral margins with 7 simple setae. Exopod length 0.42 endopod length, 3.6 width, with 6 simple setae. Protopod length 1.8 width, with 12 simple setae.



**Fig. 32:** *Desmosoma renatae* sp. nov., holotype female, pleopods: Op (A, scale 1, scale 2), PI3 (B, scale 3), PI4 (C, scale 3), Ur (D, scale 3)

**Differences in male**



**Fig. 33:** *Desmosoma renatae* sp. nov., allotype male, habitus lateral (A), habitus dorsal (B), scale = 1 mm

Habitus (Fig. 33): very similar to female, 12.6 times longer than width of Prn2. Coxae more produced than in female and tipped with long stout sensory setae, additionally on edges of second coxal lobe short stout setae. Marginal flanges at Prns 5-7 broader than in female.

Pereopods V–VII: Longer than P I-IV, heavily build, with broad carpi and propodi with dorsal and ventral rows of numerous natatory setae (extremely modified for swimming).

**Discussion:** Although in the holotype female all pereopods except P I are broken off, the main characters to distinguish the species are present. Most important are the features of the P I. The heavy bases of the posterior pereopods in holotype female resemble very much the heavy bases in allotype male. It can be concluded, that females possess similar pereopods, which may be less setose (sexual dimorphism). The new species is most similar to *D. gigantea* in habitus, size and setation of P I. In male, P II is strongest of P I-IV as it is in *Desmosoma gigantea* (Park, 1999). Differences to *D. gigantea* are: article 2 of A1 distally with 3, not with 4 broom setae; distolateral corners of Prn4 quadrangular; Lm of MdL with 4, not with 3 teeth, differing clearly from the shape of the ip; Mxp with 3 retinaculae, not with 4; carpus and propodus of P I more slender and elongated; endite terminally with 2 star-formed cuspidate setae, not with 3; Op less setose; uropodal endite smaller and less well developed. *D. renatae* sp. nov. resembles *D. tetarta* (Hessler, 1970) in the broad marginal flanges and the relatively robust P I compared to other members of the genus. Differences to *D. tetarta* are: Carpus of P I not with robust composed setae, propodus in *D. tetarta* without rows of setae; Mxp with 3 retinaculae, not with 2; Prn1 smaller than Prn2 in *D. tetarta* (0.78 of length of Prn2), but not as small as in *D. renatae* sp. nov.; Plt in adult male not quadrangular.

The new species differs from the remaining species of the genus by following apomorphies: Prn4 with marginal flanges producing quadrangular anterodorsal corners and broad marginal flanges at Prns 5-7. Carpus more than 5.5 times longer than wide and propodus of P I about 4 times longer than wide, ventrally with mixed rows of long slender distally setulate and small simple slender setae. Posterior pereopods heavily build and extremely modified for swimming.

#### **3.1.5.1.2 *Eugerdella theodori* sp. nov.**

Holotype. – Female, preparatory, 1.3 mm; ZMH K-401001; type locality. – Angola Basin, start position: 16° 18,1' S 005° 27,2' E, end position: 16° 19,3' S 005° 27,2' E, depth 5390 m; RV Meteor M48/1; station 348; gear: EBS

#### Paratypes:

Allotype. – 1 male, adult, 1.4 mm; ZMH K-401002; locality. – As type locality.

Paratypes. - 12 females ZMH K-401003; locality. – As type locality.

#### **Etymology**

The name refers to the author's father *Theodor*.

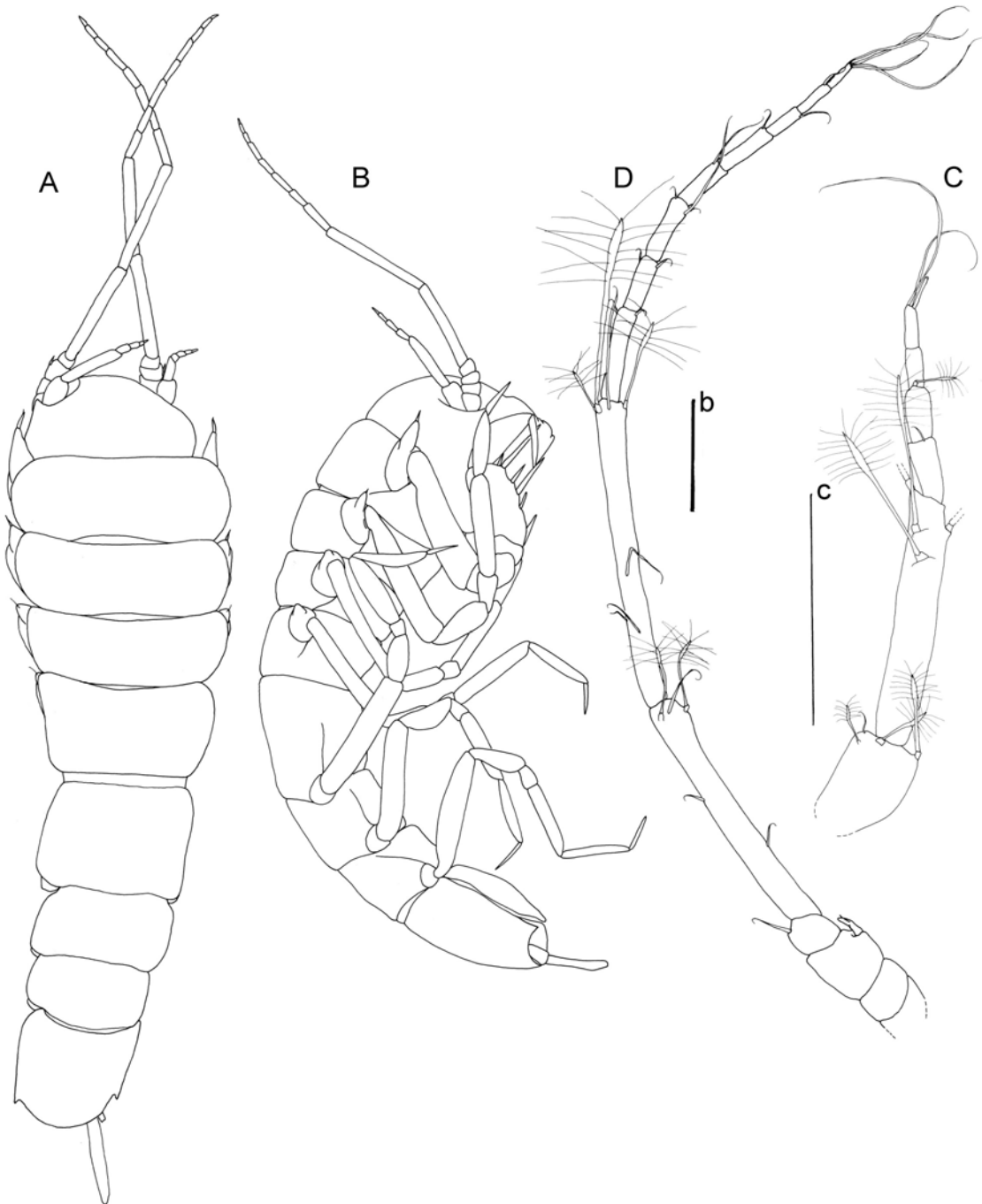
#### **Diagnosis**

Body length about 3.5 times longer than width of Prn2. Prn1 about 1.5 times wider than cephalon. Frons clypeal furrow present, without transverse ridge on frons. Prn 1 slightly longer in midsagittal length than Prn 2. Prn 4- of similar width, margins straight. Coxae 1-4 produced, anterior production of coxa 1 longest, coxae 1 and 2 tipped with stout setae. Carpus enlarged, with ventral row of robust unequally bifid setae of irregular size, proximal seta to propodus robust and simple, smaller than all other setae of the ventral row. Uropodal exopod reaching 0.1 times of endopod length.

#### **Description of holotype female**

Habitus (Fig. 34): body 1.3 mm long (measured without appendages), 3.6 times longer than width of Prn2. Prn1 width 1.4 times cephalon width in dorsal view. Frons clypeal furrow present, without transverse ridge on frons. Prn1 length 1.1 Prn2 length, 0.3 Prn2 width. Prn5 width 1.3 length, anterior margin straight, Prn 4 anteriorly broadest and Prn5 posteriorly broadest. Lateral margins of Prns 6 and 7 slightly convex. Coxae 1-4 produced, anterior production of coxa 1 longest, coxae 1 and 2 tipped with stout setae. Plt length 0.87 width, small posterolateral spines present. Lateral margins in front of spines straight, in male slightly convex. Posterior margin rounded.

**Antennula** (Fig. 34): 0.3 mm long, length 0.23 body length, with 6 articles. Article 1 with three broom setae and one small simple seta. Article 1 1.5 Article 2 length 6.1 width, 2.3 article 1 length; with four articulated big broom setae. Article 3 with one simple slender seta, article 4 with one small broom seta. Articles 2-5 length relative to article 1: 2.3: 0.6: 0.52: 0.36: 0.4.



**Fig. 34:** *Eugerdella theodori* sp. nov., holotype female, habitus dorsal (A), lateral (B); paratype female, antennula (C), antenna (D), scale a = 0.5 mm, scale b = 0.1 mm, scale c = 0.1 mm

Antenna (Fig. 34) about 1.1 mm long, length 0.85 body length, with 14 articles. Articles 3 with one stout unequally bifid seta on outer side. Article 4 with one small slender seta. Article 5 distally with one slender and two broom setae and marginally with two simple setae. Article 6 with distally with one long slender seta and three broom setae and marginally with three simple slender setae. Flagellar articles with distally with few simple slender setae, distal article terminally with four long slender setae. Relative length of articles: 1: 1.6: 2.6: 1.7: 10.7: 12.8: 3.9: 2.3: 2.7: 2.1: 2.3: 1.6: 1.6: 1.3.

Mandible (Fig. 35): Palp absent, represented by one triangular bulge. Incisor process with five lobes. Lacinia mobilis of left mandible with six teeth. Spine row containing seven spines (three spines terminally setulate with two fine hairs inserted basally and four simple spines). Molar process triangular with nine fine slender setae.

Maxillula (Fig. 35): Inner lobe slightly smaller than outer lobe (0.83 of outer lobe length), terminally with 6 simple setae, marginally with pairs of fine hairs. Outer lobe 3.36 times longer than wide, terminally with 11 strong spines.

Maxilla (Fig. 35): Medial lobe slightly broader than other lobes, basally with four long slender setae, terminally with 13 setae. Outer lobes terminally with three setae, shortest terminal seta finely setulate, dorsolaterally with six pairs of fine hairs.

Maxilliped (Fig. 35): Epipodite length 3 times width, length 1.1 endite length, outer margin fringed with short fine hairs in cuticular membrane. Endite with two retinaculæ, terminally and marginally with numerous fine setae. Terminal edges of palp articles 1 and 2 tipped with simple setae, outer margins fringed with fine setae, palp article 3 with eight setae, article 4 with three setae, article 5 with four setae. Article 1 length 0.55 width, article 2 0.9 width, article 3 0.88 width, article 5 2 times width and article 4 4 times width.

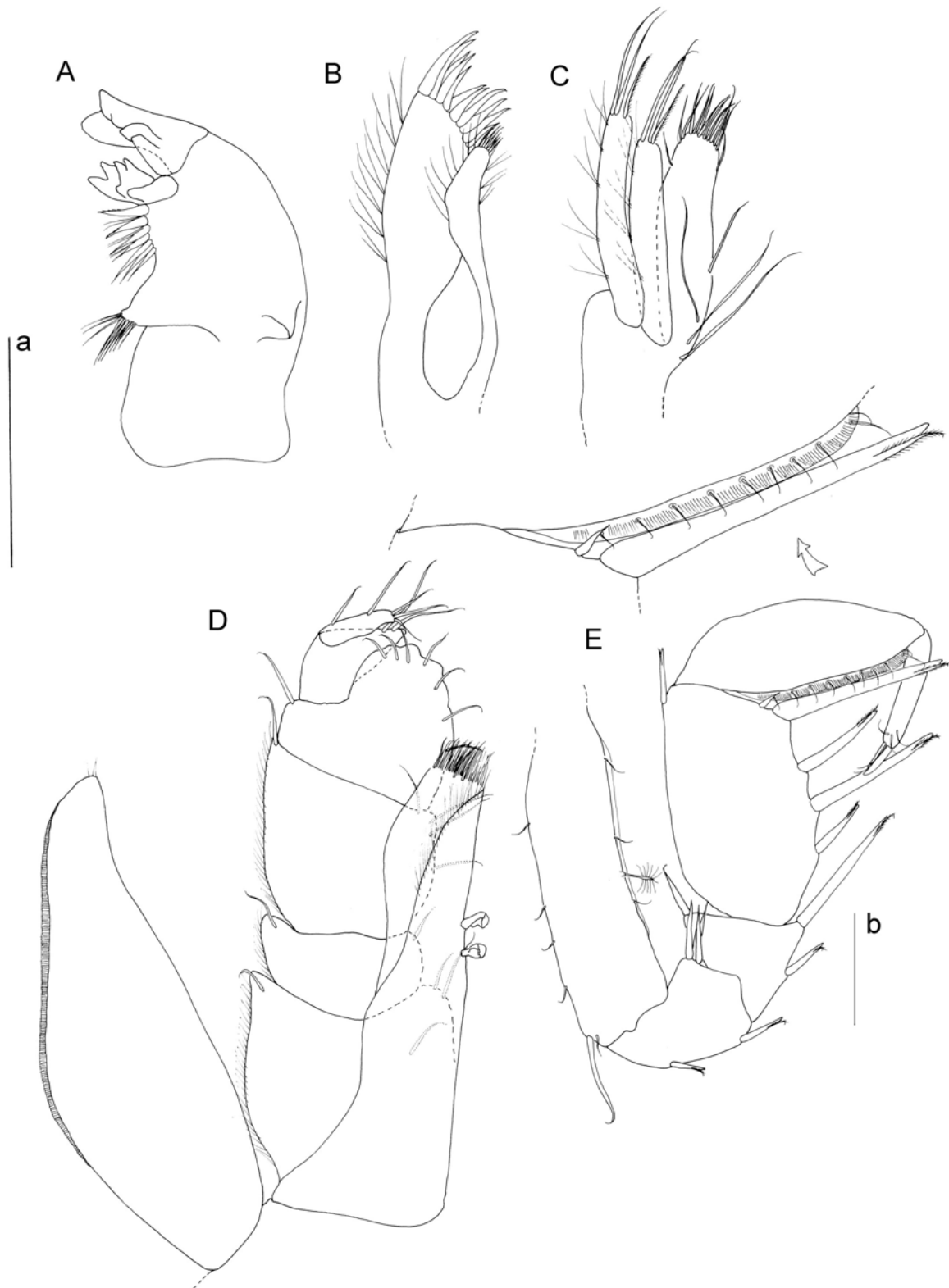
Pereopod I (Fig. 35): Basis length 3.6 width, marginally with seven simple setae and one broom seta, proximal to ischium ventrally with one long simple seta. Ischium length 1.5 width, dorsally three robust simple setae, ventrally two small unequally bifid terminally setulate setae. Merus length 0.85 width, dorsally with one stout seta, ventrally with one small and one large unequally bifid distally setulate seta. Carpus length 1.75 width, with ventral row of robust unequally bifid setae of irregular size,

proximal seta to propodus robust and simple, smaller than all other setae of the ventral row; distodorsally with one robust unequally bifid seta. Propodus length 2.6 width, lacking dorsal setae, ventrally fringed with cuticular membrane with row of 10 small setae breaking through this membrane. Dactylus length 6.6 width, terminally with three simple setae. Claw of dactylus with two conate setae and two slender setae inserted medially.

Pereopods II-IV (Fig. 36): Basis length about 5 times width, with up to three broom setae and marginally slender setae in regular distances. Ischium length about 3 times width, ventrally with two small stout unequally bifid setae, distodorsally with one stout simple seta. Merus length about 1.5 width, ventrally with two unequally bifid setae (PIV: one unequally bifid and one long simple seta), distodorsally with one small and one stout simple seta. Carpus length between 4.7 and 5.8 width, with ventral row of seven composed setae (long unequally bifid) increasing in length towards propodus (PIV: slender distally unequally bifid setae), dorsally with row of slender setae, near insertion of propodus one stout unequally bifid and one broom setae (PIV: lacking dorsal setae except one seta distally).

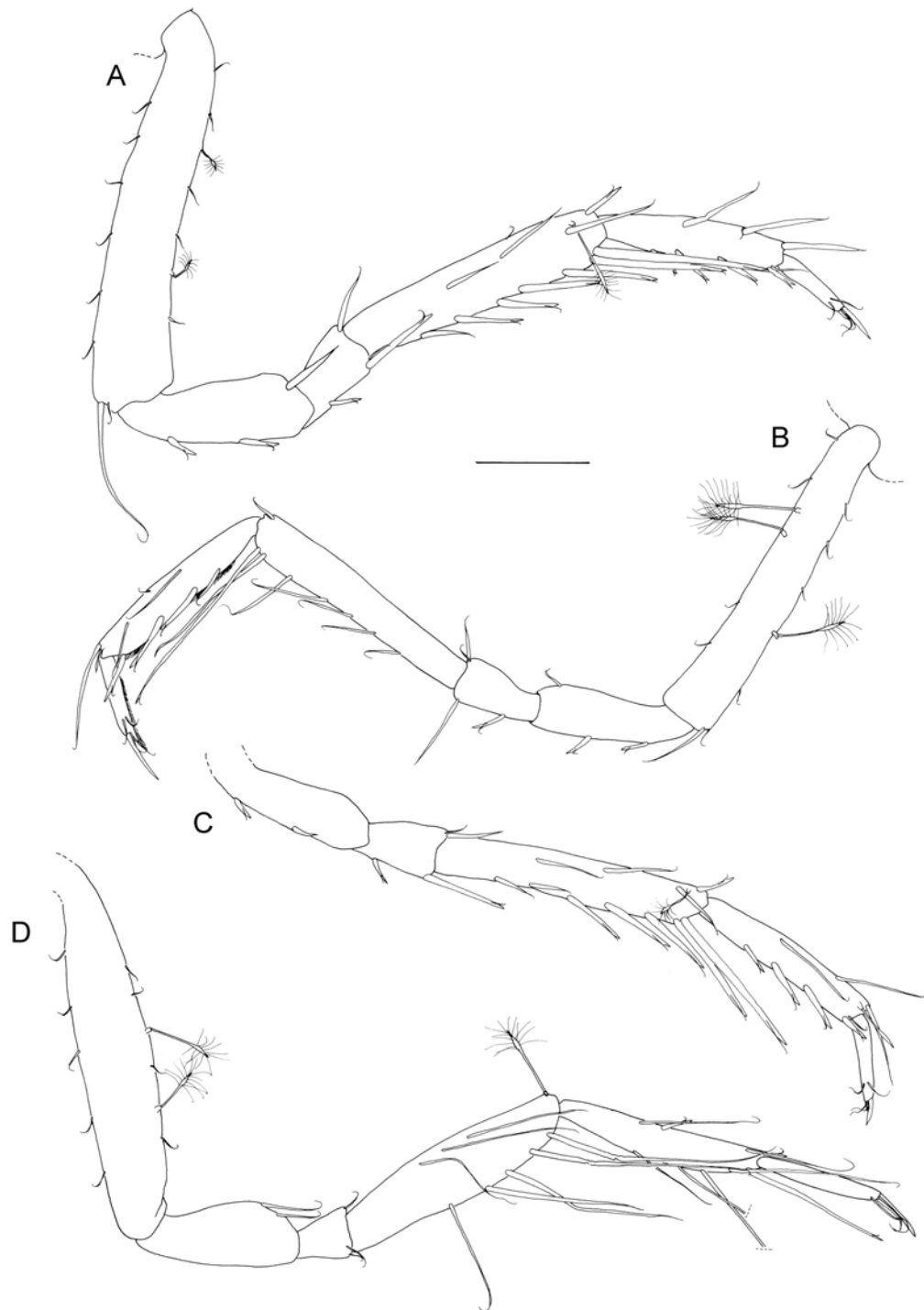
Pereopods V-VII (Fig. 36 (D), 37 (A-B): Basis length between 4.6 and 5.4 times width, P V with two broom setae, P V-VII marginally with small simple setae in regular distances. Ischium length between 2.6 and 2.9 width, few small simple setae. Merus length between 1.1 and 1.7 width, distally with one or two small simple setae on ventral and dorsal margin. Carpus length between 4.1 and 6.3 width, ventrally with row of five long slender setae, dorsally with row of 3-5 setae, P V dorsodistally with one broom seta. Propodus length between 5.9 and 7.3 width, ventrally with row of up to six long setae, dorsally with up to three long setae and two small stout unequally bifid setae. Dactylus length PV: 10 ; P VI: 23, P VII: 13 times width terminally with one slender seta. Claw out of one long conate seta and two slender seta next to conate seta.

Pleopod 2 (operculum) (Fig. 37): length 1.2 width. Lateral margins slightly convex, distal margin straight, surrounded by 32 setae.



**Fig. 35:** *Eugerdella theodori* sp. nov., paratype female, mouthparts (A-D, scale a): Md L (A), Mx 1 (B), Mx 2 (C), Mxp (D), pereopod I (E, scale b), scales = 0.1 mm





**Fig. 36:** *Eugerdella theodori* sp. nov., paratype female, pereopods (A-D): P II (A), P III (C), P IV (B), P V (D), scale = 0.1 mm

Pleopod 3 (Fig. 37): Endopod length 1.9 width, distally with 3 long plumose setae. Exopod length 0.36 of endopod length, outer margin hirsute, terminally with one simple seta.

Pleopod 4 (Fig. 37): Endopod oval-shaped, length 2.1 width. Exopod length 7.7 width, 0.75 endopod length, outer margin hirsute, terminally with one long plumose seta.

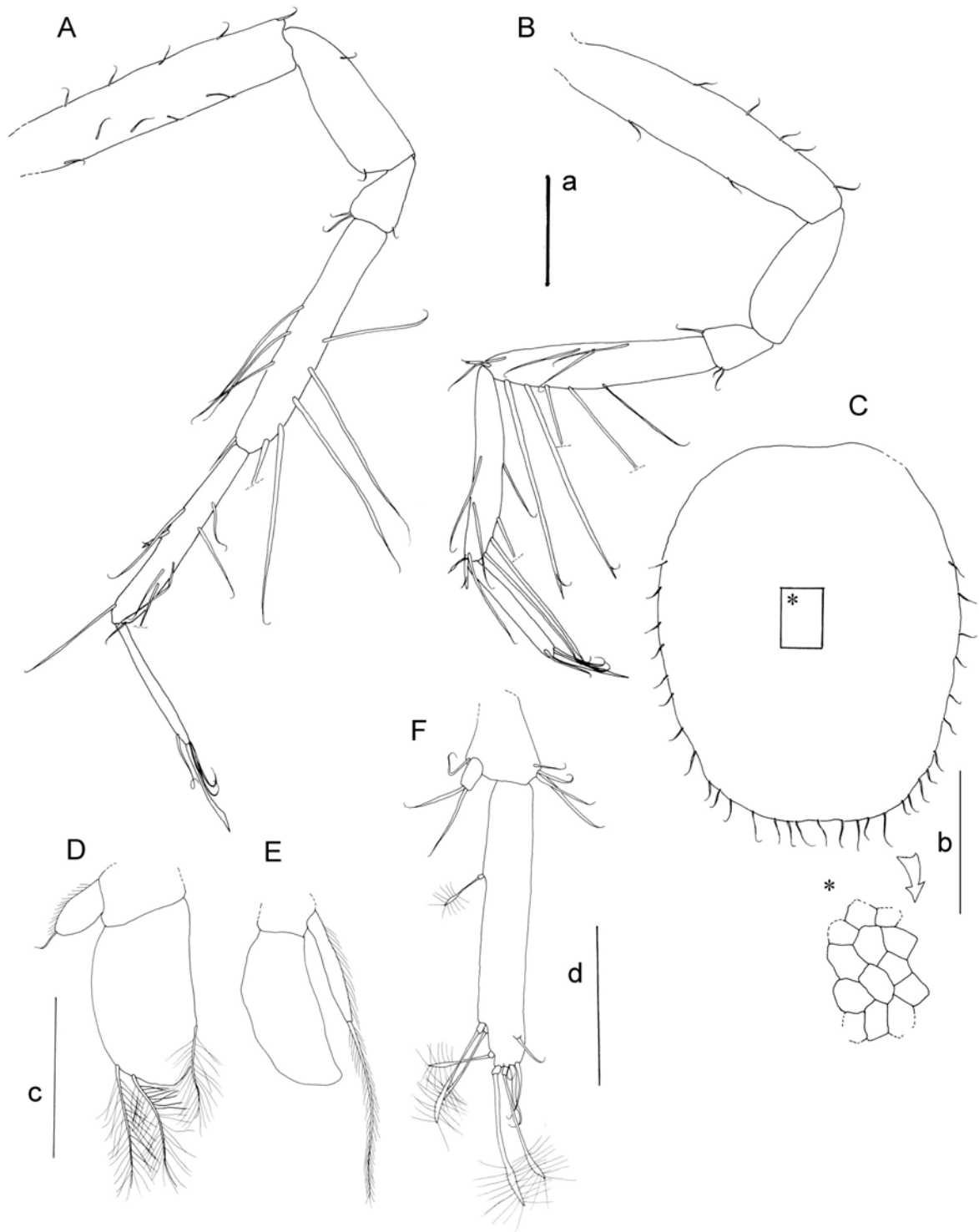
Uropods (Fig. 37): biramous. Endopod length 3.1 protopod length, 5.9 times longer than wide, medially with one small broom seta, terminally with five long broom setae, three slender setae and one small simple seta. Exopod length 0.1 endopod length, 1.7 width with terminally with two slender setae. Protopod length 1.2 width, with five setae.

#### **Differences in male:**

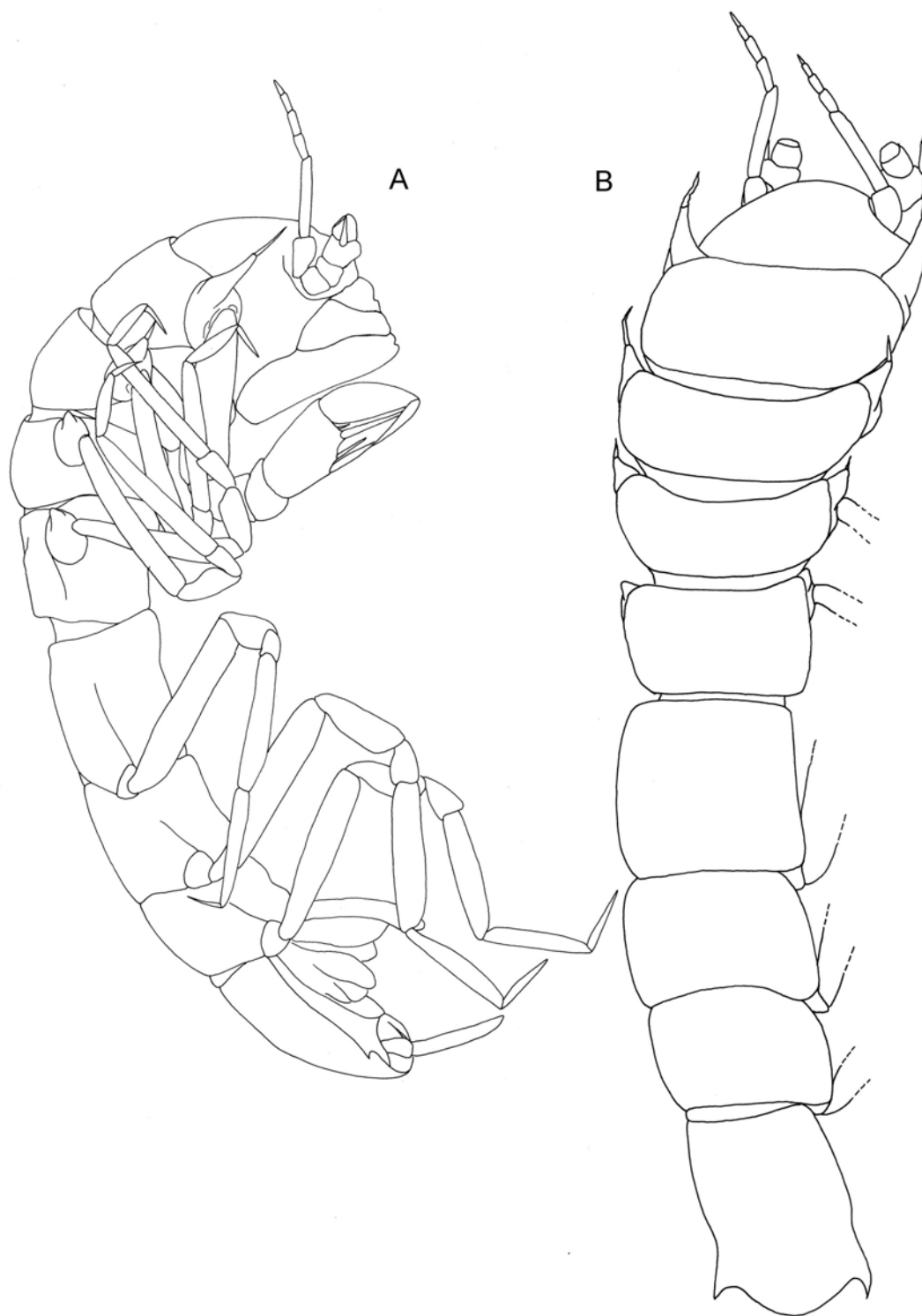
Habitus (Fig. 38): very similar to female, but coxae more produced, coxae 1-3 tipped with long stout sensory setae. Posterolateral spines at pleotelson more developed than in female.

Antenna (Fig.38): broken off after article 4, but unequally bifid seta at article 3 stronger developed than in female.

**Discussion:** The new species is assigned to the genus *Eugerdella* due to the robust pereopod with the ventral row of composed setae of irregular size on the carpus, carpus and propodus clearly broader than in pereopod II, the most distal setae being smallest and inserted next to a dais. It can be distinguished from other species of the genus by the characters of P I as there are the extremely small simple distal seta in the ventral row of irregular seta next to the propodus and the anterolateral elongation of the coxa which is longest of the anterior pereopods. *E. serrata* sp. nov., *E. pugilator*, *E. rotunda*, *E. polita*, *E. ordinaria*, *E. nonfunalis*, *E. minutula* and *E. falklandica* have a platform-like gap between the insertion of the propodus and the above mentioned short distal ventral seta, but in all these species this seta is unequally bifid, not simple and not as small as in the new species. *E. coarctata* and the type species *E. natator*, lack the platform-like gap. The new species possesses no ventral elongations as pereonites 1-5 or cephalic spine-rows as *E. serrata* sp. nov. and *E. pugilator*.



**Fig. 37:** *Euserdella theodori* sp. nov., paratype female, pereopods (A-B, scale a): P VI (A), P VII (B), pleopods (C-F, scale c); operculum (C, scale b), PI 3 (D), PI 4 (E), uropod (F, scale d), scales= 0.1 mm



**Fig.38:** *Eugerdella theodori* sp. nov., allotype male, habitus (A) lateral, (B) dorsal, scale = 0.5 mm

#### **3.1.5.1.3 *Momedossa longipedis* sp. nov.**

Holotype. – Female, preparatory, 2.4 mm; ZMH K-401007; type locality. – Angola Basin, start position: 18° 18,3' S 004° 41,3' E, end position: 18° 19,4' S 004° 41,9' E, depth 5395 m; RV Meteor M48/1; station 340; gear: EBS

Paratypes:

Allotype. – 1 male, adult, 2.5 mm; ZMH K-401008; locality. – As type locality.

Paratypes. – 3 females ZMH K-401009

#### **Etymology**

The name refers to the extremely long pereopods of this species.

#### **Diagnosis**

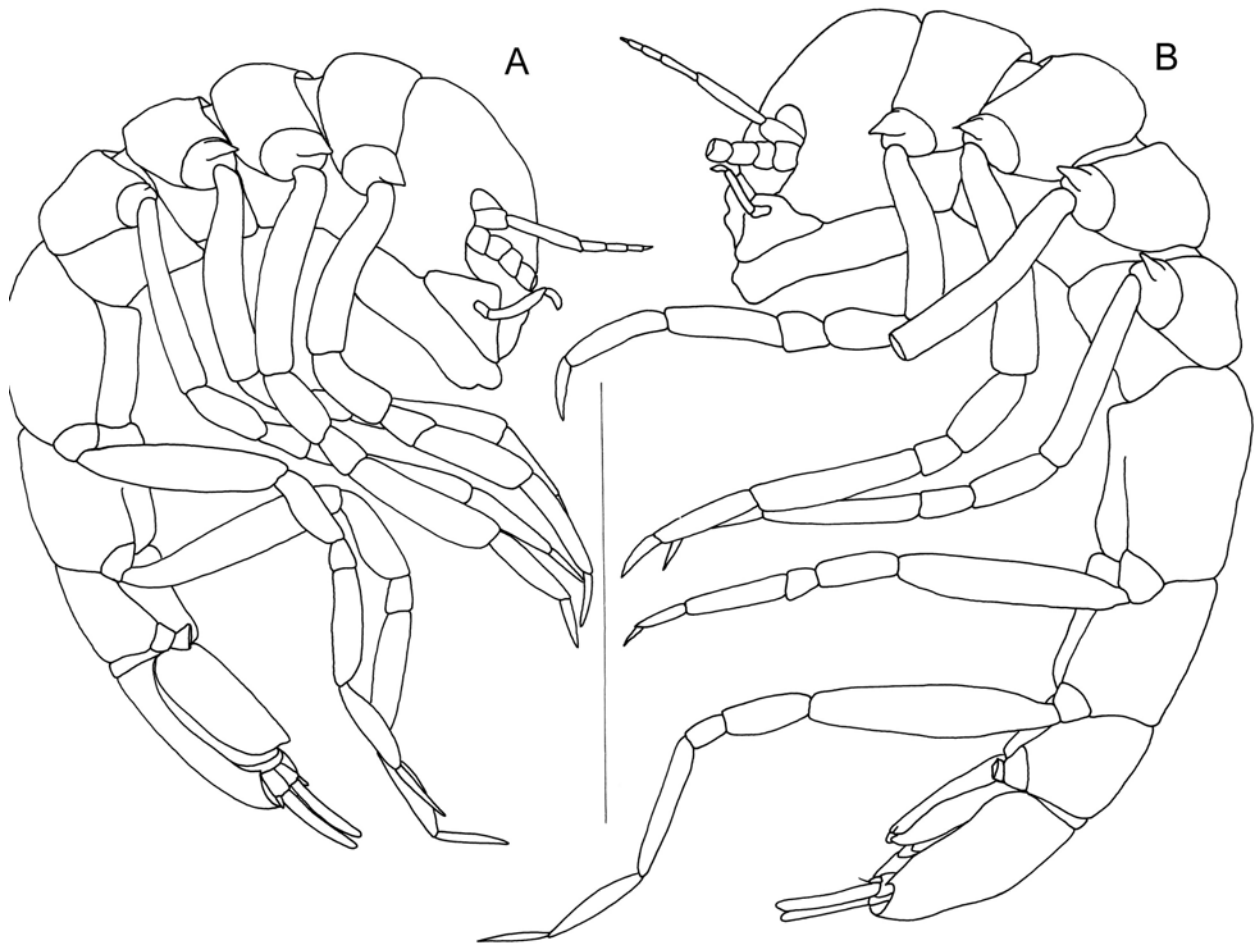
Body length about 4 times longer than width of pereonite 2. Cephalon with small bilateral bulges, Prn4 widest anteriorly, posteriorly as wide as Prn5, Prn5 slender. Carpus of P I without dorsal setae. Op rectangular, lateral margins straight.

#### **Description of holotype female**

Habitus (Fig. 39 B, 40 A): body 2.4 mm long (measured without appendages), 4.35 times longer than width of Prn2. Prn1 width 1.13 times cephalon width in dorsal view. Frons clypeal furrow present, without transverse ridge on frons. Prn1 length 1.2 Prn2 length, 0.92 Prn2 width. Prn5 width 1.2 length, anterior margin slightly convex, Prn 4 anteriorly widest, lateral margins of Prn5 straight. Lateral margins of Prns 6 and 7 slightly convex. Coxae 1-4 slightly produced, tipped with small stout setae. Plt length 1.15 width, small posterolateral spines present, lateral margins in front of spines convex, posterior margin rounded.

Antennula (Fig. 41): about 0.4 mm long, length 0.16 body length, with six articles. Article 1 with five small broom setae. Article 2 length 8 times width, 3.63 article 1 length; distally with three long broom setae. Article 3 distally with two small setae, article 4 distally with one broom seta, terminal article with one aesthetasc and two long slender setae. Articles 2-5 length relative to article 1: 3.63: 0.95: 0.77: 0.36: 0.23.

Antenna (Fig. 41): broken off

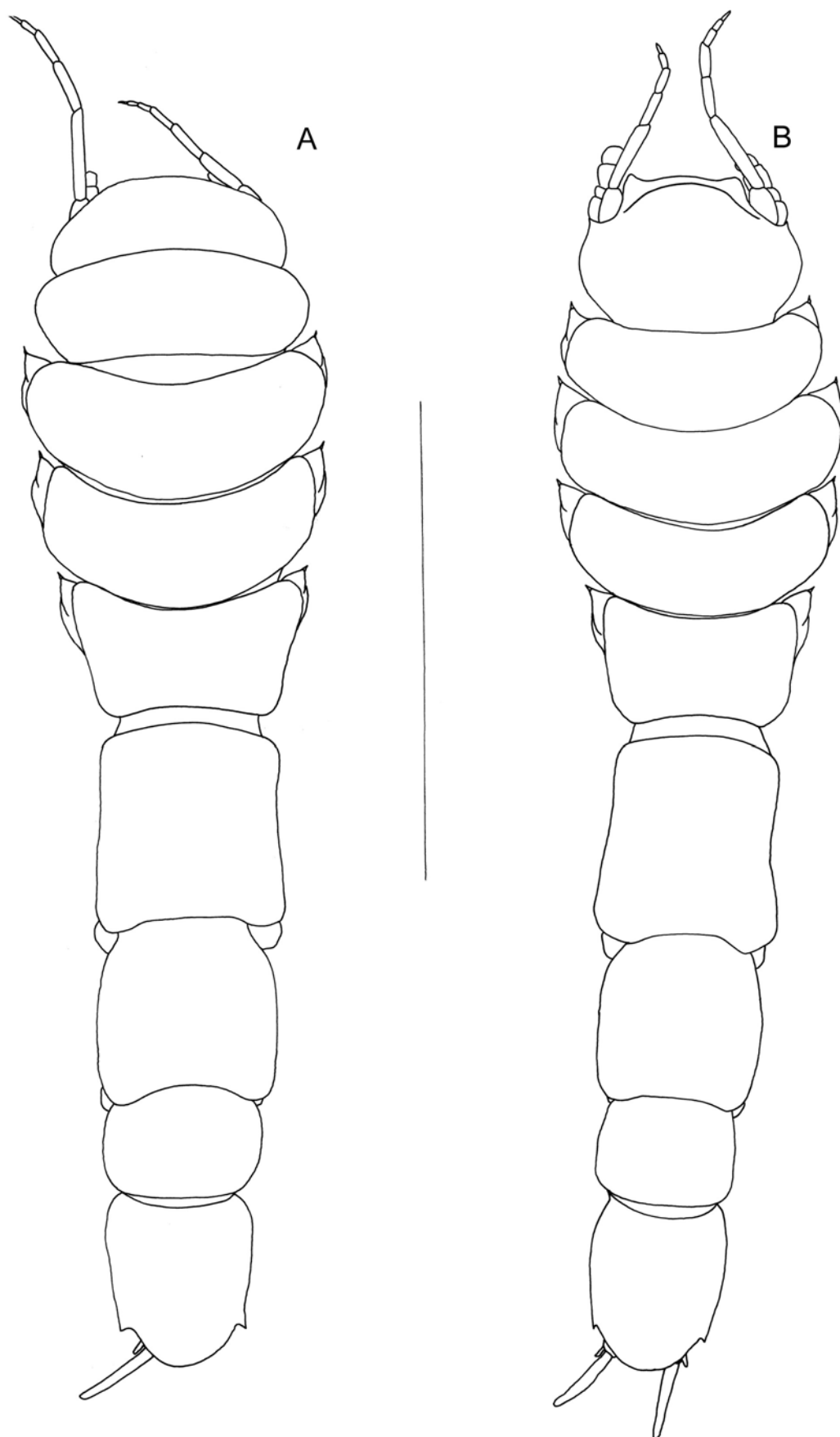


**Fig. 39:** *Momedossa longipedis* sp. nov., habitus lateral (A) allotype male, (B) holotype female, scale = 1 mm

**Mandible** (Fig. 41): First article of palp distally with one small seta, second article with distoventrally with dorsal rows of fine hairs and two small setulate setae, apical article with dorsal rows of fine hairs and five small setulate setae, distal seta longest. Ip with three lobes. Lm of MdL with four teeth, Lm-like structure of MdR triangular and terminal margin with eight small teeth (serrated). Spine row containing 12 spines.

**Maxillula** (Fig. 41): Inner lobe smaller than outer lobe (0.46 of outer lobe length), surrounded by numerous setae. Outer lobe 9.88 times longer than wide, terminally with 11 strong spines (four spines with setules), dorsally with nine setae, partly inserted in pairs, ventrally with 13 fine setae and eight small setae.

**Maxilla** (Fig. 41): Medial lobe slightly smaller than outer lobes (0.93 of outer lobe length), ventrally with four long setae near base followed by six pairs of fine setae, terminally with seven simple setae and numerous fine setae. Outer lobe 8.6 times longer than wide, marginally with six setae, terminally with four long setae.



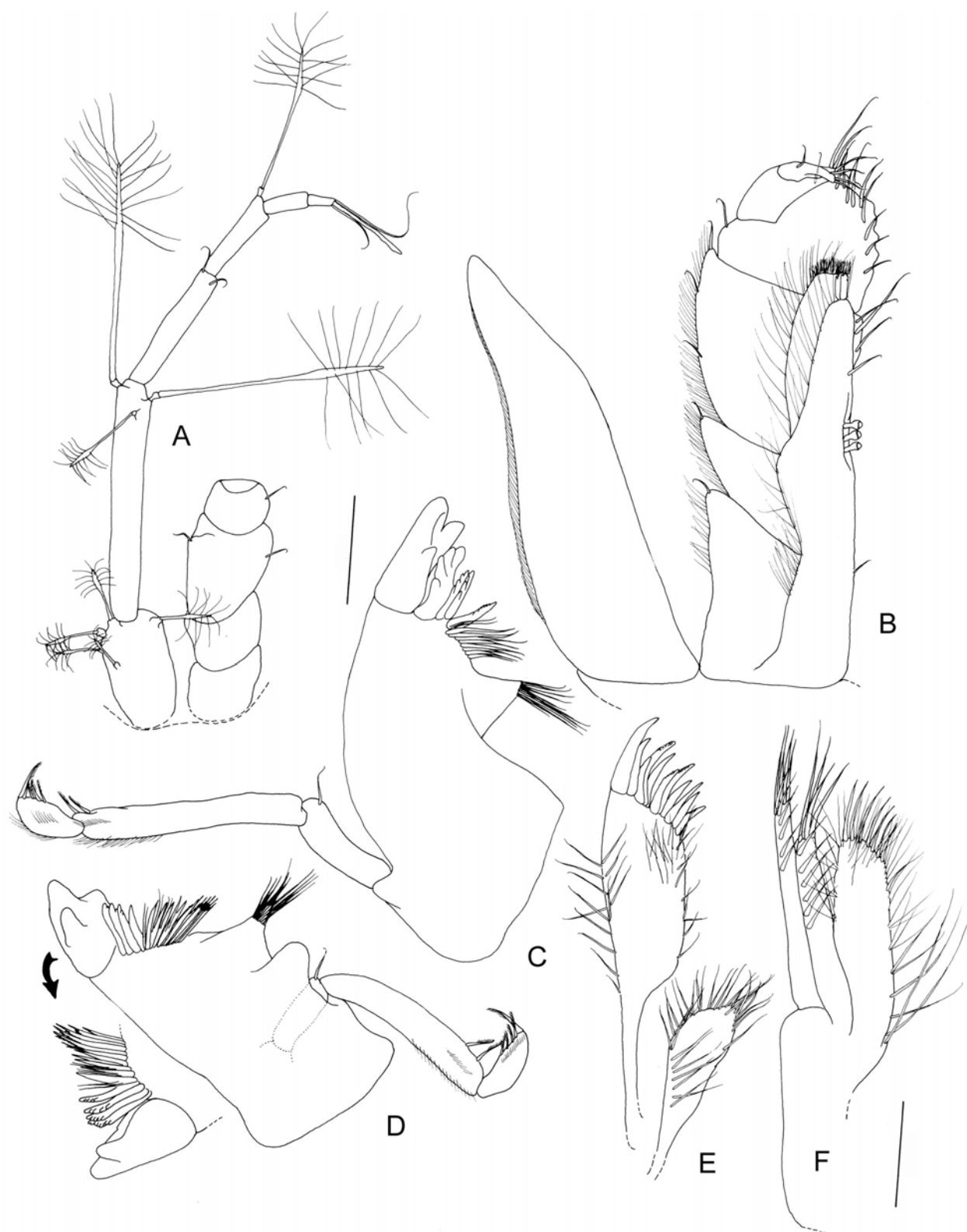
**Fig. 40:** *Momedossa longipedis* sp. nov., habitus dorsal (A) allotype male, (B) holotype female, scale = 1 mm

Maxilliped (Fig. 41): Epipodite length 3.92 width, length 1.15 endite length, outer margin with fine hairs in cuticular membrane. Endite with three retinaculae, terminally with numerous small setae and one star-shaped conate seta, marginally with numerous fine setae inserted in pairs. Outer margin of endite and palp articles 1 and 2 hirsute, edges tipped with small setae. Palp article 2 with four setae on inner margin, three setae on outer margin, article 3 with one seta on outer margin, nine setae on inner margin, article 4 with three setae, article 5 with two setae. Article 1 length 0.78 width, Article 2 length 1.75 width, Article 3 length 0.72 width, Article 4 length 0.5 width, Article 5 length 0.33 width.

Pereopod I (Fig. 42): Basis length 5 times width, marginally with 31 small setae, proximal to ischium ventrally with one long ventrally setulate seta. Ischium length 2.46 width, distodorsally with one slender seta, ventrally with four distally setulate setae. Merus length 0.92 width, distodorsally with one long slender seta, ventrally with one small and three distally setulate setae. Carpus length 3.72 width, ventrally with row of eight distally setulate setae increasing in length towards propodus, distal seta reaching half of length of propodus. Propodus length 5.86 width, with few simple slender setae. Dactylus length 5 times width, distally three small slender setae. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.

Pereopod II (Fig. 42): Basis length 4.75 width, marginally with one broom seta, 36 small setae and proximal to propodus with one long slender ventrally setulate seta. Ischium length 2.67 width, ventrally with seven distally setulate seta, proximal to merus two small and two simple setae. Merus length 1.4 width, distodorsally with one simple seta, ventrally with one small and four distally setulate setae. Carpus length 4.07 width, with dorsal and ventral rows of seta, ventrally with 17 distally setulate seta increasing in length towards propodus, dorsally with row of 19 setae, four small setae and distodorsally one unequally bifid seta. Propodus length 3.89 width, dorsally with row of 10 slender distally setulate setae and two small setae, ventral margin with four unequally bifid setae, fringed with fine hairs in cuticular membrane. Dactylus length 4 times width, distally with three small slender setae. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.





**Fig. 41:** *Momedossa longipedis* sp. nov., paratype female, antennula and first four articles of antenna (A), mouthparts: MdL (C), MdR (D), Mx1 (E), Mx2 (F), Mxp (B), scale = 0.1 mm

Pereopod VI (Fig. 42): Basis length 3.75 width, marginally with one broom seta and 13 small setae. Ischium length 2.45 width, with few small setae. Merus length 1.38 width, dorsodistally and ventrodistally with two small seta. Carpus length 4.5 width, ventrally with row of 11 long slender setae, dorsally with five simple setae and two small setae, distally with one unequally bifid seta. Propodus length 8.24 width, with ventral row of nine long setae and dorsal row of four setae. Dactylus length 11.5 width, two slender setae distally. Claw of dactylus with one long conate setae, two slender setae inserted next to it.

Pleopod 2 (operculum) (Fig. 43): rectangular, length 1.25 width, lateral margins straight, distal margin straight. Margins with 22 setae.

Pleopod 3 (Fig. 43): Endopod length 1.45 width, distally with 3 long plumose setae. Exopod length 0.25 of endopod length, outer margin smooth.

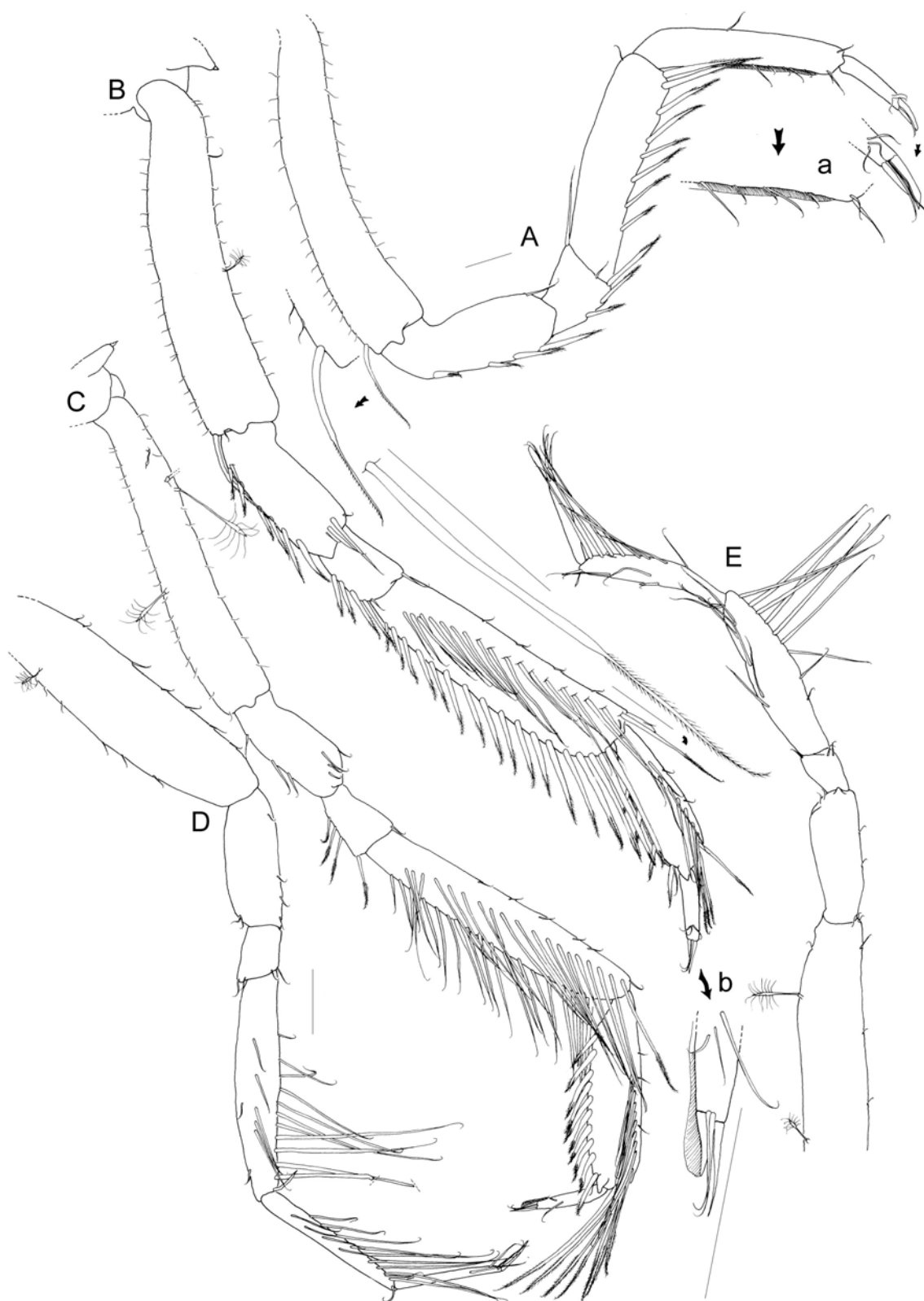
Pleopod 4 (Fig. 43): Endopod oval-shaped, length 1.94 width. Exopod length 6.57 width, outer margin smooth, distally with one long plumose seta.

Uropods (Fig. 43): biramous. Endopod length 4.11 protopod length, 7.09 times longer than wide, with four simple setae. Exopod length 0.08 endopod length, terminal with one simple seta. Protopod length 1.68 width, with one unequally bifid seta midway, one unequally bifid, one small and one slender seta distally, marginally eight broom setae.

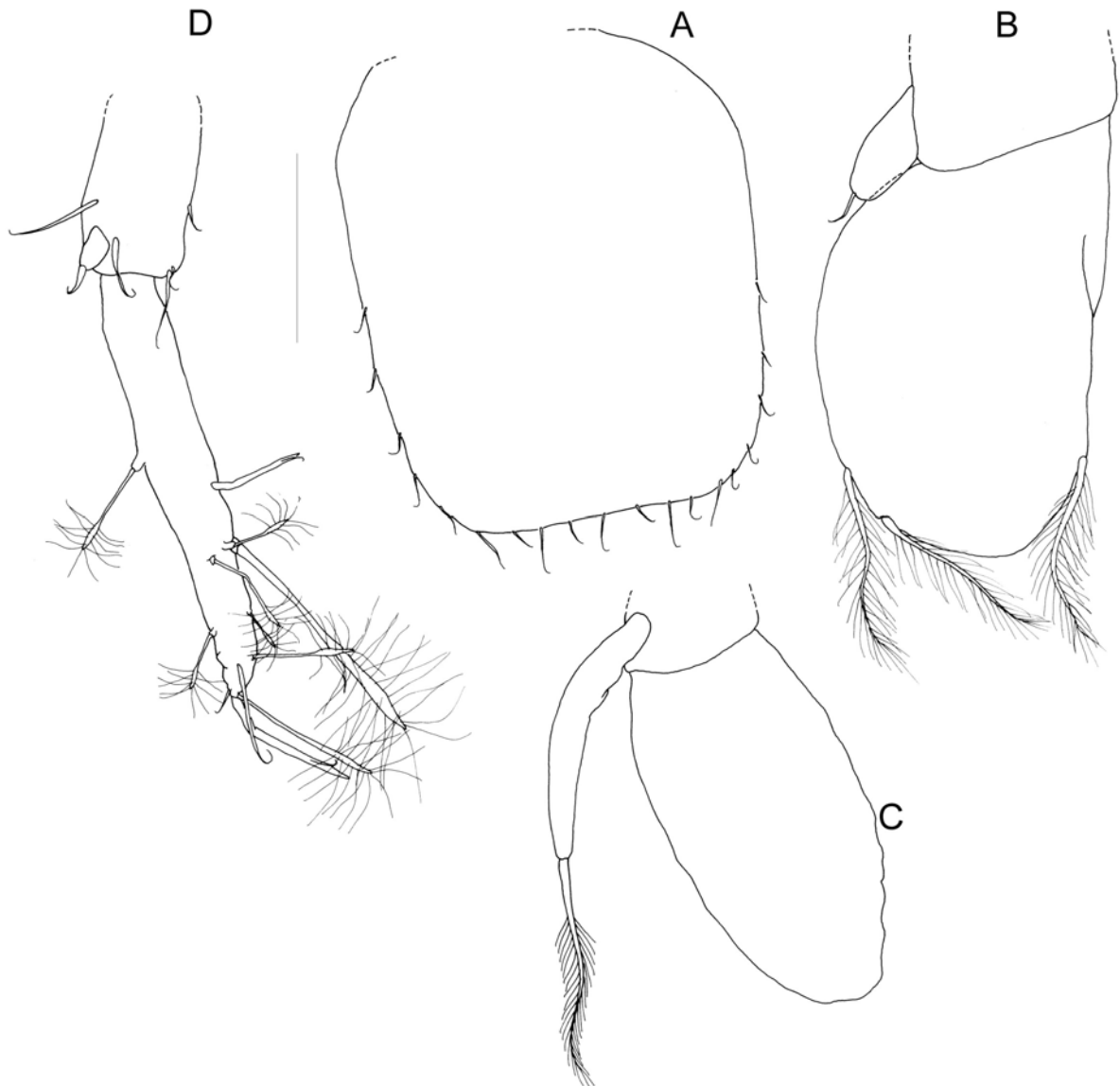
#### **Differences in male:**

Habitus (Fig. 39 A, 40 B): Except the sexual dimorphism in pleopod 1 and 2, the adult male is very similar to female, the cephalon is wider compared to the width of Prn1 and slightly more heavily built than in female.

**Discussion:** *Momedossa longipedis* sp. nov. is assigned to *Momedossa* mainly due to the characters of P I: carpus with a ventral row of composed setae, setae increasing in length towards the propodus, distal seta reaching not more than half of the length of the propodus, propodus is elongated (length more than 3.5 width).



**Fig. 42:** *Momedossa longipedis* sp. nov., paratype female, pereopods: P I (A), P II (B), P III (C), PVI (D), P VII (E), scales = 0.1 mm



**Fig. 43:** *Momedossa longipedis* sp. nov., paratype female, pleopods: PI2 (Op, A), PI3 (B), PI4 (C), Ur (D), scale = 0.1 mm

The pereopods are long compared to the total body length of the specimen, carpi and propodi setose. The new species differs from the only other species of the genus, *M. profunda* Hessler, 1970 by following apomorphies: cephalon with small bilateral bulges between the antennular folds, Prn4 widest anteriorly, posteriorly as wide as Prn5, Prn5 slender, the carpus of P I lacks dorsal setae except one distodorsal small seta and carpi and propodi of Prn5-7 are not as broad and rows of natatory setae are not as setose and well developed as in *M. profunda*, operculum rectangular, lateral margins straight.

#### **3.1.5.1.4     *Torwolia tinbieniae* sp. nov.**

Holotype. – Female, preparatory, 2.3 mm; ZMH K-401010; type locality. – Angola Basin, start position: 18° 18,3' S 004° 41,3' E, end position: 18° 19,4' S 004° 41,9' E, depth 5395 m; RV *Meteor* M48/1; station 340; gear: EBS

Paratypes:

Paratype. - 1 female, adult, 2.6 mm; ZMH K-401011; locality. - Angola Basin, start position: 16° 18,1' S 005° 27,2' E, end position: 16° 19,3' S 005° 27,2' E, depth 5390 m; RV *Meteor* M48/1; station 348 ; gear: EBS.

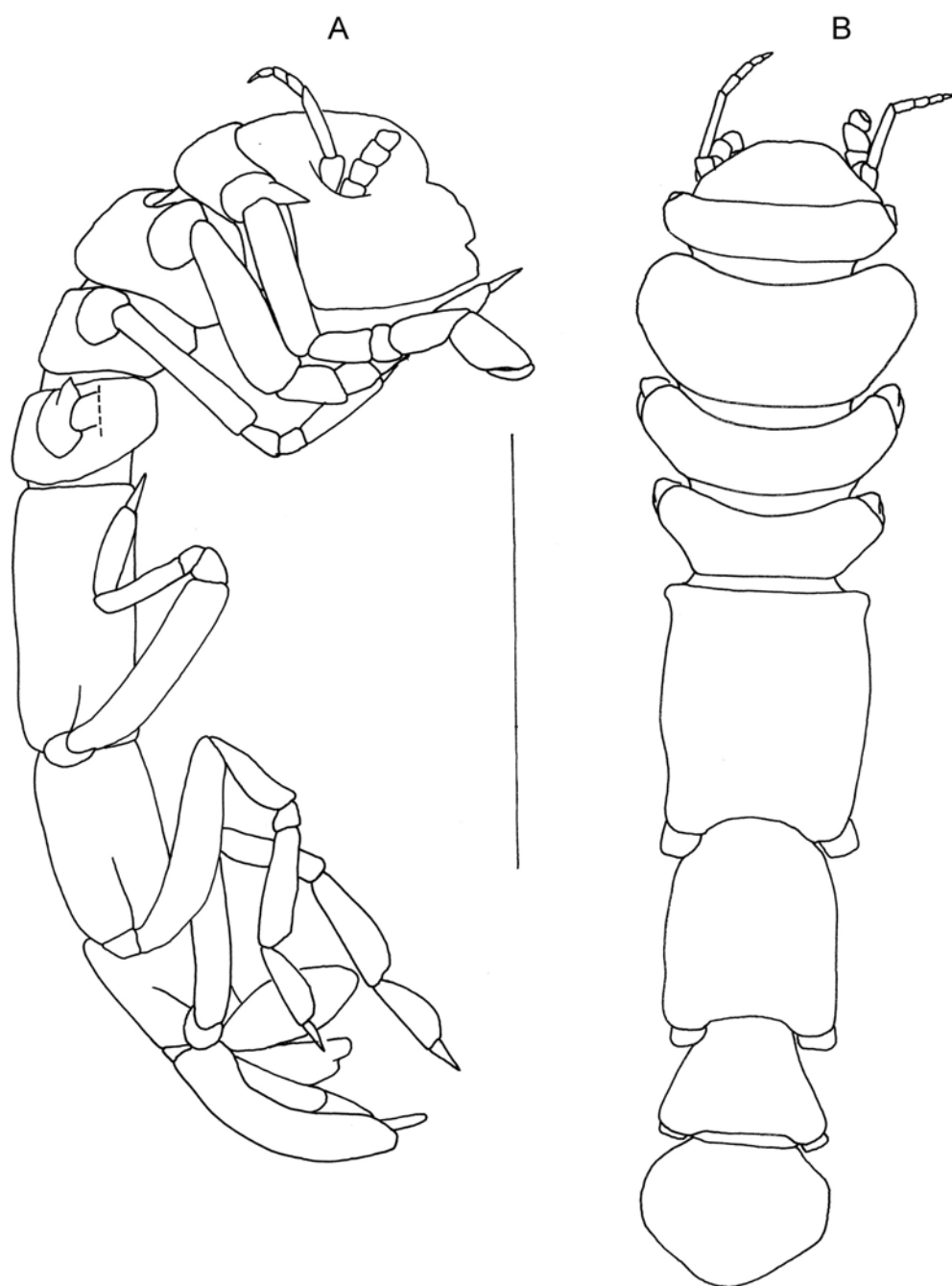
Paratype. - 1 female, preparatory, 2.4 mm; ZMH K-401012; locality. - Angola Basin, start position: 16° 18,1' S 005° 27,2' E, end position: 16° 19,3' S 005° 27,2' E, depth 5390 m; RV *Meteor* M48/1; station 348 ; gear: EBS.

#### **Etymology**

The first part of the name refers to the nickname, “Tini”, of a very close relative, the second part of the name refers to the german word for bee, “Biene”. The name alludes to a joke made between good friends.

#### **Diagnosis**

Body length about 4 times longer than width of Prn 2. Prn 1 about 0.5 of length Prn 2. Prn 2 enlarged, 2 times longer in midsagital length than Prn 3 and 4. Prn 5 elongated, lateral margins slightly convex and inflated. Mouthparts bent forwards. Antennula consisting of 6 articles. P I small, subchelate, much smaller than P II., carpus ventrally with few (3-4) slender distally setulate setae, propodus widest midway, tapering towards dactylus, without setae, ventrally fringed with fine hairs in cuticular membrane. P II heavily built, carpus and propodus broad, with ventral and dorsal rows of numerous composed setae, bearing sensory folds all over. Carpus and propodus of posterior P with few (3-4) natatory setae ventrally. Operculum rounded, as wide as long, 4 small setae at distal margin. Uropods uniramous.



**Fig. 44:** *Torwolia tinbienae* sp. nov., holotype female, habitus lateral (A), habitus dorsal (B), scale = 1 mm

#### **Description of holotype female**

Habitus (Fig. 44): body 2.3 mm long (measured without appendages), 4.2 times longer than width of Prn 2. Prn 1 width 1.2 times cephalon width in dorsal view. Mouthparts bent forwards. Frons clypeal furrow present, without transverse ridge on frons. Prn 1 length 0.43 Prn 2 length, 0.81 Prn 2 width. Prn 5 width 0.9 length, anterior margin straight, lateral margins of Prn 5 convex. Prn 6 and 7 lateral margins straight. Coxae 1-4 produced, coxa 1 tipped with short stout seta. Pleotelson length 0.74 width, without posterolateral spines, margins rounded.

Antennula (Fig. 45): about 0.4 mm long, length about 0.2 body length, with six articles. Article 1 with five broom setae and one small seta. Article 2 length 6 times width, 2.1 article 1 length; with two long terminal broom setae. Article 3 without setae, article 4 with two small broom setae, distal article terminally with one small broom seta, one aesthetasc and two long slender setae. Articles 2-5 length relative to article 1: 2.1: 0.86: 0.97: 0.59: 0.52.

Antenna (Fig. 45) about 0.9 mm long, length 0.39 body length, with 18 articles. Articles 1 and 2 without setae, article 3 with one small seta. Article 4 with two small setae. Article 5 length 5.6 width, distally with two slender setae. Article 6 length 8 times width, distally with five slender setae. Flagellar articles sporadically with slender setae, distal article terminally with four long slender setae. Relative length of articles: 1: 1.3: 1: 1.3: 6.2: 8: 2.4: 1.4: 1.3: 1.5: 1.2: 1: 1.1: 0.7: 0.4: 0.5: 0.5: 0.2.

Mandible (Fig. 45): First article of palp distally with one small seta, second article distally fringed with three rows of numerous fine hairs, ventrodistally with two small setulate setae, apical article with three terminal setae, distal seta longest and ventrally setulate, dorsally with row of numerous fine hairs. Incisor process with Three lobes. Lm of MdL with three teeth. Spine row containing four simple spines. Molar process triangular with nine slender setae.

Maxillula (Fig. 45): Inner lobe slightly smaller than outer lobe (0.76 of outer lobe length), with 21 setae. Outer lobe 5.2 times longer than wide, marginally with pairs of fine setae, terminally with 10 strong spines.

Maxilla (Fig. 45): Medial lobe 6.1 width, broader than other lobes, surrounded by more than 20 fine setae which marginally are inserted in pairs. Outer lobes about 5

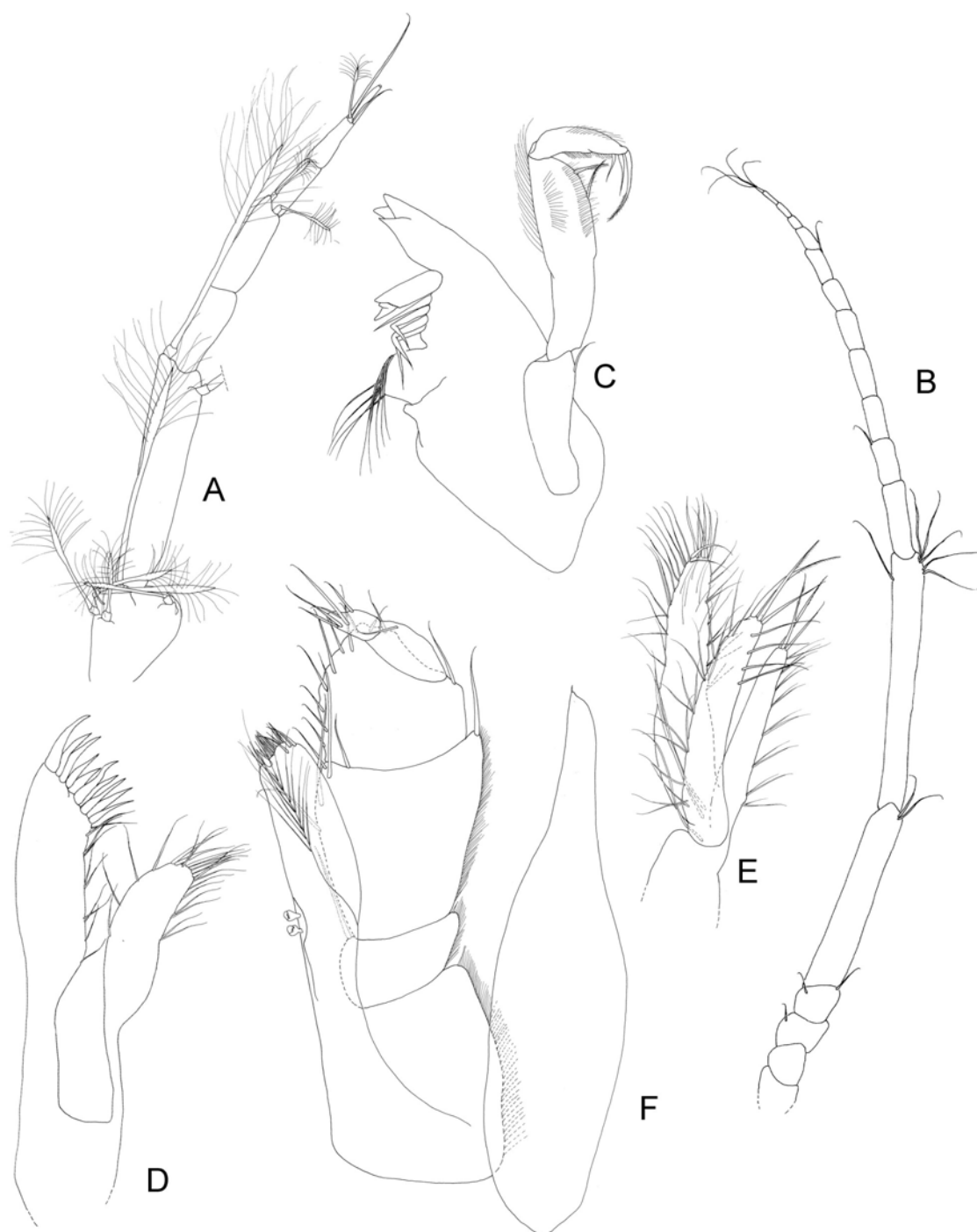
times width, terminally with three setulate setae, ventrolaterally with six pairs of fine seta of setae dorsolaterally with four slender setae.

Maxilliped (Fig. 45): Epipodite length 4.04 width, length 1.1 endite length. Endite with two retinaculae, terminally with one stout seta and numerous small setae, marginally with eight pairs of fine setae. Outer edge of endite and palp articles 1 and 2 hirsute, of palp article 2 tipped with one seta. Inner margin of palp article 2 with four setae. Palp article 3 with 10 setae on inner margin, one on outer margin. Article 4 with one seta, article 5 with five setae. Article 1 length 0.57 width, article 2 and 3 length 1 times width, article 4 length 0.52 width, article 5 length 2.1 width.

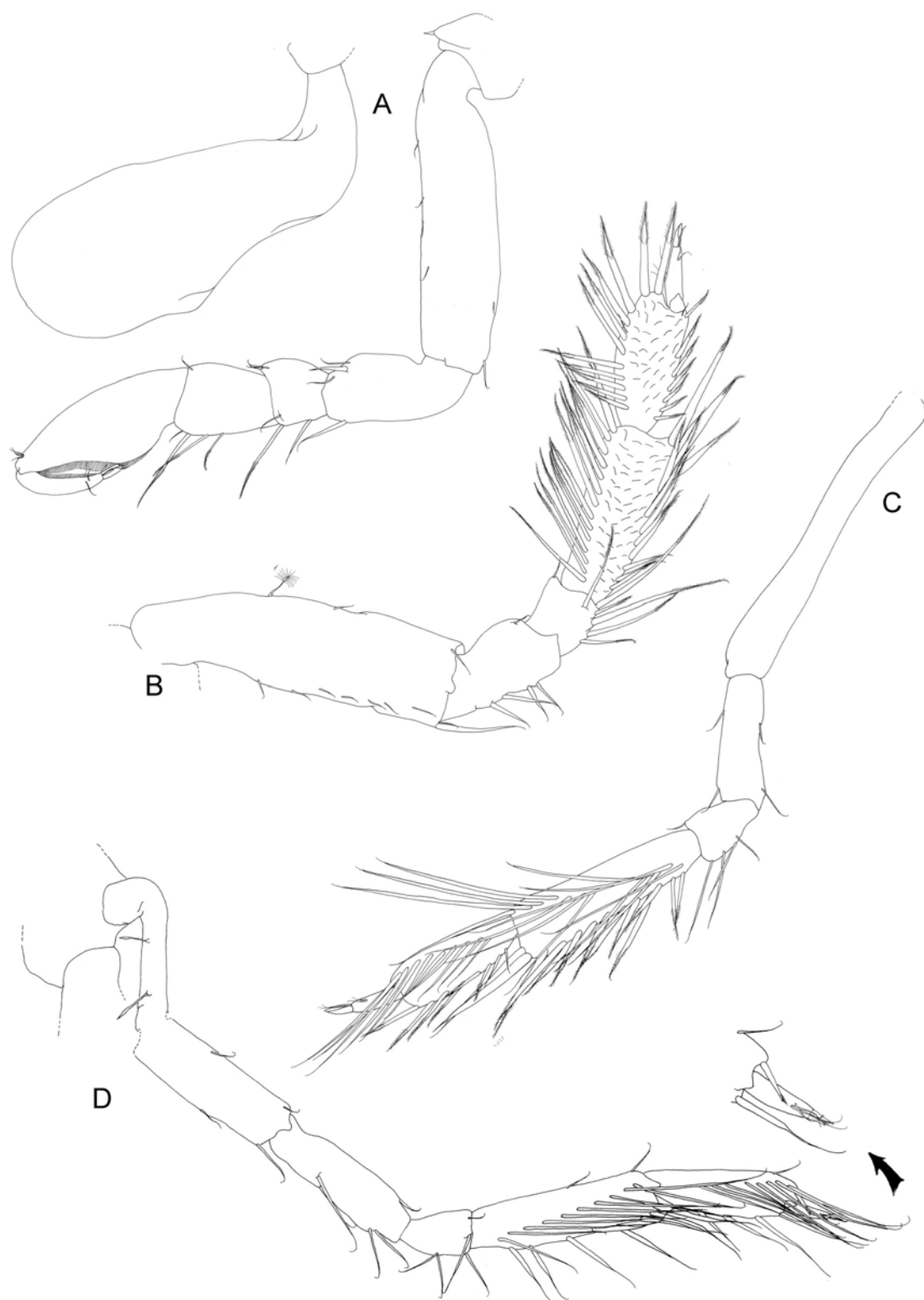
Pereopod I (Fig. 46): Basis length 4.05 width, with six small setae, proximal to ischium ventrally one slender seta. Ischium length 2.25 width, dorsally with one stout simple seta and two small slender seta, ventrally with one simple slender seta. Merus length 0.9 width, ventrally with two slender distally setulate setae and one small slender seta, distodorsally with two small slender setae. Carpus length 1.41 width, ventrally with three long slender distally setulate setae and one small seta, distodorsally with one simple seta. Propodus length 2.5 width, distodorsally few small setae, ventrally fringed with numerous fine hairs in cuticular membrane Dactylus length 5.13 width, terminally two small setae. Claw of dactylus with one cuspidate and one conate setae as well as two slender setae medially.

Pereopod II (Fig. 46): Basis length between 3.64 width, with one plumose seta and nine small setae, ventrodistally proximal to ischium one long simple seta. Ischium length 2 times width, distodorsally one small seta, ventrally four setae. Merus length 1.13 width, distodorsally one small seta, ventrally with six long slender distally setulate setae description of setae. Carpus length 2.54 width, with ventral and dorsal rows of 12-14 composed setae. Propodus length 2.22 width, with ventral and dorsal rows of composed setae. Dactylus length 4.7 width, distally with two small setae. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.





**Fig. 45:** *Torwolia tinbienae* sp. nov., paratype female, antennula (A), antenna (B), mouthparts (C-F): MdL (C), Mx1 (D), Mx2 (E), Mxp (F)



**Fig. 46:** *Torwolia tinbienae* sp. nov., paratype female, pereopods: PI (A, left oostegite), PII (B), PIII (C), PIV (D)

Pereopod III (Fig. 46): Basis length 6.76 width. Ischium length 2.45 width, with two small slender setae on each margin. Merus length 1.32 width, ventrally with four slender setae, distodorsally one small seta. Carpus length 3.8 width, dorsally with row of 14 slender setae, ventrally with row of 13 robust distally setulate setae. Propodus length 2.48 width, dorsally with row of 10 slender setae, ventrally with row of eight distally setulate setae. Dactylus length 5.38 width, terminally two small setae. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.

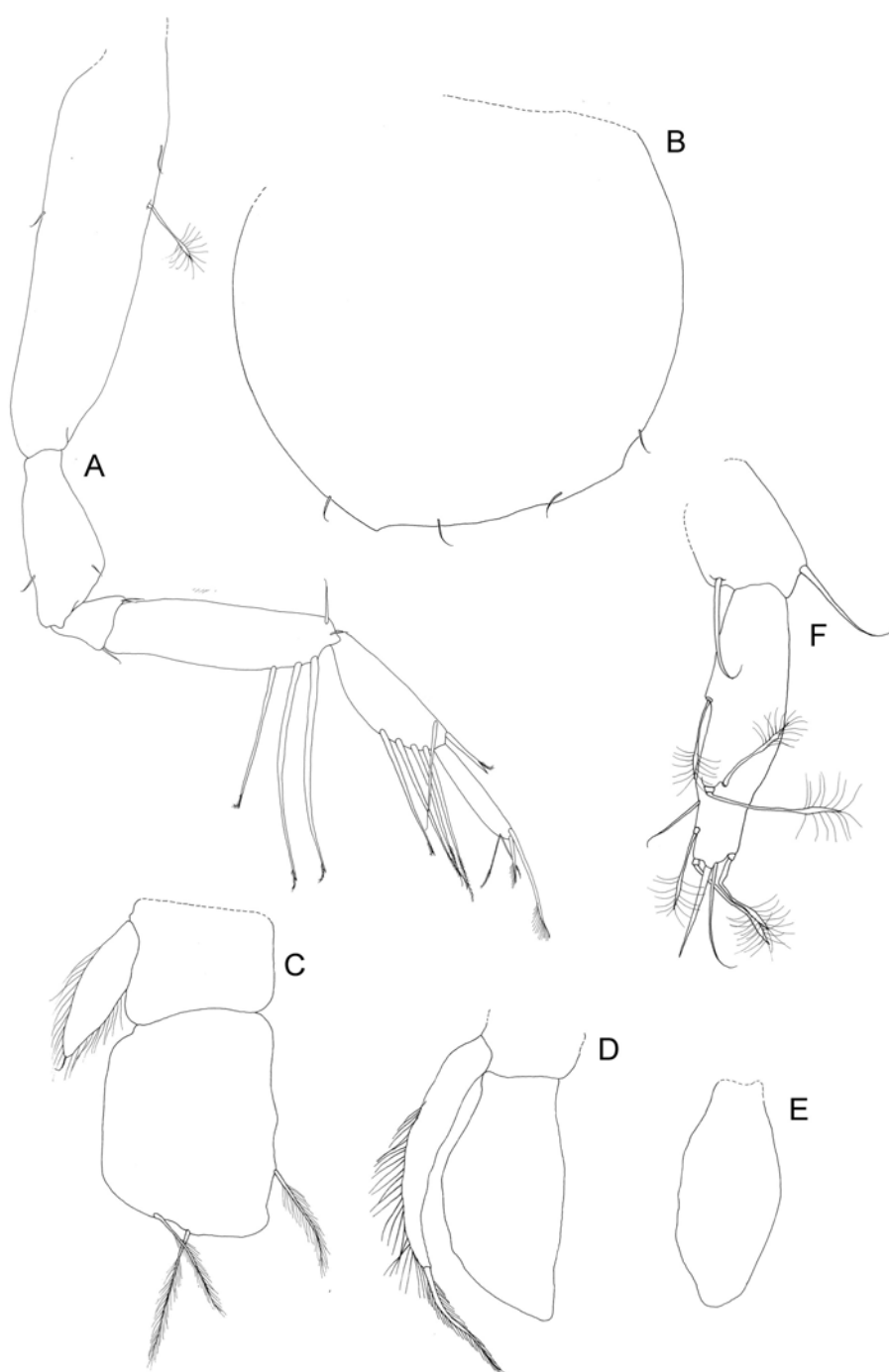
Pereopods V-VII (Fig. 47): Basis length between 11.3 and 16.8 width, few broom setae and few small setae. Ischium length about 5.5 width, with few small setae. Merus length about 3 times width, with few small setae. Carpus length 8.8 width, ventrally with row of long distally unequally bifid setae, distodorsally few setae. Propodus length between 5.8 and 7.1 width, ventrally with row of long distally unequally bifid setae, dorsally few long setae and distally one stout unequally bifid seta. Dactylus length about 4.3 width, with two small slender distally setulate setae. Claw being represented by one short and one long seta which possess long setules at their terminal part.

Pleopod 2 (operculum) (Fig. 47): length 0.98 width. Lateral margins convexly rounded, distal margin straight with bilateral triangular bulges, four small setae.

Pleopod 3 (Fig. 47): Endopod length 1.3 width, distally with 3 long plumose setae. Exopod length 0.19 of endopod length, margins hirsute, distally tipped with small seta.

Pleopod 4 (Fig. 47): Endopod oval, length 1.94 width. Exopod length 6.9 width, outer margin with numerous small slender setae.

Uropods (Fig. 47): uniramous. Endopod length 2.26 protopod length, 3.65 times longer than wide, with five broom setae, one simple and two simple slender setae. Protopod length 1.27 width, with two simple slender setae.



**Fig. 47:** *Torwolia tinbienae* sp. nov., paratype female, P VII (A), pleopods: Op (B), PI3 (C), PI4 (D), PI5 (E), Ur (F)

**Discussion:** The new species is assigned to the genus *Torwolia* due to the small subchelate P I, Prn1 being half as long as Prn2 which is largest of the anterior four pereonites, the relatively robust P II in comparison to P III and IV and the convex margins of the elongated Prn 5.

The body form (inflated Prn5 with convex margins) resembles most *T. subchelatus*. In characters of pereopod I, the new species resembles more *T. creper*. This species also possesses long slender distally setulate seta on the ventral margins of ischium, carpus and propodus, while in *T. subchelatus* there are slender setae without setules present.

*T. tinbieniae* sp. nov. differs from the two other species of the genus by following apomorphies: Anterolateral corners of Prn5 rounded, ip of three teeth, Lm of three teeth, lateral margins of operculum convexly rounded, distal margin straight with bilateral triangular bulges, four small setae, ventral margin of propodus of pereopod I without small setae and pereopods V-VII less setose.

#### 3.1.5.2 ANDEEP I & II

##### ***Eugerdella serrata* sp. nov.**

Holotype. – Female, adult, 2.5 mm; ZMH K-401004; Type locality. – Weddell Sea, start position: 65°20.17 S-65°20.08 S, end position: 54°14.30 W-54°14.34 W, depth 1121 m; 07.02.02 RV *Polarstern*; station 133-3; gear: EBS

##### Paratypes:

Allotype. – 1 male, adult, 2.6 mm; ZMH K-401005; locality. – As type locality.

Paratypes. – 26 specimens ZMH K-401006; locality. – As type locality.

##### **Etymology**

The name refers to the strongly serrated margins of the pleotelson and the cephalic spine row located at the antennular folds of this species.

##### **Diagnosis**

Body length about 3 times longer than width of Prn 2. Prn1-5 with spine-like ventral elongations. Cephalic spine row dorsally at antennular folds. Antennula of five articles. Lm with three teeth. Lateral margins of Prn5-7 smooth in female, serrated in

male, Prn5 marginal flanges anterolaterally produced triangular-shaped. Between row of composed ventral setae of irregular size on carpus of P I fringed combs of fine hairs inserted in cuticular membrane, propodus of P I with two unequally bifid setae, with row of dorsal setae. Uropods uniramous.

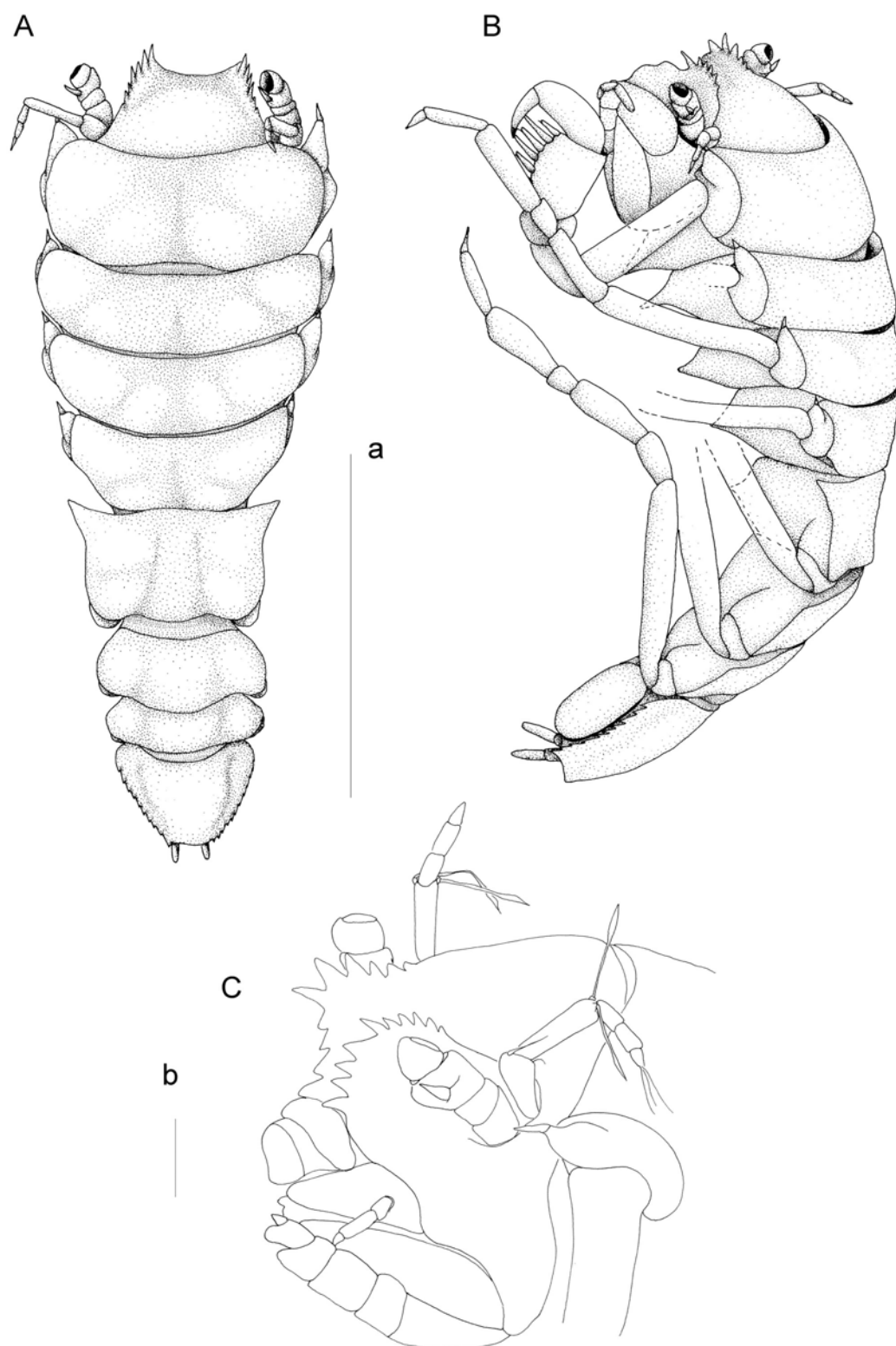
#### **Description of holotype female**

Habitus (Fig. 48): body 2.5 mm long (measured without appendages), 2.72 times longer than width of Prn2. Prn1 width 1.71 times cephalon width in dorsal view. Prn1 length 1.3 Prn2 length, 0.98 Prn2 width. Prn5 width 1.59 length, anterior margin medially slightly convex, towards anterolateral corners slightly concave going over into triangular-shaped marginal flanges, lateral margins of Prn5 slightly concave. Prn6 and 7 lateral margins straight Coxae 1-4 produced, tipped with small stout setae. Pleotelson length 0.58 width, lateral margins serrated.

Antennula (Fig. 49): 0.35 mm long, length 0.23 body length, with five articles. Article 1 with three broom setae and one small seta. Article 2 length 4.47 width, 1.6 article 1 length; distally with two small and two long articulated broom setae. Article 3 with one slender seta, article 4 with four small broom setae, distal article terminally with aesthetasc and three long slender setae. Articles 2-5 length relative to article 1: 1.6: 0.55: 0.52: 0.19.

Antenna (Fig. 49) about 1.2 mm long, length 0.48 body length, with 17 articles. Articles 1-4 lost during dissection. Article 5 with one broom seta, two slender setae and two simple setae. Article 6 marginally with three, distally with five slender setae. Distal flagellar article with five long slender setae.

Antenna (Fig. 49) about 1.2 mm long, length 0.48 body length, with 17 articles. Articles 1-4 lost during dissection. Article 5 with one broom seta, two slender setae and two simple setae. Article 6 marginally with three, distally with five slender setae. Distal flagellar article with five long slender setae.



**Fig. 48:** *Eugerdella serrata* sp. nov., holotype female, habitus dorsal (A, scale a), lateral (B, scale a), detail cephalothorax (C, scale b), scale a = 1 mm, scale b = 0.1 mm

### 3. Results

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Antenna (Fig. 49) about 1.2 mm long, length 0.48 body length, with 17 articles. Articles 1-4 lost during dissection. Article 5 with one broom seta, two slender setae and two simple setae. Article 6 marginally with three, distally with five slender setae. Distal flagellar article with five long slender setae.

Mandible (Fig. 49): First article of palp without setae, second article without setae, apical article with seven fine setae and two stronger terminal setae. Ip with four teeth. Lm of MdL with three teeth, Im-like structure of MdR distally serrated. Spine row containing of eight spines. Mp triangular with 14 setae.

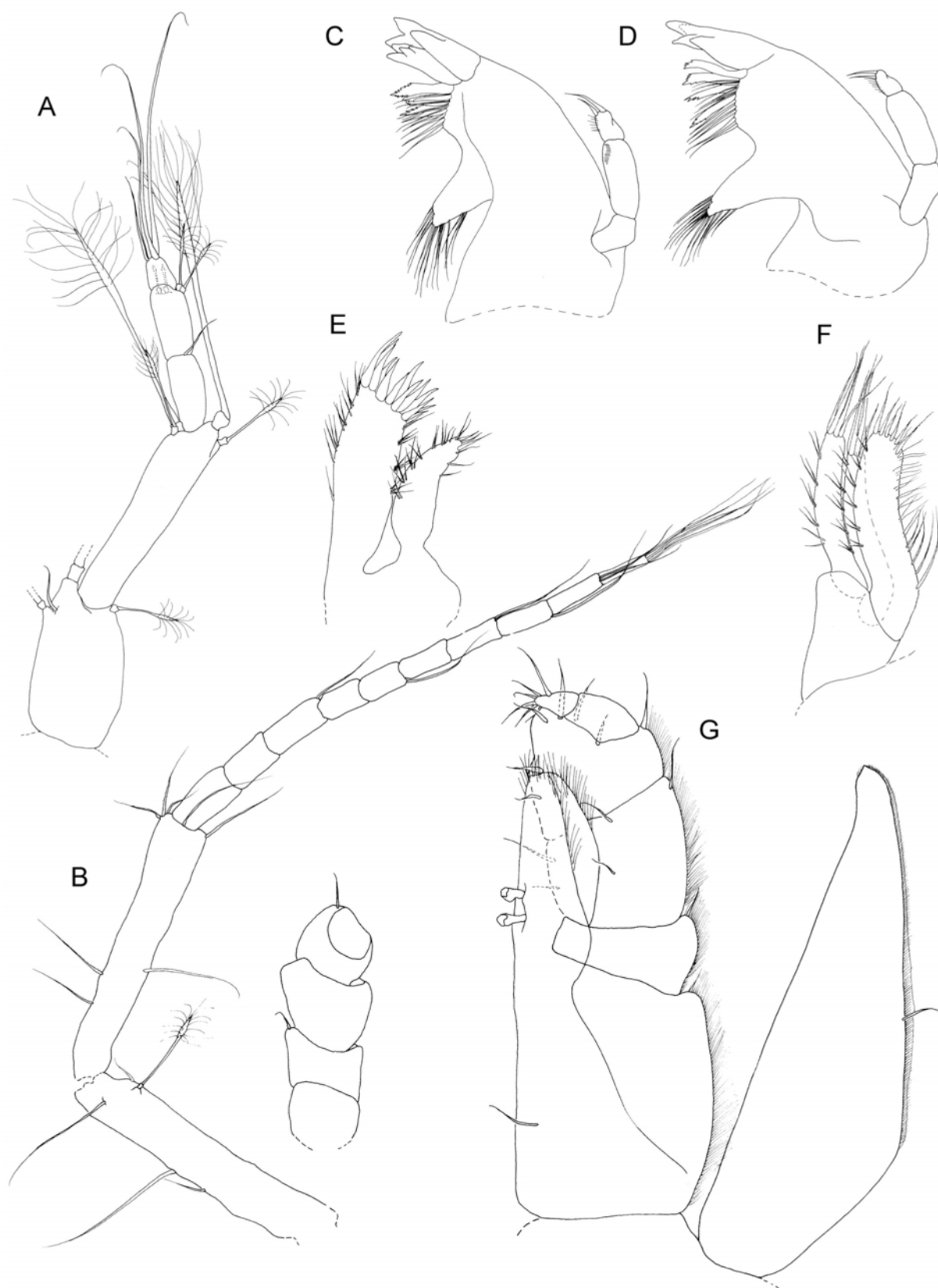
Maxillula (Fig. 49): Inner lobe slightly smaller than outer lobe (0.76 of outer lobe length), with 24 setae. Outer lobe 4 times longer than wide, marginally with fine setae inserted in bunches of three together, terminally with 13 strong spines.

Maxilla (Fig. 49): Medial lobe of similar length of other lobes, terminally with six setae, ventrolaterally with five long setae near to base and eight pairs of fine setae. Outer lobe length 6.25 width, terminally with four setae, dorsolaterally with five pairs of fine setae.

Maxilliped (Fig. 49): Epipodite length 3.24 width, length 1.15 endite length. Endite with two coupling hooks, terminally with numerous fine setae. Outer margin of endite and palp articles 1-3 hirsute, tipped with one seta each. Inner margin of palp article 3 with five setae, article 4 without setae, article 5 with six setae. Article 1 length 0.45 width, article 2 length 0.97 width, article 3 length 0.52 width, article 4 length 1.33 width, article 5 length 1.6 width.

Pereopod I (Fig. 50): Basis length 3.57 width, with few small setae, proximal to ischium one simple seta. Ischium length 1.9 width, ventrally with one small and two simple setae, dorsally with one small seta midway and distally two stout simple setae. Merus length 0.5 width, ventrally with tow simple slender, one small and unequally bifid distally setulate seta. Carpus length 1.76 width, ventrally with row of robust unequally bifid setae of irregular size and five simple seta, between composed setae combs of fine hairs inserted in a cuticular membrane, distodorsally one simple seta. Propodus length 2.22 width, ventrally with two small unequally bifid setae, three small simple setae and combs of fine hairs inserted in a cuticular membrane, dorsally row of six setae. Dactylus length 2.75 width, distally four small slender setae.





**Fig. 49:** *Eugerdella serrata* sp. nov., paratype female, antennula (A), antenna (B), mouthparts (C-G): Md L (C), Md R (D), Mx 1 (E), Mx 2 (F), Mxp (G) , scale = 0.1 mm

Claw of dactylus with one cuspidate and one conate setae, two slender setae inserted medially.

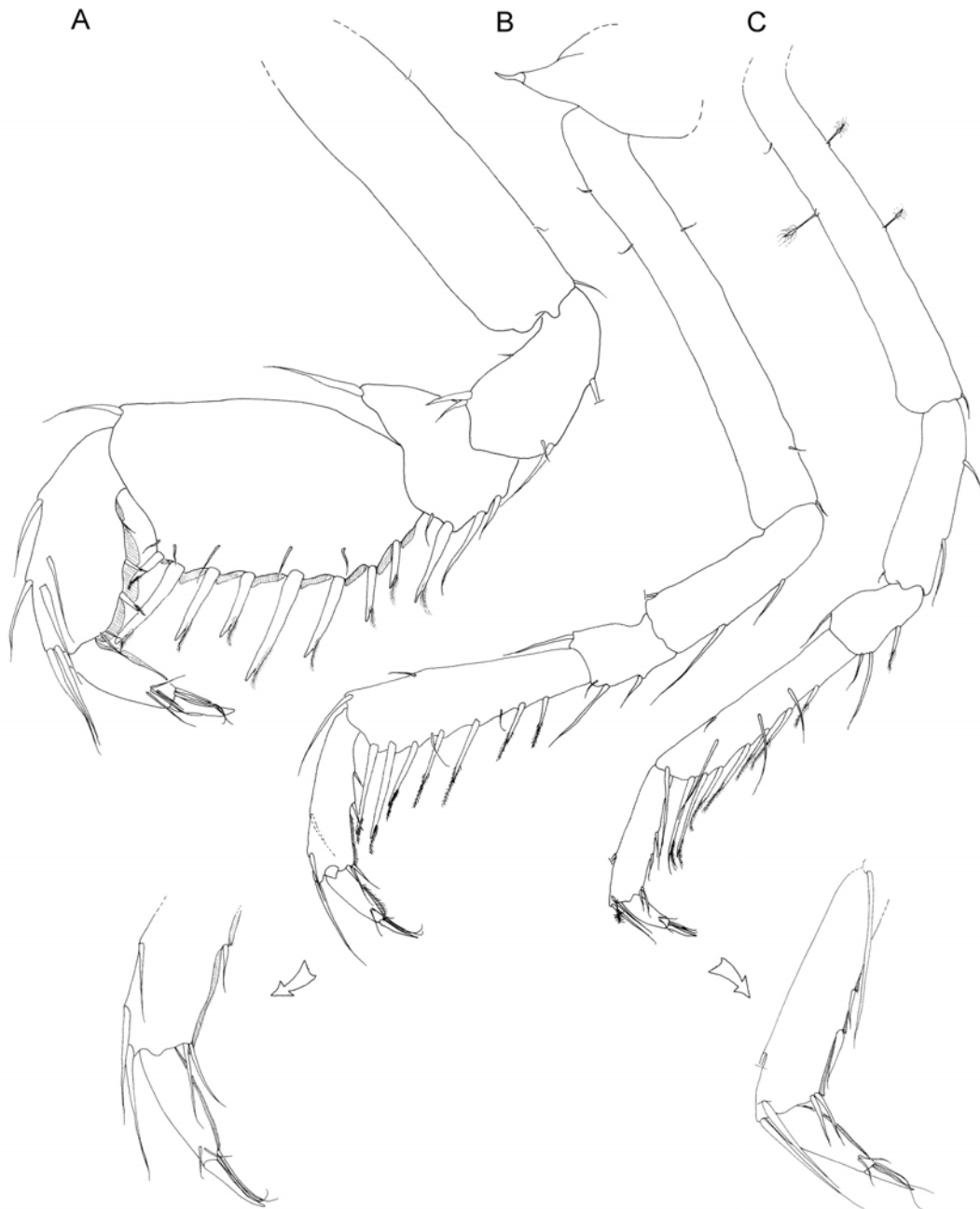
Pereopod II (Fig. 50): Basis length 8.36 width, with few small setae. Ischium length 3.5 width, distodorsally with one seta, ventrally with two simple slender setae. Merus length 1.25 width, distodorsally one seta, ventrally with one small and two simple slender setae. Carpus length 3.5 width, seven distally setulate setae increasing in size towards propodus in ventral setal row, additionally two small slender setae, dorsally one small slender seta midway and one simple slender seta distally. Propodus length 3 times width, dorsally with three setae; ventral margin with four simple setae and fringed with fine hairs inserted in cuticular membrane. Dactylus length 3.25 width, distally two small setae. Claw of one conate seta, two slender setae inserted ventrally.

Pereopod V (Fig. 51): Basis length about 3.5 width. Ischium length 3.5 width, with two small and five long simple setae. Merus length 1.11 width, dorsally with two, ventrally with one slender simple setae. Carpus length 4.44 width, with ventral row of eight slender setae and dorsal row of five slender setae. Propodus length 4.92 width, with ventral row of seven slender setae and dorsal row of five slender setae distodorsally with one small broom seta. Dactylus length 8.5 width, with one slender dorsal seta and two slender inserted ventrally next to claw.

Pleopod 2 (operculum) (Fig. 52): length 1.07 width. Margins rounded, surrounded by 26 setae. Surface with structure.

Pleopod 3 (Fig. 52): Endopod length 1.49 width, distally with 3 long plumose setae. Exopod length 0.47 of endopod length, margins hirsute.

Pleopod 4 (Fig. 52): Endopod oval, length 1.55 width. Exopod length 7.63 width, margins hirsute.



**Fig. 50:** *Eugerdella serrata* sp. nov., paratype female, pereopods (A-C): P I (A), P II (B), P III (C) , scale = 0.1 mm

Uropods (Fig. 52): uniramous. Endopod length 4.2 protopod length, 5.71 times longer than wide, medially with one small broom seta, terminally with eight broom seta, one long slender seta and four simple slender setae. Protopod length 1.12 width, with three simple slender setae.



**Fig. 51:** *Eugerdella serrata* sp. nov., paratype female, pereopods (A-D): P IV (A), P V (B), P VI (C), P VII (D), scale = 0.1 mm

#### **Differences in male:**

Habitus (Fig. 53): Similar to female, but lateral margins of Prn5-7 serrated, coxae more produced, especially coxa 1. Plt in subadult male not as quadrangular as in adult male, in subadult male Plt length 1.3 width, in adult male Plt length 0.9 width.

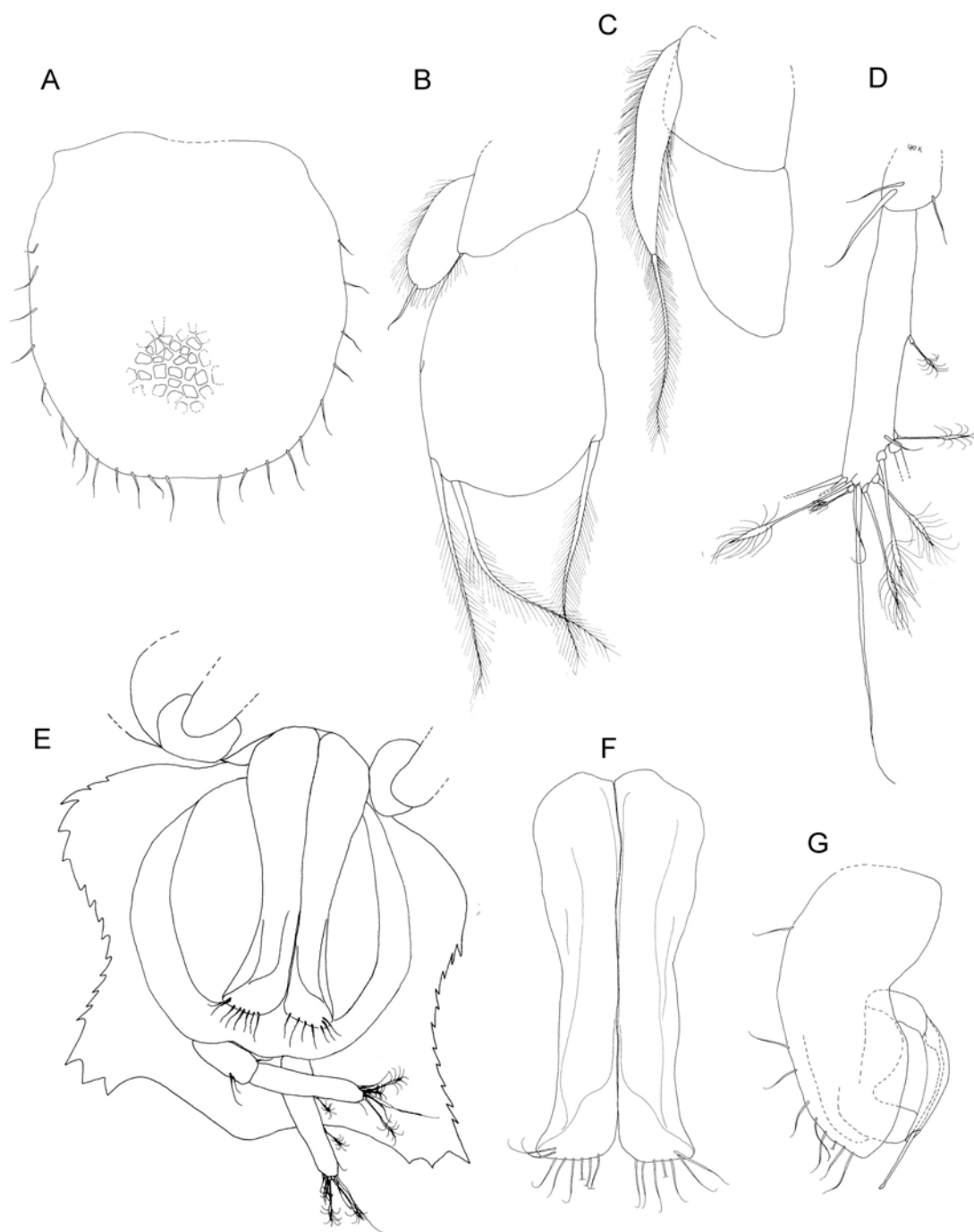
Antenna (Fig. 53): Consisting of 18 articles. Article 3 with strong stout unequally bifid seta, flagellum basally swollen

Pleopod 1 (Fig. 53): 2.27 times longer than distal width, terminally with seven slender setae.

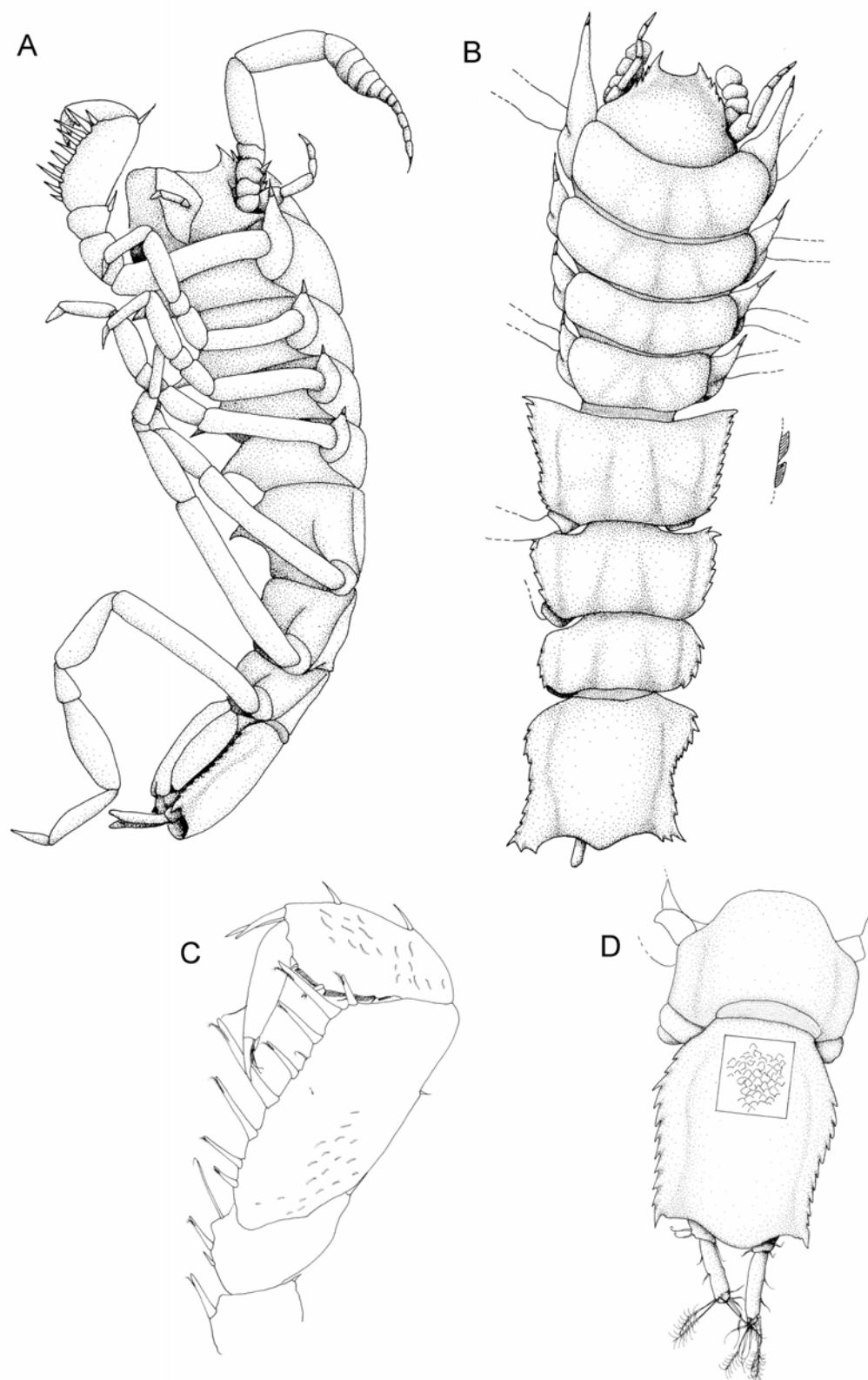
Pleopod 2 (Fig. 53): sympod oval-shaped, length 2.66 times of width, lateral margin with eight slender setae. Endopod inserting 0.7 of sympod length.

**Discussion:** The new species belongs to the genus *Eugerdella* due to the enlarged P I, the ventral row of composed setae of irregular size at the carpus, carpus and propodus clearly broader than in P II, the most distal setae being smallest and inserted next to a dais.

It is most similar to *E. pugilator* and shares following synapomorphies that distinguish the two species from all other species of the genus: Prn1 twice as long as Prn2, P I extremely enlarged, propodus bearing ventrally small unequally bifid setae, spine-like ventral elongations at Prn1-5, dorsal margin of antennular folds with cephalic spine row, pleotelson serrated. *E. serrata* sp. nov. differs from *E. pugilator* in the following apomorphies: lateral margins of Prn5-7 smooth, carpus of P I between composed ventral setae of irregular size fringed with fine hairs inserted in cuticular membrane, propodus of P I with two unequally bifid setae, not with row of seven unequally bifid setae, dorsal setae on propodus not unequally bifid, Im with three teeth.



**Fig. 52:** *Eugerdella serrata* sp. nov., paratype female pleopods (A-D): operculum (A), PI 3 (B), PI 4 (C), uropod (D), paratype male (E-G): pleotelson adult male ventral (E), pleopods (F-G): PI 1 (F), PI 2 (G)



**Fig. 53:** *Eugerdella serrata* sp. nov., allotype male, habitus lateral (A), dorsal (B), P I (C), paratype subadult male pleotelson dorsal (D), scale = 1 mm

#### **3.1.5.3 Collection material**

##### **3.1.5.3.1 gen. nov. sp. nov. A**

Holotype. – Female, preparatory, 2.1 mm; NMV J 18612; Type locality. – Australia, New South Wales, Off Nowra (34°59.52'S, 151°5.94'E), 204.0 m, WHOI epibenthic sled, Poore, G.C.B. *et al.*, RV Franklin, 14. Jul 1986 (Stn SLOPE 1)

Paratypes. – 7 specimens (3 females, 4 males); NMV J 186121; locality. – As type locality.

#### **Diagnosis**

Body elongated, length 5 times longer than width of pereonite 2. Body margins straight, Prn6,7 and Plt dorsally fused. P I carpo-euchelate, enlarged, carpus with one slender seta midway and one slender seta proximal to claw-seta. Plt without posterolateral spines. Uropods biramous, partly overlapping anus valves, exopod less than half of length of endopod.

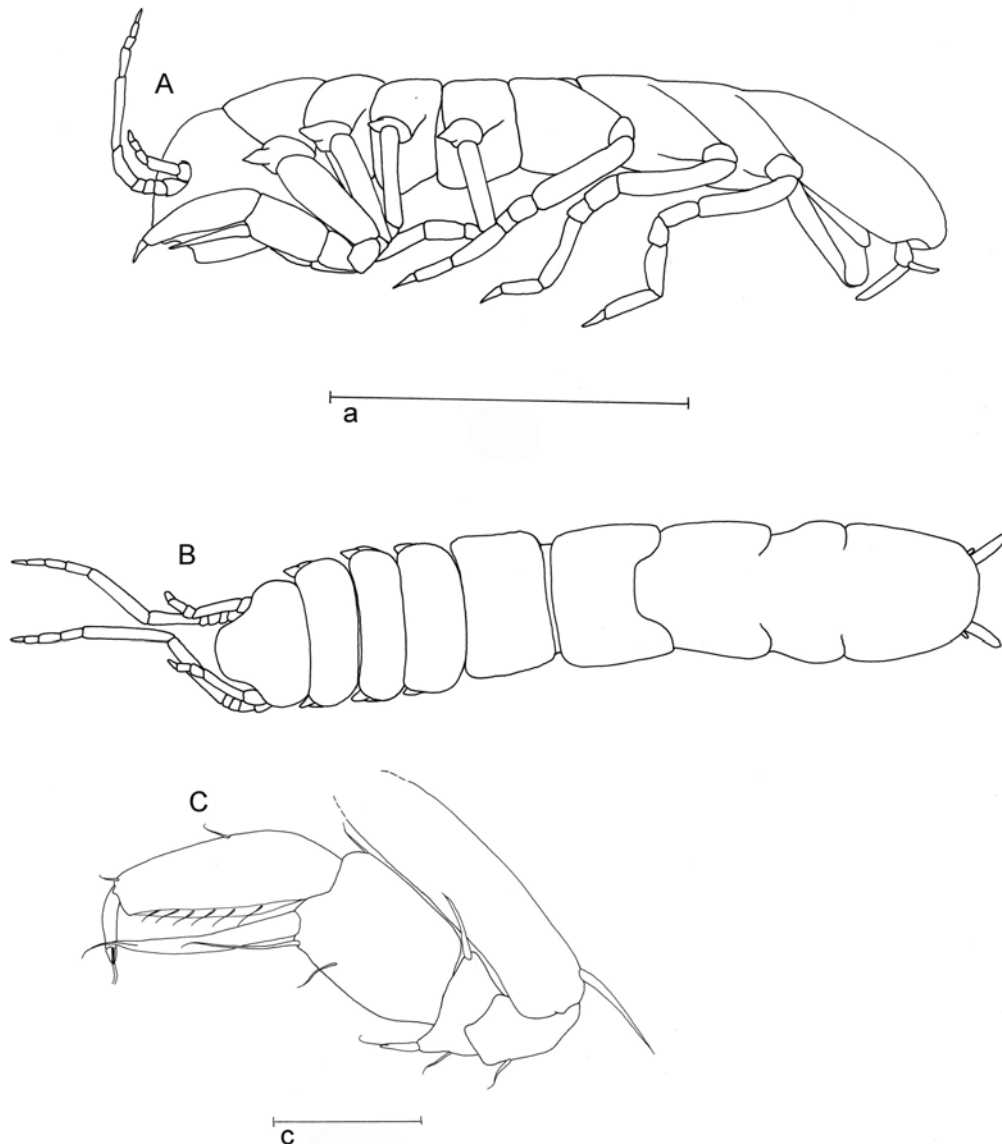
#### **Description of holotype female**

Habitus (Fig. 54): body 2.1 mm long (measured without appendages), 5.17 times longer than width of pereonite 2. Prn1 width 1.16 times cephalon width in dorsal view. Prn1 length 1.11 pereonite 2 length, 0.96 pereonite 2 width. Prn5 width 0.6 length, anterior margin straight. Prn6 and 7 fused with Plt, lateral margins form? Coxae 1-4 slightly produced, without setae. Plt length as long as wide, without posterolateral spines. Lateral margins straight, posterior margin slightly rounded.

Antennula (Fig. 54): 0.23 mm long, length 0.02 body length, five articles.

Pereopod I (Fig. 54): Carpo-euchelate. Basis length 3.75 width, proximal to ischium ventrally one large seta. Ischium length 1.77 width, with one ventral seta. Merus length 2.38 width, ventrally with one strong unequally bifid seta, midway one slender seta, distodorsally one large simple seta. Carpus length 1.38 width, ventrally with claw-seta, penultimate slender seta and one slender seta midway. Claw-seta as long as propodus. Propodus length 2.69 width, dorsally with two small setae, ventral margin with cuticular membrane and six small slender setae. Dactylus length 3.6 width, without setae. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.





**Fig. 54:** gen. nov. sp. nov., holotype female, habitus lateral (A, scale a = 1 mm), dorsal (B, scale a), Pl (C, scale c = 0.1 mm)

Uropods (Fig. 54): biramous. Exopod length less than 0.5 times endopod length.

**Discussion:** This new species possesses a unique combination of apomorphies and does not fit completely in none of the existing genera. It no desmosomatid species known that has Prn6, 7 and the Plt fused. This kind of fusion is known for

nannoniscid genera. All these nannoniscid genera include species with a specialized antennula with a bulbous distal article. The new species does not possess such a specialization, the flagellar articles of the antennula are tapering towards the distal article.

P I of the new species resembles most species of *Prochelator*, *Chelator* or *Oecidiobanchus*. *Prochelator* is the only genus of these three genera that includes species with biramous uropods. No species of this genus has fused pereonites.

At the present systematic status, a decision about the generic affiliation of the new species is not possible. It is proposed to erect a new genus for this new species. A detailed description of this species will be necessary. In the present study, the main characters of the new species are described to include it into the phylogenetic analysis (chapters 3.2, 4.2.2, 4.3).

#### **3.1.5.3.2     *Prochelator maorii* sp. nov.**

Holotype. – Female, preparatory, 3.1 mm NIWA S 147; Type locality. – “Off New Zealand”

#### Paratypes:

Allotype. – 1 male, adult, 3.2 mm; NIWA S 147; locality. – As type locality.

Paratype. - F 753 2 females, locality. – As type locality

Paratype. - F 755 2 females, locality. – As type locality

#### **Etymology**

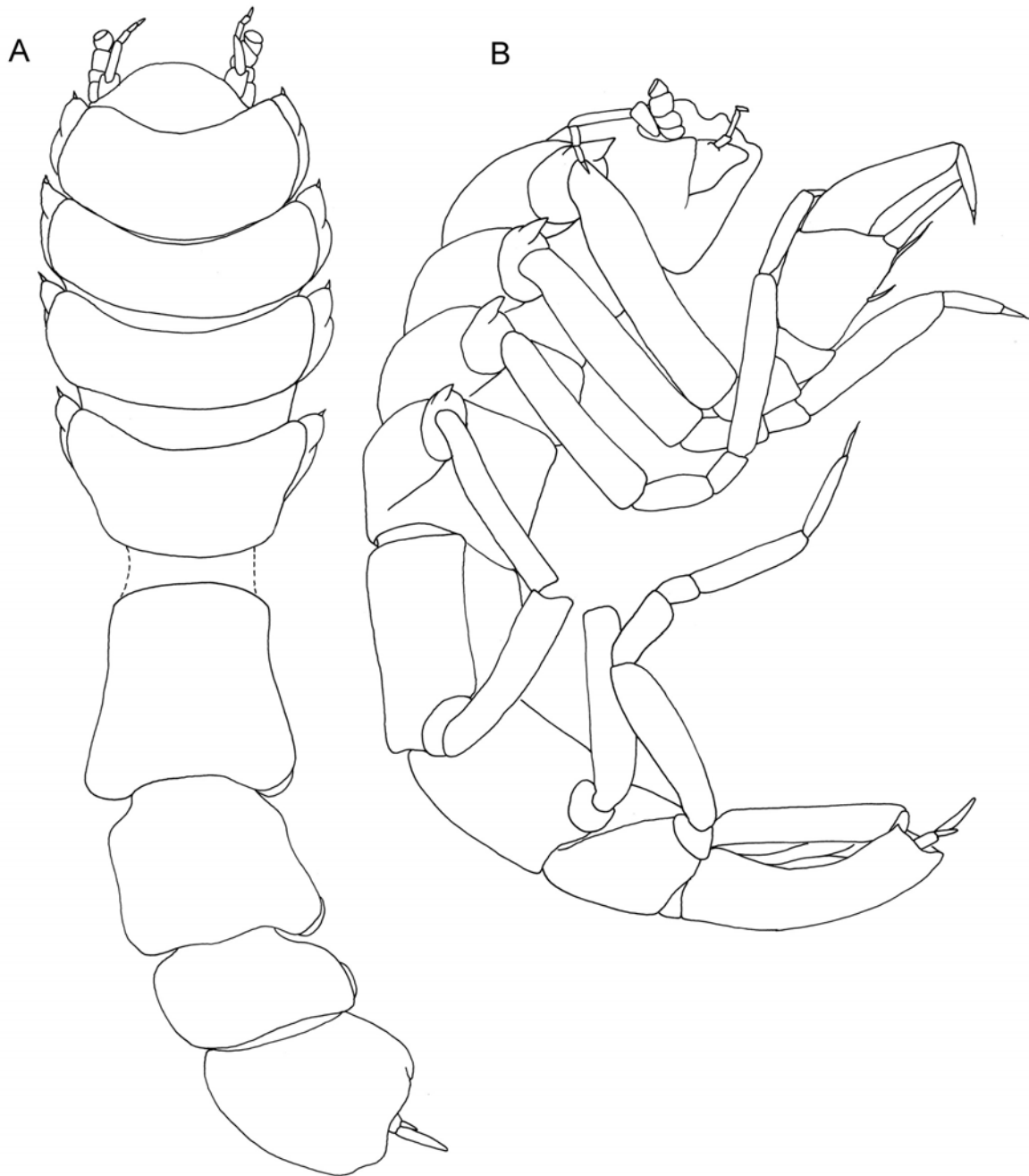
The name refers to the Maori, the first human inhabitants of New Zealand.

#### **Diagnosis**

Body length about 4.6 times longer than width of Prn 2. Prn1-4 in female slightly higher than Prn5-7 in lateral view, in male as high as Prn5-7. Prn1 length 1.4 times Prn2 length. Prn5 length 0.8 times width. Coxae 1-4 anteriorly produced, with strong stout setae. P I carpo-euchelate, carpus broadest at articulation of propodus, slightly produced at base of claw-seta, ventrally with large claw-seta, penultimate small slender seta and one small distally setulate seta midway. Carpi of P II-IV about twice as long as carpus of P I. Plt with posterolateral spines located at 0.6 of Plt length. Uropods biramous, exopod about half as long as endopod.

#### Description of holotype female

Habitus (Fig. 55): body 3.1 mm long (measured without appendages), 4.68 times longer than width of Prn 2. Prn 1 width 1.42 times cephalon width in dorsal view. Prn 1 length 1.5 Prn 2 length, 0.84 Prn 2 width. Prn 5 width 0.82 length, anterior margin straight, lateral margin slightly convex. Coxae 1-4 produced, with large stout setae. Pleotelson length 0.98 width, large posterolateral spines present. Lateral margins convex, posterior margin slightly rounded.



**Fig. 55:** *Prochelator maorii*, sp. nov., holotype female, habitus dorsal (A), lateral (B), scale = 1 mm

Antennula (Fig. 56): With six articles. Article 1 1.69 width, with four broom setae. Article 2 length 6.43 width, 2.01 article 1 length; distally with two large articulated broom setae and two small slender setae, marginally with two small slender setae. Article 3 length 3.5 width, with one small slender seta, article 4 length 3.3 width, distally with one broom seta, distal article length 3.5 width, terminally with one aesthetasc, one broom seta and two long slender setae. Articles 2-5 length relative to article 1: 2.01: 0.64: 0.5: 0.45: 0.32.

Antenna (Fig. 56): broken off.

Mandible (Fig. 56): Article 1 of palp with one small distal seta, article 2 ventrodistally with two small setulate setae, dorsally with rows of numerous fine hairs, apical article with nine ventral seta, distal one longest. Ip with three teeth. Lm of MdL with three teeth, spine row containing eight spines. Mp with 13 fine slender setae.

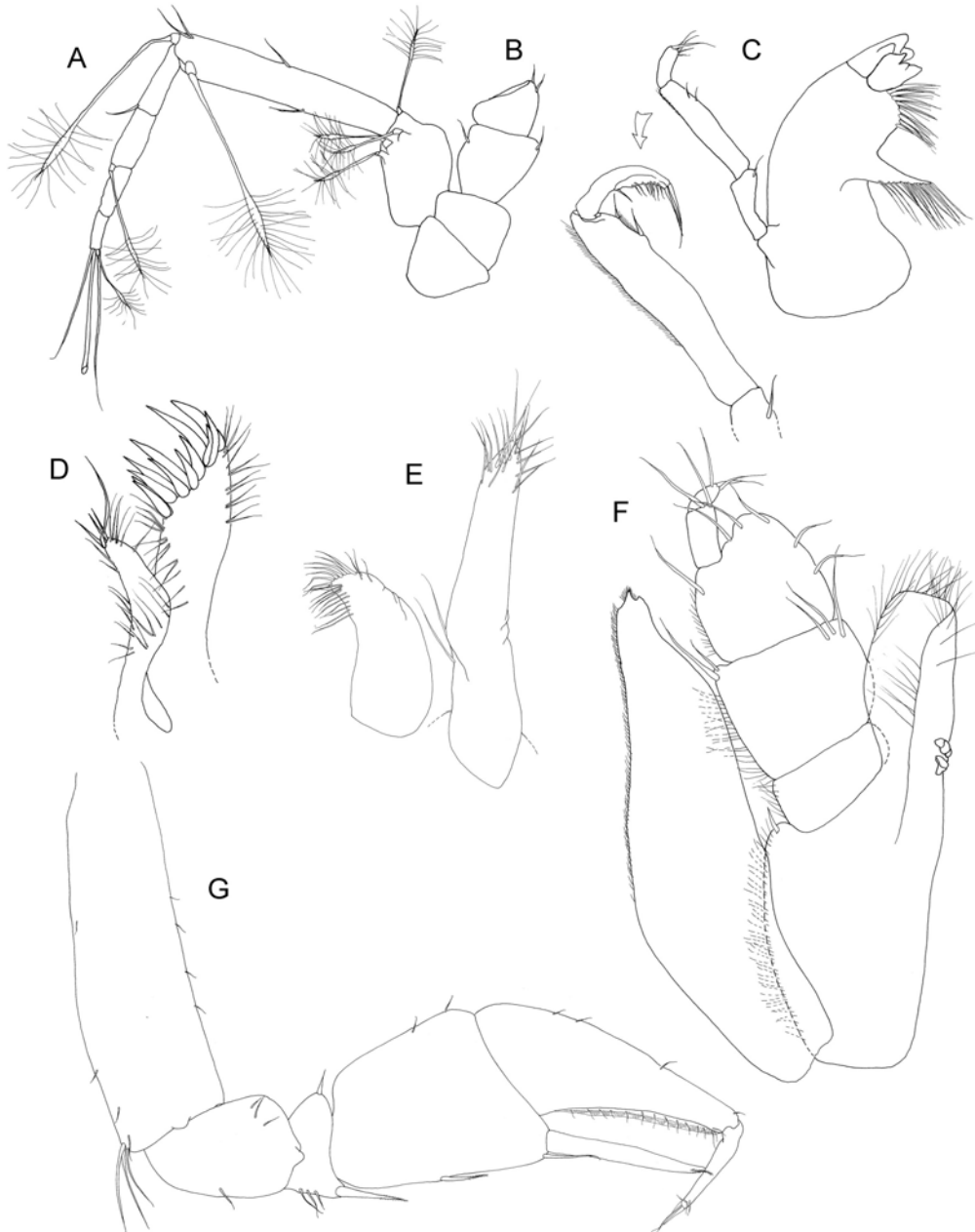
Maxillula (Fig. 56): Inner lobe slightly smaller than outer lobe (about 0.7 of outer lobe length), with 25 setae. Outer lobe 3.75 times longer than wide, marginally with pairs of fine setae, terminally with 12 strong spines.

Maxilla (Fig. 56): Medial lobe 0.48 times of length of outer lobes, terminally with 21 setae. Outer lobe (one lobe lost during dissection) basally with two slender setae, terminally with 18 setae.

Maxilliped (Fig. 56): Epipodite length 3.85 width, length 1.06 endite length. Endite with two retinaculae, terminally with numerous fine setae. Edge of endite and palp articles 1-3 with row of fine setae. Palp article 2 with three setae on inner margin and two setae on outer margin, article 3 with five setae on inner margin and one seta on outer margin, article 4 with two setae, article 5 with three setae. Article 1 length 0.45 width, article 2 length 0.76 width, article 3 length 1.04 width, article 4 length 2.4 width, article 5 length 1.5 width.

Pereopod I (Fig. 56): Basis length 3.48 width, ventrally proximal to ischium with three slender setae, marginally with eight small setae. Ischium length 1.34 width, with few small setae. Merus length 0.32 width, ventrally with three small setae, ventrodistally with one robust distally setulate seta, dorsally one stout simple seta. Carpus length 1.42 width, distoventrally with large robust claw-seta and slender penultimate seta,

medioventrally one small distally setulate seta, dosally two small setae. Propodus length 2.82 width, dorsally with four small setae, ventrally fringed with fine hairs inserted in cuticular membrane and 14 small setae. Dactylus length 6 times width. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.



**Fig. 56:** *Prochelator maorii* sp. nov., paratype female, antennula (A), antenna (B), mouthparts (C-F): Md L (C), Mx 1 (D), Mx 2 (inner and outer lobe) (E), Mxp (F), pereopod I (G)



**Fig. 57:** *Prochelator maorii* sp. nov., paratype female, pereopods (A-D): P II (A), P III (B), P IV (C), P V (D)

Pereopod II (Fig. 57): Very similar to P III and IV. Basis length 4.58 width, ventrally proximal to ischium three slender setae. Ischium length 2.3 width, ventrally with three simple setae, dorsally with one small seta. Merus length 4.31 width, ventrally with four distally setulate setae, distodorsally one simple seta. Carpus length 5.12 width, with ventral and dorsal rows of setae, ventrally 12 distally setulate setae, dorsally 18 simple setae. Propodus length 5.12 width, ventrally with three small setae, distodorsally one simple seta. Dactylus length 6 times width. Claw of dactylus with one conate seta.

Pereopod V (Fig. 58): Very similar to P VI and VII. Basis length 3.9 width, medially with two broom setae. Ischium length 2.37 width, dorsally with row of five slender setae. Merus length 1.3 width, with two small setae. Carpus length 3.17 width, with ventral row of 13 long slender setae and dorsal row of 11 setae, distodorsally one small broom seta. Propodus length 2.75 width, with ventral row of nine long setae and dorsal row of 10 setae, additionally two simple setae. Dactylus length 5.25 times width, mediodistally with two small slender setae. Claw of dactylus with one long conate seta, two slender setae inserted next to it.

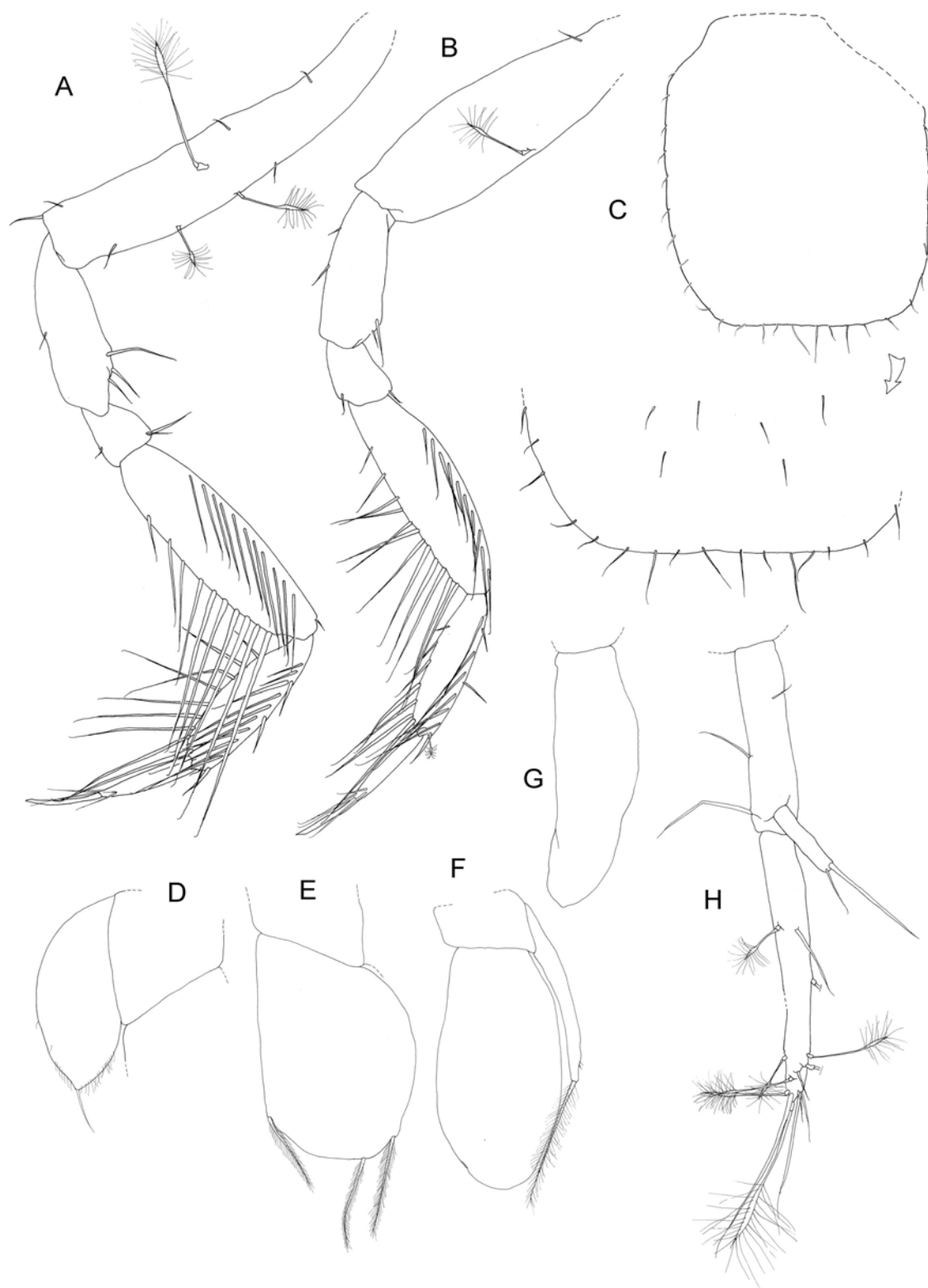
Pleopod 2 (operculum) (Fig. 58): length 1.2 width. Lateral margins straight, distal margin straight, with 30 setae.

Pleopod 3 (Fig. 58): Endopod length 1.31 width, distally with 3 long plumose setae. Exopod length 0.73 of endopod length, margins hirsute, with one small distal seta.

Pleopod 4 (Fig. 58): Endopod oval-shaped, length 1.97 width. Exopod length 12 times width, distally with one long plumose seta.

Pleopod 5 (Fig. 58): Endopod only, length 3.08 width.

Uropods (Fig. 58): biramous. Endopod length 1.4 protopod length, 7.9 times longer than wide, marginally with one slender and two broom setae, distally with three small, one slender and six broom setae. Exopod length 0.3 endopod length, 5 times width terminally with two setae. Protopod length 4.6 width, with few small slender setae.



**Fig. 58:** *Prochelator maorii* sp. nov., paratype female, pereopods (A-B): P VI (A), P VII (B), pleopods (C-H): operculum (C), exopodit of PI 3 L (D), endopodit of PI 3 R (E), PI 4 (F), PI 5 (G), uropod (H)



**Differences in male:**

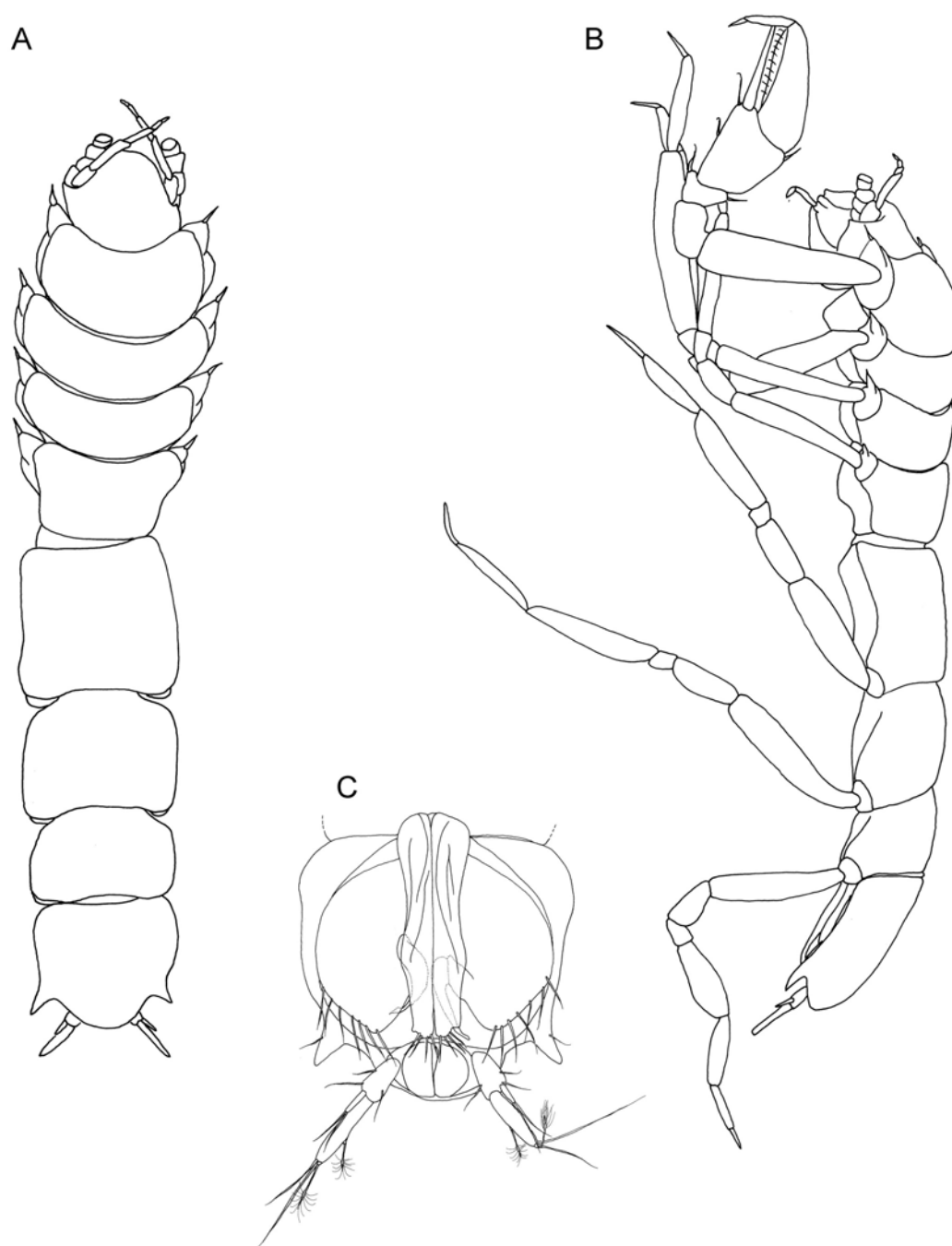
Habitus (Fig. 59): very similar to female, but Prn1-4 as high as Prn5-7, Plt with larger posterolateral spines.

Pleopod 1 (Fig. 59): 4.72 times longer than distal width, tips with distal bulges bearing four slender setae.

Pleopod 2 (Fig. 59): Sympod oval-shaped length 1.37 times of width, lateral margin rounded, with seven slender setae. Endopod inserting 0.49 of symposiums length.

**Discussion:** *Prochelator maorii* sp. nov. is assigned to the genus *Prochelator* mainly due to the characters of P I as there are the carpo-euchela, one composed seta midway on the ventral margin of the carpus and the slender penultimate seta next to the large claw-seta. Furthermore, important are the enlarged Prn1, the Im with three teeth and the biramous uropods.

The new species is easily to distinguish from *P. incomitatus* and *P. angolensis* by the biramous uropods. Both species possess a very compact anterior part of the body, Prn1 being twice as long as Prn2. Apomorphies, distinguishing the new species from other species of the genus with biramous uropods are: Body relatively elongated, without spine-like ventral elongations at Prn1-4 (as in *P. lateralis*, *P. uncatus* and *P. hampsoni*). The remaining species of the genus are anteriorly compact, Prn1-4 are higher than Prn5-7 from lateral view. In *P. maorii* sp. nov. Prn1 is as high as Prn5, the medial lobe of Mx2 is much shorter than in the other species of the genus, reaching only half of length of the outer lobe. The carpus of P I is distinctly produced at the base of the claw-seta, the propodus is broadest at the articulation to the carpus and tapers distally.



**Fig. 59:** *Prochelator maorii* sp. nov., allotype male, habitus dorsal (A), lateral (B), pleotelson ventral (C)

#### **3.1.5.3.3     *Pseudomesus satanus* sp. nov.**

Holotype. – Female, preparatory, 1.7 mm; NMV J18597; Type locality. – Australia, Victoria, 67 km S of Point Hicks (38°23.95'S, 149°17.02'E), 1277-1119 m, WHOI epibenthic sled, Poore, G.C.B. *et al.*, RV Franklin, 25. Oct 1988 (Stn. SLOPE 67)

#### **Etymology**

The name refers to the devil-like cephalic spines at the cephalon of the new species.

#### **Diagnosis**

Body length about 6.2 times longer than width of Prn 2. Cephalon with two cephalic spines and a row of small setae on frons. A1 with five articles, article 2 length 3.38 width, 1.5 article 1 length; distally with serration resembling four “teeth”, with three broom setae. Plt dorsally inflated, length subequal width, posterolateral spines absent, lateral margins convex, tapering to posterior margin. Ur uniramous, bulbous, not overlapping posterior margin of Plt, overlapping anus valves. Endopod, length 1.5 protopod length, 1.9 times longer than wide

#### **Description of holotype female**

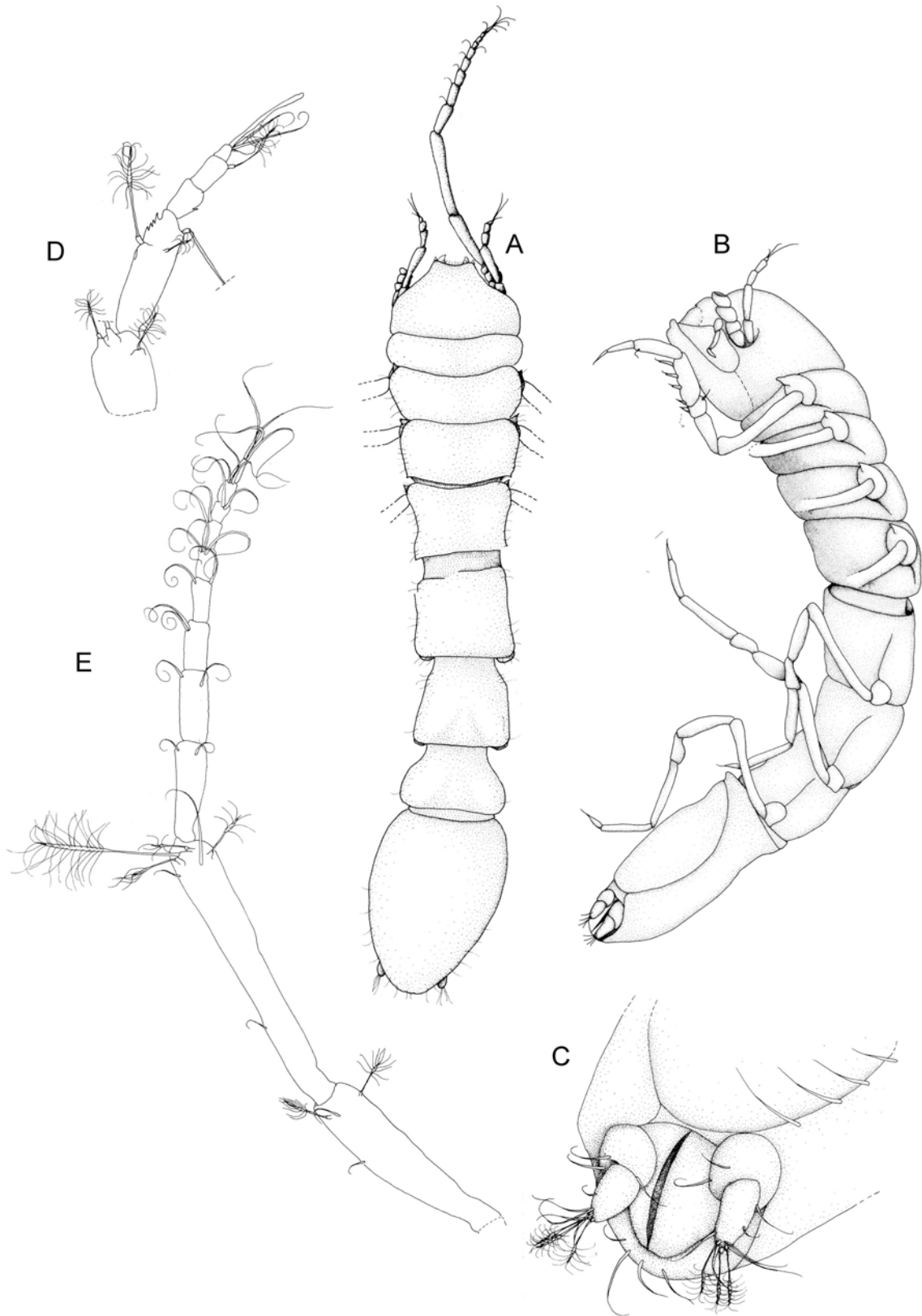
Habitus (Fig. 60): body 1.7 mm long (measured without appendages), 6.18 times longer than width of Prn 2. Prn 1 width 1.07 times cephalon width in dorsal view. Frons clypeal furrow present, two cephalic spines and row of small setae on frons. Prn 1 length 0.8 Prn 2 length, 1.1 Prn 2 width. Prn 5 anterior margin and lateral margins straight. Coxae 1-4 slightly produced, without setae. Plt dorsally inflated, length 1.18 width, posterolateral spines absent. Lateral margins convex, tapering to posterior margin.

Antennula (Fig. 60): about 0.25 mm long, length about 0.19 body length, with five articles. Article 1 with three broom setae. Article 2 length 3.38 width, 1.5 article 1 length; distally with serration resembling four “teeth”, with three broom setae. Article 3 with one small elongation, article 4 with one broom seta, distal article terminally with one aesthetasc and two slender setae. Articles 2-5 length relative to article 1: 1.5: 0.62: 0.62: 0.16.

Antenna (Fig. 60): about 1 mm long, length 0.77 body length, with 14 articles. Article 3 with two broom setae and two simple setae. Article 4 distally with three small and

### 3. Results

one large broom seta, one slender and two small setae. Flagellar articles with two slender setae each, distal article terminally with four long slender setae.



**Fig. 60:** *Pseudomesus satanus* sp. nov., holotype female, habitus dorsal (A), lateral (B), Plt ventral with uropods (C), antennula (D), antenna (E), scale = 1 mm

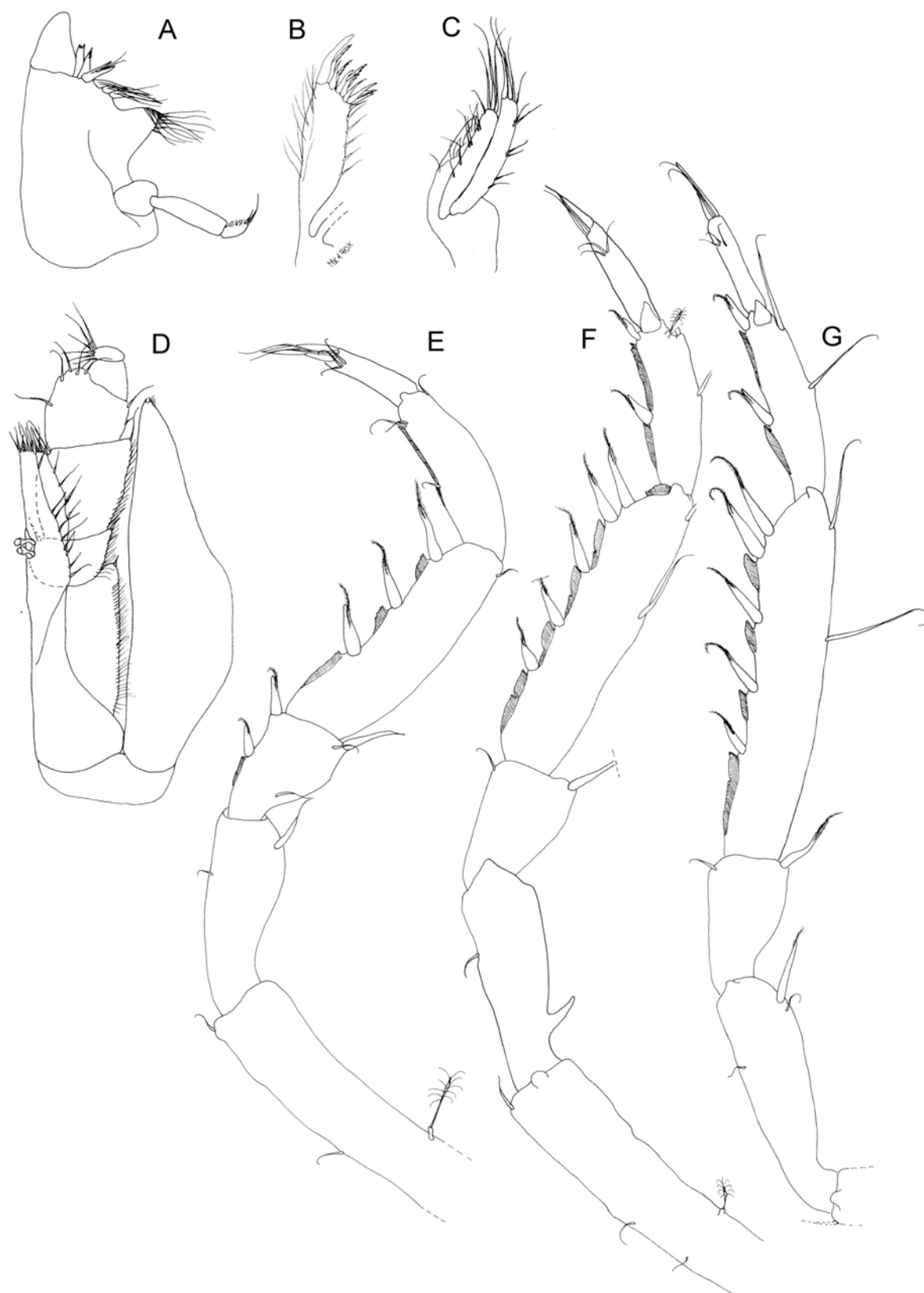
Mandible (Fig. 61): Article 1 and 2 without setae, apical article with nine ventral setae, distal one longest. Ip with one strong tooth. Lm-like structure of MdR with three small teeth, (MdL was not dissected from the holotype). Spine row containing five spines. Mp with 10 slender setae.

Maxillula (Fig. 61): Inner lobe slightly smaller than outer lobe (lost during dissection). Outer lobe 4.1 times longer than wide, dorsal margin with six pairs of fine setae, ventral margin with six small simple setae, terminally with 11 strong spines (four of them with setules).

Maxilla (Fig. 61): Medial lobe shorter than outer lobes, terminally without setae, marginally with seven fine setae. Outer lobe length 6.75 width, terminally with three setae.

Maxilliped (Fig. 61): Epipodite length 3.6 width, length 1.13 endite length. Endite with two coupling hooks, marginally and terminally with numerous fine setae. Edge of endite and palp articles 1 and 2 fringed with row of fine setae and one seta on tip. Article 1 length 0.56 width, article 2 length 1.11 width, article 3 length 0.94 width, inner margin with five setae, outer margin with two setae, article 4 length 1.3 width, with three setae, article 5 length 2 times width, with three terminal setae.

Pereopod I (Fig. 61): Basis length 3.75 width, marginally with one broom seta and one small seta, proximal to ischium ventrally one simple seta. Ischium length 2.53 width, dorsally on composed seta, ventrally one small seta. Merus length 1.5 width, ventrally two unequally bifid distally setulate seta and one comb of fine hairs in cuticular membrane, distodorsally one composed and one simple seta. Carpus length 4.4 width, with ventral row of unequally bifid distally setulate setae and three combs of fine hairs inserted in a cuticular membrane, distodorsally one small seta. Propodus length 2.9 width, ventrally with few small slender setae, fringed with fine hairs inserted in a cuticular membrane, distodorsally one small seta. Dactylus length 4.17 width, distally three small slender setae. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.



**Fig. 61:** *Pseudomesus satanus* sp. nov., holotype female, mouthparts (A-D): MdR (A), Mx 1 (B), Mx 2 (C), Mxp (D), pereopods (E-G): P I (E), P II (F), P III (G)

Pereopod II (Fig. 61): Very similar to P III and IV. Basis length 3.53 width, marginally with one small broom seta and few small setae. Ischium length 2.81 width, with dorsal hook, ventrally one small seta. Merus length 1.17 width, ventrodistally one small seta, dorsodistally one seta (terminally broken off). Carpus length 4.4 width, with ventral row of five robust unequally bifid setae and six combs of fine hairs inserted in a cuticular membrane, dorsally with one seta medially and one seta distally. Propodus length 2.91 width, ventrally with two short unequally bifid setae, fringed with fine hairs inserted in a cuticular membrane, distodorsally one small broom seta. Dactylus length 4.17 width, three small slender setae mediodistally, claw with one conate seta, two slender setae inserting ventrally.

Pereopod V (Fig. 62): Very similar to P VI and VII. Basis length 5.27 width, marginally with three broom setae, one small seta medially and one small seta ventrally proximal to ischium. Ischium length 3.46 width, with dorsal hook. Merus length 2 times width, distodorsally with two setae, ventrodistally with one small seta. Carpus length 5.64 width, ventrally with two long slender setae and three combs of fine hairs inserted in cuticular membrane, distodorsally with one small broom seta and one small seta. Propodus length 5.11 width, ventrally with three long slender setae and one small slender seta, one comb of fine hairs inserted in cuticular membrane, distodorsally with one small broom seta and one long slender seta. Dactylus length 5 times width, claw with one long conate seta, two slender setae ventral to conate seta.

Pleopod 2 (operculum) (Fig. 6): length 1.08 width. Margins rounded., istal margin with four slender setae.

Pleopod 3 (Fig. 63): Endopod length 1.24 width, distally with 3 long plumose setae. Exopod length 0.56 of endopod length, inner margin hirsute, distally one small seta.

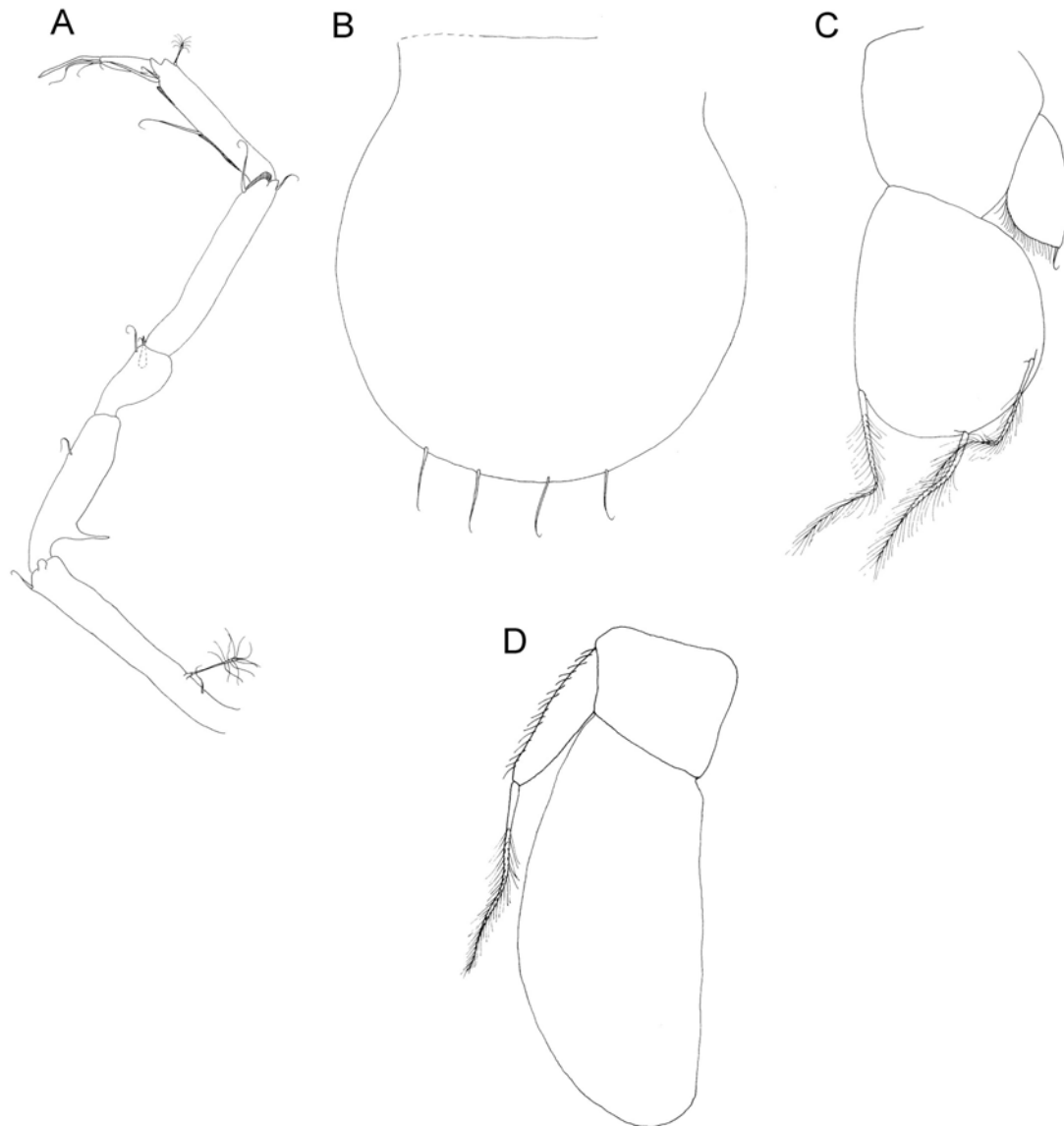
Pleopod 4 (Fig. 63): Endopod oval-shaped, length 2.25 width. Exopod length 3.86 width, outer margin with row of fine setae, distally one long plumose seta.

Uropods (Fig. 63): Uniramous, bulbous, not overlapping posterior margin of Plt, overlapping anus valves. Endopod, length 1.5 protopod length, 1.9 times longer than wide, terminally with three broom setae and one small and four slender setae. Protopod length 1.5 width, with three slender setae.



**Fig. 62:** *Pseudomesus satanus* sp. nov., holotype female, P IV (A), P V (B) P VI (C), scale = 0.1 mm





**Fig. 63:** *Pseudomesus satanus* sp. nov., holotype female, pereopod VII (A), pleopods (B-D): operculum (B), PI 3 (C), PI 4 (D), scale = 0.1 mm

**Discussion:** *Pseudomesus satanus* sp. nov. belongs to the genus *Pseudomesus* due to the elongated body (more than 6 times width Prn2), the enlarged dorsally inflated Plt, the extremely short uropods and the characters of the P I.

The new species is most similar to *Pseudomesus pitombo*, described from DIVA-1 material (Kaiser 2005). *P. satanus* differs from *P. pitombo* by the cephalic spines. *P. pitombo* possesses bilateral bulges on the cephalon. Both species can be distinguished from the remaining species of the genus (*P. brevicornis* and *P. similes*) by the presence of a well developed mandibular palp of three articles.

#### **3.1.5.3.4     *Paradesmomsoma australis* sp. nov.**

Holotype. – Female, preparatory, NMV J 18608; Type locality. – Australia, Victoria, South of Point Hicks (38°17.70'S, 149°11.30'E), depth 400 m, WHOI epibenthic sled, RV *Franklin*, 24. Jul 1986 (Stn. SLOPE 40)

#### **Etymology**

The name refers to the fact that this species is the first record of the genus *Paradesmosoma* from the southern hemisphere.

#### **Diagnosis**

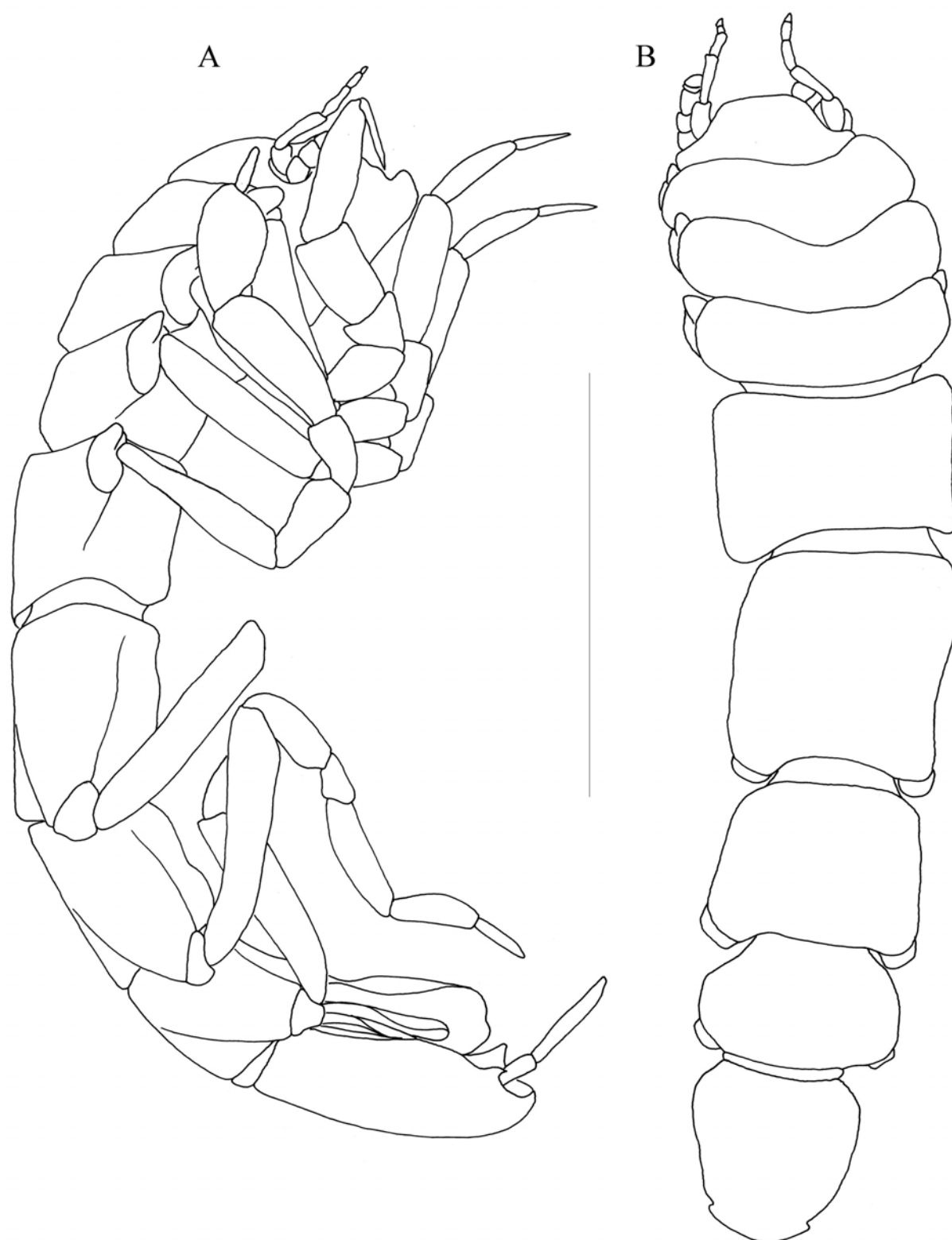
Body length about 4.4 times longer than width of Prn2. MdL palp of two articles, article 2 length 2.1 width, tapering to distal end, terminally one small seta, margins hirsute. Prn1 length 1.36 Prn2 length. Coxae 1-4 faintly produced, without setae. Plt anteriorly widest, about as wide as long, posterolateral spines present, lateral margins slightly convex, posterior margin slightly rounded. Ur uniramous, long, endopod length 4.82 protopod length, 10.25 times longer than wide.

#### **Description of holotype female**

Habitus (Fig. 64): body 2.6 mm long (measured without appendages), 4.36 times longer than width of Prn2. Prn1 width 1.44 times cephalon width in dorsal view. Prn1 length 1.36 Prn2 length, 0.97 Prn2 width. Prn5 anterior margin straight, lateral margins slightly concave. Coxae 1-4 faintly produced, without setae. Plt anteriorly widest, about as wide as long, posterolateral spines present, lateral margins slightly convex, posterior margin slightly rounded.

Antennula (Fig. 65): about 0.26 mm long, length about 0.1 body length, with five articles. Article 1 with one small slender seta and four small broom setae. Article 2 length 3.7 width, 1.48 article 1 length; marginally with two slender setae, distally with two long articulated broom setae. Article 3 with two slender setae, article 4 distally with one broom seta, distal article with one aesthetasc, one broom seta and two long slender setae. Articles 2-5 length relative to article 1: 1.48: 1.3: 0.64: 0.5.

Antenna (Fig. 65): broken off



**Fig. 64:** *Paradesmosoma australis* sp. nov., holotype female, habitus lateral (A), dorsal (B), scale = 1 mm

Mandible (Fig. 65): Palp of two articles. Article 1 without setae, article 2 length 2.1 width, tapering to distal end, terminally one small seta, margins hirsute. Ip with three teeth. Lm of MdL with three teeth, MdR not dissected from specimen. Spine row containing eight spines. Mp large, with 12 slender setae.

Maxillula (Fig. 65): Inner lobe not dissected from specimen. Outer lobe broken off from inner lobe, marginally with six ventral setae and six dorsal setae, terminally with 12 strong spines.

Maxilla (Fig. 65): Medial lobe as long, slightly broader than other lobes, terminally with three slender setulate setae, marginally with 14 setae, setae inserting near base longest. Outer lobe terminally with three long slender setulate setae, dorsal margin with five pairs of fine setae.

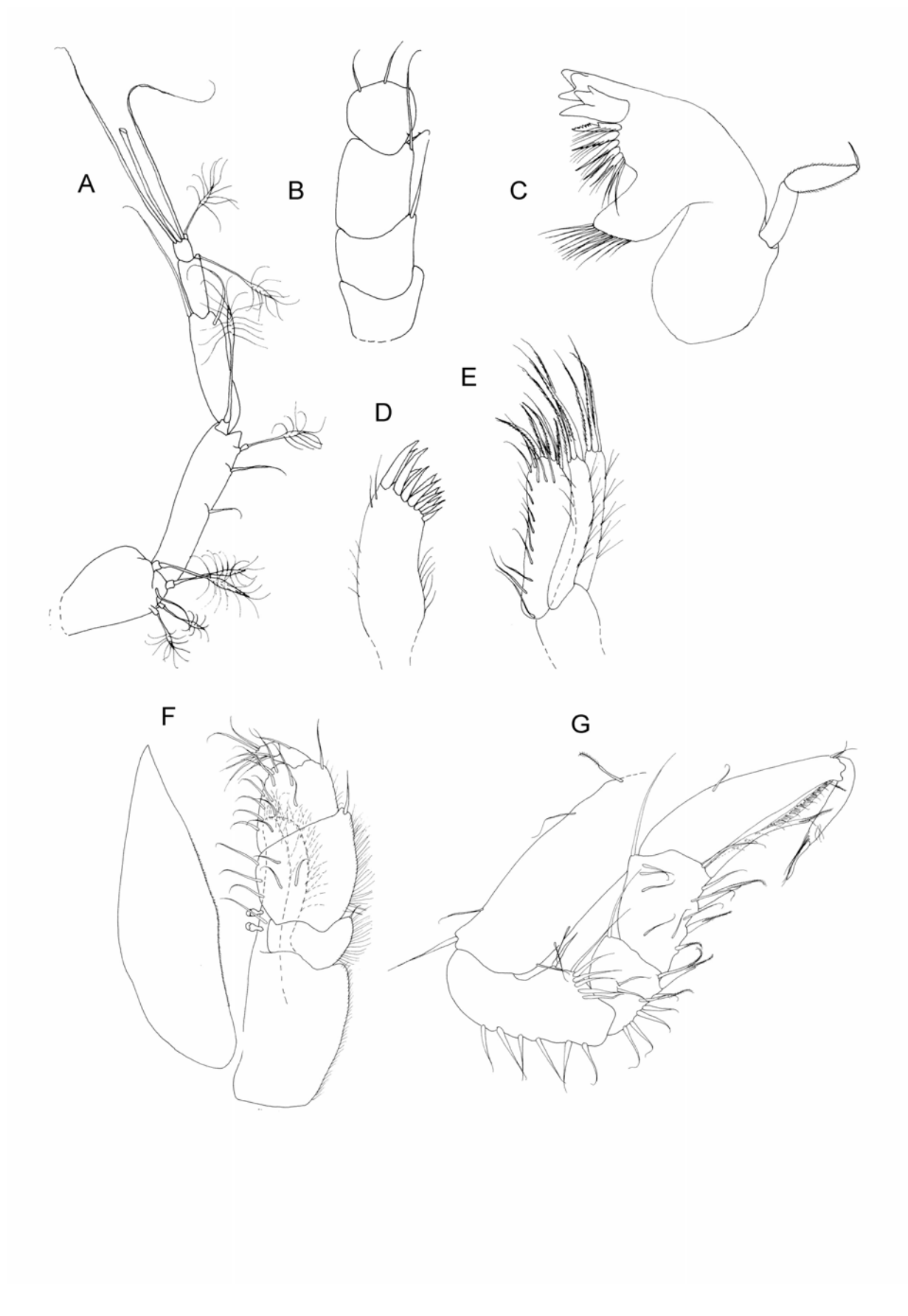
Maxilliped (Fig. 65): Epipodite length 3.31 width, length 1.17 endite length, outer margin hirsute. Endite with two coupling hooks, with numerous fine setae. Edge of endite and palp articles 1-3 fringed with row of fine setae and one seta on distal corner. Palp article 2 with six setae on inner margin, article 3 with 12 setae on inner margin, article 4 three setae, article 5 with four setae. Article 1 length 0.37 width, article 2 length 1.03 width, article 3 length 0.85 width, article 4 length 1.5 width, article 5 length 1.5 width.

Pereopod I (Fig. 65): Basis length 2.57 width, near coxa with one distally slender plumose seta, five simple slender setae and proximal to ischium one slender seta. Ischium length 2.43 width, ventrally with row of six simple setae, dorsolaterally with row of seven simple setae. Merus length 0.72 width, distodorsally one simple slender seta, ventrally with a row of five simple setae, two distally setulate setae and one stout unequally bifid seta. Carpus length 1.44 width, with dorsolateral row of five simple slender setae, distoventrally with claw-seta and a ventral row of setae of irregular size and type: three robust unequally bifid setae and five slender setae (one slender seta inserting proximal to propodus. Propodus broadest at articulation to carpus, tapering towards dactylus, length 3.05 width, ventrally fringed with fine hairs and 12 small setae inserted in cuticular membrane. Dactylus length 5 times width, mediodistally with three small setae. Claw of one conate setae, three slender setae inserting ventrally.

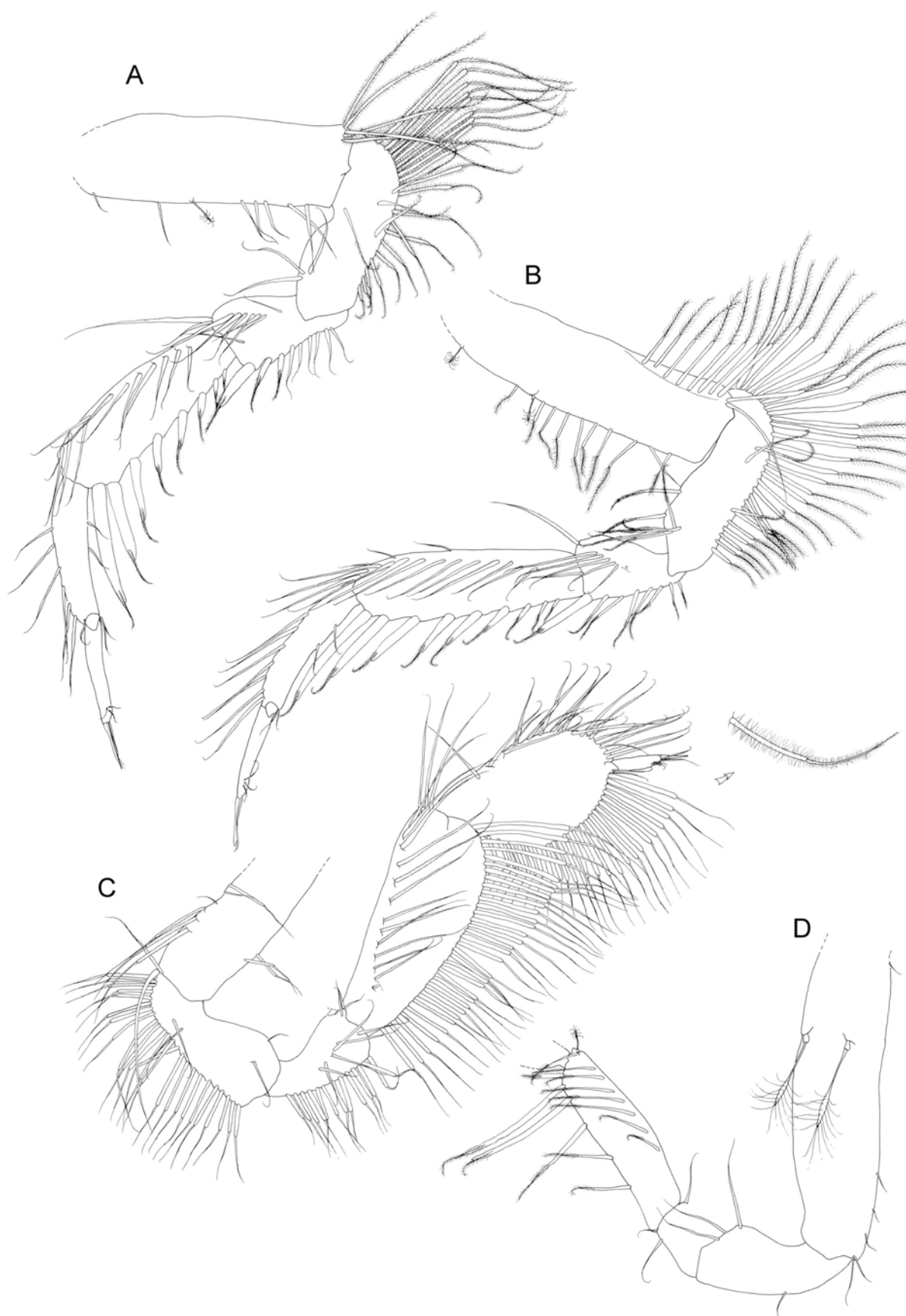
Pereopod II (Fig. 66): Very similar to P III, different from PIV. Basis length 3.04 width, marginally with seven slender setae and one small broom seta, proximal to ischium ventrally with bunch of five distally slender plumose setae. Ischium length 3 times width, ventrally with row of 23 distally slender plumose setae, dorsally with five setae. Merus length 1.86 width, with dorsolateral row of nine long simple setae, ventrally with six simple slender setae and two distally setulate setae. Carpus length 3.05 width, with ventral row of eight robust unequally bifid setae increasing in length towards propodus, distal seta of row as long as propodus, dorsally with row of 12 simple setae. Propodus length 4.18 width dorsally, ventrally four small slender setae, dorsally seven setae. Dactylus length 5.6 width, mediodistally with three small seta. Claw of one long conate seta, two slender setae inserting ventrally.

Pereopod IV (Fig. 66): Basis marginally with eight distally slender plumose setae. Ischium length 1.77 width, ventrally with row of 24 distally slender plumose setae and dorsally three slender setae. Merus length 1.67 width, with nine simple slender setae and ventral row of 13 distally slender plumose setae. Carpus length 2.41 width, with dorsal row of 16 slender setae and a ventral row of 33 distally slender plumose setae. Propodus length 1.66 width, dorsally with 24 simple slender setae, ventrally with row of 25 distally slender plumose setae, distally two small slender setae. Dactylus width 0.125 propodus width, length 1.5 width, three small setae mediodistally. Claw with one conate seta, two slender setae ventrally.

Pereopods VI (Fig. 67): Very similar to P V and P VII. Basis length 1.93 width, with few small slender setae and one long slender seta ventrally proximal to ischium. Ischium length 2.15 width, ventrally with one simple seta, distodorsally two simple slender setae. Merus length 1.21 width, with two ventral setae, distodorsally one simple slender seta. Carpus length 3.53 width, ventrally with row of six long distally setulate setae and one short unequally bifid seta, dorsally with row of seven simple slender setae. Propodus length 3.91 width, ventrally with row of 11 long distally setulate setae, dorsally with row of four simple slender seta, distally one small broom seta. Dactylus length 6.75 width, proximal to claw four simple slender setae. Claw of one long conate seta.



**Fig. 65:** *Paradesmosoma australis* sp. nov., holotype female, antennula (A), antenna (B), mouthparts (C-F): Md L (C), Mx 1 (D), Mx 2 (E), Mxp (F), pereopod I (G)



**Fig. 66:** *Paradesmosoma australis* sp. nov., holotype female, pereopods (A-D): P II (A), P III (B), P IV (C), P V (D)

Pleopod 2 (operculum) (Fig. 67): length 0.93 width, lateral margins slightly convex, distal margin deeply concave, with four small simple setae.

Pleopod 3 (Fig. 67): Endopod length 1.62 width, distally with 3 long plumose setae. Exopod length 0.75 of endopod length, margins hirsute, distally with one small seta.

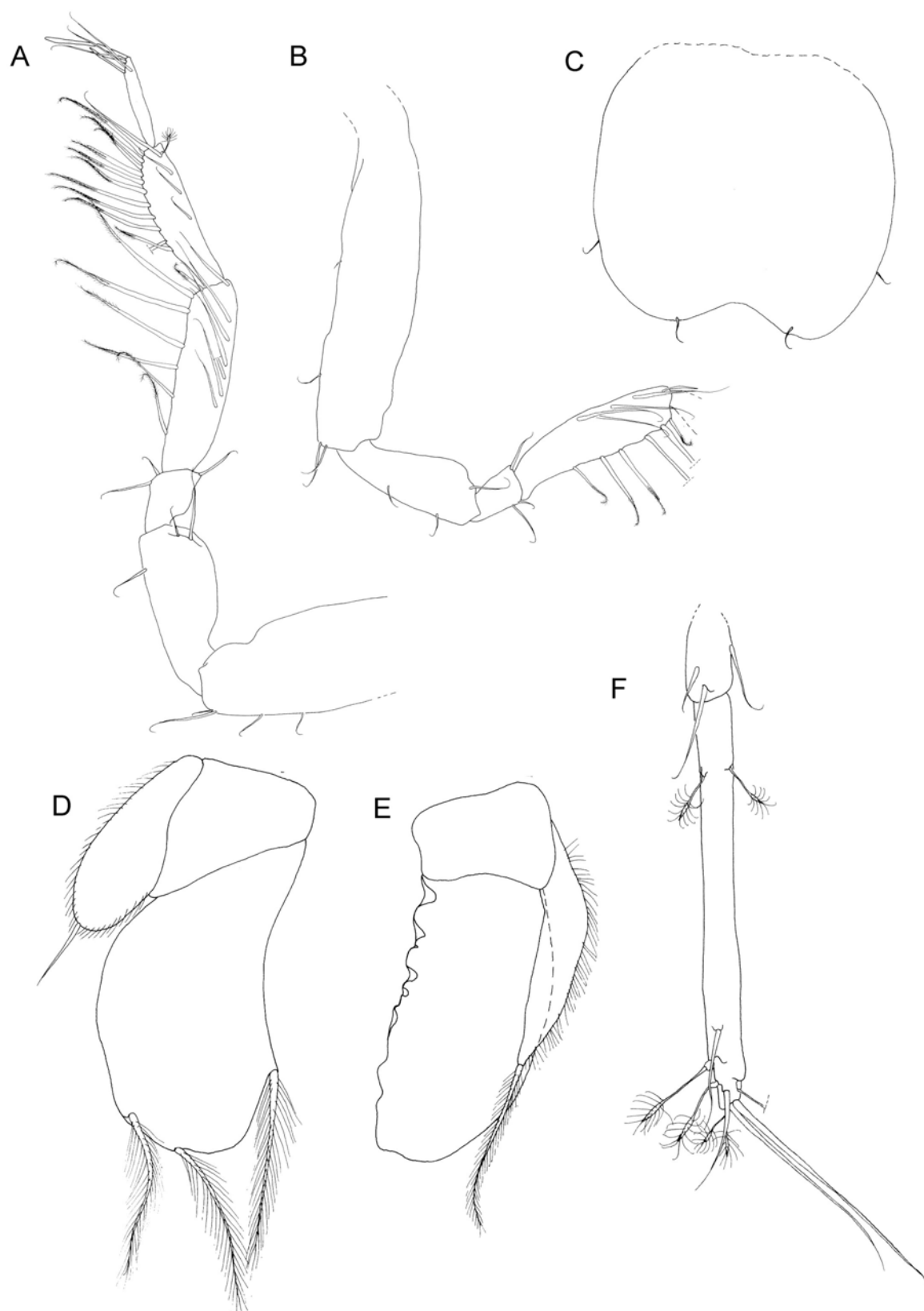
Pleopod 4 (Fig. 67): Endopod oval-shaped, length 2.31 width. Exopod length 5 width, distally one long plumose seta, outer margin hirsute.

Uropods (Fig. 67): Uniramous. Endopod length 4.82 protopod length, 10.25 times longer than wide, marginally with two small broom setae, distally with four slender setae and five broom setae. Protopod length 1.7 width, with three simple slender setae.

**Discussion:** The new species is assigned to the genus *Paradesmosoma* due to the very characteristic shape of P IV, the kind of setation of this pereopod, carpus and propodus “paddle-like” and surrounded by numerous distally slender plumose seta (occurring in *Paradesmosoma* only), the mandibular palp of only two articles, the characteristic shape of the operculum (distal margin strongly concave) and the apomorphies of P I: P I carpo-euchelate, carpus less enlarged than propodus, with ventral row of irregular setae of varying types.

*P. australis* sp. nov. is most similar to *P. orientale* in the shape of palp article 2 of the Md. As in *P. orientale*, palp article 2 is about 2.17 times longer than wide and tapers to the distal end which is tipped by a small simple setae. In contrast to *P. orientale*, the lateral margins of this article are hirsute in *P. australis*. According to Kussakin’s (1965) drawings, whether *P. orientale* nor *P. conforme* possess posterolateral spines at the Plt. *P. australis* has posterolateral spines at the Plt. Unlike in the two species from the northern hemisphere, the propodus of P I is posteriorly widest in *P. australis* and tapers towards the dactylus.





**Fig. 67:** *Paradesmosoma australis* sp. nov., holotype female, pereopods (A-B): P VI (A), P VII (B), pleopods (C-F): operculum (C), PI 3 (D), PI 4 (E), uropod (F) scale = 0.1 mm

#### **3.1.5.3.5     *Oecidiobanchus slopei* sp. nov.**

Holotype. – male, 1.4 mm, NMV J 18606 ; Type locality. – Australia, New South Wales, 65 km E. of Nowra (34°55.52'S, 151°22.20'E), 2055 m depth, Poore, G.C.B. *et al.*, RV *Franklin*, 23 Oct. 1988 (Stn. SLOPE 63)

#### **Etymology**

The name refers to the sampling area on the South Australian continental slope.

#### **Diagnosis**

Body length 3.83 times longer than width of Prn2. Prn1 length 1.1 Prn2 length, similar to Prn2 width. Prn5 anterior margin slightly convex, lateral margins straight. Lm of MdL with five teeth. Coxae 1-4 produced, tipped with stout setae. Pl carpus length 1.41 width, distodorsally one long robust simple seta, ventrally with the large claw-seta and a row of distally setulate setae and combs of fine hairs inserted in a cuticular membrane, propodus length 2.61 width, more enlarged than carpus. Plt with posterolateral spines.

#### **Description of holotype male**

Habitus (Fig. 68): body 1.4 mm long (measured without appendages), 3.83 times longer than width of Prn2. Prn1 width 1.13 times cephalon width in dorsal view. Prn1 length 1.1 Prn2 length, similar to Prn2 width. Prn5 width 1.36 length, anterior margin slightly convex, lateral margins straight. Coxae 1-4 produced, tipped with stout setae. Plt length 0.71 width, posterolateral spines present. Lateral margins convex, posterior margin rounded.

Antennula (Fig. 68): 0.31 mm long, length 0.22 body length, with five articles. Article 1 with three broom setae. Article 2 length 1.53 width, 2.36 article 1 length; distally with three broom setae and one small seta. Article 3 with one slender seta, article 4 with two small broom setae, distal article with one aesthetasc, one broom seta and four long slender setae. Articles 2-5 length relative to article 1: 1.53: 0.45: 0.54: 0.63.

Antenna (Fig. 68) about 1 mm long, length about 0.71 body length, with 22 articles. Articles 3 with three small setae, article 4 with three small setae. Article 5 with four slender setae and distally one broom seta. Article 6 with six slender setae. Flagellum basally swollen (sexual dimorphism), articles with one or two slender setae each,

distal article with five long slender setae. Relative length of articles: 1: 1: 1.5: 0.88: 4.13: 4.25: 1.63: 0.75: 0.625: 0.5: 0.5: 0.5: 0.63: 0.5: 0.63: 0.63: 0.5: 0.38: 0.5: 0.5: 0.75: 0.75.

Mandible (Fig. 69): Article 2 of palp ventrodistally with four small setae, dorsally with rows of fine hairs, apical article with six setae, distal one longest. Ip with three teeth. Lm of MdL with five teeth. MdR not dissected from specimen. Spine row containing five spines. Mp with six fine slender setae.

Maxillula (Fig. 69): Inner lobe slightly smaller than outer lobe, terminally with five setae. Outer lobe dorsally with four fine setae, terminally with 11 strong spines (four spines with setules).

Maxilla: not dissected from specimen.

Maxilliped (Fig. 69): Epipodite length 3.13 width, length 1.43 endite length. Endite with two coupling hooks, terminally with one conate seta and numerous fine setae. Outer edge of endite and palp articles 1-3 fringed with numerous fine setae, distal corners tipped with one seta. Palp article 3 with six setae on inner margin, article 4 with two setae and article 5 with four setae. Article 1 length 0.5 width, article 2 length 1.16 width, article 3 length 1.07 width, article 4 length 1.1 width, article 5 length 1.6 width.

Pereopod I (Fig. 69): Enlarged, carpo-euchelate. Basis length 4.53 width, marginally with one small broom seta and five simple setae, proximal to ischium ventrally one long simple seta. Ischium length 1.87 width, distodorsally one simple seta, ventrally two simple setae. Merus length 1.13 width, ventrally two combs of fine hairs inserted in a cuticular membrane, distally one distally setulate and one simple seta, distodorsally two setae. Carpus length 1.41 width, distodorsally one long robust simple seta, ventrally with the large claw-seta and a row of distally setulate setae and combs of fine hairs inserted in a cuticular membrane. Propodus length 2.61 width, more enlarged than carpus, ventral and dorsal margin convex, distodorsally two small setae, ventrally fringed with fine hairs and nine small setae inserted in a cuticular membrane. Dactylus length 7.5 width, folding to propodus, mediodistally with three small setae. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.

Pereopod III (Fig. 69): P II missing from specimen, P III very similar to P IV. Basis length 5.7 width, marginally with four broom setae, five small slender setae and proximal to ischium ventrally one large simple seta. Ischium length 2.25 width, distodorsally one long simple seta and distoventrally one long simple seta. Merus length 2.5 width, dorsally with two, ventrally with one simple seta. Carpus length 4.3 width, with ventral row of four long slender setae, dorsally with row of four setae. Propodus length 3.5 width, ventrally with row of five slender setae, dorsally with four slender setae and one small broom seta. Dactylus length 4 times width, mediodistally with three small slender seta. Claw of one conate set, two slender setae inserting ventrally.

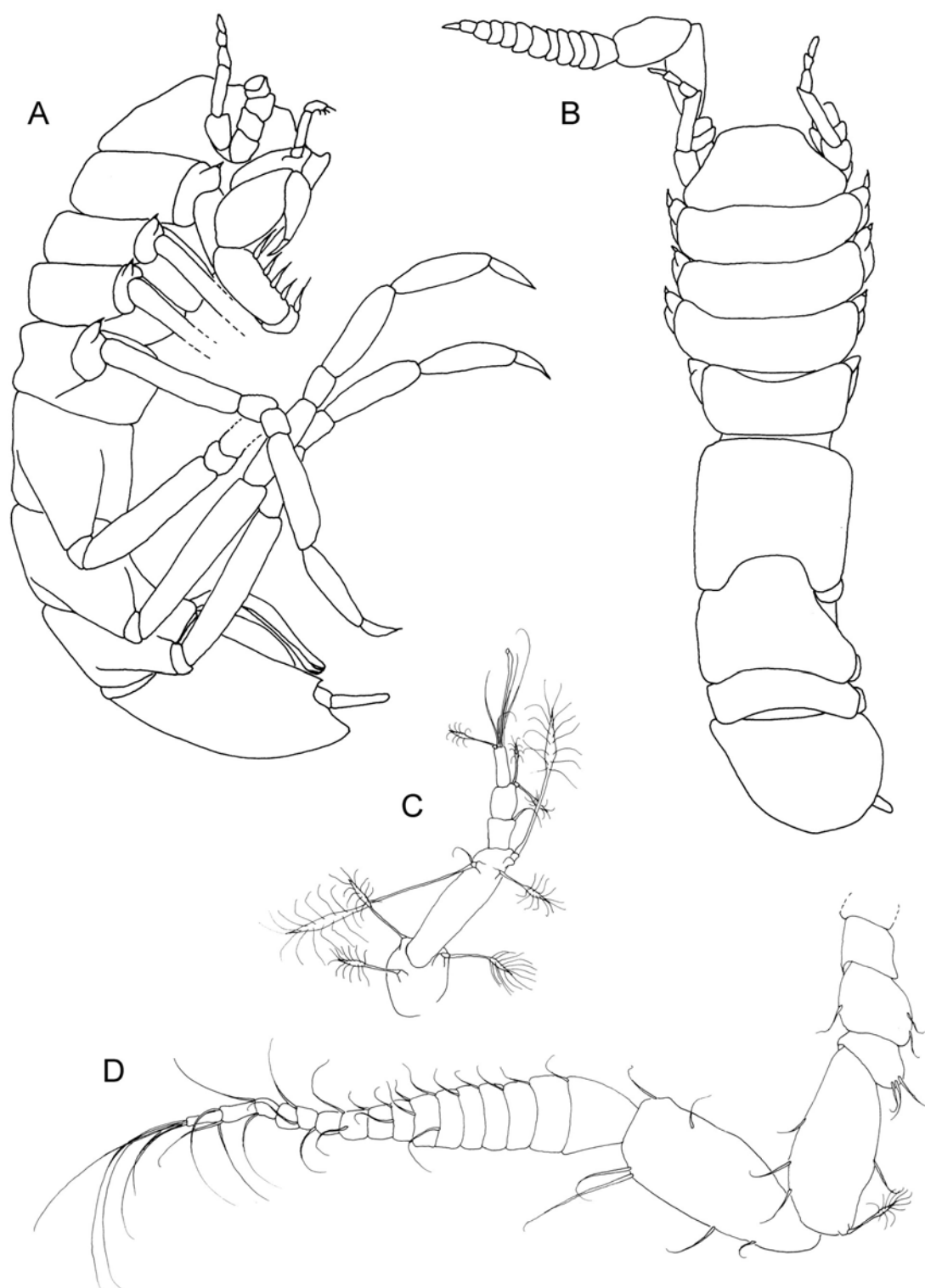
Pereopod V (Fig. 70): Very similar to P V and P VII. Basis length 4 times width, marginally with three simple slender setae and three broom setae. Ischium length 2.64 width, dorsally with four slender setae, ventrally with two small slender setae. Merus length 1.89 width, one small slender seta distodorsally and one small slender seta distolaterally. Carpus length 3 times width, ventrally with row of five long slender setae, dorsally as well and distally one small broom seta. Propodus length 3.4 width, ventrally with a row of six long slender setae, dorsally with seven long slender setae and two unequally bifid seta (one midway, one distally). Dactylus length 4 times width, mediodistally with three small slender setae, claw of one long conate seta, two slender setae inserting ventrally.

Pleopod 1 (Fig. 70): Length 2.04 width. Outer margins straight, terminal margin rounded, with three small setae on each side.

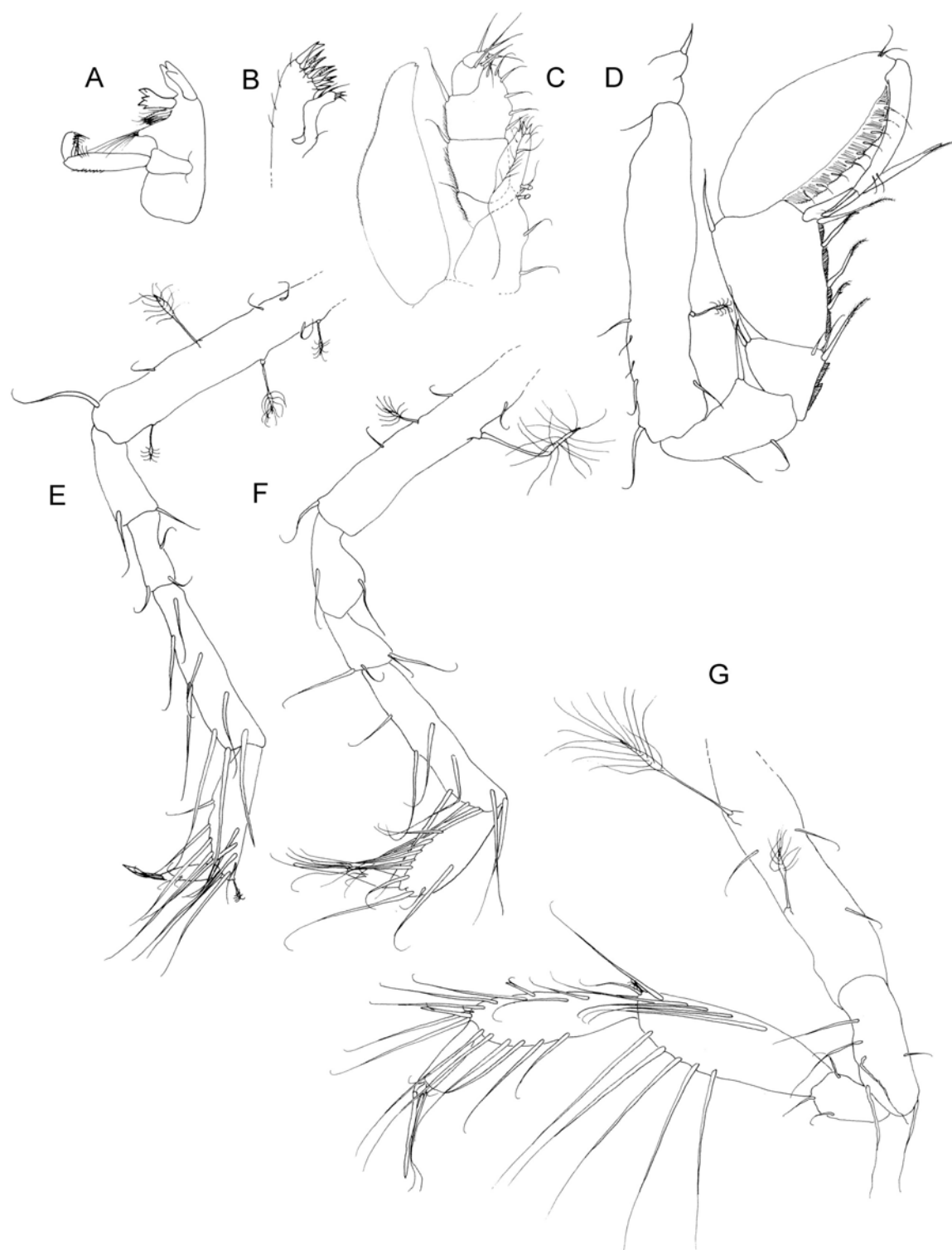
Pleopod 2 (Fig. 70): Sympod oval-shaped, length 2.24 width. Outer margin distally with one small seta. Endopod inserting 0.56 of sympods length.

Pleopod 3 (Fig. 70): Endopod length 1.4 width, distally with 3 long plumose setae. Exopod length 0.52 of endopod length, terminally tapering, with one simple seta, outer margin hirsute.

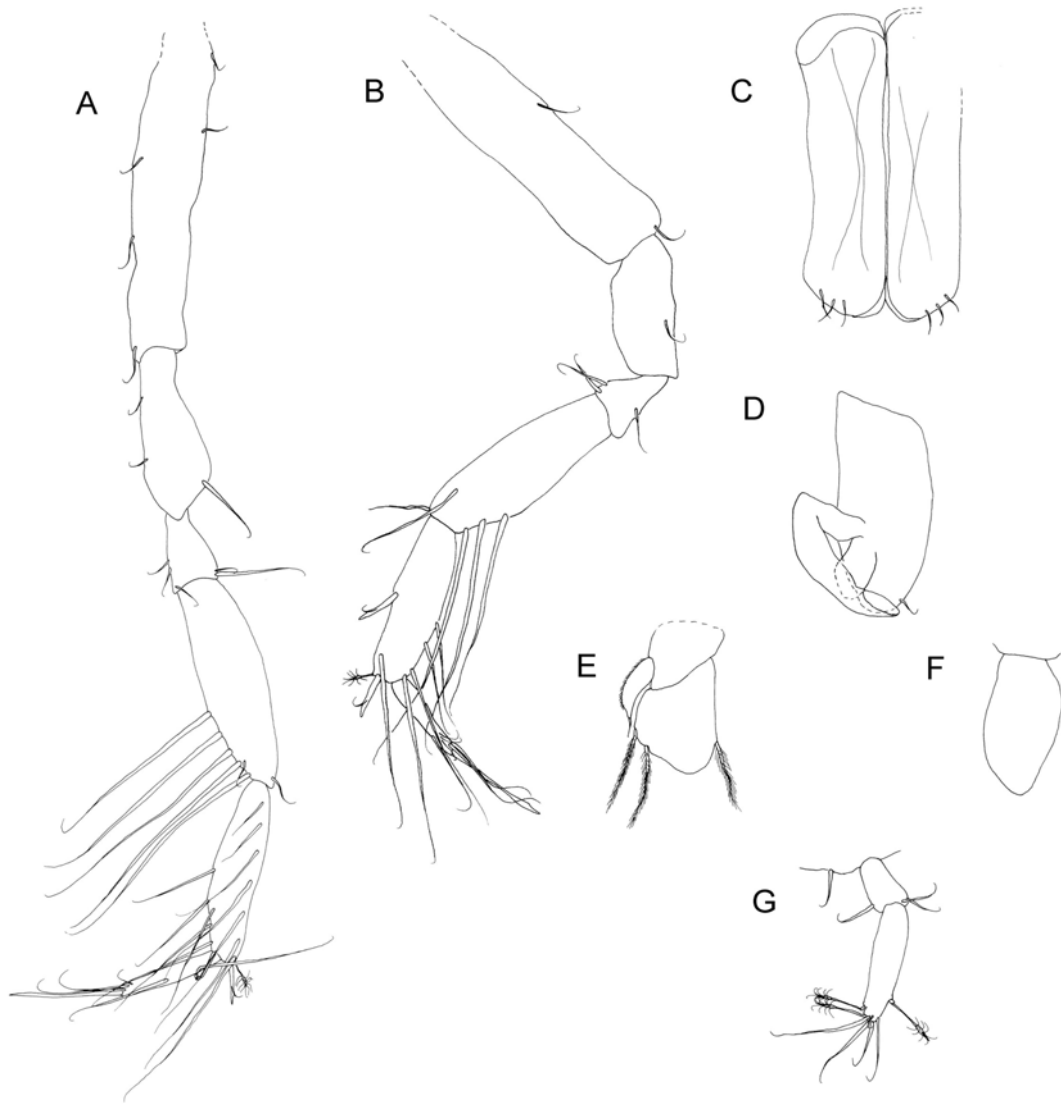
Pleopod 4 (Fig. 70): Endopod oval-shaped, length 1.92 width. Exopod missing.



**Fig. 68:** *Oecidiobanchus slopei* sp. nov, holotype male, habitus lateral (A), dorsal (B), antennula (C), antenna (D), scale = 1 mm



**Fig. 69:** *Oecidiobranthus slopei* sp. nov., holotype male, mouthparts (A-C): Md L (A), Mx 1 (B), Mxp (C), pereopods (D-G): P I (A), P III (E), P IV (F), P V (G)



**Fig. 70:** *Oecidiobranthus slopei* sp. nov., holotype male, pereopods (A-B): P VI (A), P VII (B), pleopods (C-G): PI 1 (C), PI 2 (D), PI 3 (E), PI 4 (F), uropod (G)

**Uropods** (Fig. 70): Uniramous. Endopod length 2.33 protopod length, 3.5 times longer than wide, distally with three broom setae, one small seta and four slender setae. Protopod length 1.5 width, with three simple slender setae.

**Discussion:** *Oecidiobranthus slopei* sp. nov. is assigned to the genus *Oecidiobranthus* due to the small and rounded breathing chamber. It shares the uniramous uropods, the propodus of P I is ore enlarged than the propodus and the dactylus and the propodus show the tendency to a subchela, although the typical claw-seta of the carpo-euchela is present.

The male of the new species differs from the other two species of the genus in the characters of P I. Unlike *O. plebejum* and *O. nanseni*, *O. slopei* sp. nov. possesses a ventral row of distally setulate seta on the carpus. Furthermore, the new species possesses posterolateral spines at the pleotelson. Whether *O. plebejum*, nor *O. nanseni* possess posterolateral spines at the pleotelson.

#### **3.1.5.3.6     *Disparella kensleyi* sp. nov.**

Holotype. – Female, preparatory, 1.9 mm; NMV J 18605; Type locality. - Australia, New South Wales, 74 km E. of Nowra (34°56.11'S, 151°28.06'E), 3150 m, box corer, Poore, G.C.B. *et al*, RV Franklin, 23. Oct 1988 (Stn. SLOPE 64)

#### **Etymology**

The name refers to Dr. Brian Kensley.

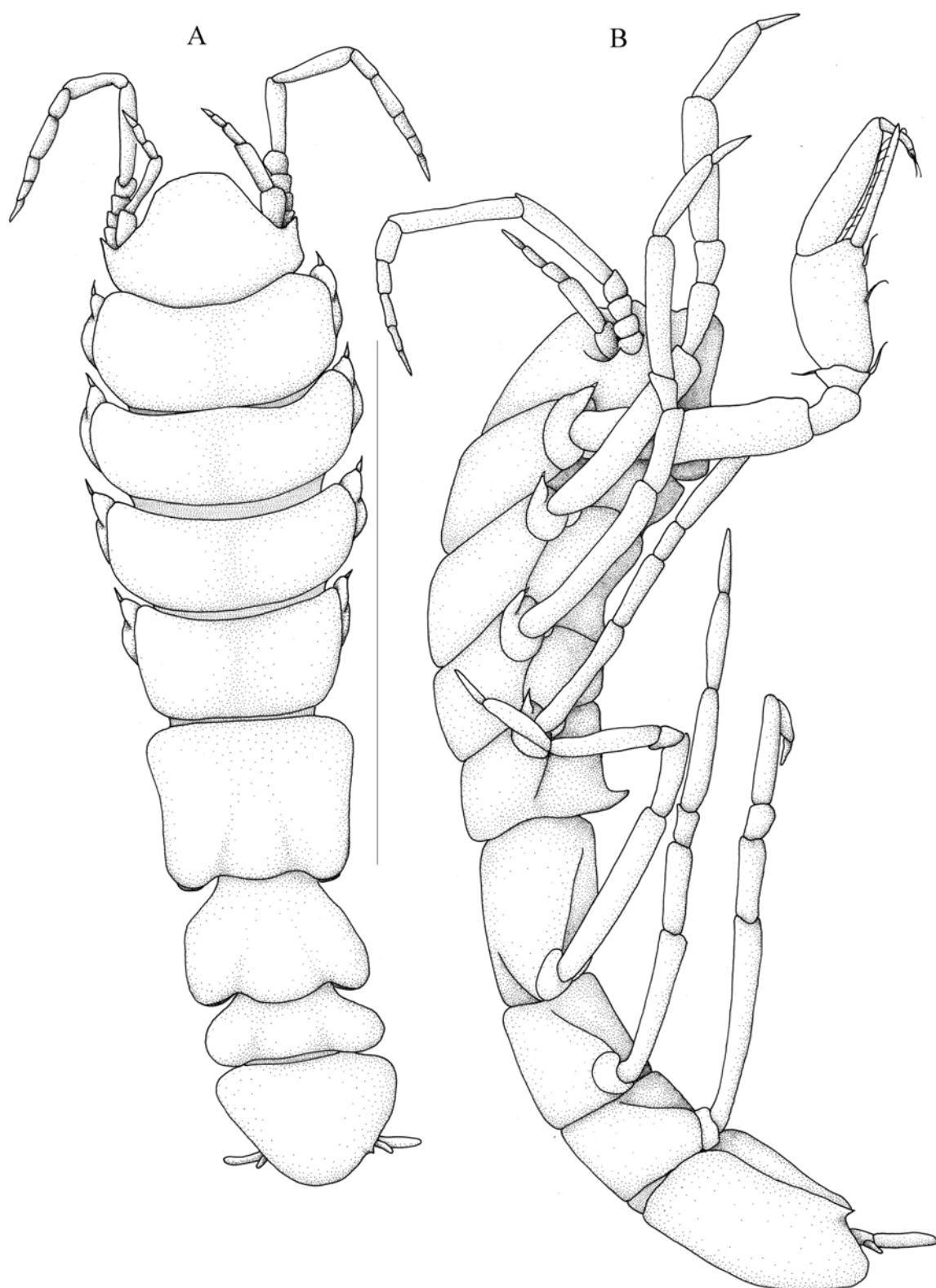
#### **Diagnosis**

Body length 3.98 times longer than width of Prn2. Prn1 length 1.05 Prn2 length, 0.93 Prn2 width. Prn5 with spine-like ventral elongation. Cephalon with one short anteriorly directed spine at insertion of antennae. Md palp of two articles, article 1 with one small seta, article 2 terminally with one small seta. Ip with four teeth. Lm of MdL with four teeth. Carpus of P I length 5 times width, with ventral row of five long unequally bifid setae increasing in length towards the propodus and three combs of fine hairs inserted in a cuticular membrane, dorsally with two long simple setae. Plt with posterolateral spines. Distal margin of Op slightly concave, with six slender setae. Ur biramous, exopod length 0.43 endopod length.

#### **Description of holotype female**

Habitus (Fig. 71): body 1.9 mm long (measured without appendages), 3.98 times longer than width of Prn2. Prn5 with spine-like ventral elongation. Cephalon with one short anteriorly directed spine at insertion of antennae. Prn1 slightly wider than cephalon. Prn1 length 1.05 Prn2 length, 0.93 Prn2 width. Prn5 anterior margin straight, lateral margins slightly concave. Coxae 1-4 produced, tipped with small stout setae. Plt length 0.71 width, posterolateral spines present, lateral margins convex, posterior margin rounded.





**Fig. 71:** *Disparella kensleyi* sp. nov., holotype female, habitus dorsal (A), lateral (B), scale = 1 mm

Antennula (Fig. 72): 0.3 mm long, length 0.16 body length, with five articles. Article 1 with three small broom setae. Article 2 length 3.83 width, 1.64 article 1 length; distally with two large articulated broom setae. Article 3 with one small slender seta, article 4 distally with two small broom setae, distal article terminally with one aesthetasc, one broom seta and two long slender setae. Articles 2-5 length relative to article 1: 1.64: 0.57: 0.7: 0.64.

Antenna (Fig. 72): about 1.1 mm long, length 0.58 body length, with about 12 articles (broken off after article 12). Article 3 with two small slender setae. Article 4 with two slender setae. Article 5 with three small slender setae. Article 6 marginally with two and distally with three slender setae. Flagellar articles 1-3 distally with two slender setae, following articles with long slender setae. Relative length of articles: 1: 0.6: 0.9: 0.9: 4.1: 5.4: 1.7: 1.3: 1.3: 0.9: 0.6: broken off.

Mandible (Fig. 72): Palp of two articles, article 1 with one small seta, article 2 terminally with one small seta. Ip with four teeth. Lm of MdL with four teeth, lm-like structure of MdR triangular and distally serrated (five small teeth). Spine row containing three spines. Mp with seven setae.

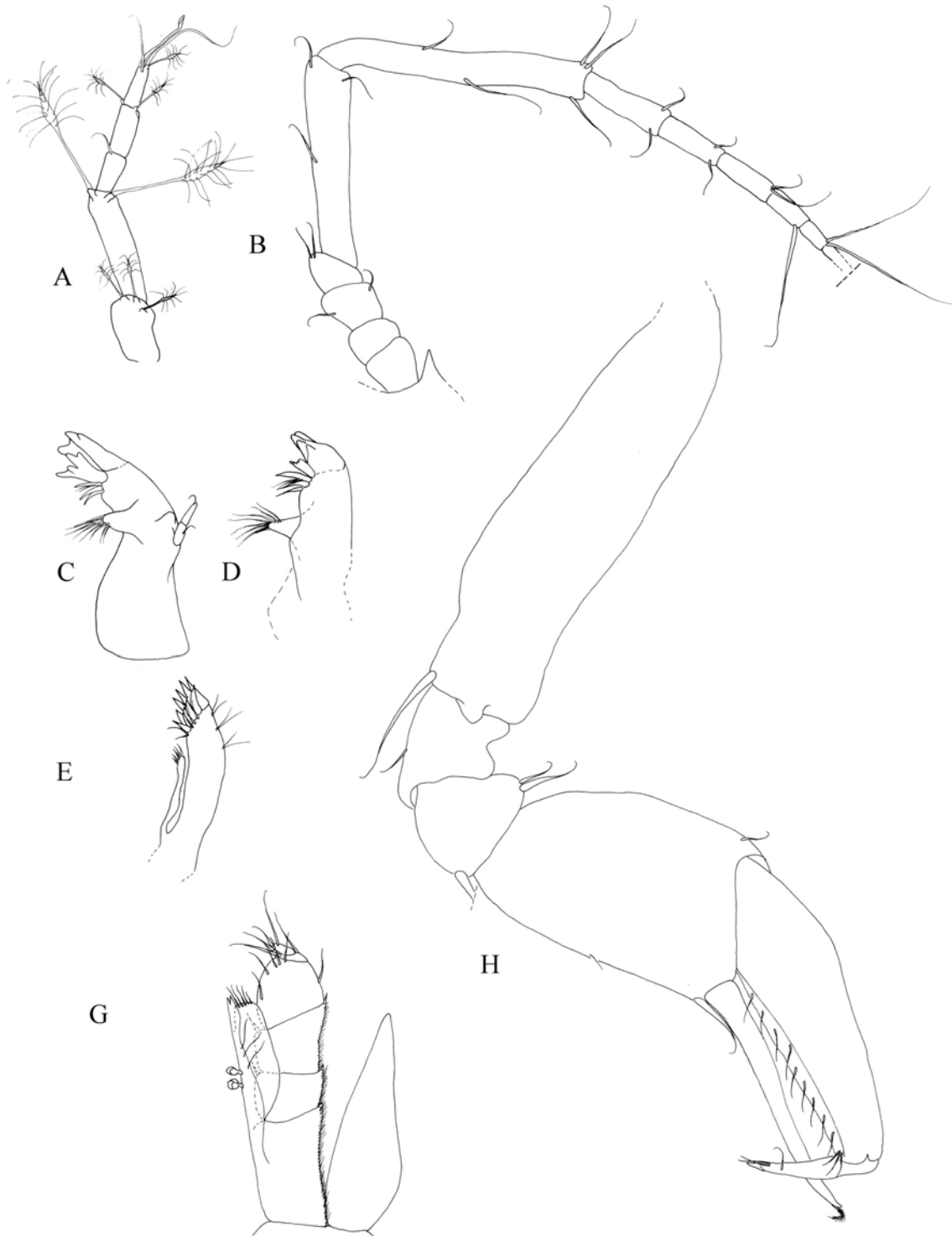
Maxillula (Fig. 72): Inner lobe smaller than outer lobe (0.71 of outer lobe length), terminally with five setae. Outer lobe five times longer than wide, marginally with three pairs of fine setae, terminally with nine strong spines and four simple setae.

Maxilla: Not dissected from specimen.

Maxilliped (Fig. 72): Epipodite length 3.13 width, length similar endite length. Endite with two coupling hooks, terminally with two conate setae and five small setae, marginally few fine setae. Outer edge of endite and palp articles 1 and 2 with row of fine setae and one small seta on distal corners, inner margin of article 3 with five setae, outer margin with one seta, article 4 with three setae, article 5 with two setae. Article 1 length 0.6 width, article 2 length 0.93 width, article 3 length 1.07 width, article 4 length 2.5 width, article 5 length 3 times width.

Pereopod I (Fig. 72): Basis length 4.04 width, proximal to ischium ventrally one long simple seta. Ischium length 0.63 width, ventrally one small slender seta. Merus length 0.71 width, dorsally two robust simple setae, ventrally one seta (broken off). Carpus

length 1.43 width, ventrodistally with large claw-seta and slender proximal seta, ventrally one small seta midway. Propodus length 3.47 width, ventrally fringed with fine hairs and row of 12 small setae inserted in a cuticular membrane. Dactylus length 7.6 width, mediolaterally one small seta. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.



**Fig. 72:** *Disparella kensleyi* sp. nov., holotype female, antennula (A), antenna (B), mouthparts (C-G): Md L (C), Md R (D), Mx 1 (E), Mxp (G), pereopod I (H)

Pereopod II (Fig. 73): Very similar to P III and P IV). Basis length 6.33 width, marginally with few simple setae and one small broom seta, proximal to ischium ventrally with one long simple seta. Ischium length 2.62 width, distodorsally with one seta, ventrally one seta midway. Merus length 1.45 width, distoventrally with one stout unequally bifid seta and two small slender setae, distodorsally one composed seta. Carpus length 5 times width, with ventral row of five long unequally bifid setae increasing in length towards the propodus and three combs of fine hairs inserted in a cuticular membrane, dorsally with two long simple setae. Propodus length 5.38 width, ventrally with one small slender seta midway, fringed with fine hairs, dorsally two long simple setae and distally one small broom seta. Dactylus length 6.67 width, mediodistally two small setae. Claw of dactylus with one conate seta, two slender setae ventrally.

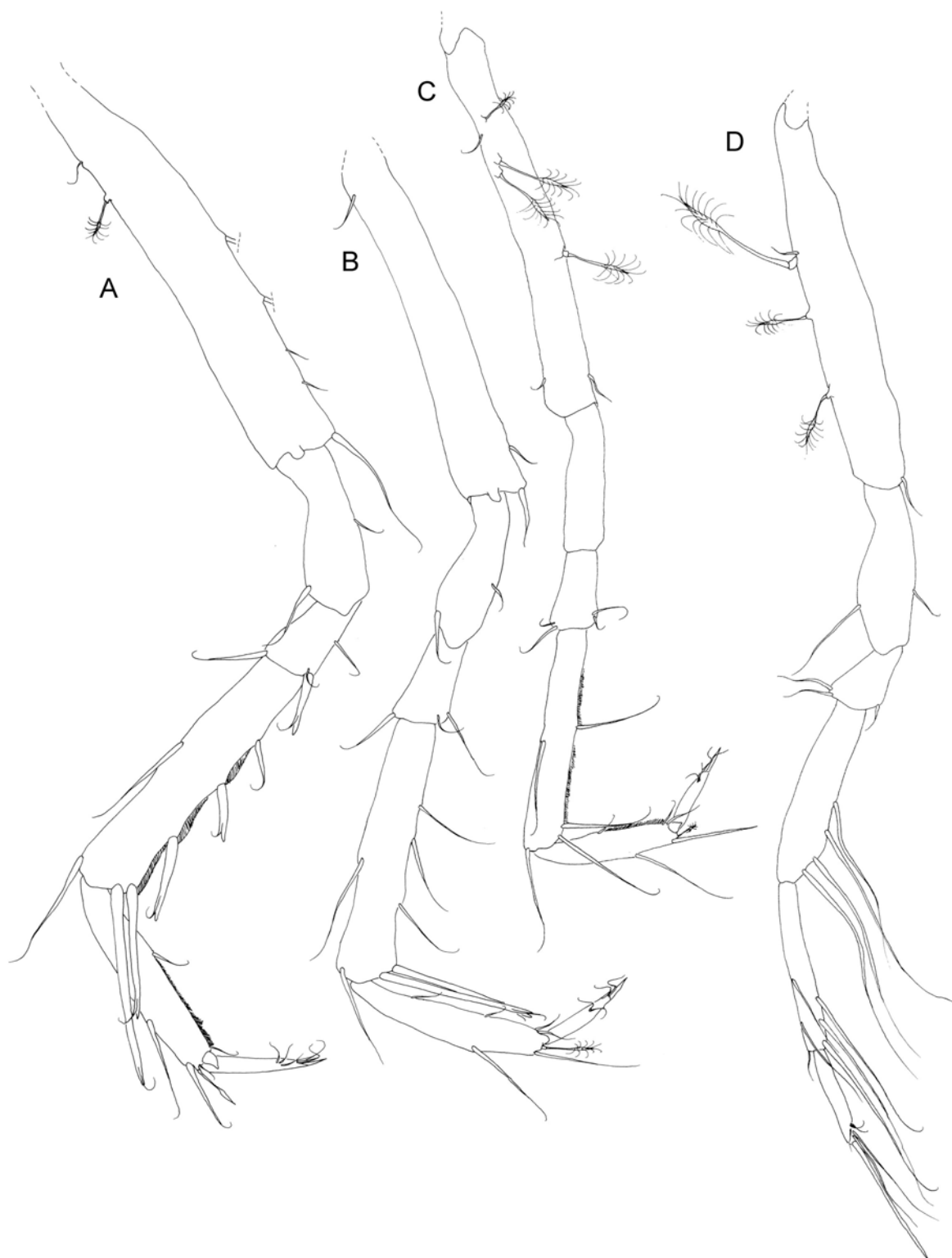
Pereopod V (Fig. 73): very similar to P VI and P VII. Basis length 6.3 width, marginally with one small and two broom setae. Ischium length 4.1 width. Merus length 1.6 width, with three slender setae. Carpus length 4.8 width, with ventral row of five long slender setae and dorsally two long setae (broken off), distally one small slender seta and one small broom seta. Propodus length 4.13 width, ventrally with one small seta and three long slender setae, dorsally with two slender setae. Dactylus length 7.6 width, mediodistally three small seta, claw of one long conate seta, two slender setae inserting ventrally.

Pleopod 2 (operculum) (Fig. 74): length 1.19 width. Lateral margins slightly convex, distal margin slightly concave, distal margin with six slender setae.

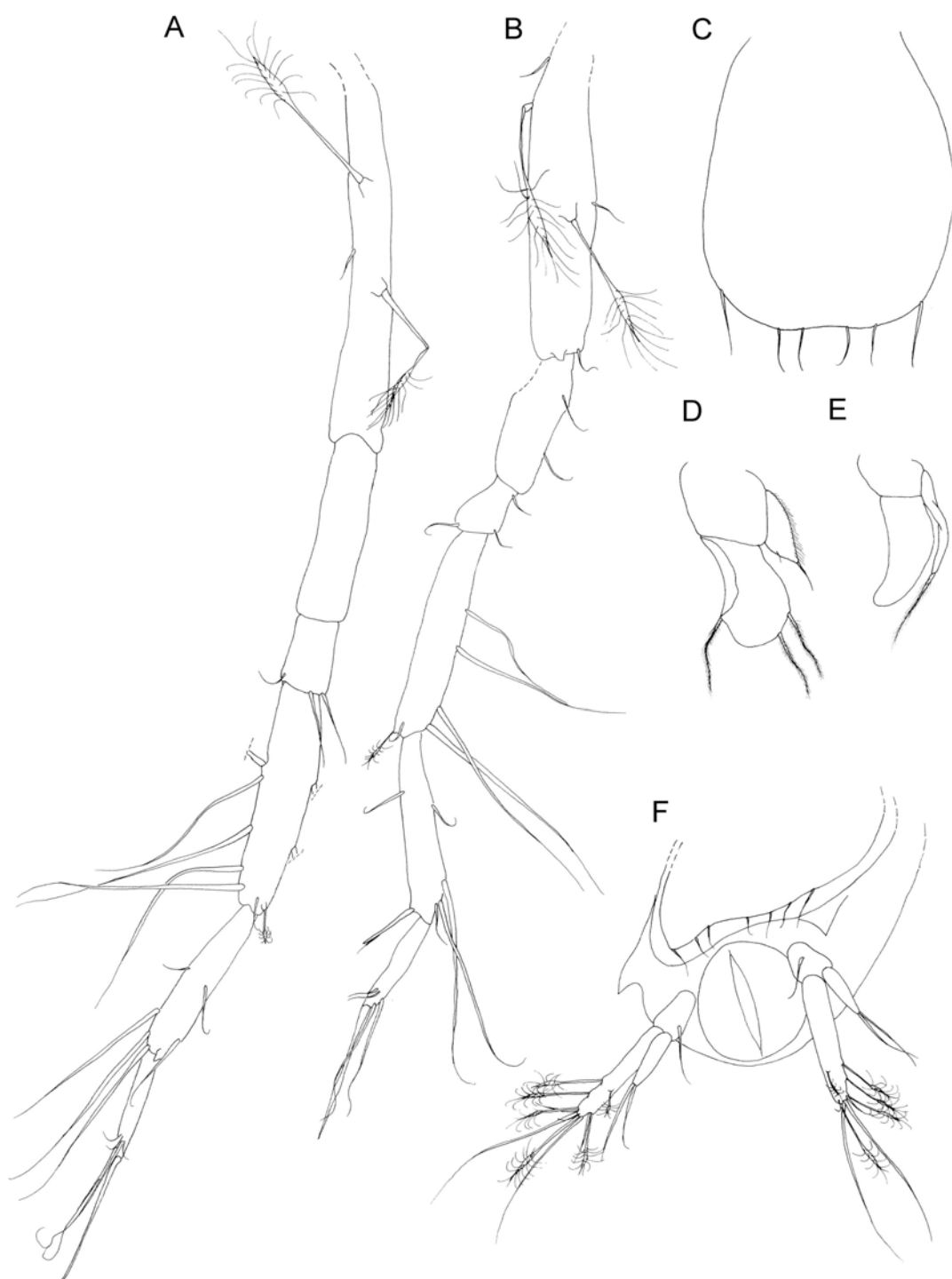
Pleopod 3 (Fig. 74): Endopod length 1.44 width, distally with 3 long plumose setae. Exopod length 0.74 of endopod length, with one small terminal seta, outer margin hirsute.

Pleopod 4 (Fig. 74): Endopod length 2.66 width. Exopod length 8 times width, distally with one long plumose seta.

Uropods (Fig. 74): Biramous. Endopod length 3.5 protopod length, 4.66 times longer than wide, distally with five broom setae, two small slender setae and two long slender setae. Exopod length 0.43 endopod length, 4 times width, terminally with two slender setae. Protopod length similar width, with one slender seta.



**Fig. 73:** *Disparella kensleyi* sp.nov., holotype female, pereopods (A-D): P II (A), P III (B), P IV (C), P V (D)



**Fig. 74:** *Disparella kensleyi* sp. nov., holotype female, pereopods (A-B): P VI (A), P VII (B), pleopods (C-E): operculum (C), PI 3 (D), PI 4 (E), Plt with uropods from ventral (F)

**Discussion:** The new species is assigned to the genus *Disparella* due to the short anteriorly directed spine at the antennular fold, the carpo-euchelate P I, the biramous Ur and a Im with four teeth.

*Disparella kensleyi* sp. nov. shows affinity to species of *Chelator* and *Prochelator*. The carpo-euchela of the new species resembles more a carpo-euchela as found in *Chelator* (ventral margin of carpus with small setae only), but *Chelator* species possess uniramous uropods and the Im has three teeth. A single midventral seta on the carpus together with the claw-seta and the penultimate slender seta is known for *Prochelator*, but in *Prochelator* species the midventral seta is always of composed setal type. Due to the anteriorly directed spine at the antennular folds, which is known for all species of *Disparella*, and the biramous uropods, *D. kensleyi* sp. nov. fits best into *Disparella*.

It is easily to distinguish from the other members of the genus by the spine-like ventral elongation at Prn5 and the single small midventral seta on the carpus of P I together with the claw-seta and the penultimate slender seta.

#### 3.1.5.3.7 *Echinopleura cephalomagna* sp. nov.

Holotype. – Female, preparatory, 1.8 mm; NMV J 18600 Australia, Victoria, South of Point Hicks (38°17.70'S, 149°11.30'E), 400 m depth, WHOI epibenthic sled, MF *et al.*, RV Franklin, 24. Jul 1986 (Stn. SLOPE 40).

#### Paratypes:

Paratype. – 1 female, adult, 2.2 mm; NMV J 18601; locality. - Australia, New South Wales, 54 km ESE of Nowra (34°52.72'S, 151°15.04'E), 996-990 m, WHOI epibenthic sled, Poore, G.C.B. *et al.*, RV Franklin, 22. Oct 1988 (Stn. SLOPE 53).

Paratype. – 1 female, preparatory; 2.1 mm; NMV J 53074; locality. – Australia, New South Wales, 54 km ESE of Nowra (34°52.72'S, 151°15.04'E), 996-990 m, WHOI epibenthic sled, Poore, G.C.B. *et al.*, RV Franklin, 22. Oct 1988 (Stn. SLOPE 53).

#### **Etymology**

The name refers to the extremely large cephalothorax of the new species.

#### **Diagnosis**

Body length 3.2 times longer than width of Prn2. Cephalothorax highest part of body from lateral view. Prn1 slightly smaller than Prn2. Lateral margins of Prn5-Plt serrated. Ip with one rounded tooth. Lm of MdL represented by one small bulge-like tooth.

#### **Description of holotype female**

Habitus (Fig. 75): body 2.2 mm long (measured without appendages), 3.2 times longer than width of Prn2. Cephalothorax highest part of body from lateral view. Prn1 width 1.16 times cephalon width in dorsal view. Prn1 length 0.94 Prn2 length, 0.91 Prn2 width. Prn5 width 0.67 length, anterior margin straight, lateral margins serrated. Coxae 1-4 produced, tipped with small stout setae. Plt length 1.06 width, lateral margins serrated, lightly convex, posterior margin smooth, rounded.

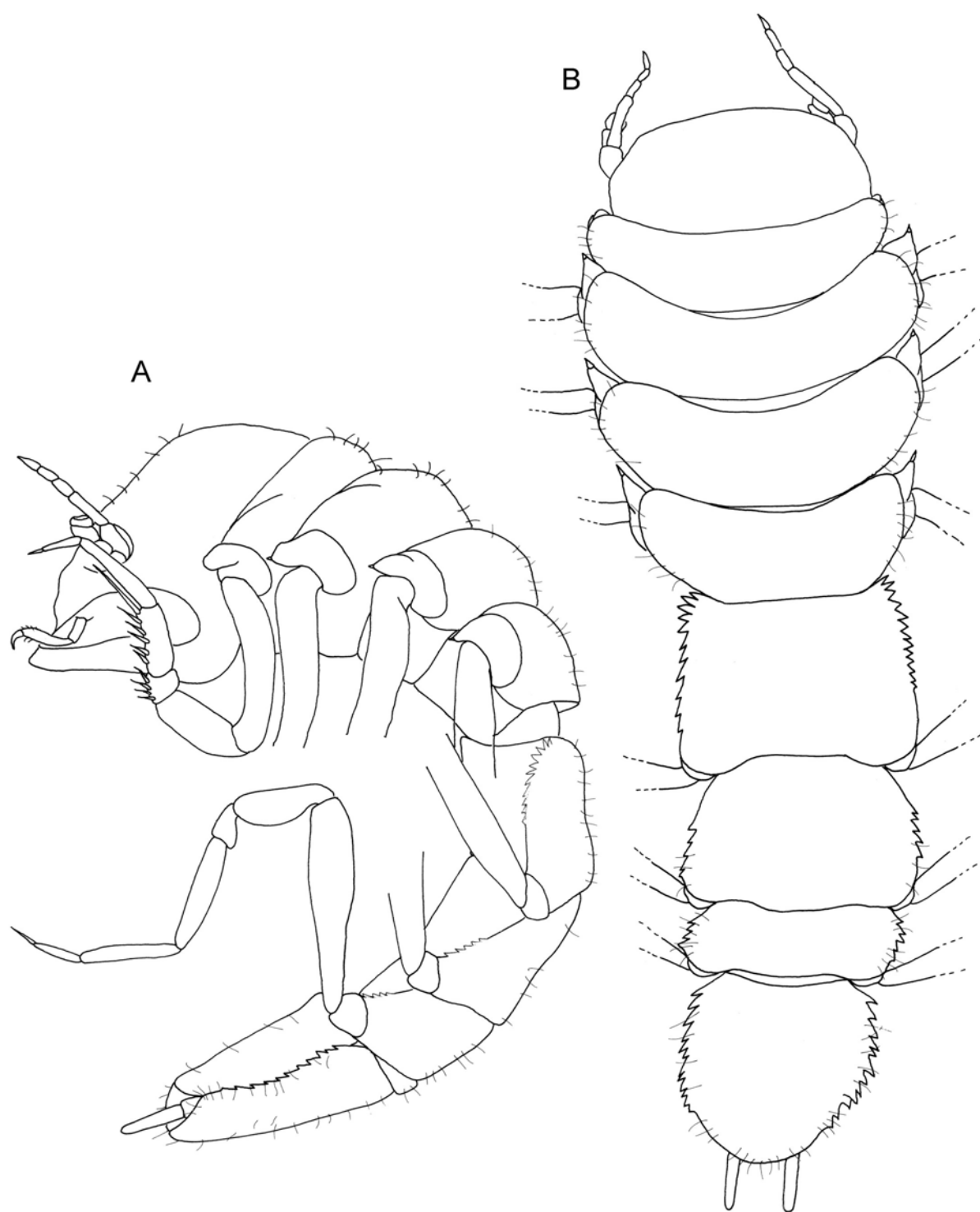
Antennula (Fig. 76): 0.27 mm long, length 0.12 body length, with six articles. Article 1 with one small slender seta and three broom setae. Article 2 length 2.57 width, 0.69 article 1 length; distally with four articulated broom setae. Article 3 with one small seta, article 4 distally with two broom setae, distal article with one aesthetasc and four slender setae. Articles 2-5 length relative to article 1: 0.69: 0.69: 0.23: 0.19: 0.27.

Antenna (Fig. 76): broken off.

Mandible (Fig. 76): Article 1 of palp distally with one slender seta, article 2 distoventrally with two small seta, fringed with rows of fine hairs, article 3 with four small and distally one setulate seta. Ip with one rounded tooth. Lm of MdL represented by one small bulge-like tooth. Lm-like structure absent at MdR. Spine row containing nine spines. Mp with 10 setae.

Maxillula (Fig. 76): Inner lobe slightly smaller than outer lobe (0.63 of outer lobe length), distally with seven simple setae, dorsally with 12 fine setae and ventrally with five pairs of fine hairs. Outer lobe marginally with 21 pairs of fine hairs, terminally with 11 strong spines (seven spines with setules).





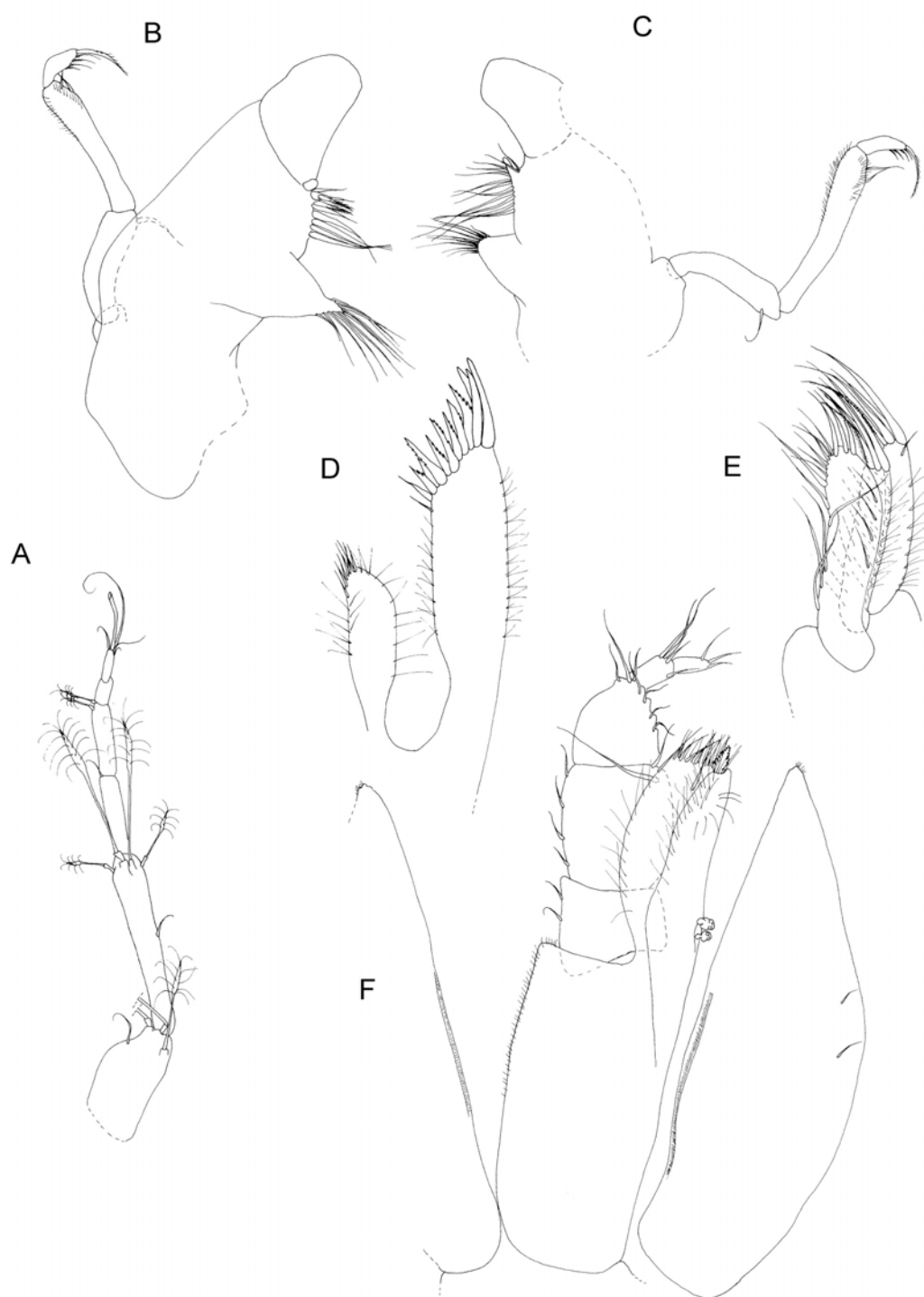
**Fig. 75:** *Echinopleura cephalomagna* sp. nov., holotype female, habitus lateral (A), dorsal (B), scale = 1 mm

Maxilla (Fig. 76): Medial lobe broader than other lobes, terminally with three slender setae, ventrolaterally with 12 setae, setae near base longest. Outer lobe dorsally with eight pairs of fine hairs, terminally with three long ventrally setulate setae.

Maxilliped (Fig. 76): Epipodite length 3.08 width, length similar endite length. Endite with two coupling hooks, terminally with one star-shaped conate seta and numerous fine setae, marginally with pairs of fine setae. Edge of endite fringed with fine hairs, palp article 1 with two setae on outer margin, article 2 with three setae on outer margin and three setae on inner margin, article 3 with seven setae on inner margin, article 4 with four setae, article 5 with three setae. Article 1 length 0.91 width, article 2 length 0.89 width, article 3 length 1.11 width, article 4 length 1.6 width, article 5 length 2.67 width.

Pereopod I (Fig. 77): Basis length 5.94 width, marginally with 14 setae. Ischium length 3.17 width, ventrally with seven small slender setae, dorsally with two simple slender setae. Merus length 1.18 width, ventrally with a row of four simple setae, distodorsally with one seta (broken off). Carpus length 3.2 width, ventrally with dorsal row of seven setae, distal and penultimate seta longest, distally setulate, dorsally with three small slender setae. Propodus length 8 times width, with few setae distally. Dactylus length 4.2 width, mediodistally three small setae. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.

Pereopod II (Fig. 77): very similar to P III and P IV. Basis length 4 times width, marginally with 27 small setae, proximal to ischium ventrally one long simple seta. Ischium length 3.13 width, ventrally 16 simple seta, dorsally four simple setae. Merus length 1.38 width, ventrally with row of six setae, distodorsally two simple setae. Carpus length 3.57 width, with ventral row 11 long unequally bifid setae increasing in length towards the propodus., dorsolaterally with row of 11 long simple setae, dorsally with six small slender setae. Propodus length 2.7 times width, ventrally with one small slender seta, two small stout unequally bifid setae and two combs of fine hairs inserted in a cuticular membrane, dorsally with row of eight long simple setae. Dactylus length 2.5 width, mediodistally three small setae. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.



**Fig. 76:** *Echinopleura cephalomagna* sp. nov., paratype female, antennula (A), mouthparts (B-F): Md R (B), Md L (C), Mx 1 (D), Mx 2 (E), Mxp (F)

Pereopod VI (Fig. 78): very similar to P V and P VII. Basis length 4.19 width, with two large broom setae, marginally with 13 small seta. Ischium length 3.39 width, laterally with nine small setae, dorsally with six slender setae. Merus length 1.38 width, ventrally with three small slender setae. Dorsally with one small seta and one long simple seta. Carpus length 4.11 width, ventrally with row of 12 long slender setae, dorsally with row of nine slender setae and four small setae. Propodus length 3.79 width, ventrally with row of five long slender setae, dorsally with row of six setae. Dactylus length 8.5 width, distally with one slender seta, claw of one long conate seta, two slender setae inserting ventrally.

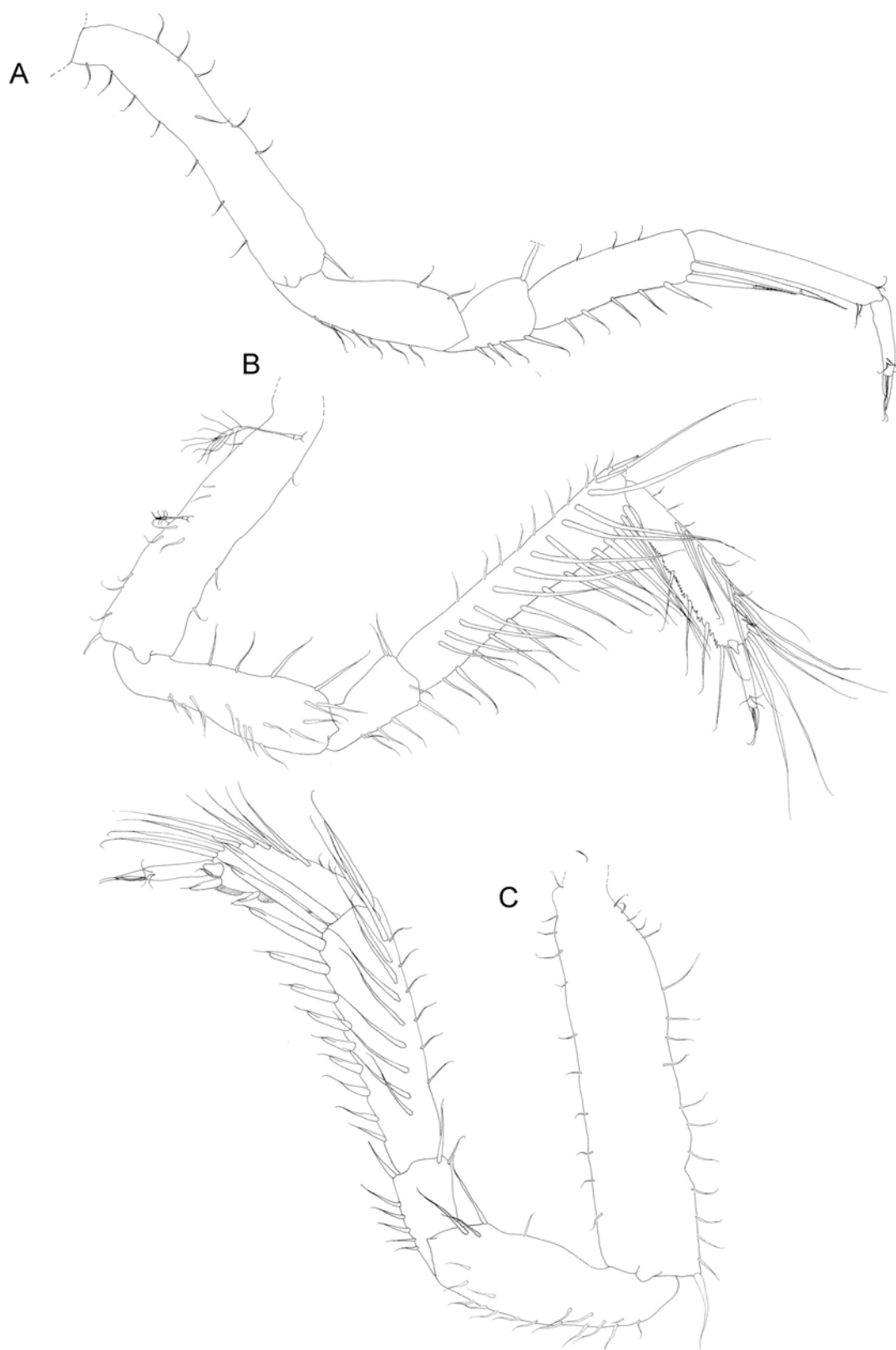
Pleopod 2 (operculum) (Fig. 78): length 1.37 width. Lateral margins straight, op tapering towards distal tip, setose (ventral surface with about 34 setae), marginally with 58 setae.

Pleopod 3 (Fig. 78): Endopod length 1.8 width, distally with 3 long plumose setae. Exopod length 0.44 of endopod length, margins hirsute, distally with one simple seta.

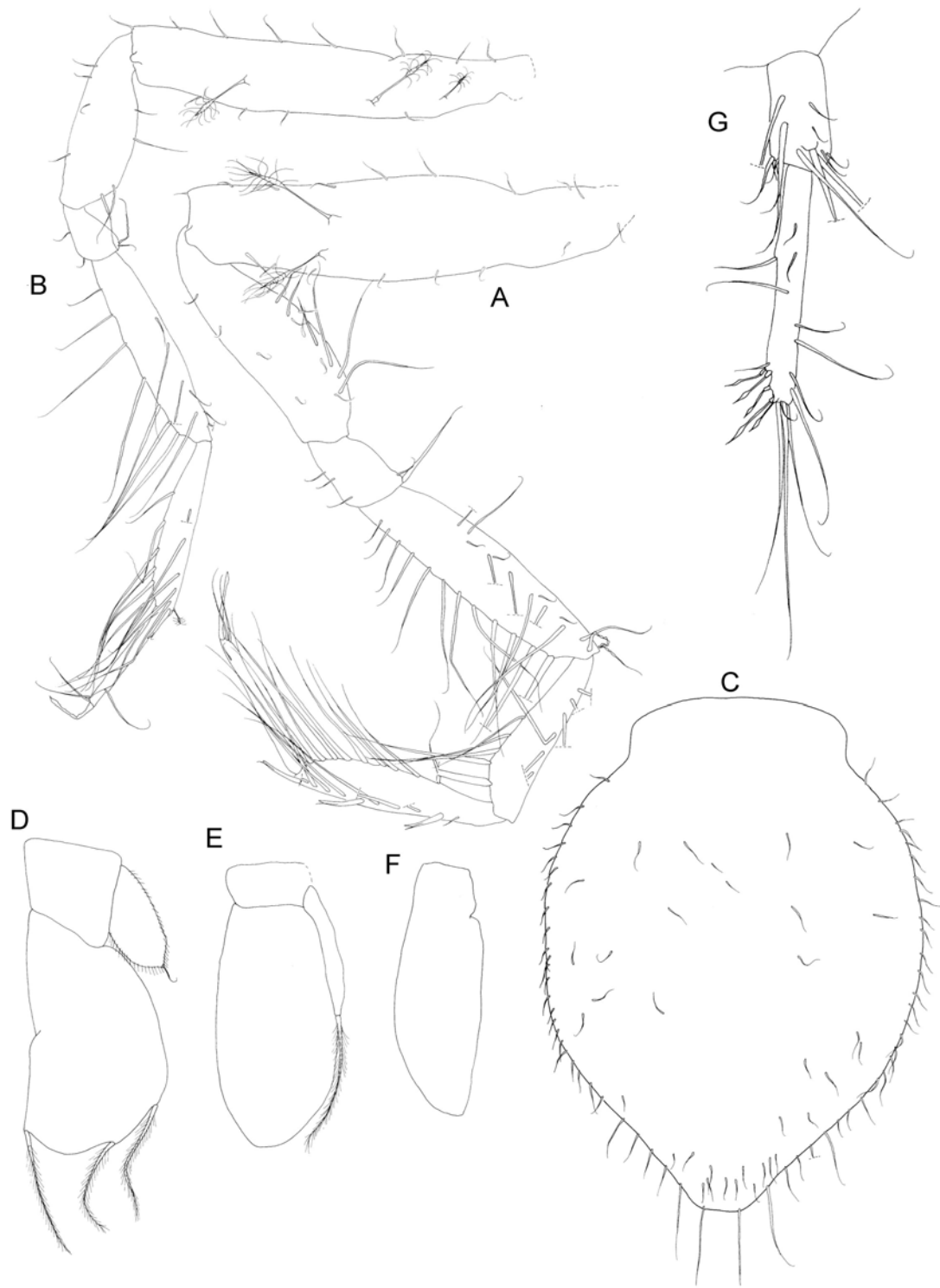
Pleopod 4 (Fig. 78): Endopod oval-shaped, length 2 times width. Exopod length 7.8 width, distally one long plumose seta.

Uropods (Fig. 78): Uniramous. Endopod length 2.04 protopod length, 8.17 times longer than wide, marginally with six slender setae, distally with five long slender setae, two small seta and five broom setae. Protopod length 1.85 width, with 12 setae.

**Discussion:** *Echinopleura cephalomagna* sp. nov. is the second species of the genus *Echinopleura*. It belongs to this genus due to the slender P I and the features of the Md as there are the ip with one rounded tooth and the extremely small Im, the serrated body margins from Prn5 to the Plt. The simplified Md is unique to *Echinopleura*. The new species is easily to distinguish from the only other species of the genus, *E. aculeata*, by the presence of a well developed mandibular palp. In *E. aculeata* the whole body is serrated, even the cephalon and the coxae. *E. aculeata* possesses a dorsal hook on the ischium of P II, *E. cephalomagna* lacks this hook. While the antennula of *E. aculeata* consists of five articles, the antennula of *E. cephalomagna* consists of six articles.



**Fig. 77:** *Echinopleura chephalomagna* sp. nov., paratype female, pereopods (A-D): P I (A), P II (C), P III (B)



**Fig. 78:** *Echinopleura cephalomagna* sp. nov., paratype female, pereopods (A-B): P VI (A), P VII (B), pleopods (C-G): operculum (C), PI 3 (D), PI 4 (E), PI 5 (F), uropod (G)

#### **3.1.5.3.8     *Whoia victoriensis* sp. nov.**

Holotype. – Female, preparatory, 1.6 mm NMV J 18598; Type locality. – Australia, Victoria, 76 km S of Point Hicks (38°29.33'S, 149°19.98'E), 1840-1750 m depth, WHOI epibenthic sled, Poore, G.C.B. *et al.*, RV Franklin, 26. Oct 1988 (Stn. SLOPE 69)

#### Paratypes:

Paratype. – female, preparatory, 1.5 mm NMV J 18599; locality. - Australia, Victoria, 67 km S of Point Hicks (38°23.95'S, 149°17.02'E), 1277-1119 m depth, WHOI epibenthic sled, Poore, G.C.B. *et al.*, RV Franklin, 25. Oct 1988 (Stn. SLOPE 67)

#### **Etymology**

The name refers to the state Victoria in Australia because the species was collected in the region and it is described out of the collection of the “Museum Victoria”. The name may refer to two locations, the sampling area and the museum.

#### **Diagnosis**

Body length 4 times longer than width of pereonite 2. Prn1 slightly smaller than Prn2. Pereonite 5 anterior margin straight, lateral margins straight. A1 with six articles. Ip with two teeth. Lm of MdL with one tooth. Coxae 1-4 angular, coxa 1 with small stout seta, 2-4 without setae. Ischium, merus and carpus of anterior pereopods laterally with numerous folds in which rows of fine hairs are inserted. P I and P II similar in setation, carpus with ventral row of five large robust unequally bifid distally setulate setae increasing in length towards propodus, distal seta of row reaching full length of propodus, dorsally with a row of five slender distally setulate setae, propodus ventrally with two small stout unequally bifid setae and a row of 14 small setae inserted between them, dorsally with a row of five slender distally setulate setae and distally one small seta. Lateral margins of Plt hirsute, form tapering to posterior margin. Ur biramous, setose, exopod well developed (length 0.64 endopod length).

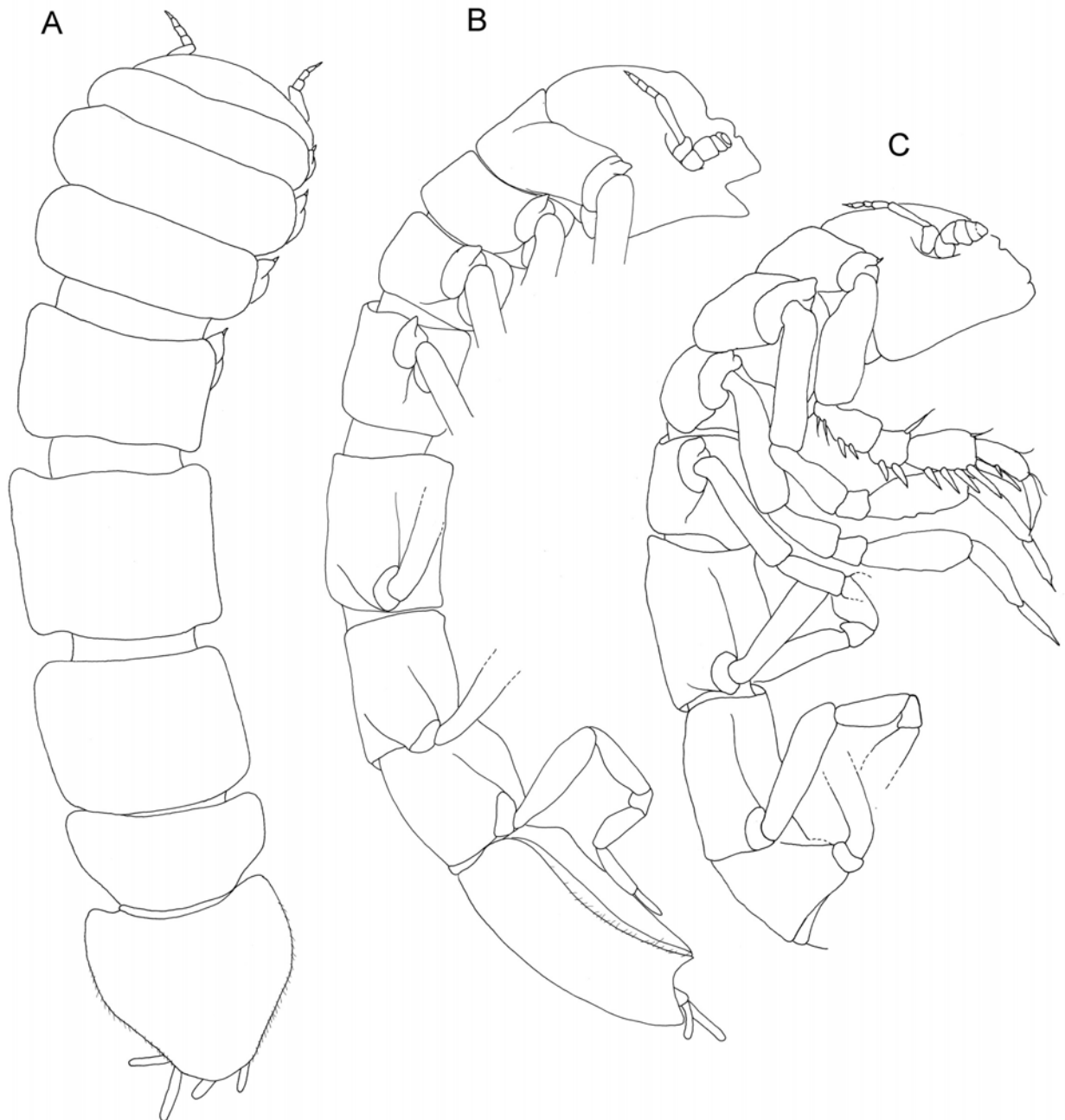
#### **Description of holotype female**

Habitus (Fig. 79): body 1.6 mm long (measured without appendages), 4.02 times longer than width of pereonite 2. Pereonite 1 width 1.13 times cephalon width in dorsal view. Pereonite 1 length 0.6 pereonite 2 length, 0.91 pereonite 2 width.

### 3. Results

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Pereonite 5 anterior margin straight, lateral margins straight. Coxae 1-4 angular, coxa 1 with small stout seta, 2-4 without setae. Pleotelson length 1.19 width, without posterolateral spines. Lateral margins hirsute, convex, posterior margin triangularly convex (Pleotelson tapering to posterior margin).



**Fig. 79:** *Whoia victoriensis* sp. nov., holotype female habitus dorsal (A), lateral (B), paratype female lateral (C), scale = 1 mm



Antennula (Fig. 80): Length 0.23 body length, with six articles. Article 1 with one small seta and four broom setae. Article 2 length 4.25 width, 1.9 article 1 length; distally with four articulated broom setae and one small seta. Article 3 with one small seta, article 4 with two slender setae and one small seta, article 5 with one slender seta, distal article terminally with one aesthetasc, one broom seta and two long slender setae. Articles 2-5 length relative to article 1: 1.89: 0.39: 0.4: 0.6: 0.28.

Antennula (Fig. 80): Length 0.23 body length, with six articles. Article 1 with one small seta and four broom setae. Article 2 length 4.25 width, 1.9 article 1 length; distally with four articulated broom setae and one small seta. Article 3 with one small seta, article 4 with two slender setae and one small seta, article 5 with one slender seta, distal article terminally with one aesthetasc, one broom seta and two long slender setae. Articles 2-5 length relative to article 1: 1.89: 0.39: 0.4: 0.6: 0.28.

Antenna (Fig. 80): broken off.

Mandible (Fig. 80): First article of palp with one small seta, second article ventrodistally with two small setulate setae, dorsally with rows of fine hairs, apical article dorsally with one small seta and rows of fine hairs, ventrally with five setae, distal one longest. Ip with two teeth. Lm of MdL with one tooth, Im-like structure of MdR of the same shape as Im of MdL. Spine row containing nine spines. Mp with five finely setulate setae.

Maxillula (Fig. 80): Inner lobe slightly smaller than outer lobe, terminally with seven setae, ventrally with four slender setae, dorsally with five pairs of fine hairs. Outer lobe marginally with 10 pairs of fine hairs, terminally with nine strong spines (three spines with setules).

Maxilla (Fig. 80): Medial lobe broader than other lobes, distally with seven simple setae, marginally with pairs of fine hairs, basally with seven slender setae. Outer lobe terminally with three setae, ventrally with three simple setae, dorsally with fine setae.

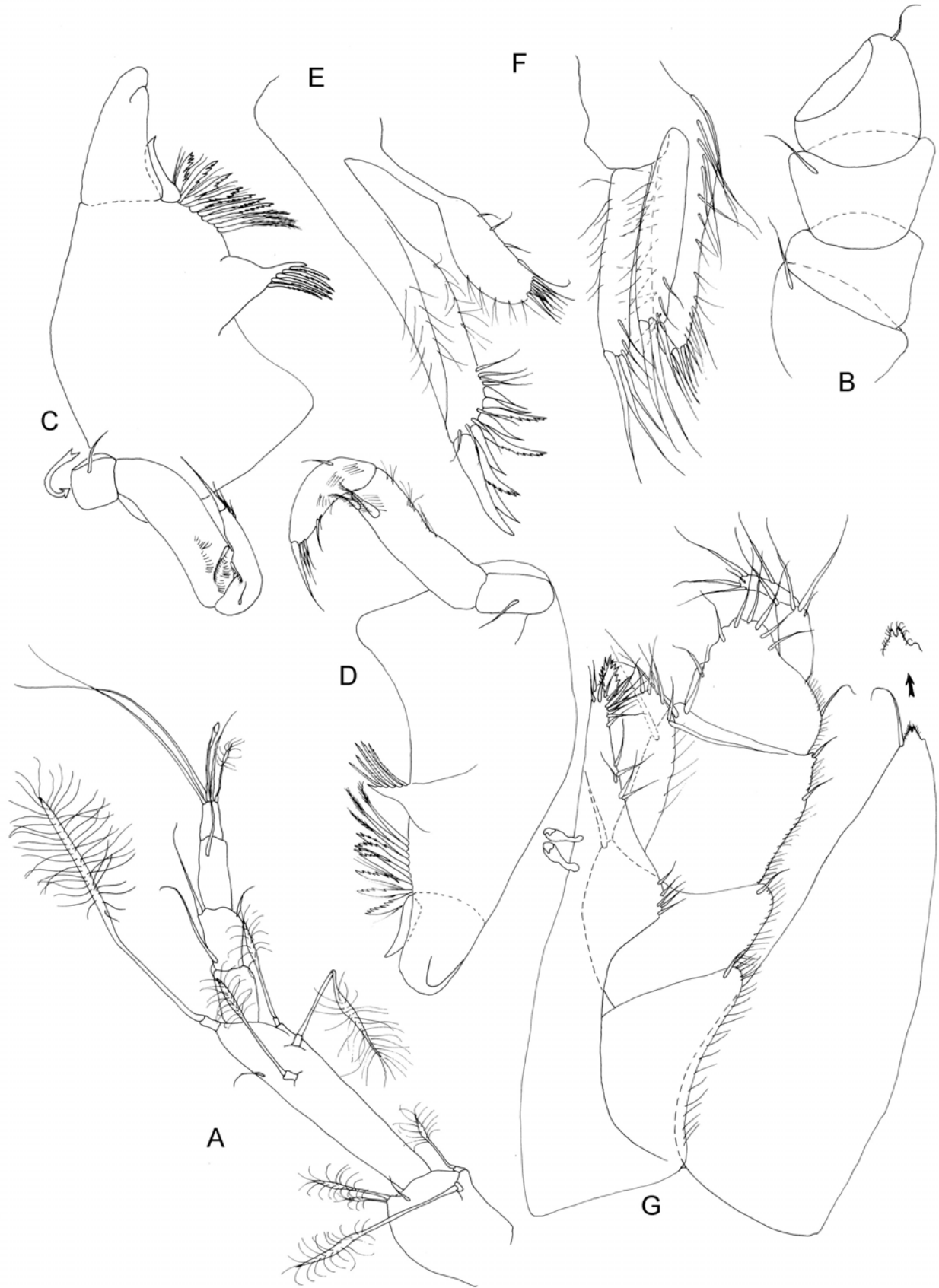
Maxilliped (Fig. 80): Epipodite length 2.67 width, length 0.9 endite length. Endite with two retinaculae, terminally with one star-shaped cuspidate seta and numerous small setae. Edge of endite and palp articles 1.3 hairs, distal corners with one small seta. Article 2 inner margin with three setae, article 3 inner margin with seven setae, article

4 with four setae, article 5 with five setae. Article 1 length 0.69 width, article 2 length similar to width, article 3 length 0.79 width, article 4 length 1.8 width, article 5 length 4 times width.

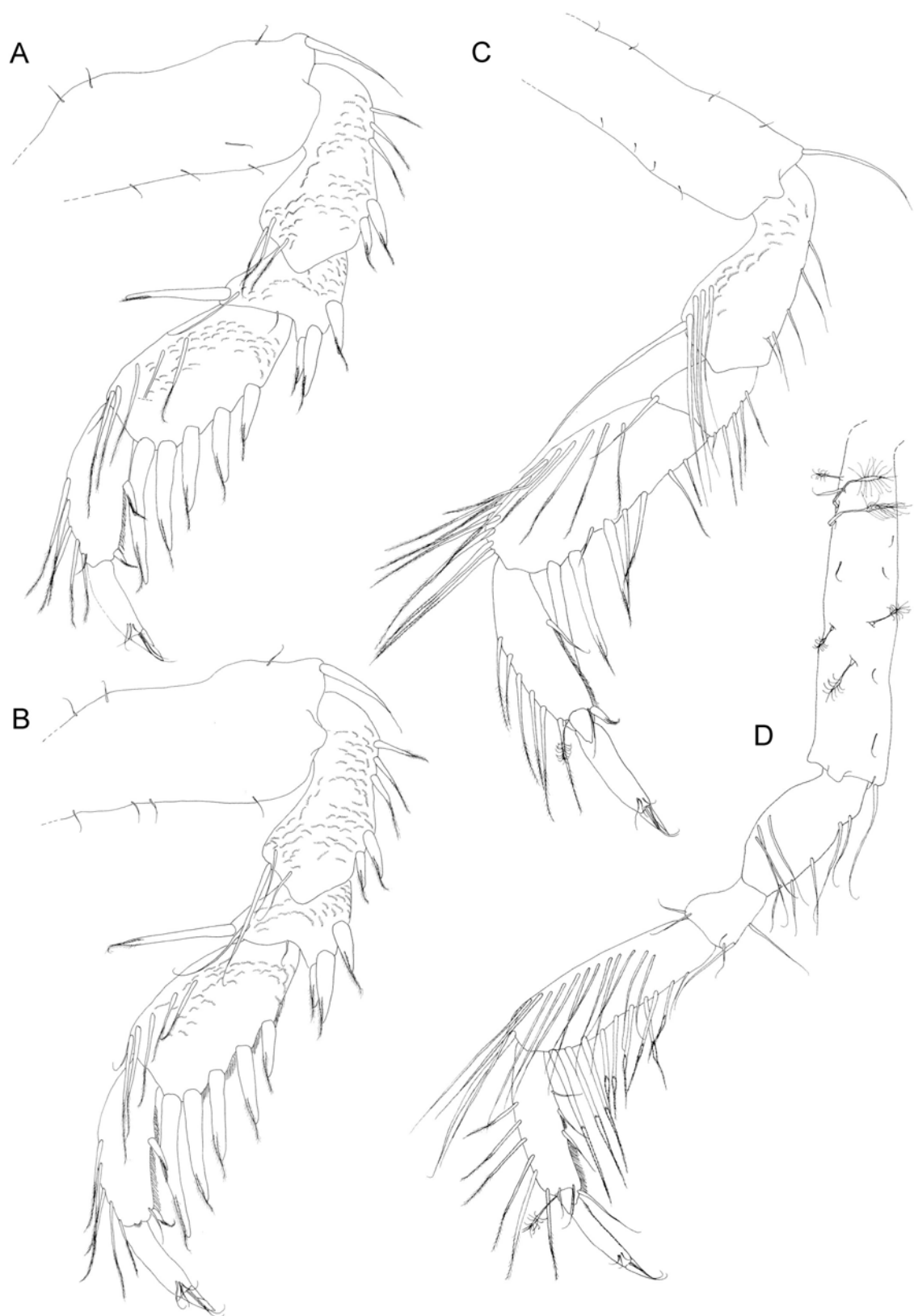
Pereopod I (Fig. 81): Basis length 2.28 width, with few small setae and proximal to ischium ventrally with one long simple seta. Ischium length 2.14 width, ventrally with three slender distally setulate setae and two robust unequally bifid distally setulate setae, dorsally with three slender distally setulate setae. Ischium, merus and carpus laterally with numerous folds in which rows of fine hairs are inserted. Merus length 0.42 width, ventrally with three robust stout unequally bifid distally setulate setae, distodorsally one simple slender seta and one robust unequally bifid distally setulate seta. Carpus length 1.96 width, with ventral row of five large robust unequally bifid distally setulate setae increasing in length towards propodus, distal seta of row reaching full length of propodus, dorsally with a row of five slender distally setulate setae. Propodus length 2.69 width, ventrally with two small stout unequally bifid setae and a row of 14 small setae inserted between them, dorsally with a row of five slender distally setulate setae and distally one small seta. Dactylus length 4.13 width, mediodistally with three small setae, claw of dactylus with one cuspidate and one conate setae, two slender setae medially.

Pereopod II (Fig. 81): In setation similar to P I. Difference in length to width ratios: basis length 1.9 width ischium length 2.1 width, merus length 0.35 width, carpus length 1.93 width, propodus length 2.94 width, dactylus length 3.43 width. Claw of dactylus with one cuspidate and one conate setae, two slender setae medially.

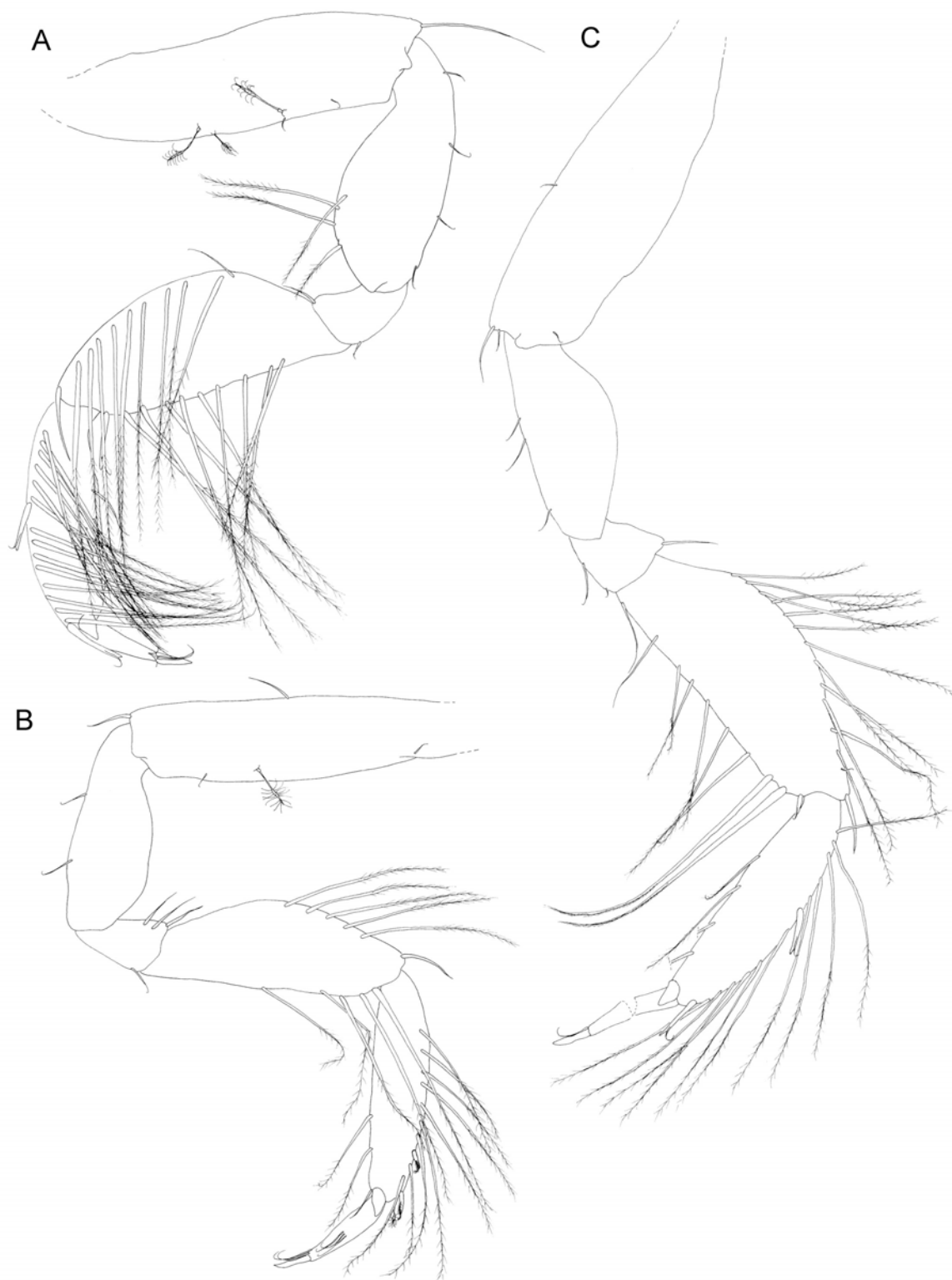
Pereopod VII (Fig. 82): Very similar to P V and P VI. Basis length 3.06 width, with few setae. Ischium length 2.19 width, ventrally with three small slender setae. Merus length 0.73 width, distodorsally one simple slender seta, ventrally one small and one simple slender seta. Carpus length 2.58 width, ventrally with row of nine long slender distally hairy setae, dorsally with a row of 11 long slender distally hairy setae. Propodus length 3.79 width, ventrally with row of four long slender distally hairy setae, dorsally with row of 10 long slender distally hairy setae and two small unequally bifid setae, one midway, one distally. Dactylus length 4.2 width, claw of one conate seta, one slender seta inserted ventrally.



**Fig. 80:** *Whoia victoriensis* sp. nov., paratype female, antennula (A), articles 1-4 of antenna (B), mouthparts: MdR (C), MdL (D), Mx1 (E), Mx2 (F), Mxp (G)



**Fig. 81:** *Whoia victoriensis* sp. nov., paratype female, pereopods (A-D): P I (A), P II (B), P III (C), P IV (D)



**Fig. 82:** *Whoia victoriensis* sp. nov., paratype female, pereopods (A-C): P V (A), P VI (B), P VII (C),

Pleopod 2 (operculum) (Fig. 83): length 1.16 width. Surrounded by 64 setae, lateral margins slightly convex, distal margin straight.

Pleopod 3 (Fig. 83): Endopod length 1.62 width, inner margin hirsute, distally with 3 long plumose setae. Exopod length 0.41 of endopod length, outer margin hirsute, distally one slender seta.

Pleopod 4 (Fig. 83): Endopod oval-shaped, length 1.91 width. Exopod length 7.5 width, outer margin basally hirsute, distally with one long plumose seta.

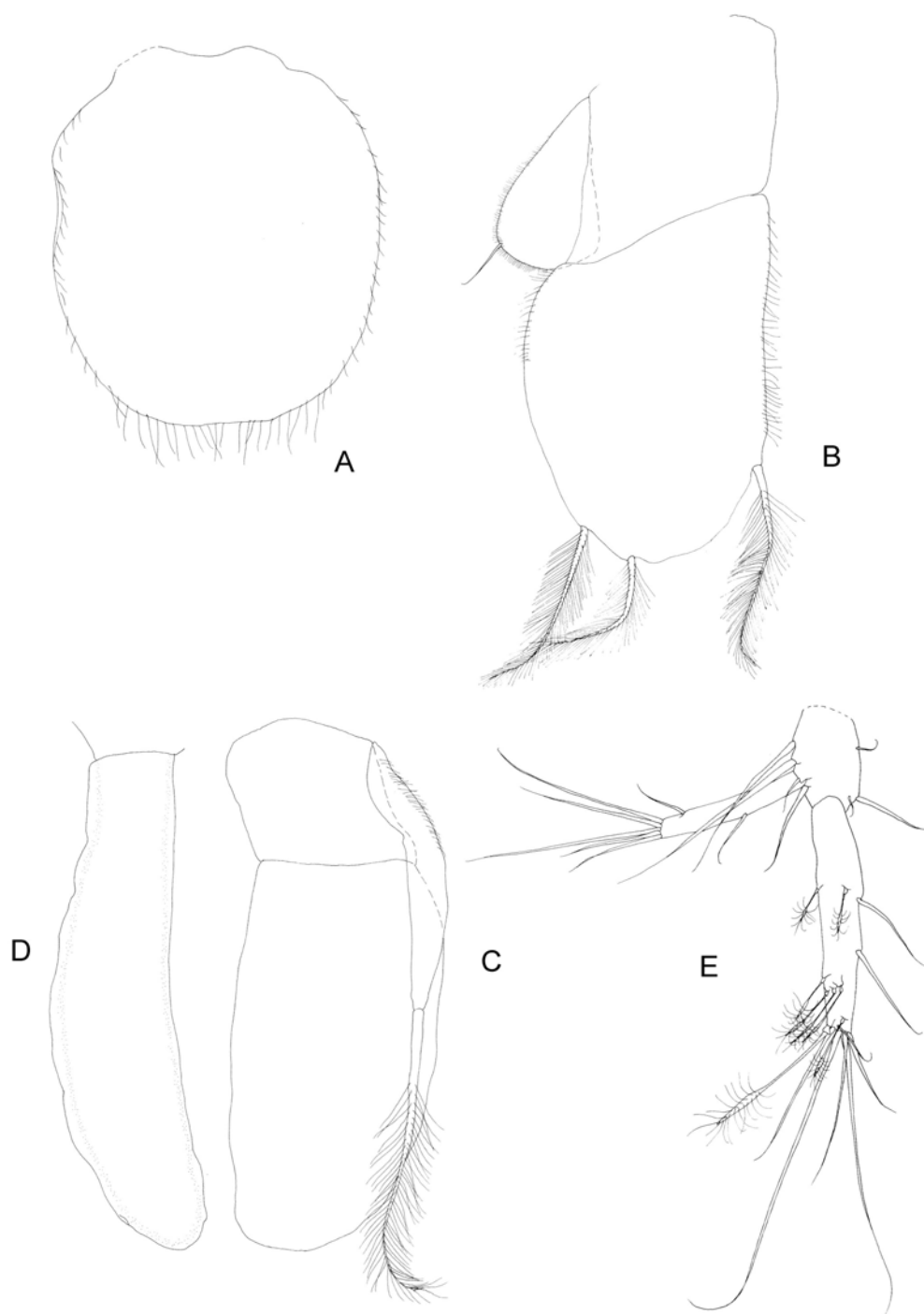
Pleopod 5 (Fig. 83): Endopod only, length 4.18 width.

Uropods (Fig. 83): Biramous. Endopod length 2.64 protopod length, 5.5 times longer than wide, marginally with six small broom setae and two simple slender setae, distally with two broom setae, one small slender seta and five long slender setae. Exopod length 0.64 endopod length, 7 times width with marginally with two simple slender setae, distally with five long slender setae. Protopod length 1.39 width, with two small slender setae and four long simple slender setae.

**Discussion:** The new species is assigned to the genus *Whoia* due to the robust P I with nearly quadrangular articles, P I and II of similar size and shape, P I with long robust composed setae, carpus with ventral and dorsal row of setae, propodus elongated, without dorsal setal row. Coxae not produced, slightly angular tipped with small seta. Lateral margins of pereonite 5 convex, inflated laterally.

*Whoia victoriensis* sp. nov. is in regard to the body shape most similar to *W. angusta*. Autapomorphies distinguishing the new species from the other three species of the genus are: Im only one tooth, P I with rows of extremely robust ventral seta on carpus and propodus, propodus dorsally with row of setae, uropods biramous, exopod well developed, reaching more than half of endopod length.

The new species shares an antennula consisting of six articles with *W. dumbshafensis*, in *W. variabilis* and *W. angusta* the antennula has five articles. In *W. angusta* the Im has four teeth and the lateral margins of Prn5 are straight. In *W. variabilis* the uropodal exopod is much smaller than in *W. victoriensis* sp. nov and the uropods are less setose, P I does not bear large robust setae, the Im has four teeth. The Im of *W. dumbshafensis* has only two teeth.



**Fig. 83:** *Whoia victoriensis* sp. nov., paratype female, pleopods (A-D): operculum (A), PI 3 (B), PI 4 (C), uropod (D)

#### 3.1.5.4 Redescriptions

In the following eight species are redescribed. Many characters were missing in the original descriptions. Based on the main characters (first pereopod, posterolateral spines at the pleotelson, uropods and form of the coxal plates), species described by Menzies & George (1972) are assigned as follows:

One species belongs to *Chelator* Hessler, 1970 (*Chelator brevicauda* (Menzies & George, 1972)); two species to *Disparella* Hessler, 1970 (*Disparella neomana* (Menzies & George, 1972) and *Disparella funalis* (Menzies & George, 1972)); one species to *Desmosoma* Sars, 1864 (*Desmosoma dolosa* (Menzies & George, 1972)); one species to *Pseudogerda* Kussakin, 1965 (*Pseudogerda anversense* (Schultz, 1979)); two species to *Mirabilicoxa* Hessler, 1970 (*Mirabilicoxa acuta* (Menzies & George, 1972), *Mirabilicoxa similipes* (Menzies & George, 1972)) and one species to *Eugerdella* Kussakin, 1965 (*Eugerdella rotunda* (Menzies & George, 1972)).

##### 3.1.5.4.1 *Chelator brevicauda* (Menzies & George, 1972)

Synonyms: *Desmosoma brevicauda* Menzies & George, 1972

#### Material

Holotype. - male, 2.2 mm long, 0.5 mm wide, USNM Cat. No. 120963, *Anton Bruun* Station 4, 02. Oct. 1965; 03°46'S 81°32'W (type locality), depth 1238 m, SBT.

Holotype only. Distribution known only from type locality.

#### Diagnosis

Body 4.4 times longer than wide, A1 with six articles, Lm of left Md with 3 teeth, of right Md serrated (eight teeth). Md palp well developed with three articles, Mxp palp with five articles, Mxp endopodite medially with two coupling hooks. Prn1-3 similar in size, anterior margin of Prn4 convex. Prn5 and 6 from dorsal quadratic, lateral margin of Plt convex. Coxae with anterolateral elongation clearly overlapping proximal segment/cephalothorax. Carpus of PI robust, ventral margin with three small distally setulate setae. Well developed propodus forming a chela together with "claw-seta" at proximal margin of carpus. Dactylus elongated PII setose, carpus ventrally and dorsally with row of sensory setae; propodus bearing few simple setae and proximal spine, dactylus elongated.



#### **Description of holotype male**

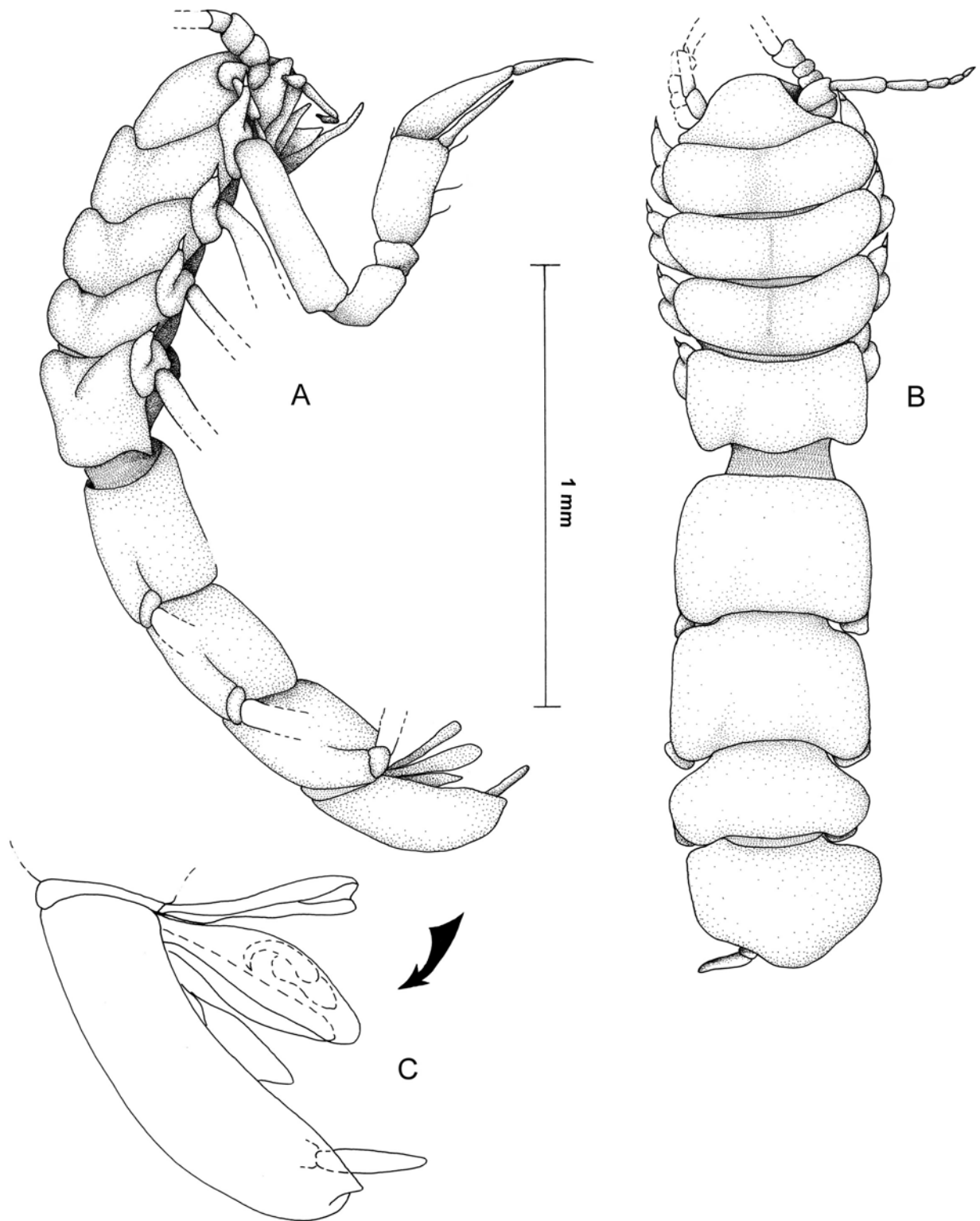
Habitus (Fig. 84): 2.2 mm long (measured without appendages), body 4.4 times longer than wide (width of Prn2). Prn1-3 similar in size (each 3.3 times wider than long), Prn4 2.2 times wider than long. Prn5-7 1.4 times wider than long. Cephalothorax about 2 times wider than long. From lateral body characteristically arched and Prn1-4 higher than Prn5-7 from lateral view. Pleotelson rounded, nearly as long as wide, lateroventrally with very small posterolateral spines, posterior margin smooth. Insertion of Urp located at same high as posterolateral spines.

Antennula (Fig. 85): 0.32 times of length, peduncle with two articles, flagellum with four articles, relative length of all articles: 1:1.4:0.7:0.6:0.6:0.1. Both peduncular articles with three broom setae. Flagellar article 1 with one simple seta, flagellar article 2 with one plumose seta and three long simple setae, flagellar article 3 with four long simple setae. Flagellar article 4 terminally tipped with two long slender setae and one plumose seta.

Antenna (Fig. 85): about 0.5 times of body length, six peduncular articles. Basal articles (1-4) of nearly same size with few small setae; peduncular articles 5-6 of similar size and 5.2 times longer articles 1-4. Article 5 with two broom setae and four small setae. Article 6 with four simple setae. Flagellum out of 16 flagellar articles, decreasing in width, comparable in length. Article 1 with one small, article 2 without and articles 3-12 with crest of numerous simple setae. Flagellar articles 13 and 14 each with one long simple seta. Article 15 with three long simple setae and article 16 with four long simple setae and one aesthetasc.

Mandible (Fig. 85): left and right Md of comparable size, Md palp well developed (around 1.5 times longer than Md). Second article with five distal rows of about 30 small fine hairs and two small ventral setae. Third article ventrally with eight setae, increasing in length towards distal end. Pm compact and with 11 fine setae. Spine row with five simple setae. Lm-like structure of right Md serrated (eight small teeth at dorsal margin). Pi with four teeth of different size.

Maxillula (Fig. 85): Inner lobe with 12 fine hairs and much smaller than outer lobe. Lateral margin of outer lobe bearing seven small simple setae, terminally with 11 spines.



**Fig. 84:** *Chelator brevicauda* (Menzies & George, 1972), habitus holotype male, (A) lateral, (B), dorsal, (C) pleotelson from lateral view

Maxilla (Fig. 85): With three lobes. All lobes setose. Outer and inner lobe comparable in size, medial lobe stout. Inner and outer lobe tipped with three, medial lobe with four

simple setae. Inner and outer lobe additionally dorsally with six fine hairs. Medial lobe with three dorsal fine hairs and six ventral small simple setae.

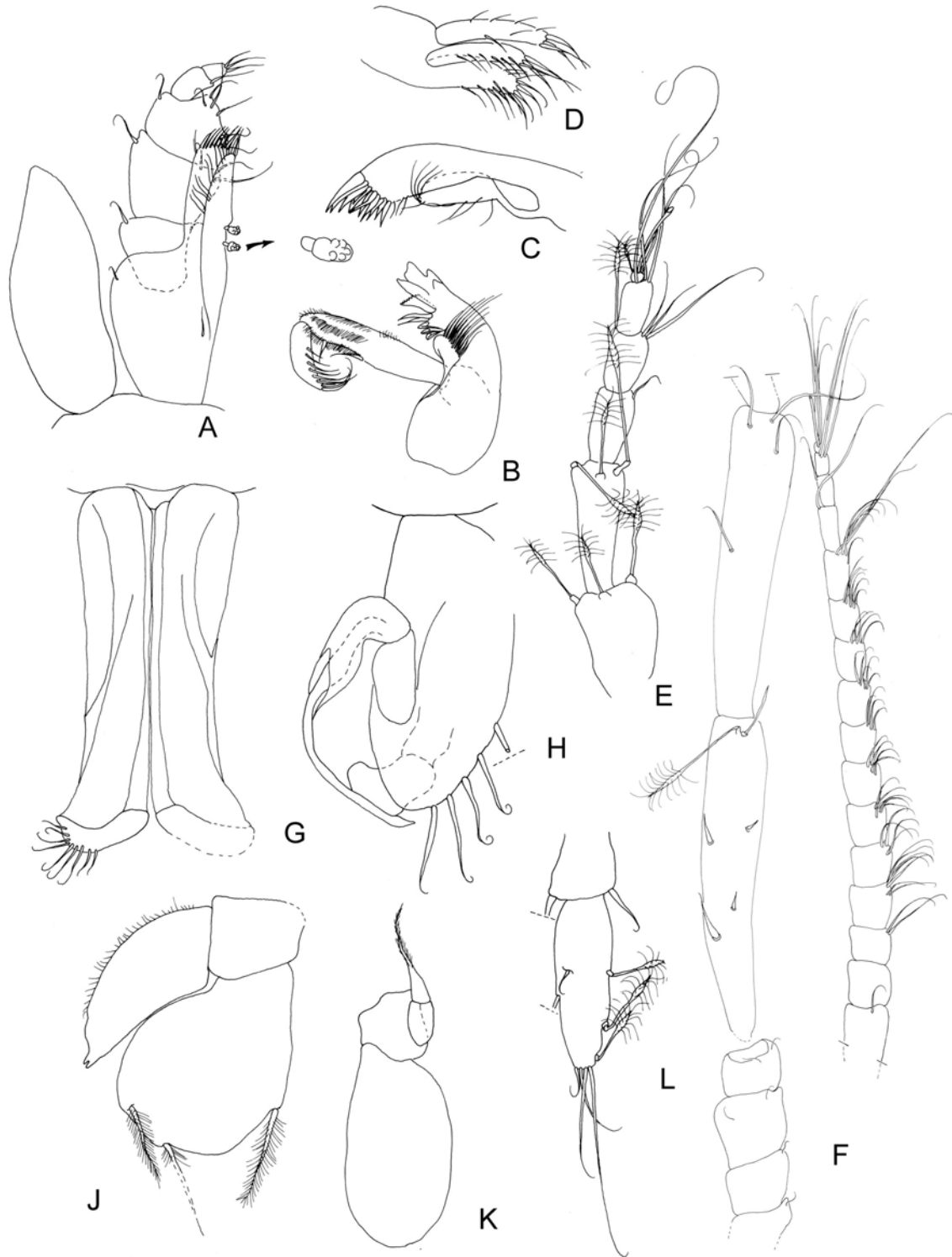
Maxilliped (Fig. 85): Epipodite oval-shaped and terminally pointed. Endite medially with two coupling hooks (retinacula). Those with five teeth each. On endite two setal rows, one laterally, one terminally. Palp of five articles, articles 4-5 much smaller than articles 1-3. Each article at distal corners tipped with several small setae.

Pereopod I (Fig. 86): well developed, carpo-euchelate. Base about four times longer than wide with several small setae. Ventral margin proximal to ischium with one stout sensory seta. Ventral margin of ischium with four distally setulate setae. Dorsal margin strongly convex with one seta. Ventral margin of merus with two setae of same type. Dorsally with one seta. Carpus enlarged and robust (1.8 times longer than wide). Dorsal margin with one small seta close to propodus base, ventral margin anteriorly with the typical “claw-seta” and three small setae, which are of same type like those at ischium and merus. Propodus about four times longer than wide and pointed distally, tipped with one small seta close to dactylus. Ventral margin with row of nine small, slightly arcuate setae, attached to a hyaline cuticular membrane. Dactylus elongated (eight times longer than wide), ventral margin with row of fine hairs attached to a hyaline membrane and two distoventral setae. Claw of dactylus composed of one cuspidate and two long slender setae.

Pereopods II-IV (Fig. 86): (PIII and IV missing) Base 4.6 times longer than wide and with several small setae. All setae of ventral margin broken off. Distally one stout sensory seta. Ischium with two small setae on ventral margin, on dorsal margin one long simple seta. Merus as long as ischium and nearly two times longer than wide. Ventral margin of merus with three setae, two simple ones and one distally setulate seta. Dorsal margin tipped with one small seta. Carpus ventrally with six distally setulate setae and one unequally bifid seta proximal to propodus. Dorsally with row of seven distally setulate setae. Propodus bearing three simple setae ventrally, dorsally three long simple setae and two simple setae. Dactylus elongated (10 times longer than wide). Claw of dactylus composed of one cuspidate and two long slender setae.

Pereopods V-VII: missing.

Pleopod 1 (Fig. 85): Sides gradually converging for first two-thirds of length, then flaring, limbs widest distally. 2.7 times longer than wide. Distal margin slightly convex, bearing nine slender setae at the corner.

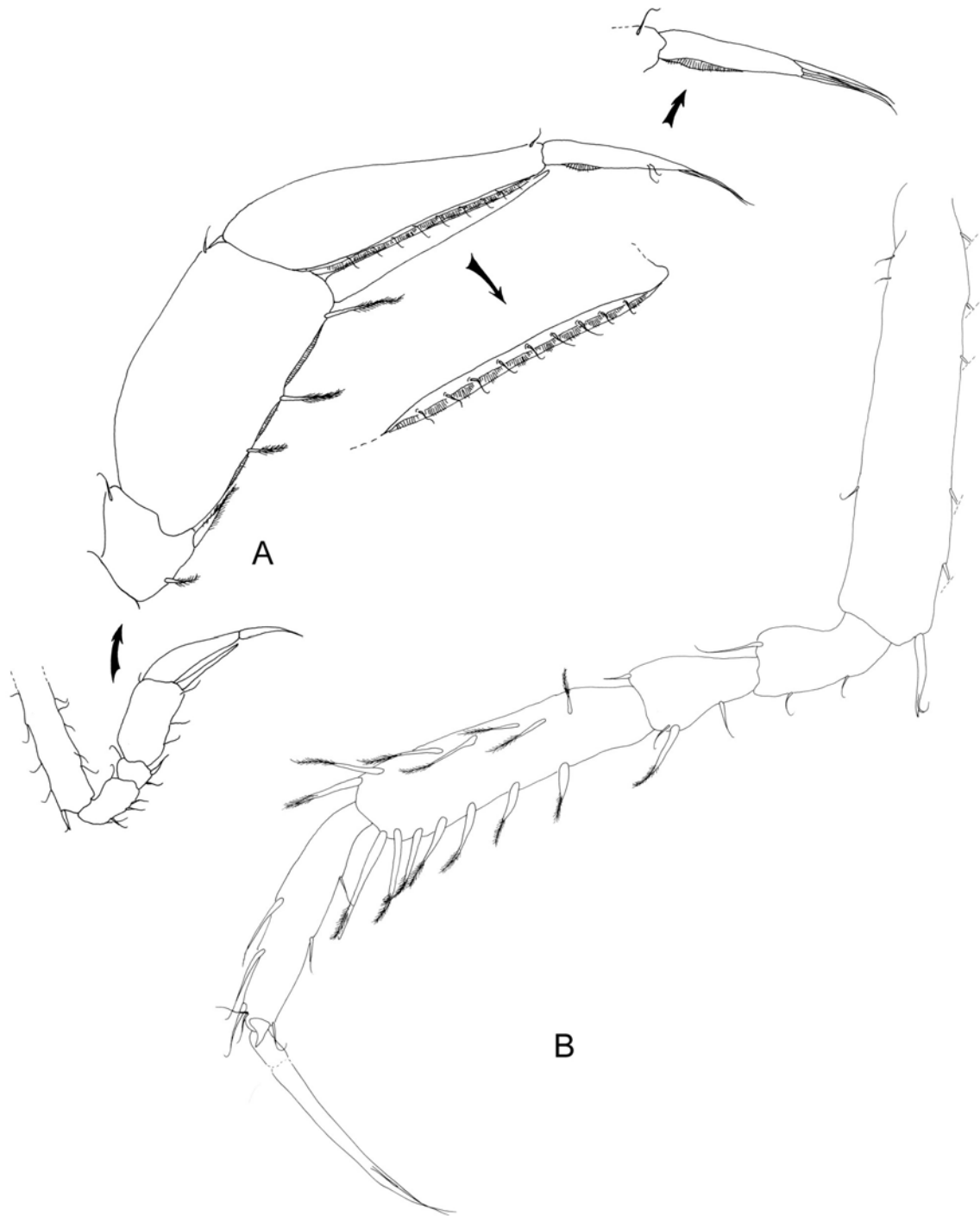


**Fig. 85:** *Chelator brevicauda* (Menzies & George, 1972)

mouthparts (A-D): Mxp (A), MdR (B), Mx1 (C), Mx2 (D); antennula (E), antenna (F); pleopods (G-L): PI1 (G), PI2 (H), PI3 (J), PI4 (K), Ur (L)

Pleopod 2 (Fig. 85): 2.1 times longer than wide, widest midway. Free margin with five slender simple setae.

Pleopod 3 (Fig. 85): Endopodite “pear-shaped”, with three long plumose setae on posterior margin. Outer margin of exopodite slightly convex, with row of over 30 fine hairs. Tip cleft and inner margin slightly concave. Base nearly quadratic.



**Fig. 86:** *Chelator brevicauda* (Menzies & George, 1972), pereopod I (A), pereopod II (B)

Pleopod 4 (Fig. 85): Endopodite oval (1.8 times longer than wide) without setae, transparent. Exopodite with single plumose seta inserting at half of length of endopodite. Around four times longer than wide.

Pleopod 5: absent.

Uropods (Fig. 85): simple, uniramous, around 4.4 times longer than wide. Base with two setae (one simple, one broken off). Endopodite medially with one plumose seta, one small seta, one broken off. One plumose seta on two-third of length and terminally with one plumose seta and four simple slender setae of different length.

#### Remarks

The holotype was damaged; the remaining appendages are described. No other specimen of this species is known.

#### 3.1.5.4.2 *Disparella neomana* (Menzies & George, 1972)

Synonyms: *Desmosoma neomana* Menzies & George, 1972

#### Material

Holotype. - male, 2.6 mm long, 0.8 mm wide, USNM Cat. No. 120971, *Anton Bruun* Station 59, 09. Oct. 1965; 06°46'S 82°11'W, depth 4526-4609 m (type locality), gear: SBT. Distribution known only from type locality.

Allotype. - female, 3.5 mm, 1.0 mm wide, USNM Cat. No. 120972, from type locality

Paratypes. - 4 specimens, USNM Cat. No. 120973, from type locality

Other material: USNM cat. No. 120974: 1 male, Pacific Ocean, Peru-Chile Trench, 02. Nov. 1965, 08°46'S 80°44'W. Depth 3909-3970 m, St. 169 *Anton Bruun*, gear: MT

#### Diagnosis

Body about 3.5 times longer than wide; body form from dorsal straight. Cephalothorax 1.5 times longer than wide, without frons clypeal furrow or ridge on frons, cephalic spines nearly reaching proximal margin of eye-fold. Posterior margins of Prn1-3 from dorsal convex, posterior margin of Prn4 strongly concave, of Prn5-7 nearly straight. Form of Prn4 is similar to Prn5-7. A1 with five articles. Md with

shelflike Pi, three lobes. Endite of Mxp with three coupling hooks. PI enlarged, chelate, lower margin of carpus with four small setae in regular distances and proximal setae to “claw spine” slightly larger. PI and PII of nearly similar size. Plt distally with spines. Uropods biramous, exopod small with one slender seta, endopod 11 times longer than exopod.

#### **Description of allotype female**

Habitus (Fig. 87): Body 4.1 mm long (measured without appendices) and 3.7 times longer than wide (measured without appendages). Cephalic spine shorter than basal article of A1. Prn1-3 from dorsal increasing in size, Prn3 1.4 times wider than Prn4, which is more similar to Prn5-7 than to Prn1-3. Spine like elongations of coxal plates 1-4 overlapping proximate segments. Prn1 2.9, Prn2 2.7, Prn3 4.2 and Prn4 2.9 times wider than long. Anterior margins of Prn1-4 concave, posterior margins of Prn1-3 convex and of Prn4 concave. Lateral margins of Prn1-3 rounded, of Prn4-7 straight. Pleotelson 1.4 times longer than wide and with spines close to insertion of Urp. Lateral margins convex. Distally rounded.

Antennula (Fig. 89): slightly longer than cephalothorax (0.2 of body length). With five articles, two peduncular and three flagellar articles. Article 1 shorter and broader than second. Relative length of articles: 1:2.5:1.75: 0.55:0.5. Article 1 with three broom setae, article 2 with two large and two small broom setae, article 3 without setae, article 4 with one broom seta and article 5 with three slender setae and one aesthetasc.

Antenna (Fig. 89): 1.1 mm long, six peduncular and 11 flagellar articles. Relative length of peduncular articles 5 and 6 and flagellum: 1:1.3:1.5. Article 5 distally with one slender and one broom seta. Article 6 with one slender seta and five broom setae. Flagellum with one to two slender setae per article. Last article of flagellum with three slender setae.

Mandible (Fig. 89): Both mandibles with well-developed palp of three articles. Article 1 with two small setae, article 2 distally with several rows of fine hairs and two small setulate setae on lower margin. Article 3 with one row of fine hairs and ventrally with six setulate setae and one terminal simple seta. Pi shelflike, with three lobes. Lm of left Md with three teeth; Lm of right Md serrated on top, with eight teeth. Spine row of

both mandibles containing 10 spines of three different types. First two spines of left spine row very Lm-like with four teeth, next two spines after Lm of right Md also Lm-like, but serrated, with seven small teeth. Pm with 14 slender setae.

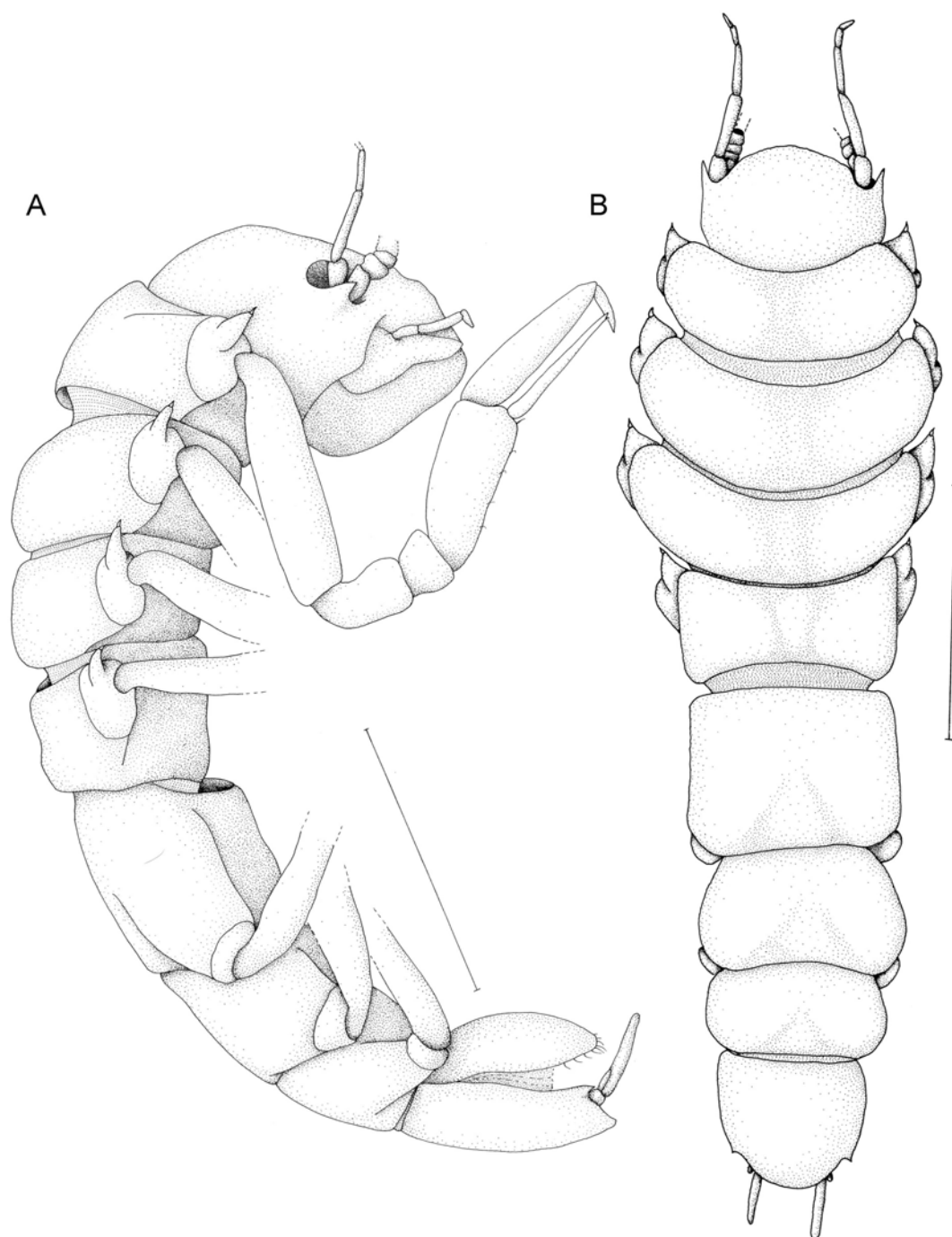
Maxillula (Fig. 89): Inner lobe terminally with 10 strong spines, nine of them terminally serrated. Upper margin of lobe with 16 fine setae and lower margin with 14 fine setae.

Maxilla (Fig. 89): Base with three long slender setae. Three lobes of similar size. Inner and outer lobe each with four long terminal setae, with 10 pairs of fine hairs on upper margins and nine pairs on lower margins. Medial lobe terminally with six simple setae and 23 slender setae on lower margin.

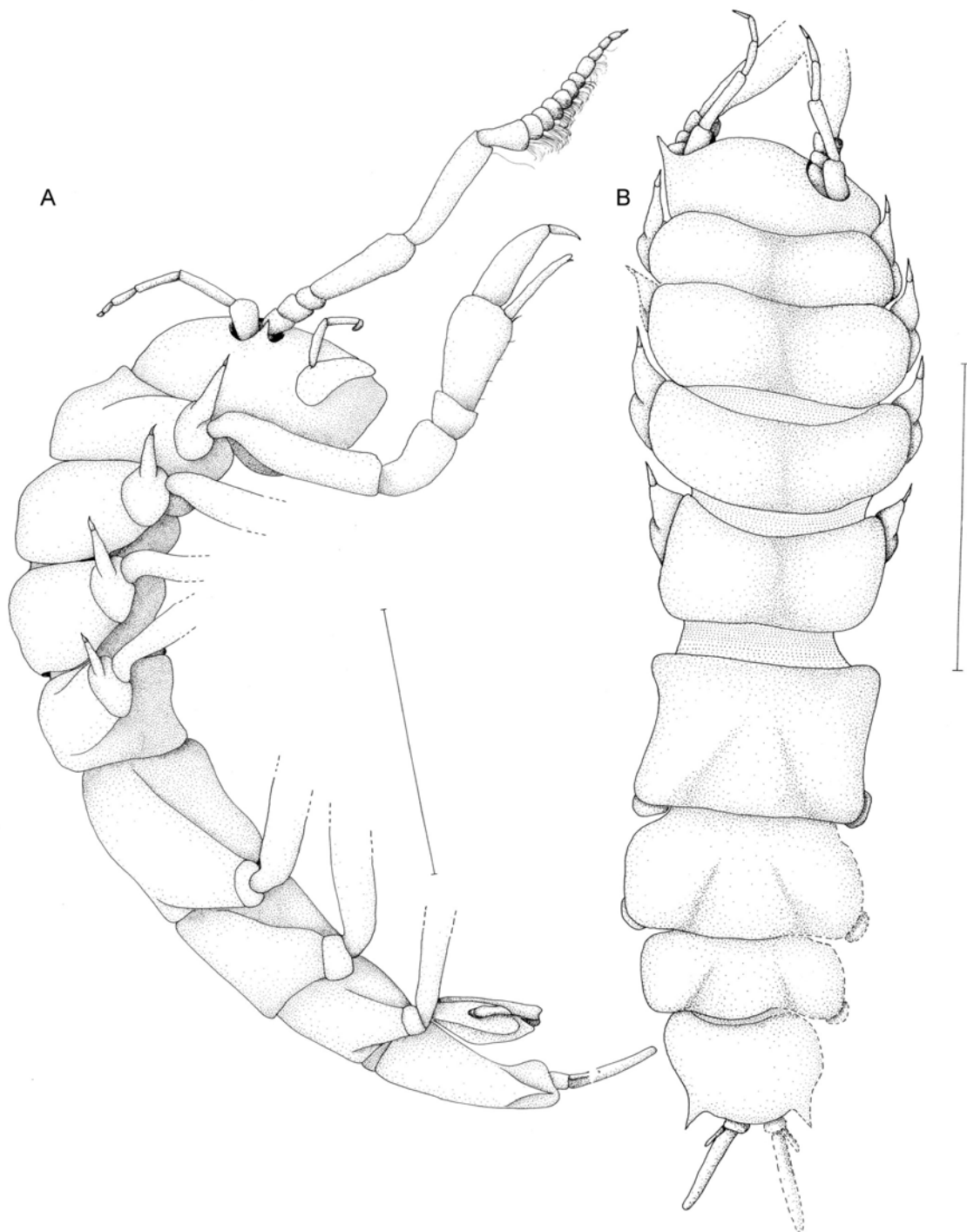
Maxilliped (Fig. 89): Endite with three coupling hooks and terminally with several stout setae. Outer margin with eight small setae and numerous small setae in lateral fold. Palp of five articles, inner margin of article 1 with six small setae, outer margin tipped with two small setae. Article 2 with four, article 3 with 13 and article 4 with three small setae on the inner margins. Article 5 with four setae. Epipodite oval, outer margin slightly concave, fringed with fine hairs, inner margin distally with three fine setae.

Pereopod I (Fig. 90): carpo-euchelate; propodus forming chela together with the large “claw-seta”. Base 3.25 times longer than wide and medially with one broom setae and two small setae. Lateral margin to ischium tipped with one long slender seta. Ischium 1.75 times longer than wide, upper margin convex with one stout seta. Lower margin with five stout distally setulate setae. Merus 1.4 wider than long, upper margin tipped with one stout and one slender setae. Lower margin with two small stout distally setulate setae. Carpus 2.4 times longer than wide, upper margin smooth and lower margin with four small setae in regular distances. Proximal to propodus with two setae, the large “claw-seta” and the small slender seta. Propodus 3.9 times longer than wide, basally slightly broader than distally. Upper margin with four small setae and lower margin with four small setae and 14 fine setae inserted in a hyaline membrane. Dactylus 4.4 times longer than wide, both margins smooth. Medially, close to unguis with three slender setae.





**Fig. 87:** *Disparella neomana* (Menzies & George, 1972) allotype female, habitus lateral (A, scale = 1 mm), habitus dorsal (B, scale = 1 mm)



**Fig. 88:** *Disparella neomana* (Menzies & George, 1972) holotype male habitus lateral (A, scale = 1 mm), habitus dorsal (B, scale = 1 mm)

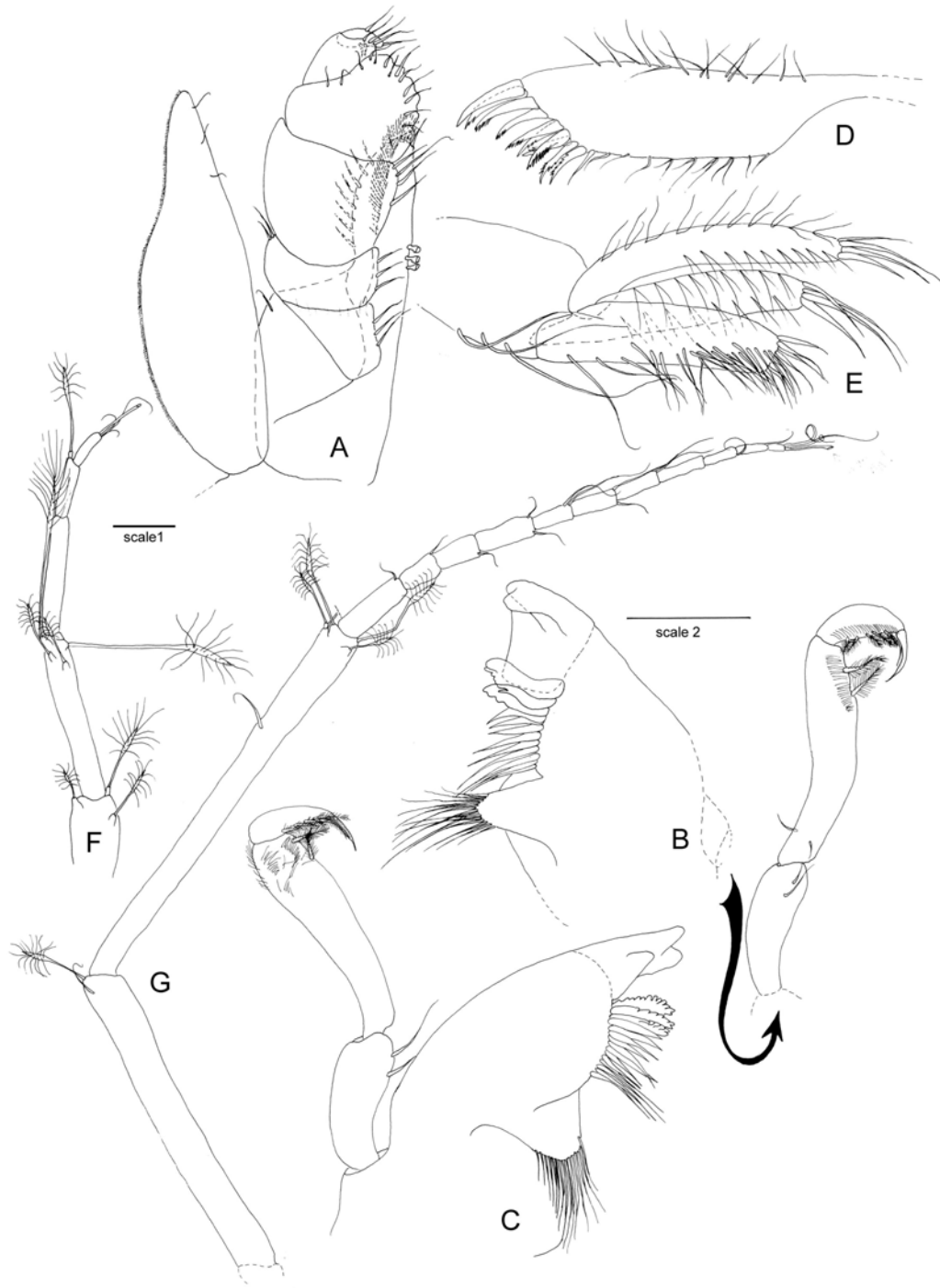
Pereopods II-IV (Fig. 90): setose. Base around 3.7 times longer than wide, number of terminal setae increasing from one to four slender setae from PII to PIV. Ischium about 2.6 times longer than wide. Upper margin convex with decreasing number of

simple setae (PII six, PIII three and PIV without), lower margin straight with stout setulate setae (PII seven and PIII five), on PIV with three simple setae. Merus around 1.5 times longer than wide. On the upper margin terminally one slender seta and on lower margin with four stout distally setulate (PII-III) and four slender setae (PIV). Carpus around four times longer than wide. Lower margin with up to 17 distally setulate setae, increasing in size towards propodus. Margin fringed with fine hairs. Dorsoventral row of setae composed of eight to 27 slender setae. Upper margin with two to five small setae.

Propodus around three times longer than wide, lower margin with five to eight stout distally setulate setae and margin fringed with fine hairs. Upper margin with eight to 11 slender setae. Dactylus around 3.5 times longer than wide with smooth margins and three slender setae medially (close to Claw). Claw of PII-III composed of two parts with two slender setae in between of them. Claw of PIV additionally with cuticula membrane on lower side in which numerous fine hairs are inserted. Claw of dactylus composed of three cuspidate and one conate setae.

Pereopods V-VII (Fig. 90): Base around 4.2 times longer than wide with few small setae and PV-VI, additionally with one respectively two broom setae. Ischium about 2.1 times longer than wide, with one or two small setae on straight lower margin. Convex upper margin with one slender seta. Merus about 1.2 times longer than wide, upper margin tipped with one or two small setae. Lower margin tipped with two small setae. Carpus about three times longer than wide with eight to 11 long slender setae on lower margin and nine to 11 long slender setae on upper margin. Carpus of PV terminally fringed with numerous fine hairs. Propodus about 3.1 times longer than wide with nine to 13 long slender setae on lower margin, upper margins described separately: PV with 10 long slender setae, terminally with one stout distally setulate seta. PVI with 10 long slender setae, two stout distally setulate setae, one medially and one terminally. PVII with four setulate setae and one long slender seta. Dactylus about 6.2 times longer than wide with smooth margins. Terminally, close to claw with one or two slender setae. Claw stout and pointed.

Pleopod 2 (operculum) (Fig. 91): rounded with terminally slightly concave margin. 24 small setae.



**Fig. 89:** *Disparella neomana* (Menzies & George, 1972) allotype female, mouthparts (A-E): Mxp (A, scale 1), MdL (B, scale 2), MdR (C, scale 2), Mx1 (D, scale 2), Mx2 (E, scale 2); antennula (F, scale 1), antenna (G, scale 1)

Pleopod 3 (Fig. 91): Endopod 3.3 times longer than exopod. Exopod oval, hirsute, tipped with single small setae. Terminal margin of endopod with three plumose setae.

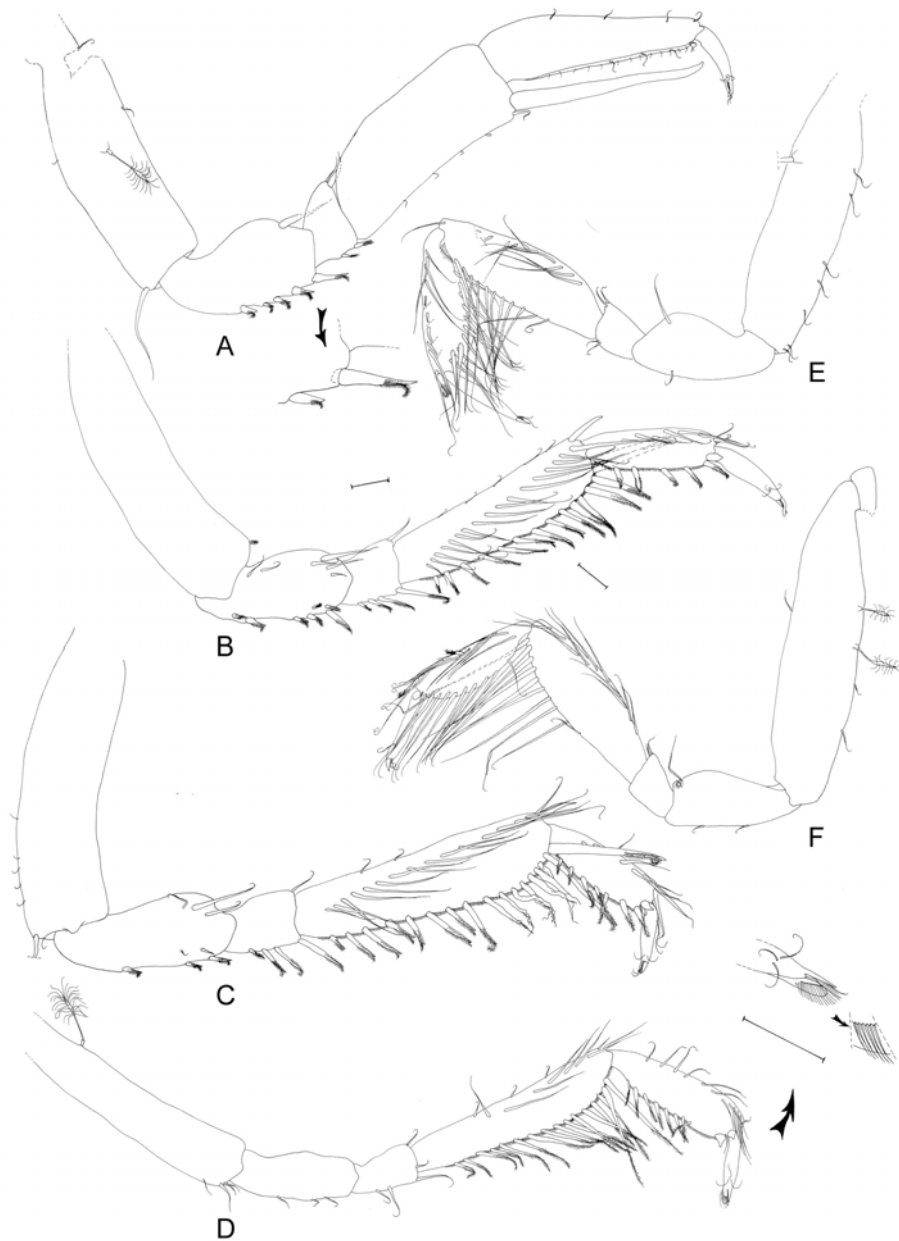
### 3. Results

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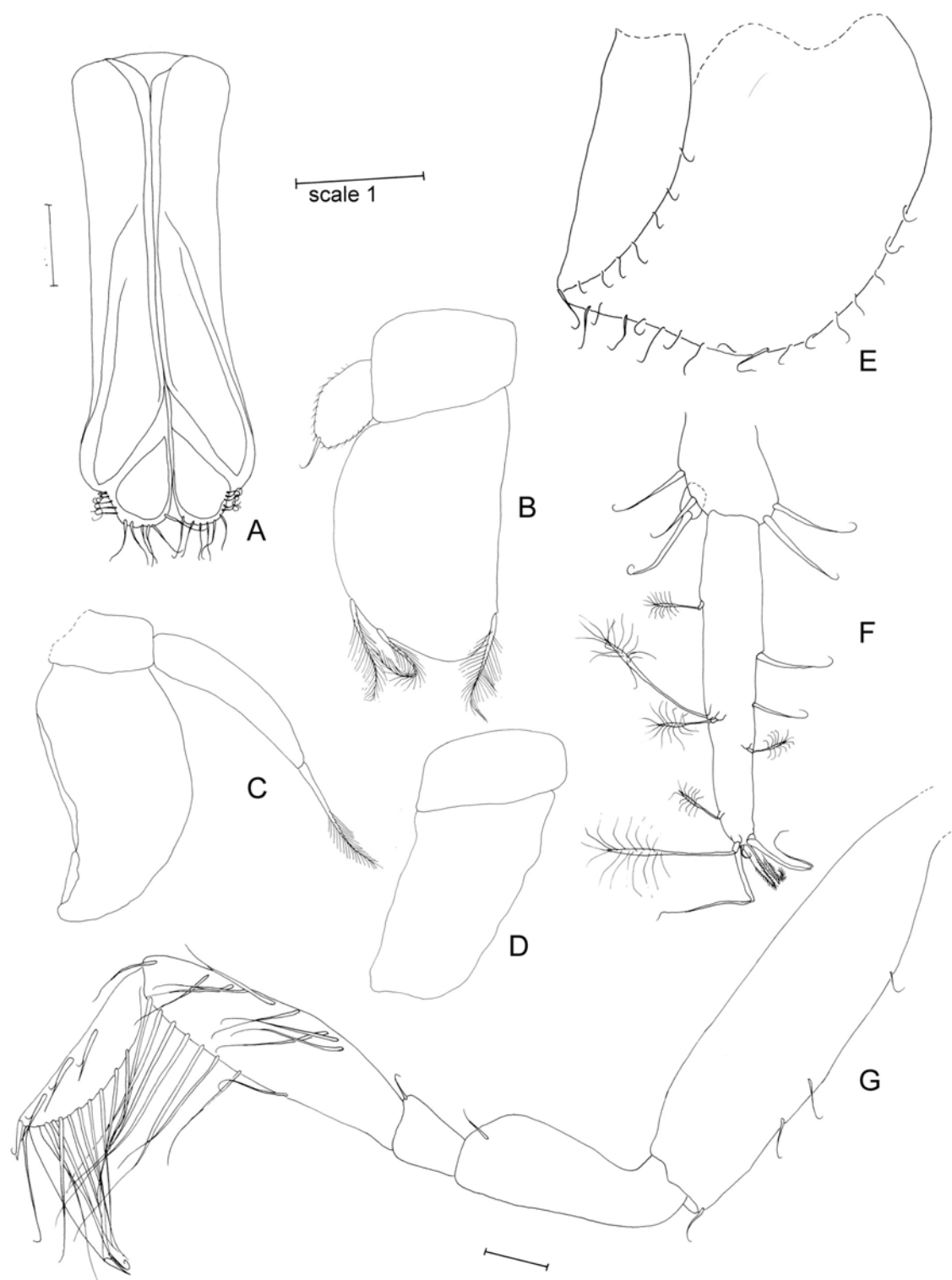
Pleopod 4 (Fig. 91): endopod oval, 1.3 times longer than exopod. Exopod tipped with long plumose seta.

Pleopod 5 (Fig. 91): endopod only, margin smooth

Uropods (Fig. 91): biramous, exopod small with one slender seta, endopod 11 times longer than exopod. Exopod bears six broom setae, four slender setae, terminally tipped with one small setae and two stout distally setulate setae.



**Fig. 90:** *Disparella neomana* (Menzies & George, 1972) allotype female, pereopods: PI (A), PII (B), PIII (C), PIV (D), PV (E), PVI (F), scale = 0.1 mm



**Fig. 91:** *Disparella neomana* (Menzies & George, 1972), pereopod VII (G), pleopods: PI1 (A), PL3 (B), PI4 (C), PI5 (D), Op (E), Urp (F), scale = 0.1 mm

#### **3.1.5.4.3     *Disparella funalis* (Menzies & George, 1972)**

Synonyms: *Desmosoma funalis* Menzies & George, 1972

##### **Material**

Holotype. female, length 5.5 mm, width 1.5 mm. USNM Cat. No. 120968, *Anton Bruun* Station 59, 09. Oct. 1965; 06°46'S 82°11'W (type locality), depth 4526-4609 m, SBT.

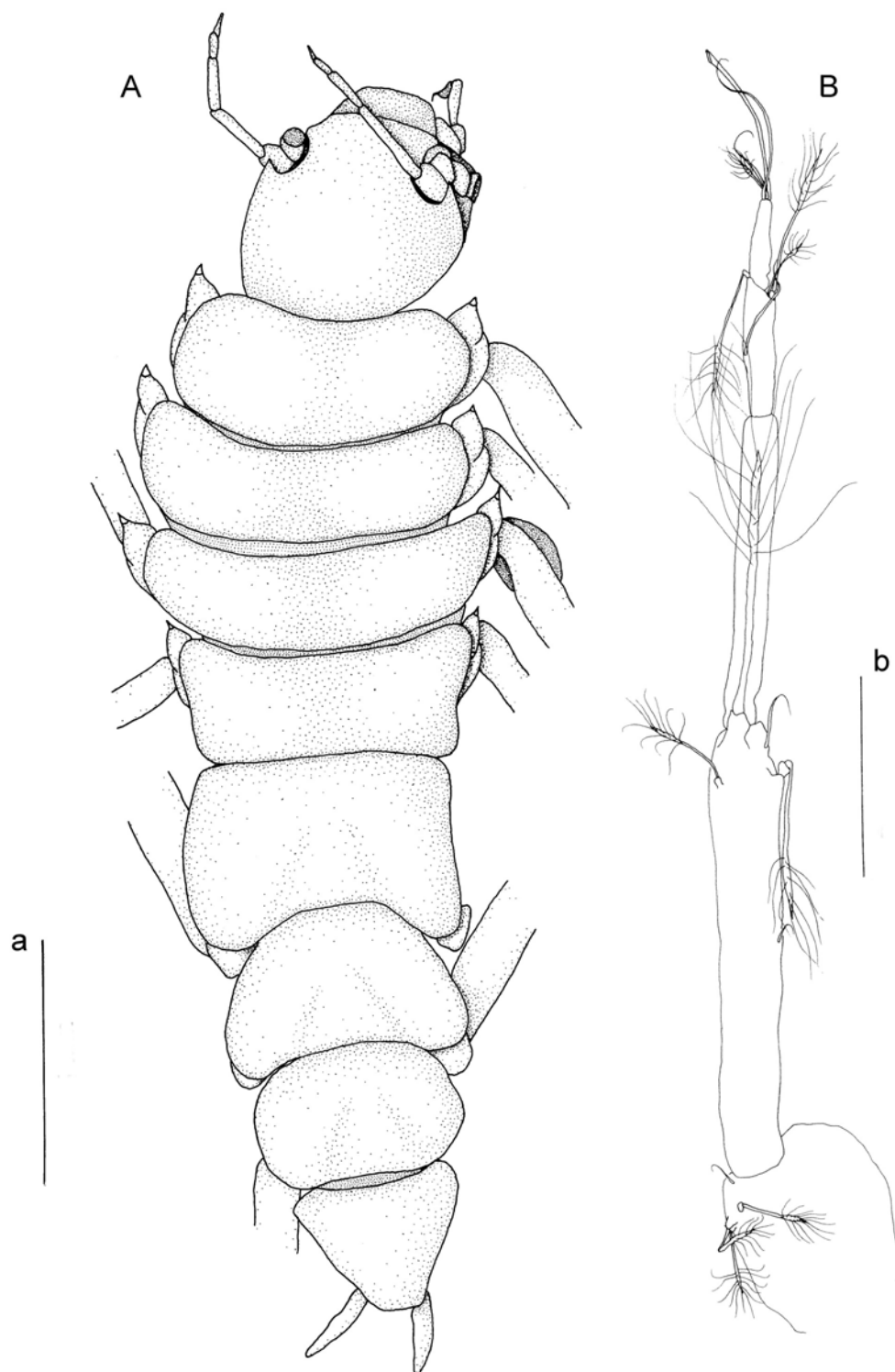
Paratypes. - USNM Cat. No. 120970: three females, length and width: 1) 5.5 mm, 1.5 mm; 2) 3.0 mm, 1.0 mm; 3) 2.5 mm, 1.0 mm. USNM Cat. No. 120969, same locality. 30 specimens: 27 females and 3 males in different stages (5 manca, 19 prep. female, 3 adult female with marsupium, 2 subadult male, 1 adult male), *Anton Bruun* Station 69, 02. Nov. 1965; 08°46'S 80°44'W, depth 3909-3970 m, SBT.

##### **Description**

Body about 4 times longer than wide. Cephalothorax as long as wide. Cephalic spines one third of length of article 1 of A1. Prn1 1.5 times longer than Prn2. Prn2 and 3 nearly similar in size. Prn4 slightly longer than Prn3. Prn5-7 decreasing in size, lateral margins convex. Plt broadest anteriorly, converging to insertion of Urp. Lm of Md with four teeth. Pi shelf-like, three teeth. Mxp with four coupling hooks. PI carpo-euchelate, lower margin of carpus with large "claw-seta" and additionally six small distally setulate setae. Op rounded, posterior margin slightly concave, with 38 small setae. Uropods biramous, endopod nine times longer than exopod.

##### **Description of holotype female**

Habitus. (Fig. 92): Body 3.5 times longer than width of Prn2. Cephalic spines one third of length of article 1 of antennula. Prn1 1.5 times longer than Prn2 in midsagittal length. Prn5-7 decreasing in size, lateral margins convex. Plt broadest anteriorly, converging to insertion of Urp. Lm of MdL with four teeth. Pi shelf-like, three teeth. Mxp with four coupling hooks. PI carpo-euchelate, lower margin of carpus with large "claw-seta" and additionally six small distally setulate setae. Op rounded, posterior margin slightly concave, with 38 small setae. Uropods biramous, endopod nine times longer than exopod.



**Fig. 92:** *Disparella funalis* (Menzies & George, 1972), holotype female, habitus dorsal (A); paratype female, antennula (B), scale a = 1 mm, scale b= 0.1 mm



Antennula (Fig. 92): as long as cephalothorax, (0.2 of body length). Two peduncular and three flagellar articles. Article 1 broadest. Relative length of articles: 1:3:2.1:0.9:0.6. Article 1 with three broom setae and one small seta. Article 2 with three broom setae and one slender seta. Article 3 without setae. Article 4 with four broom setae and article 5 tipped with one aesthetasc, two slender setae and one broom seta.

Antenna: broken off.

Mandible (Fig. 93): well developed mandibular palp with three articles. Article 1 with one small and one slender seta. Article 2 distally with several rows of fine hairs and two setulate setae. Article 3 with row of fine hairs and eight setulate setae and one simple seta. Pi shelf-like with three teeth (third tooth shelf-like elongated). Lm of left Md with four teeth. On first tooth two bunches of five, respectively four slender setae. Spine row containing 13 spines (three cuspidate, distally serrated and lobed, four slender distally setulate and six simple slender). Pm bulge-like, slightly triangular, with 10 slender setae. Spine row of right Md with two Lm-like structures, each with four terminal lobes. 10 cuspidate terminally serrated spines and four simple slender spines.

Maxillula (Fig. 93): stout. Inner lobe with 11 strong spines, three of them serrated. On lateral margin proximal two slender setae, upper margin with nine pairs of fine hairs. Outer lobe upper margin with row of nine slender setae and three pairs of fine hairs. Terminally with 15 slender setae. Lower margin with five pairs of fine hairs.

Maxilla (Fig. 93): three lobes of similar length, medial lobe twice as wide as inner and outer lobe. Medial lobe terminally with 20 simple setae and 11 pairs of small slender setae on lower margin. On upper margin with eight pairs of fine hairs. Inner and outer lobe terminally with four long setae. On upper margin with 10 triples of fine hairs. On lower margin with 10 pairs of fine hairs.

Maxilliped (Fig. 93): Endite with four coupling hooks, terminally with three stout setae and 22 fine hairs. Outer margin of endite 13 slender setae. Lateral fold with five pairs of slender setae and four slender setae. Palp of five articles. Outer margin of endite and palp articles 1 and 2 hirsute. Corners tipped with one or two small setae. Inner margin of palp with four slender setae on article 1, eight on article 2, 15 on enlarged

article 3 and nine on article 5. Outer margin with one single slender seta and three rows of fine hairs on article 3 and six small setae on article 4.

Epipodite slightly smaller than endite and palp (0.7 of their length, reaching terminal margin of third article). Both lateral margins of epipodite hirsute, outer margin additionally with 10 fine setae inserting in a cuticula membrane. Inner margin tipped with four small setae.

Pereopod I (Fig. 94): carpo-euchelate. Dactylus and propodus form movable counterpart to a large immovable spine (claw-seta) on distal end of carpus. Base 3.2 times longer than wide, lower margin with two slender setae and tipped with single long slender seta. Ischium 1.4 times longer than wide, upper margin convex proximally tipped with one long slender seta, lower margin with four stout unequally bifid distally setulate setae and two small setae. Merus 1.2 times wider than long, upper margin tipped with one long and one small slender seta, lower margin with two stout setae and one unequally bifid distally setulate seta. Carpus enlarged, 2.4 times longer than wide. Upper margin with six small setae. Lower margin with large claw spine and six small distally setulate setae. Propodus 4.1 times longer than wide, widest anteriorly. One single small seta on upper margin proximal to dactylus. Lower margin fringed, with row of 17 slightly arcuate short setae, attached to a hyaline cuticular membrane, additionally with five long setae. Dactylus 3.7 times longer than wide and with smooth upper margin. Lower margin with comb of fine hairs. Proximal to claw with three small slender setae. Claw of single conate seta and two slender distally setulate setae.

Pereopods II-IV (Fig. 94): Setose. PII: Only base and ischium present. Base 3.2 times longer than wide, lower margin tipped with one long distally setulate seta. PIII: Base 3.9 times longer than wide, lower margin with nine hairs, tipped with single seta (broken off). PIV: only base present, 5.3 times longer than wide with one broom seta on upper margin and one small medial seta on lower margin and three small slender setae proximal to ischium. Ischium about 2 times longer than wide. Upper margin distally with one small seta (Ischium of PII additionally with one distally setulate seta) and lower margin with four stout unequally bifid setae.



**Fig. 93:** *Disparella funalis* (Menzies & George, 1972), paratype female, mouthparts (A-D): Md R (A), Md L (B), Mx 1 (C), Mx 2 (D), Mxp (E), scale= 0.1 mm

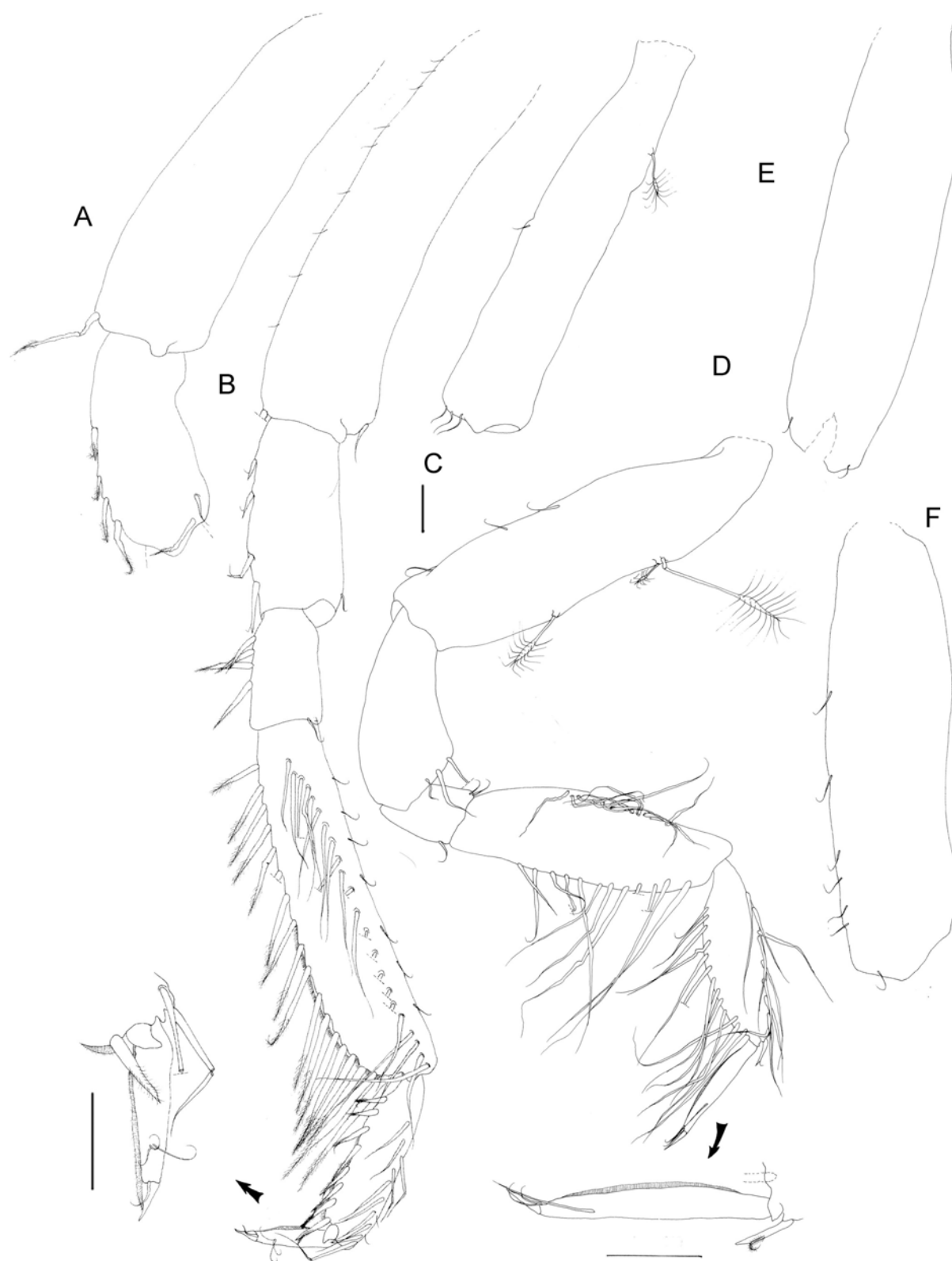
For Merus to Dactylus it follows description of PIII: Merus 1.7 times longer than wide with one slender seta on proximal margin and four distally setulate setae on lower margin. Carpus 4.7 times longer than wide with seven small setae on upper margin. Dorsoventral setal row composed of 22 long slender setae. Lower margin with 18 distally setulate setae, increasing in length towards propodus. Distal half of lower margin fringed with fine hairs. Propodus 3.1 times longer than wide with two small setae on upper margin and 10 slender setae on dorsoventral setal row. Lower margin with eight stout unequally bifid distally setulate setae. Dactylus 4.2 times longer than wide with smooth upper margin and lower margin with comb of fine hairs. Medially of dactylus three small slender setae. Claw formed out of one conate and one slender seta.

Pereopods V-VII (Fig. 94): Base 3.9 times longer than wide, with three broom setae on upper margin and three small slender setae on lower margin. (PVI and PVII: Only base present: 3.8 times longer than wide with several small setae). For Ischium to Dactylus it follows description of PV: Ischium two times longer than wide, upper margin slightly convex, with three setae. Merus as long as wide with two small setae on upper margin and one on lower margin. Carpus three times longer than wide with each 12 long slender setae on lower and upper margin. Propodus three times longer than wide with nine slender setae on upper margin and tipped with one stout unequally bifid seta. Lower margin with 13 long slender setae. Dactylus 8.3 times longer than wide with smooth upper margin and comb of fine hairs on lower margin. Medially one slender seta. Claw formed out of one conate and two slender seta.

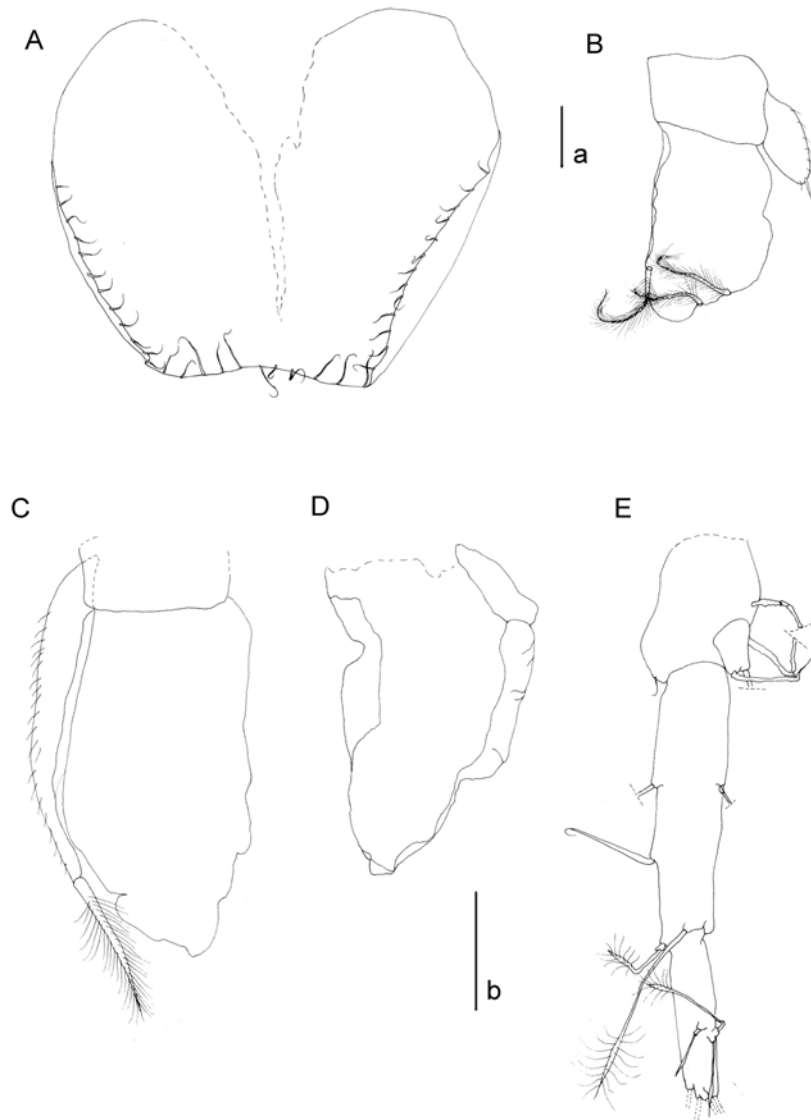
Pleopod 2 (operculum) (Fig. 95): rounded with 36 small setae. Terminal margin concave.

Pleopod 3 (Fig. 95): Endopod 3 times longer than exopod. Exopod tipped with one small seta, outer margin with six and inner margin with one hair. Endopod with three plumose setae.

Pleopod 4 (Fig. 95): Endopod as long as exopod. Endopod oval, smooth, exopod tipped with one plumose seta and outer margin with 21 hairs.



**Fig. 94:** *Disparella funalis* (Menzies & George, 1972), paratype female, pereopods (A-F): P II (A), P III (B), P IV (C), P V (D), P VI (E), P VII (F), scales = 0.1 mm



**Fig. 95:** *Disparella funalis* (Menzies & George, 1972), paratype female, popods (A-E): operculum (A), PI 3 (B), PI 4 (C), PI 5 (D), uropod (E), scale a (A-B)= 0.1 mm, scale b (C-E)= 0.1 mm

Pleopod 5 (Fig. 95): Only endopod, slightly longer than wide, smooth.

Uropods (Fig. 95): biramous, endopod nine times longer than exopod. Protopod with small setae and two long slender setae (damaged). Exopod tipped with two long slender setae (one broken off). Endopod with 12 setae (six broken off, one long slender medially, five broom medially and distally).

#### **3.1.5.4.4     *Eugerdella rotunda* (Menzies & George, 1972)**

Synonyms: *Desmosoma rotundus* Menzies & George, 1972

#### **Material**

Holotype. - female, type only, length 3.0 mm, width 1.0 mm. USNM Cat. No. 120975, *Anton Bruun* Station 59, 09. Oct. 1965; 06°46'S 82°11'W, depth 4526-4609 m, SBT, known only from type locality.

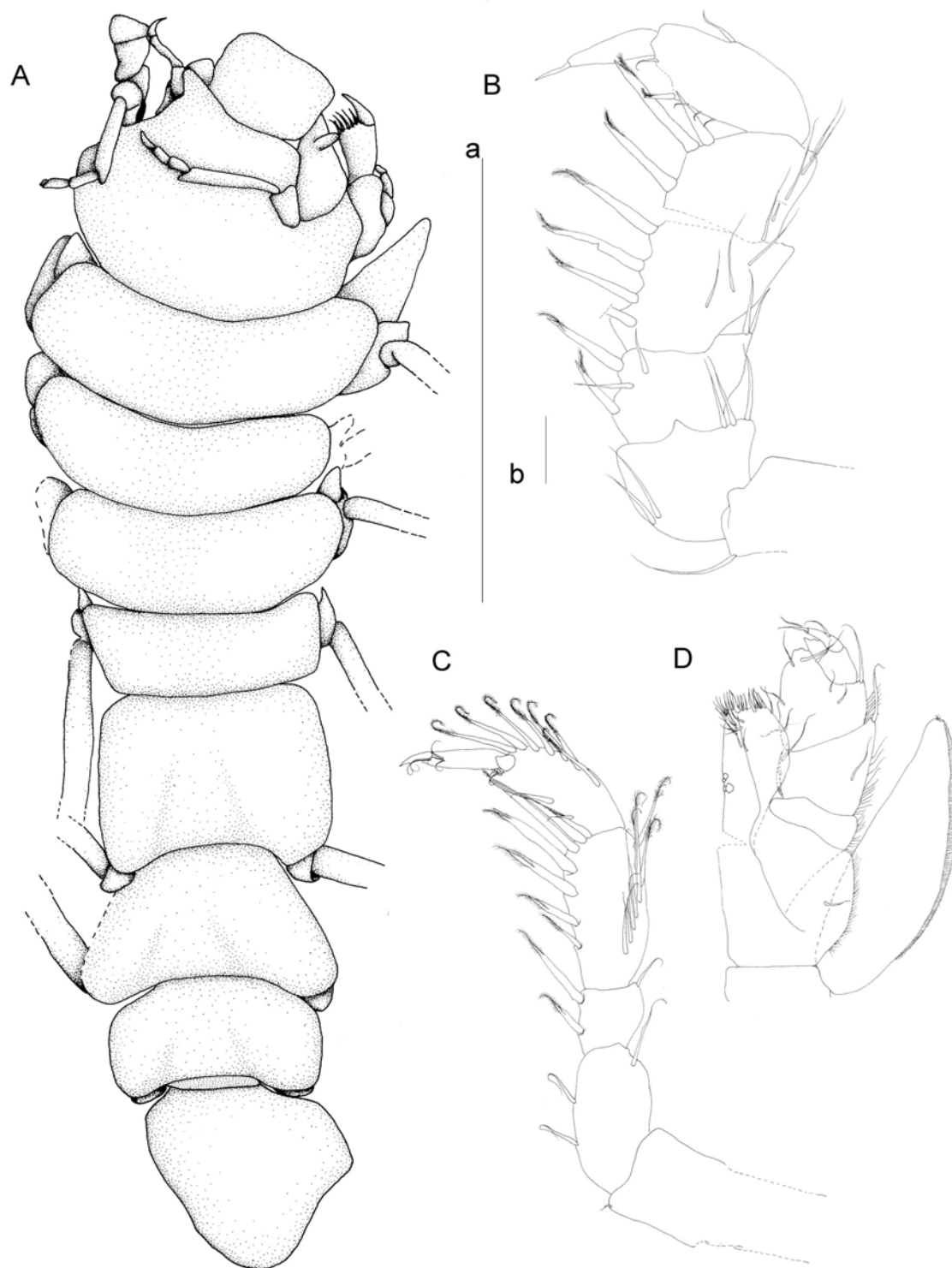
#### **Diagnosis**

Body about three times longer than width of Prn2. PI propodus with seven setae on lower margin and three stout setae on upper margin. Op distal margin slightly concave, bearing minute setae. Urp with long terminal setae

#### **Description of holotype female**

Habitus (Fig. 96): Body about three times longer than wide (measured without appendages). Prn1-4 decreasing in size and anterior margins slightly concave. Coxal plates produced, elongation terminally slightly rounded. Prn5 quadratic. Lateral margins straight, posterior margin maybe slightly concave.

Maxilliped (Fig. 96): Endite with two coupling hooks. Two stout and 16 small setae on terminal margin. Around lateral fold with four pairs of small setae. Outer margin of endite with three slender setae. Palp with five articles. Lower part of endite with single small seta, outer margin with 35 hairs, outer margin of article 1 of palp with 10 hairs, of article 2 with 12 hairs and two slender setae (one medially and one distally) and of article 3 with six hairs. Inner margin of article 2 with three slender setae, of article 3 with eight setae. Article 5 with three setae, two of them terminally. Epipodite as long as endite, tipped with three hairs. Outer margin hirsute, hairs inserting in cuticular membrane.



**Fig. 96:** *Eugerdella rotunda* (Menzies & George, 1972), holotype female, habitus dorsal (A, scale a), pereopod I (B, scale b), scale a= 1 mm, scale b= 0.1 mm



Pereopod I (Fig. 96): Base damaged. Lower margin tipped with one long slender seta. Ischium 1.5 times wider than long and with two long slender setae on lower margin. Proximal margin with three long slender setae. Merus 1.7 times wider than long. On lower margin with two slender and two unequally bifid distally setulate setae and upper margin terminally with two long slender setae. Carpus 1.6 times longer than wide and on lower margin with six unequally bifid distally setulate setae (one broken off) and proximal to propodus one stout simple seta, which is half of length of the six other setae. Eight slender setae on upper side of carpus. Propodus 2.0 times longer than wide, with four small and one stout unequally bifid distally setulate setae. Margin in direction to dactylus damaged. On upper margin medially one slender seta. Dactylus 3.5 times longer than wide, smooth. Claw out of one conate, distally pointed seta.

Pereopods II-IV (Fig. 96): PII: Base damaged. Lower margin tipped with one small seta. Ischium 1.7 times longer than wide and with two long slender setae on lower margin. Upper margin with one long slender seta. Merus as long as wide. On lower margin with two unequally bifid distally setulate setae and upper margin terminally with one slender seta. Carpus 1.9 times longer than wide and on lower margin with six unequally bifid distally setulate setae, length increasing towards propodus. Eight distally setulate setae on upper side of carpus. Propodus 2.3 times longer than wide, with three simple setae on lower margin. Margin fringed with two combs of fine hairs. Upper margin with seven distally setulate setae. Dactylus 3.8 times longer than wide, medially with three small slender setae. Claw out of one conate, distally pointed seta and two small slender setae.

#### Remarks

The holotype is extremely damaged. No paratypes or other material of this species is known. In this redescription, all that was possible to draw (appendages and a dorsal habitus) are drawn. A lateral drawing is not possible, because the specimen is extremely flattened. To avoid further damage of the holotype, just those parts which were already separated or easy to prepare from the body were fixed as permanent slides.

#### **3.1.5.4.5 *Pseudogorda anversense* (Schultz, 1979)**

Synonyms: *Desmosoma anversense* Schultz, 1979

##### **Material**

Holotype: fragment, sex undetermined. Type only, length 1.8 mm from cephalon to Prn7, Plt broken off, width 0.6 mm. USNM Cat. No. 171426, RV “Hero”, Station 721-1066, 26. Jan. 1972; 64°47.4'S 64°06.8'W (type locality), depth not given, probably between 109-137 m, Petersen Grab, known only from type locality.

##### **Description of species**

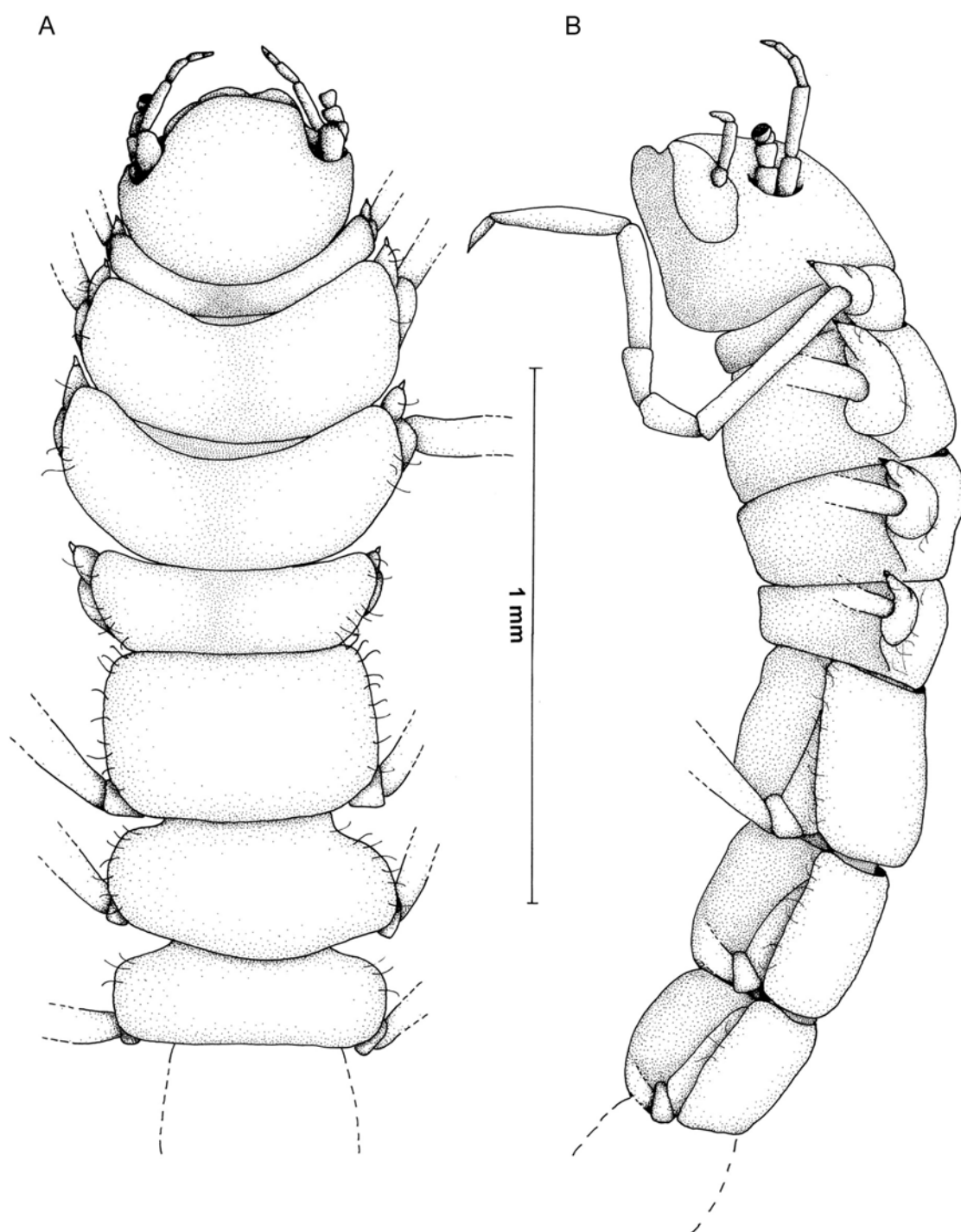
Body about three times longer than wide. Prn1 one third of size than Prn2. Pl slender, attenuated, carpus and propodus with few setae, without any row of setae. PII clearly setose, bigger in size than PI. Prn5-7 decreasing in size, with dorsal cuticular elongations, overlapping shape of body (wider than body). Prn5 rectangular. Mxp with two coupling hooks. Md with palp of three articles, Lm of left Md with four teeth.

##### **Description of holotype; sex undetermined**

Habitus (Fig. 97): Frontal margin of cephalothorax to posterior of Prn7 1.8 mm long (measured without appendices). Cephalothorax slightly wider than long (1.2 times). Three times longer than wide. Prn1 one third of size of Prn2. Prn2 slightly bigger than Prn3. Prn4 half of size of Prn3. Prn5 largest, rectangular (1.5 times wider than long from dorsal view). Prn6-7 smaller than Prn5. Plt missing.

Antennula (Fig. 98): slightly three quarters of length of cephalothorax. With five articles. Relative length of articles: 1:1.7:0.6:0.4:0.4. Article 1 shorter and broader than article 2. Article 1 with two broom setae and five small slender setae. Article 2 with three small slender and distally two broom setae. Article 3 with three small slender. Article 4 with three long slender and article 5 with one small slender, three long slender and one aesthetasc.

Antenna: broken off.



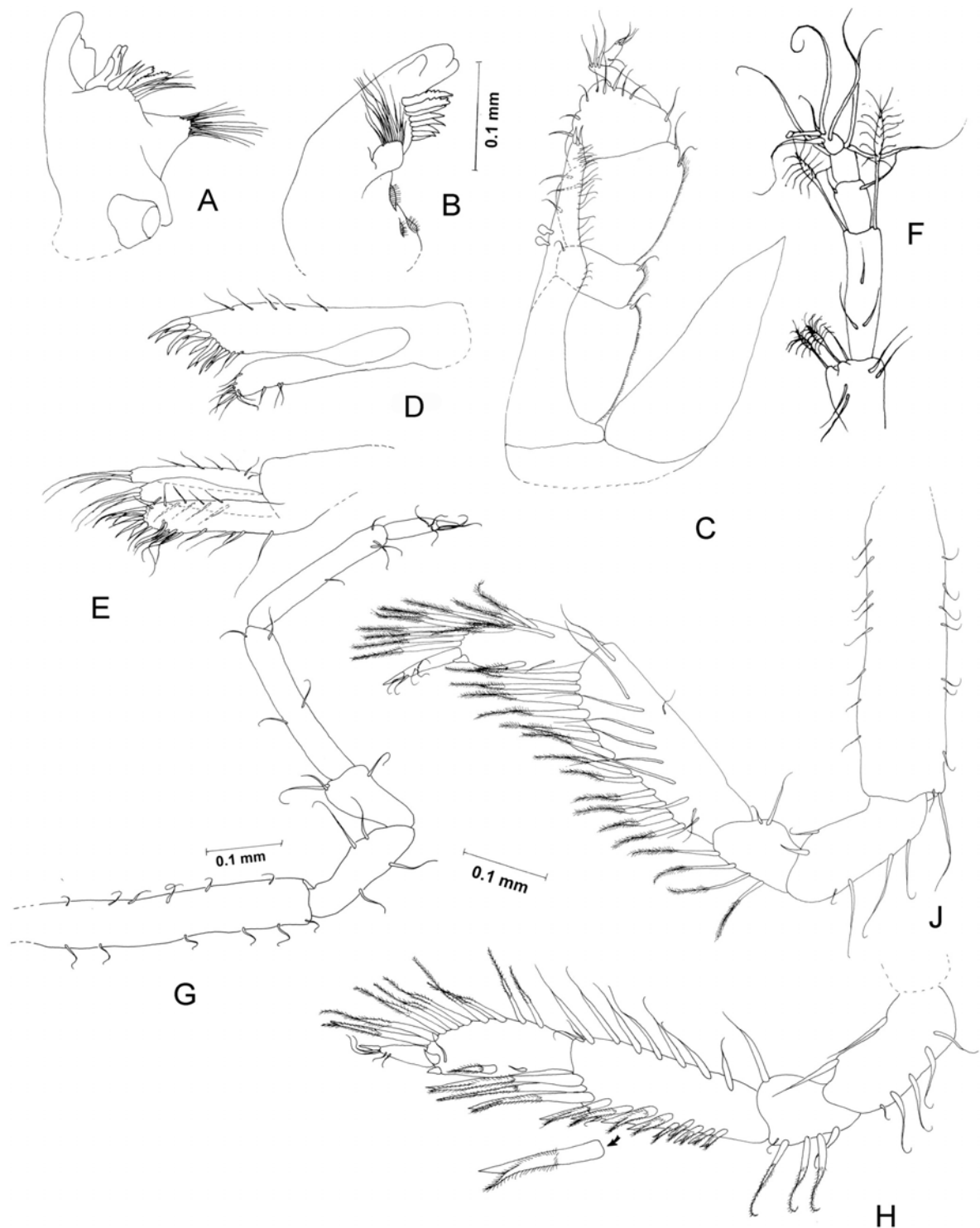
**Fig. 97:** *Pseudogorda anversense* (Schultz, 1979), holotype female, habitus dorsal (A), lateral (B)

Mandible (Fig. 98): Both mandibles after Schultz (1979) with well-developed palp of three articles. Palp of Md with middle article longest; apical article shortest with curved apical setae (Schultz, 1979). Both Md palps of holotype broken off. Pi of left Md shelf-like, three teeth. Pi of right Md strong with two big teeth of similar size and one small tooth. Lm of left Md with four teeth, first and third smaller than second and fourth. Lm of right Md longer than wide, two spines of spine row distally serrated, remaining spines (six) simple. Spine row of left Md containing eight spines, two simple, two with inner side serrated (nine small teeth) and four slender setae. Pm with 12 slender setae.

Maxillula (Fig. 98): Outer lobe smaller than inner lobe. Inner lobe terminally with 12 strong spines. Lower margin proximal to spine row with two small slender setae. Upper margin with five small slender setae. Upper margin of outer lobe smooth, lower margin with three small slender and terminally with eight small slender setae.

Maxilla (Fig. 98): All lobes of similar size, outer and inner lobe terminally with each three long setae. Outer and inner lobe with six small setae on lower margin, upper margin smooth. Medial lobe with 11 long slender setae on lower margin, upper margin with five small setae and terminally six strong setae.

Maxilliped (Fig. 98): Endite medially with two coupling hooks; terminally with three strong simple setae; numerous hairs on outer margin. Lower part of endite's outer margin hirsute, proximal to insertion of palp article single small seta. Palp of five articles; outer margins of articles 1-2 hirsute. Article 1 with one seta and article 2 with two setae on outer margin. Article 1 with one seta and article 2 with three setae on inner margin. Inner margin of article 3 higher than outer margin and overall with nine setae. Article 4 terminally with three setae and article 5 overall with five setae. Epipodite two third of length of endite, nearly oval and terminally pointed. All margins smooth.



**Fig. 98:** *Pseudogerda anversense* (Schultz, 1979), MdL (A), MdR (B), Mxp (C), Mx1 (D), Mx2 (E), A1 (F), PI (G), PII (H), PIII (J)

Pereopod I (Fig. 98): slender and elongated. Base with six setae on inner and outer margin each; 6.8 times longer than wide. Ischium with two slender setae on inner and

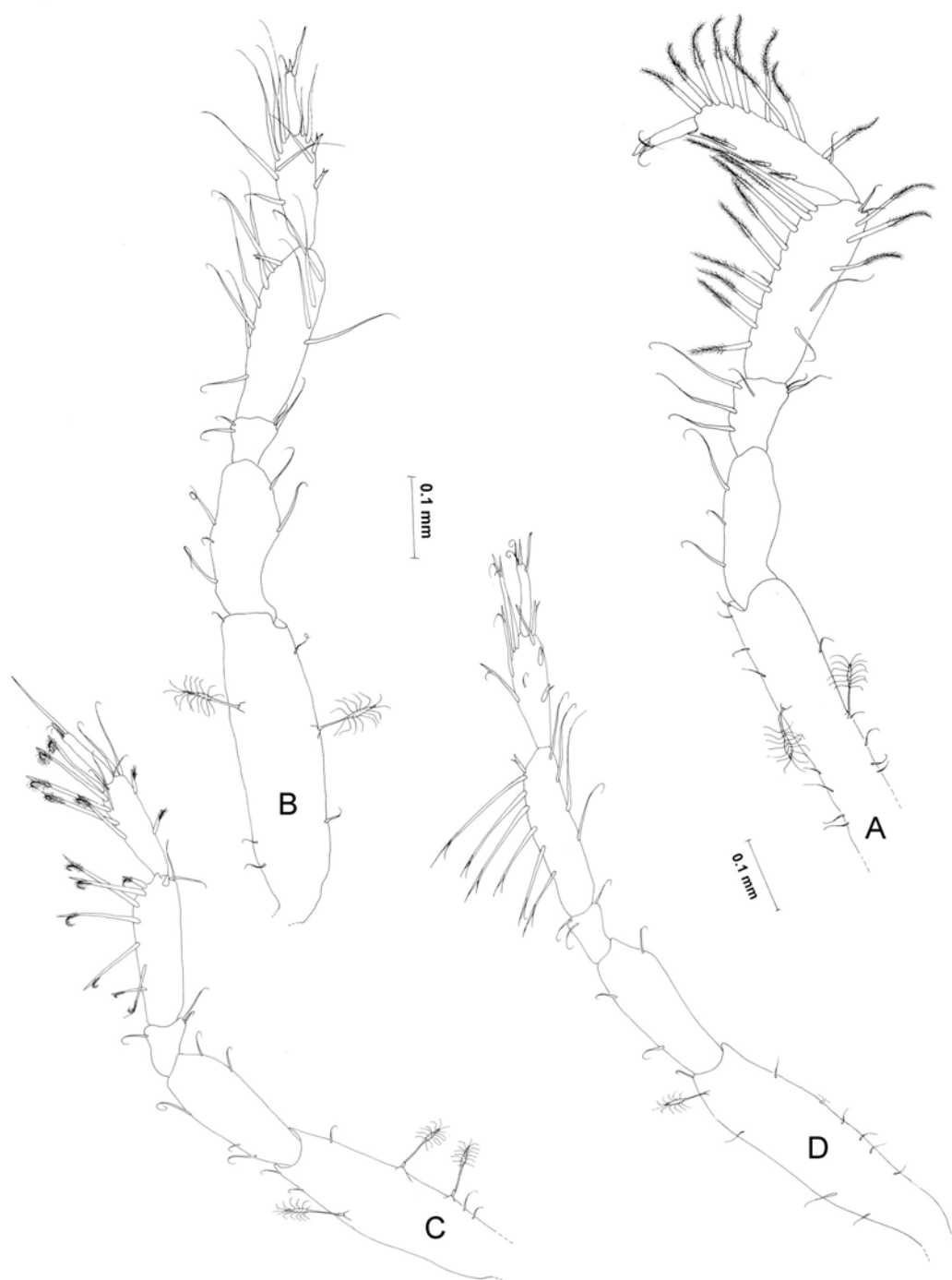
outer margin each, 3.2 times longer than wide. Merus on upper margin with two terminal setae and on lower margin one seta; 1.7 times longer than wide. Carpus with one terminal and one medial seta on upper and lower margin each; six times longer than wide. Propodus with one small terminal seta on upper margin and with one medial small and two distal small slender setae; seven times longer than wide. Dactylus with smooth margins and three slender setae proximal to claw; 3.3 times longer than wide. Claw out of two parts with two small slender setae inserting between them.

Pereopods II-IV (Fig. 98): setose. Base about 3.8 times longer than wide, on upper and lower margin with numerous small setae, PIII lower margin tipped with one long slender seta and PIV base additionally with two broom setae. Ischium about 2.2 times longer than wide and with two simple setae on upper margin on PII-III, PIV upper margin smooth, lower margin with line of three to five setae. Merus about 1.3 times longer than wide, PII with one simple seta and PIII-IV with one small and one slender setae each on upper margin; PII-III with line of distally setulate setae and PIV with three slender setae on lower margin, one small and four distally setulate. Carpus about 2.7 times longer than wide, PII with seven simple terminally pointed setae and two small slender distal setae on upper margin, PIII with one single small seta and dorsoventral row of 10 slender setae, PIV with two small distal setae and a line of five setae, three distally setulate and two slender setae. Lower margin of PII with row of 12 stout unequally bifid distally setulate setae and one small seta, PIII with nine and PIV with 12 distally setulate setae, increasing in size. Setae increasing in size towards propodus. Propodus about 2.5 times longer than wide and with eight distally setulate setae and proximal to dactylus one unequally bifid distally setulate seta on upper margin, PIII with 11 and PIV with nine distally setulate setae on upper margin, and lower margin of PII-III with one medial unequally bifid distally setulate seta, one stout simple seta and one small stout seta proximal to dactylus, PIV lower margin with three stout distally setulate setae. Dactylus about 2.8 times longer than wide, with two small slender setae proximal to claw, lower margin of PIII-IV smooth, upper margin of PII-IV smooth and with two small setae on lower margin. Claw of PII-III out of one conate seta and two small slender setae, claw of PIV out of two parts, with one small slender inserting between them and another small slender seta inserting proximal to lower margin of dactylus.

Pereopods V-VII (Fig. 99): Base about 3.7 times longer than wide and with several small setae and few broom setae. Ischium about 2.4 times longer than wide, PV-VI with two slender setae and PVII with one slender seta on upper margin. Lower margin of PV-VII with two slender and PV-VI additionally with one small medial setae. Merus about as long as wide, upper margin distally with one small and one slender seta on PV-VI, PVII with one slender seta on upper margin. PV with two, PVI with one and PVII with two small slender setae on lower margin. Carpus about 3.1 times longer than wide; upper margin of PV and PVII with four long slender setae, PVI distally with two slender setae. Lower margin of PV-VII distally with single stout unequally bifid setae and PV with row of six long slender, PVI with six long unequally bifid distally setulate, PVII with six long unequally bifid setae. Propodus about three times longer than wide with three slender and two stout unequally bifid on upper margin of PV-VI. PVII with two long and two stout unequally bifid setae on upper margin. PV lower margin with six long slender, PVI with two slender and row of six long stout unequally bifid distally setulate setae, PVII with four long stout unequally bifid and additionally one small medial setae. Dactylus about seven times longer than wide, both margins smooth. Claw of PV-VII out of one long and one small conate seta and on additionally PV with one and PVI-VII with two small slender seta inserting on lower margin of dactylus proximal to small conate seta of claw.

#### Remarks

The specimen was assigned to the genus *Desmosoma* by Schultz (1979), although he mentioned, that the PI does not completely fit in the diagnosis of the genus Hessler (1970) has given. Although the Plt and therefore its characters (posterolateral spines, uropods) are missing from the holotype and the sex cannot be determined from the only specimen, the authors change the genus from *Desmosoma* into *Pseudogerda*, because of the remaining characters (Prn1 much smaller than Prn2 (one third of length), PI slightly reduced, attenuated, carpus and propodus with few slender setae).



**Fig. 99:** *Pseudogorda anversense* (Schultz, 1979), pereopods IV - VII: PIV (A), PV (B), PVI (C), PVII (D)



#### **3.1.5.4.6     *Desmosoma dolosa* (Menzies & George, 1972)**

Synonyms: *Desmosoma dolosus* Menzies & George, 1972

#### **Material**

Holotype: male, length 6.0 mm, width 1.5 mm. USNM Cat. No. 120966, Anton Bruun Station 59, 09. Oct. 1965; 06°46'S 82°11'W (type locality), depth 4526-4609 m, SBT.

Other material: one female, length 7.4 mm, width 1.7 mm. USNM Cat. No. 120967, Anton Bruun Station 53, 07. Oct. 1965; 06°32'S 82°13'W, depth 4506-4555 m, SBT.

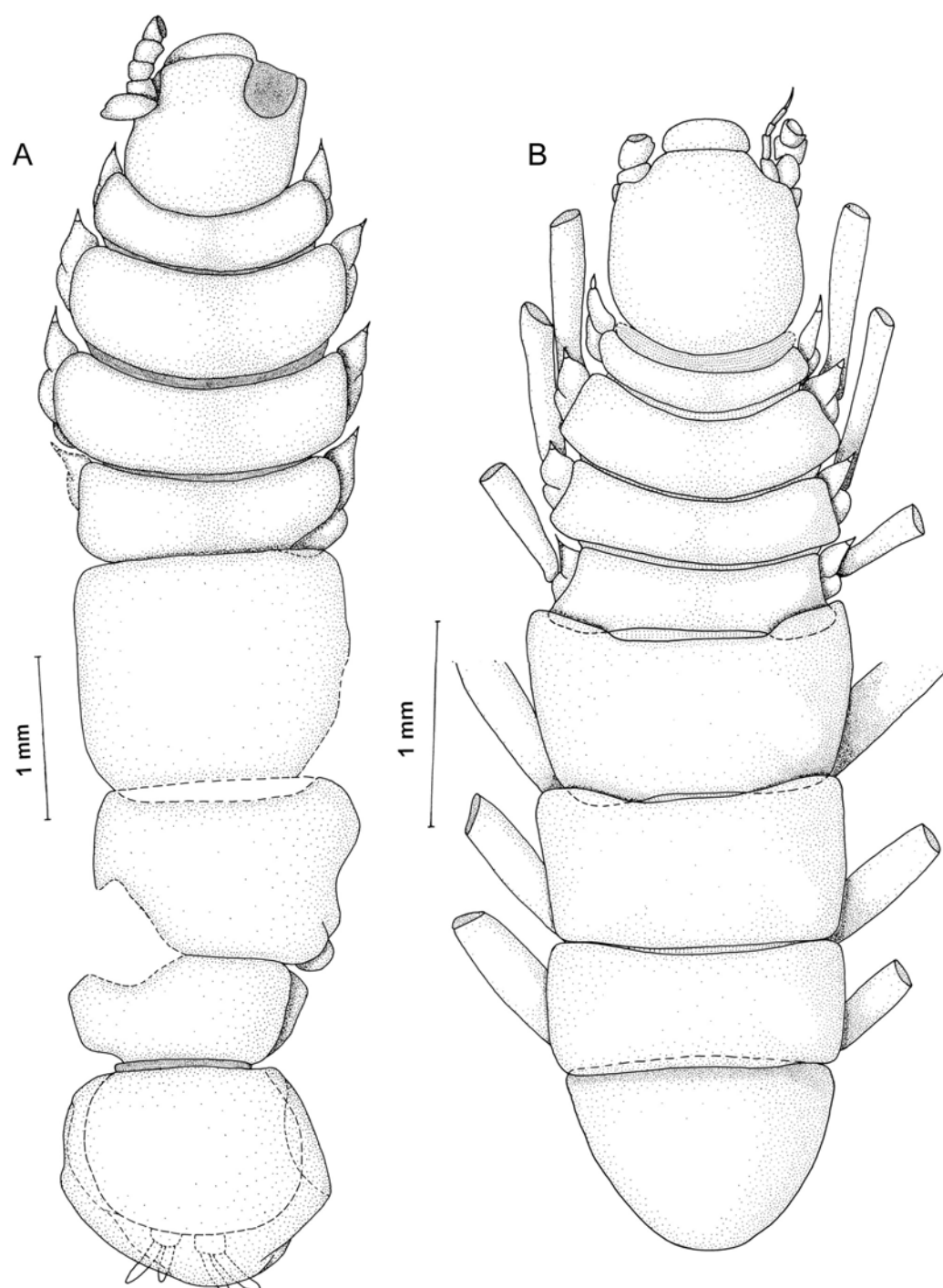
#### **Description of species**

Body about 4.4 times longer than wide. Cephalothorax nearly as long as wide. Pl probably elongated (Base 6.1 times longer than wide), PIII very setose. Prn1 half of size of Prn2. Prn2 slightly bigger than Prn3; Prn3 slightly bigger than Prn4. Prn5-7 quadratically from dorsal view (Prn5-7 of male more rectangular and proximal corners of Prn5 from dorsal slightly triangular elongated), because of cuticular elongation overlapping shape of body. A1 with six articles. A1 of male about half length of cephalon, of female as long as cephalothorax. Spine row of left Md mostly similar to form of Lm. Lm with three teeth. Right Mxp with four and left Mxp with three coupling hooks. Urp biramous, exopod with six terminal setae. Op slightly wider than long.

#### **Description of female (other material)**

Habitus (Fig. 100): Body 7.4 mm long (measured without appendices) and 1.6 mm wide; 4.4 times longer than wide (measured without appendages). Cephalothorax nearly as long as wide. Prn1-3 from dorsal view increasing in size, relative length of Prn1-4: 1:1.9:1.5:1.3. Prn5 nearly quadratic, Prn6-7 rectangular. Plt rounded.

Antennula (Fig. 101): with six articles, 1 mm long, as long as cephalothorax. Relative length of articles: 1:1.9:1.4:0.5:0.3:0.3. Article 1 widest, with nine broom and two small setae, all distally. Article 2 with three small setae and distally with three broom and two slender setae. Article 3 with two small setae and article 4 with two small and two distal broom setae. Article 5 smooth, article 6 tipped with one broom, two slender setae and one aesthetasc.



**Fig. 100:** *Desmosoma dolosa* (Menzies & George, 1972), habitus dosal male (B), female (A)

Antenna (Fig. 101): Only basal articles present. Article 1 and 3 with one small setae respectively, article 3 additionally with two small slender setae. All basal article of nearly same size.

Mandible (Fig. 101): Both mandibles with well-developed palps of three articles. Article 1 with three small setae, article 2 on lower side distally with two small distally setulate setae and several rows of fine hairs. Article 3 with row of fine hairs and ventrally with 15 small setae increasing in size towards the end. Pi of both mandibles strong, with three teeth. Lm of right Md bipartite, larger part slender and smaller part resembles conate pointed seta; distal margin with seven tooth like lobes. Lm of left Md with three teeth. Two hairs inserting basally on Lm. Following spine looks like Lm, with six teeth. Next four spines with one smooth margin and other margin with three or four tooth-like lobes and two setae inserting basally. Last six spines simple and slender. Spine row of right Md containing 12 spines, eight of them with one smooth margin and other margin with four to six tooth-like lobes and two setae inserting basally. Other five setae pappose. Pm of right Md with 16 slender setae, Pm of left Md also with 16 setae, 10 of them setulate.

Maxillula (Fig. 101): Inner lobe bigger than outer lobe, terminally with 12 strong spines, six show various types of serration. Upper margin with 10 pairs of fine setae. Lower margin basally with four pairs of fine setae and 24 small setae. Outer lobe distally with 16 slender setae and on lower margin with seven pairs of hairs. Upper margin with several pairs of fine hairs.

Maxilla (Fig. 101): Inner and outer lobe terminally with four long setae each, which have one smooth margin and one margin, which is lined with fine hairs over total length of seta. Lower margin basally with six pairs of fine setae and six single small setae. Upper margin with six fine setae. Medial lobe with four small setae on lower margin and 16 slender setae on upper margin.

Maxilliped (Fig. 101): Endite medially with four coupling hooks on right Mxp, left Mxp with three coupling hooks on endite medially. Endite terminally with two serrated, cuspidate setae and 16 small setae; on outer margin with 14 small setae and towards inner margin with 35 small setae inserting in irregular distances. Palp out of five articles. Margins of article 1 smooth, outer margin of article 2 with five slender setae. Inner margin of article 3 short, tipped with single seta. Outer margin of article 3 twice

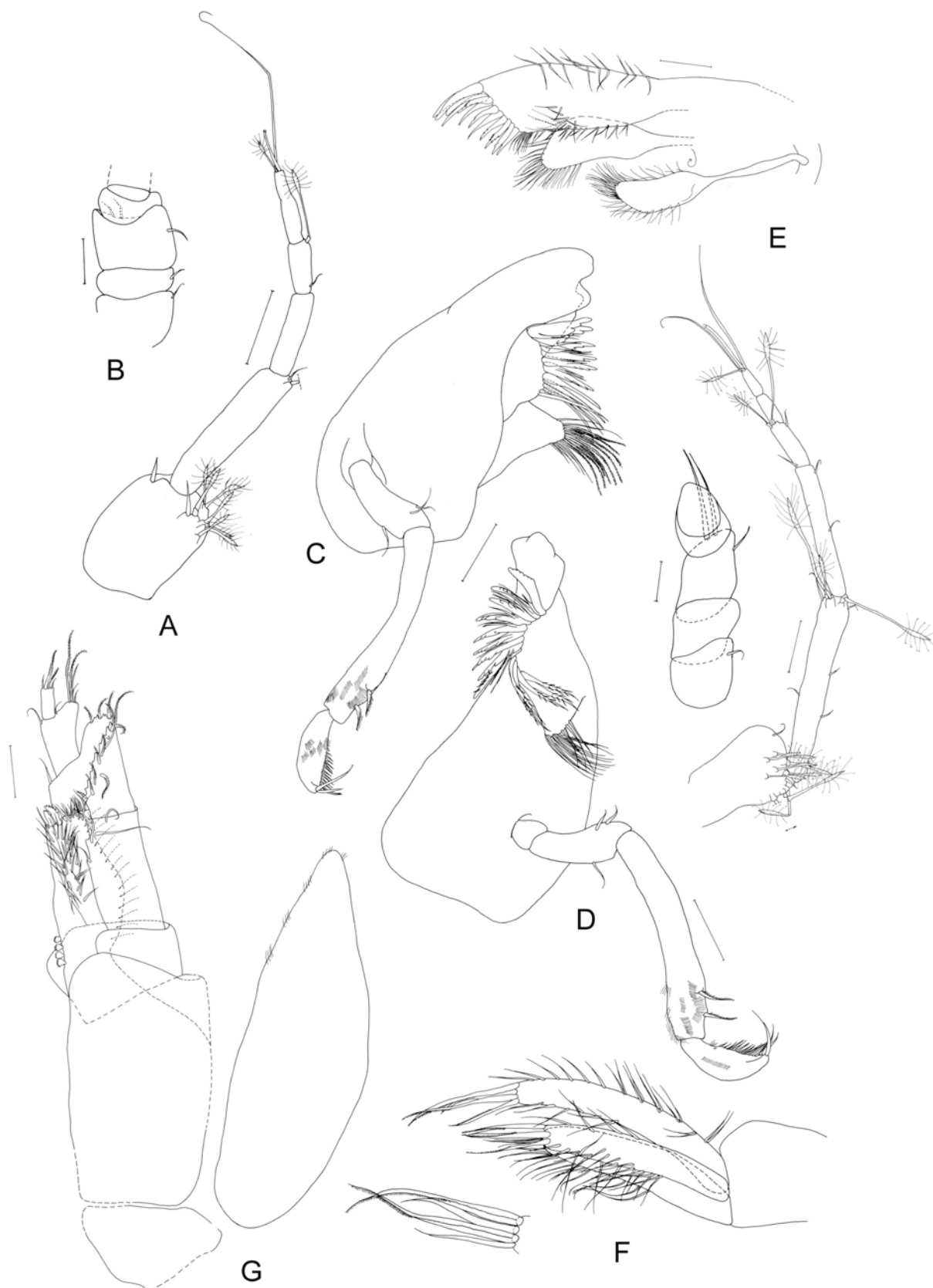
as long as inner margin and with 13 setulate setae inserting in marginal lobes. Article 4 with seven setae, one of them on inner margin, two of them terminally on outer margin slender and setulate. Article 5 with four setae on terminal margin (two small and two slender setulate). Epipodite oval, with four lines of four fine hairs on upper part of inner margin and three fine hairs distally on outer margin.

Pereopod I (Fig. 102): probably attenuated, broken off after base. Base 6.7 times longer than wide. With several small setae on both margin and one broom seta on upper margin. Lower margin distally to Ischium tipped with one small setae, which is slightly bigger than other small setae on base.

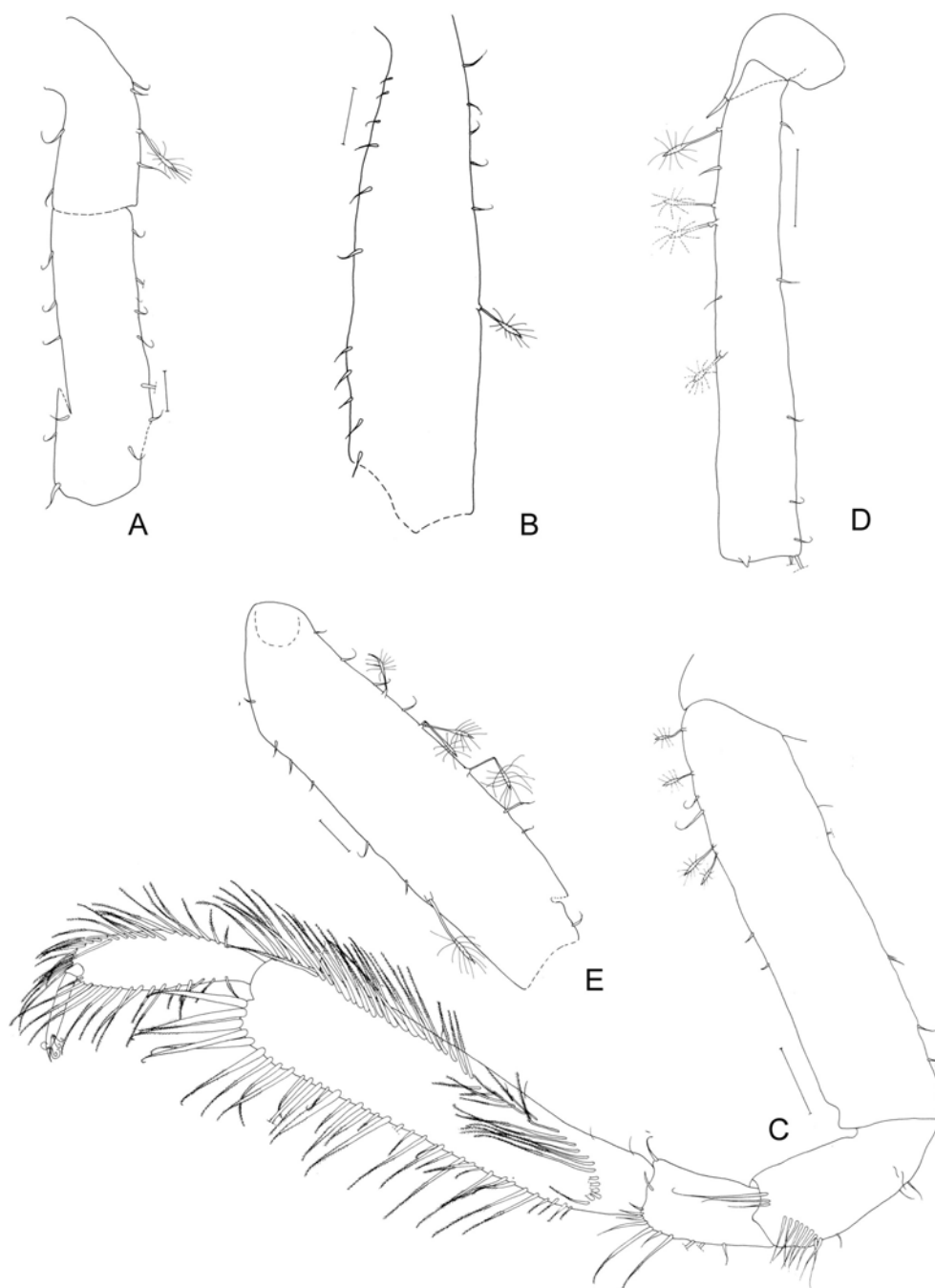
Pereopods II-IV: PII and PIV broken off after base. Base of PII-IV about 4.2 times longer than wide, with several small setae, PII additionally with one and PIII-IV with four broom setae. It is following the description of PIII: Ischium 2.2 times longer than wide, with smooth upper margin, lower margin with five small setae. Distolaterally one line of three slender setae and one row of nine slender setae. Merus 1.7 times longer than wide, with one terminal simple seta on upper margin and 10 setae on lower margin (two broken off, two distally setulate and six small and simple). On terminal margin one simple seta. Carpus 4.8 times longer than wide, with dorsoventral setale row, starting basally on lower margin and ending terminally on upper margin, containing 45 distally setulate setae. Upper margin with six small setae. Lower margin with 37 distally setulate setae, increasing in size towards propodus. Propodus 3.3 times longer than wide, with 25 distally setulate setae on upper margin and 15 distally setulate setae on lower margin. Dactylus 5.8 times longer than wide, smooth margins, three small slender inserting medially, proximally towards claw. Claw out of two small slender setae and one conate terminally pointed seta.

Pereopods V-VII: broken off, one single base of undetermined posterior leg, completely damaged.

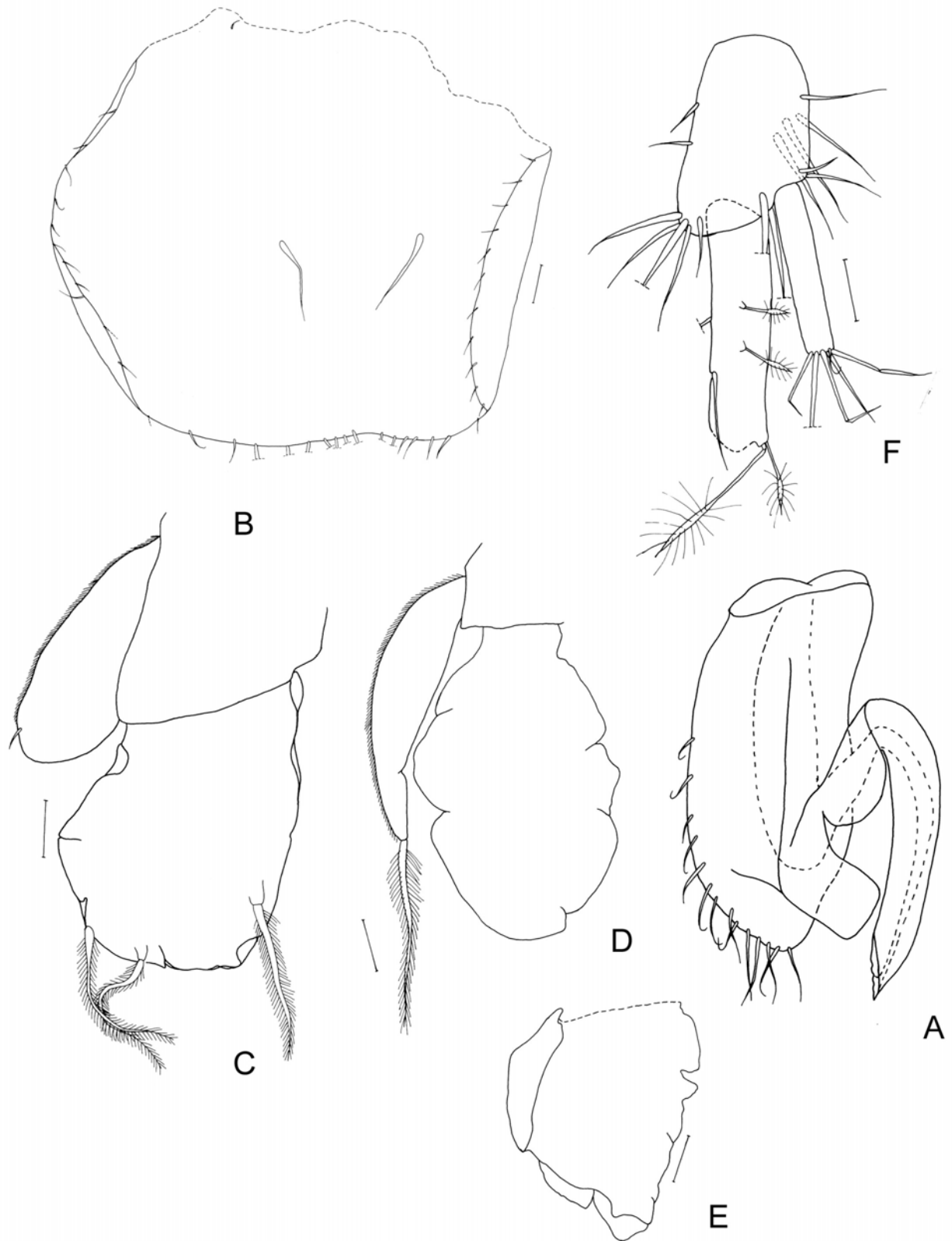
Pleopod 2 (operculum) (Fig. 103): slightly wider than longer, medially with two long slender setae and margins overall with 42 setae.



**Fig. 101:** *Desmosoma dolosa* (Menzies & George, 1972), mouthparts: MdL (C), MdR (D), Mx1 (E), Mx2 (F), Mxp (G), antennula (A), scale = 0.1 mm



**Fig. 102:** *Desmosoma dolosa* (Menzies & George, 1972), female, base pereopod I (A), base pereopod II (B), pereopod III (C), base pereopod IV (D), base pereopod V (E), scale = 0.1 mm



**Fig. 103:** *Desmosoma dolosa* (Menzies & George, 1972), pleopods: PI2 male (A), Op (B), PL3 (C), PI4 (D), PI5 (E), Ur (F), scale = 0.1 mm

Pleopod 3 (Fig. 103): Endopod 1.3 times longer than exopod, terminally with three plumose setae. Exopod with single small seta and hirsute outer margin.

Pleopod 4 (Fig. 103): Endopod 1.1 times longer than exopod. Exopod terminally with one long plumose seta and outer margin hirsute.

Pleopod 5 (Fig. 103): Only endopod, reduced and smooth.

Uropods (Fig. 103): Protopod with 15 slender setae, exopod tipped with five slender and one small seta. Endopod broken off close to end, remaining part (clearly larger than endopod) contains four broom and two slender setae.

#### Remarks

In the present study, the female which is mentioned by Menzies and George (1972) as other material is described, because the holotype is more damaged than this female and by drawing and describing the female, a better comparison to other species to animals of this family will be possible.

#### 3.1.5.4.7 *Mirabilicoxa acuta* (Menzies & George, 1972)

Synonyms: *Desmosoma acutus* Menzies & George, 1972

#### Material

Holotype: female, type only; length 2.5 mm, width 0.6 mm. USNM Cat. No. 120962, Anton Bruun Station 169, 02. Nov. 1965; 08°46'S 80°44'W, depth 3909-3970 m (type locality), SBT. Distribution only known from type locality.

#### Description of species

Body 4.0 times longer than wide. Prn1 from dorsal view slightly smaller than Prn2, from lateral view clearly smaller than Prn2. Anterior corners of Prn5 triangular; anterior margin straight. Prn5-7 decreasing in size, Plt nearly three times longer than Prn7, posterolateral spines large, pointed. Pl slender, carpus with four distally setulate setae on lower margin, upper margin of carpus smooth, proximally tipped with single slender seta. Propodus ventrally with one medial and two proximal slender setae, upper margin smooth and two slender setae proximal to dactylus. Md without palp. Mxp with two coupling hooks. Uropods uniramous.



#### **Description of holotype female**

Habitus (Fig. 104): Body 4.0 times longer than wide. Width of body decreasing with number of segments. Prn1 from dorsal view slightly smaller than Prn2, from lateral view clearly smaller than Prn2. Prn2-3 from dorsal size similar in size, from lateral view Prn2 clearly bigger than Prn3. Prn4 clearly bigger than Prn3. Anterior corners of Prn5 triangular; anterior margin straight. Prn6 slightly smaller than Prn5 and Prn7 slightly smaller than Prn6. Plt nearly three times longer than Prn7, posterolateral spines large, pointed (length of spine reaching one third of length of Urp).

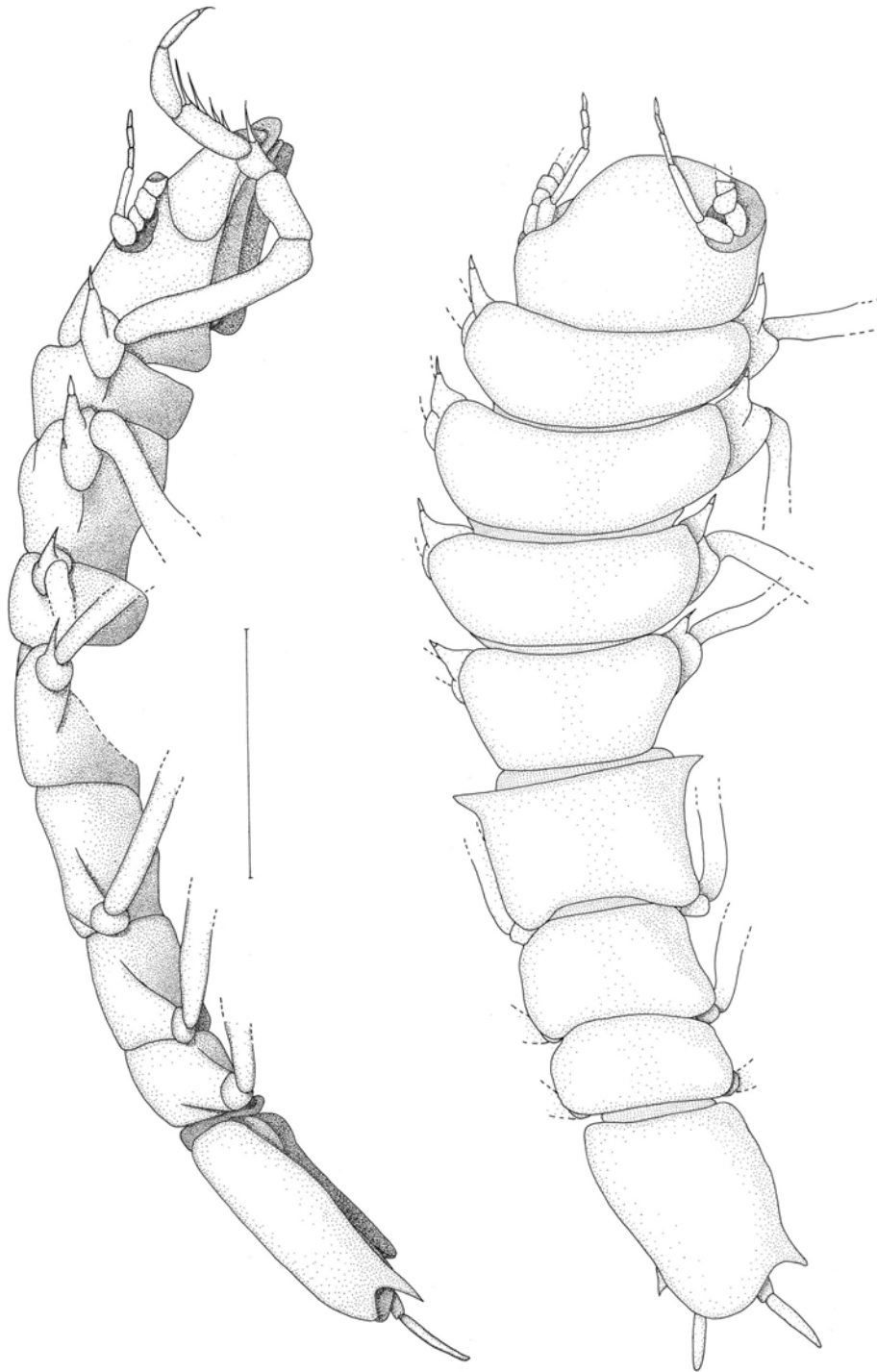
Antennula (Fig. 106): With six articles, article 1 broader than articles 2 to 6. Article 2 longest. Relative length of articles: 1:2.5:0.7:0.7:0.5:0.3. Article 1 with two small setae, article 2 distally with three broom setae, article 3 smooth, article 4 with one broom seta, article 5 smooth and article 6 tipped with two setae or one seta and one aesthetasc (both structures are broken off).

Antenna: only basal articles present. Article 1,2 and 4 of nearly similar size, article 3 slightly bigger than other three. Article 4 with two small setae.

Mandible (Fig. 106): Without palp. Pi with four teeth of irregular size. Lm of left Md with four teeth. Spine row of left Md of 10 spines, first spine most similar to Lm, with four teeth. Remaining spines with one smooth margin and other margin with three or four tooth-like lobes and two setae inserting basally. Spine row of right Md containing 10 spines, two Lm-like spines with six to seven teeth, two of them with one smooth margin and other margin with four tooth-like lobes and two setae inserting basally. Pm of both Md with nine setae.

Maxillula (Fig. 106): Inner lobe terminally with 11 strong spines, lowest three of them distally setulate. Lower margin with four small slender setae proximal to spines and four pairs of hairs. Upper margin with eight simple setae. Outer lobe with 13 small slender setae and four slender setae dorsally.

Maxilla (Fig. 106): Inner and outer lobe with four long terminal setae each, upper margin with seven pairs of fine hairs and lower margin with seven small slender setae. Medial lobe with seven terminal setae, upper margin with several pairs of fine hairs and lower margin with three long slender setae basally and 11 setae.



**Fig. 104:** *Mirabilicoxa acuta* (Menzies & George, 1972), holotype female: (A) habitus lateral, (B) habitus dorsal; scale: 0.5 mm

Maxilliped (Fig. 106): Endite with two coupling hooks, terminally with two strong conate serrated setae and two simple setae. Terminal and inner margin of endite hirsute. Lateral fold of endite with 19 small slender setae. Outer margin of article 1-2

hirsute; of article 2 additionally tipped with single small seta. Inner margin of article 1-2 smooth, article 2 with two terminal setae. Outer margin of article 3 clearly shorter than inner margin with single small setae. Inner margin with seven setae of different size. Article 4 terminally tipped with two small slender setae. Epipodite hirsute and length reaching to middle of article three of palp.



**Fig. 105:** *Mirabilicoxa acuta* (Menzies & George, 1972), , scale 0.1 mm, pereopods: (A) pereopod I, (B) pereopod II, (C) pereopod III, (D) pereopod IV, (E) pereopod V, (F) pereopod VI

Pereopod I (Fig. 105): slender. Base 6.3 times longer than wide, with three fine hairs (two distally on lower margin, one on upper margin). Lower margin tipped with one long seta. Upper margin additionally with two broom setae (broken off). Ischium 2.6 times longer than wide, with one small seta medially on lower margin. Upper margin smooth (without setae). Merus 1.5 times longer than wide, lower margin with two distally setulate setae, upper margin tipped with two distally setulate setae (one broken off). Carpus 3.3 times longer than wide, lower margin with four distally setulate setae increasing in size towards propodus, upper margin with single distal small seta. Propodus 4.2 times longer than wide, with three small slender setae on lower margin (one medially, two distally) and on upper margin with two distal small slender setae. Dactylus 3.6 times longer than wide, smooth, three medial small slender setae proximal to claw. Claw out of one strong irregular formed conate seta and two slender setae.

Pereopods II-IV (Fig. 105): Base about 5.4 times longer than wide, with few small setae, lower margin proximal to Ischium tipped with single robust simple setae. Base of PIII with one and PIV with two broom setae. Ischium about 2.9 times longer than wide. Lower margin medially with one small slender seta, upper margin with one (PII) or two (PIII) simple setae; upper margin of Ischium of PIV smooth. Merus about 1.9 times longer than wide, Lower margin with two distally setulate setae, upper margin tipped with one simple (PII-III) or one distally setulate seta (PIV). Carpus about 5.6 times longer than wide, lower margin with six distally setulate setae. Increasing in size towards propodus. Upper margin of PII-III with five distally setulate setae, PIV with five distally setulate and one unequally bifid setae on upper margin. Propodus about 3.7 times longer than wide, lower margin with numerous fine hairs inserting in cuticular membrane and three small slender setae (one medially, two proximally to dactylus). Upper margin with five distally setulate setae (PII), four distally setulate and terminally one unequally bifid setae (PIII) and four distally setulate setae (PIV). Dactylus about 7.7 times longer than wide. Both margins of PII-III smooth. Margins of Dactylus of PIV fringed with fine hairs inserting in cuticular membrane. Claw out of two parts with two fine setae inserting between them.

Pereopods V-VII (Fig. 106): Base about 6.8 times longer than wide, with few small setae, PV with three broom setae and PVI-VII with one broom seta. Ischium about 3.2 times longer than wide, of PVII smooth, PV-VI with one small seta medially on

lower margin, PV with two distally setulate setae on upper margin and PVI with one slender seta on upper margin. Merus about 1.5 times longer than wide. Merus of PV with three, PVI with four and PVII with two terminal small slender setae. Carpus about 5.3 times longer than wide, lower margin of PV-VI with six long slender setae, PVI additionally with one small slender seta and PVII with four long slender setae. Upper margin of PV terminally with one small and medially with one broken off seta; PVI with two long slender setae and PVII tipped with one seta (broken off). Propodus about 6.4 times longer than wide, PV with six long slender setae and one small slender seta on lower margin. PVI with five long slender setae and one small slender on lower margin. PVII with with four long slender setae on lower margin (three broken off). Upper margin of propodus (PV) with two long slender and two unequally bifid setae, of PVI two long slender and one unequally bifid setae and PVII with four setae, one long slender, one unequally bifid and two broken off setae on upper margin of propodus. Dactylus about 9.2 times longer than wide, and of PV-VII with smooth lower margin and upper margin with one slender seta. Claw out of long conate, terminally pointed and two slender setae.

Pleopod 2 (operculum) (Fig. 106): nearly as long as wide. Lateral margins nearly straight, four slender setae on terminal margin.

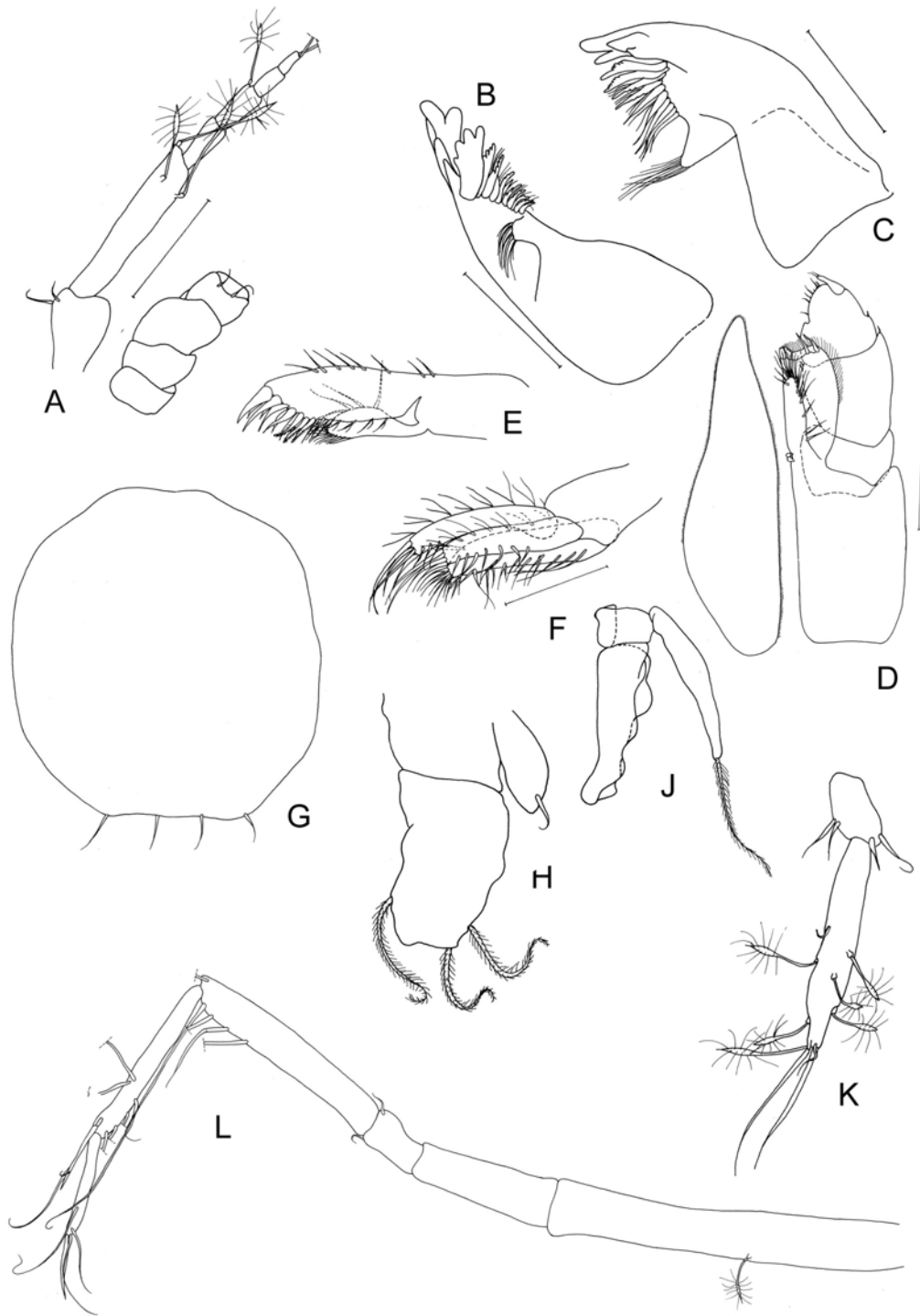
Pleopod 3 (Fig. 106): Endopod twice as long as exopod, endopod with three long plumose setae, exopod tipped with one simple slender seta.

Pleopod 4 (Fig. 106): Exopod and endopod of same length, margin of endopod totally smooth and exopod terminally tipped with one long slender plumose seta.

Uropods (Fig. 106): uniramous, protopod with four simple setae (two of them at startingpoint of extremely reduced exopod), endopod with six broom setae, two small setae and terminally two long slender setae.

#### **Remarks**

Specimen is slightly squeezed, therefore no drawing of lateral view, because a lateral view might be irretating in proportions.



**Fig. 106:** *Mirabilicoxa acuta* (Menzies & George, 1972), mouthparts: (A) antennula and articles 1-4 of antenna, (B) Md L, (C) MdR, (D) Mxp, (E) Mx1, (F) Mx2; pleopods: (G) Op, (H) pleopod 3, (J) pleopod IV, (K) Ur; (L) pereopod VII; scale 0.1 mm

#### **3.1.5.4.8     *Mirabilicoxa similipes* (Menzies & George, 1972)**

Synonyms: *Desmosoma similipes* Menzies & George, 1972

##### **Material**

Holotype: male, USNM Cat. No. 121711, distribution only known from type locality (Anton Bruun Station 113, 19. Oct. 1965; 08°44'S 80°45'W, depth 5986-6134 m), SBT.

Allotype: female, USNM Cat. No. 121712, distribution only known from type locality (Anton Bruun Station 113, 19. Oct. 1965; 08°44'S 80°45'W, depth 5986-6134 m), SBT.

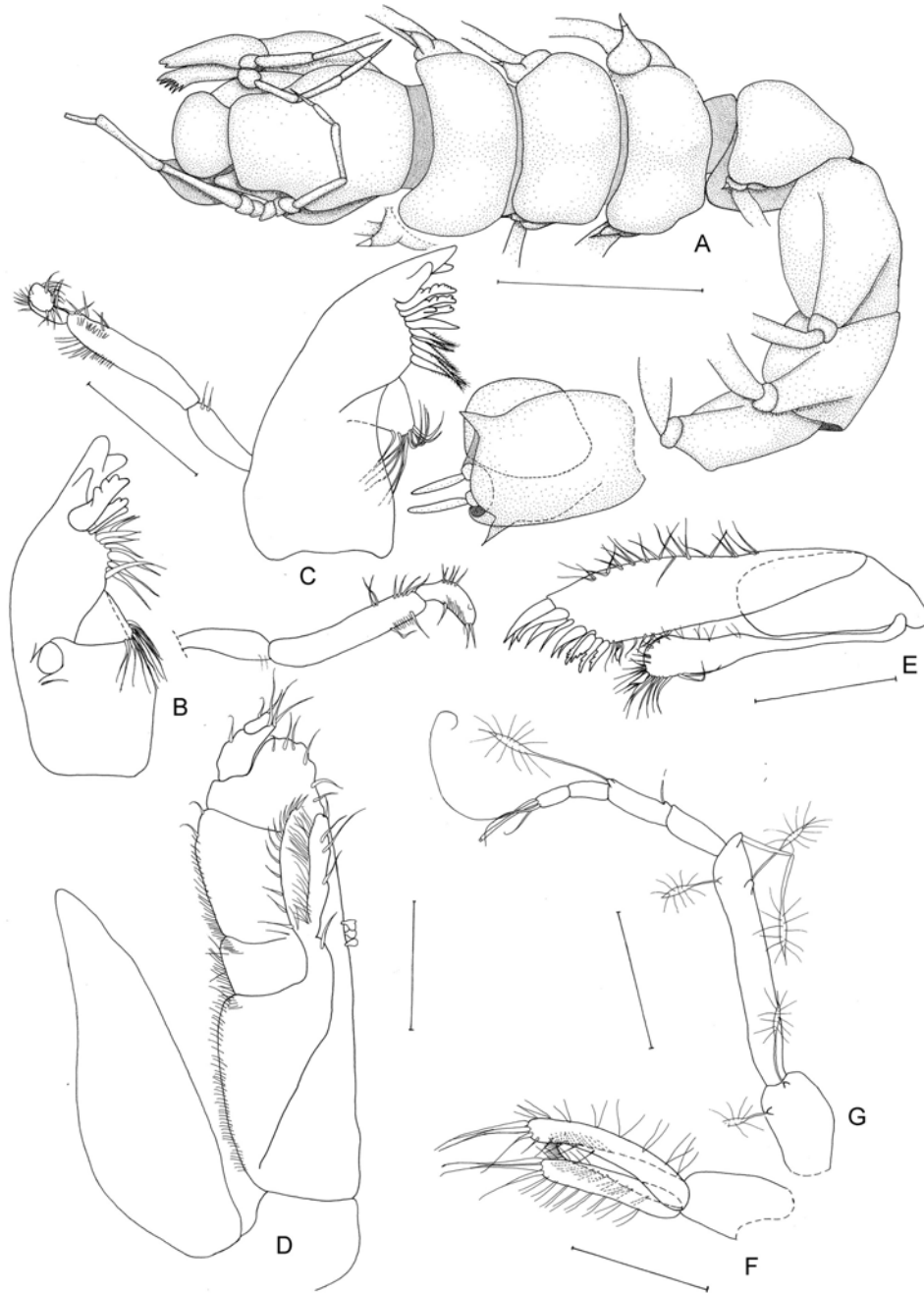
Other material: USNM Cat. No. 121750, distribution only known from type locality (Anton Bruun Station 169, 02. Nov. 1965; 08°46'S 80°44'W, depth 3909-3970 m), SBT.

##### **Description of species**

Body about 2.5 mm long and 0.5 mm wide. Prn1 slightly smaller than Prn2. Prn2 slightly smaller than Prn3. Prn4 trapezoid (widest anteriorly and half of width posteriorly). Prn5 nearly quadratic, but slightly narrower anteriorly, lateral sides slightly concave. Prn 6 slightly smaller than Prn5, Prn7 half of size of Prn5. Plt long (1.5 times longer than wide) and three times longer than Prn7. Well developed posterior spines in female and male, reaching one third of length of Plt. Very well developed Md palp of three articles, articles 2-3 with few small setae on upper margin. Medial lobe of Mx2 clearly shorter than inner and outer lobe and lined with fine setae. PI slightly smaller than PII-IV. PI slender, carpus with four unequally bifid setae on lower margin (increasing in length towards propodus) and three combs of fine hairs in cuticular membrane. Lower margin of propodus fringed with fine hairs in cuticular membrane, medially one small seta and proximal to dactylus two small setae. Upper margins of carpus and propodus smooth, proximally tipped with one and two small seta. Lower side of Op hairy.

##### **Description of allotype female**

Habitus (Fig. 107): damaged. Body 3.0 mm long and 0.6 mm wide (Hessler, 1970). Cephalothorax totally squeezed. Prn1-3 slightly squeezed and Prn4-7 crooked, Plt broken off. Prn1 slightly smaller than Prn2. Prn2 slightly smaller than Prn3.



**Fig. 107:** *Mirabilicoxa similipes* (Menzies & George, 1972), (A) habitus dorsal allotype female; mouthparts: (B) MdL, (C) MdR, (D) Mxp, (E) Mx1, (F) Mx2, (G) antennula, scale = 0.1 mm (habitus 0.5 mm)



Prn4 trapezoid (widest anteriorly and half of width posteriorly). Prn5-7 decreasing in size. Well developed posterior spines, reaching one third of length of Plt.

Antennula (Fig. 107): With six articles, article 1 broader than articles 2-6. Article 2 longest. Relative length of articles: 1:2.6:0.7:0.6:0.4:0.3. Article 1 with two broom setae, article 2 distally with three broom setae, article 3 smooth, article 4 with one small slender seta basally and one broom seta distally, article 5 smooth and article 6 tipped with one small and two long setae and one aesthetasc.

Antenna (Fig. 109): With six peduncular articles and eight flagellar articles. Basal four articles smooth and peduncular article 5 with three fine hairs and one medial broom seta, article 6 with smooth margins, tipped with three broom setae and one long slender seta. Flagellar articles 1 to 2 smooth, article 3 tipped with one small seta, article 4 tipped with two long setae, article 5 with one long slender seta, article 6 tipped with two long slender setae. Article 7 smooth and article 8 tipped with five long slender setae. Relative length of articles: 1:0.8:1.1:1.1:4.9:6.6:1.9:1.8:1.8:1.5:1.4:0.9:0.7:0.6.

Mandible (Fig. 107): Well developed palp of three articles. Pi with three teeth, Lm of left Md strong with four teeth and spine row containing 11 spines: Two of Lm-like form and terminally lobed and nine simple terminally pointed spines. Spine row of right Md containing nine spines, three of Lm-like structure with three, five and seven teeth, one simple spine and five distally setulate spines. Md palp of both mandibles with eleven slender setae. Palp article 1 on lower side terminally with two small setae, article 2 terminally with rows of fine hairs, two small setae on lower margin and six small setae on upper margin. Article 3 with three small setae on lower margin and row of fine hairs between them, upper margin with five small setae.

Maxillula (Fig. 107): Inner lobe terminally with 11 strong spines, four of them with one smooth margin and other margin with four tooth-like lobes. Lower margin of inner lobe with eight small setae and upper margin with 11 pairs of setae. Outer lobe terminally and ventrally lined with 18 small slender setae and eight pairs of hairs on upper margin.

Maxilla (Fig. 107): Inner and outer lobe longer than medial lobe. Inner and outer lobe each with three long terminal setae. Lower margin with five small setae and upper

margin with eight pairs of fine hairs. Medial lobe completely lined with fine hairs and on lower margin with several pairs of fine hairs.

Maxilliped (Fig. 107): Endite with three coupling hooks. Upper part of outer margin with 12 small setae, terminally several small setae. Endite with lateral fold in which numerous fine setae are inserting. Lower part of outer margin of endite hirsute. Outer margins of palp articles 1-2 hirsute. Outer margin of article 2 with two terminal small setae. Inner margin of article 1 terminally with one terminal slender seta, inner margin of article 2 with three slender setae. Outer margin of article 3 shorter than inner margin, smooth, inner margin seven five small slender setae. Outer margin of article 4 with one small and two small slender setae terminally on inner margin. Article 5 with two small setae.

Pereopod I (Fig. 109): slender. Base 5.7 times longer than wide, on lower margin tipped with one stout unequally bifid seta. Ischium 3.8 times longer than wide, with two stout terminally pointed setae on lower margin and upper margin terminally with one pointed seta. Merus 1.4 times longer than wide, with two pointed setae on lower margin and on upper side terminally with two small slender setae. Carpus 3.6 times longer than wide. Carpus with four unequally bifid setae on lower margin (increasing in length towards propodus) and three combs of fine hairs in cuticular membrane. Upper margin of carpus smooth, proximally tipped with one small seta. Propodus 4.0 times longer than wide. Lower margin of propodus fringed with fine hairs in cuticular membrane, medially one small seta and proximal to dactylus two small setae and terminally on upper margin two small setae. Dactylus 5.7 times longer than wide, with smooth margins. Three proximal setae towards claw. Claw out of one long conate seta and two small slender setae inserting basally.

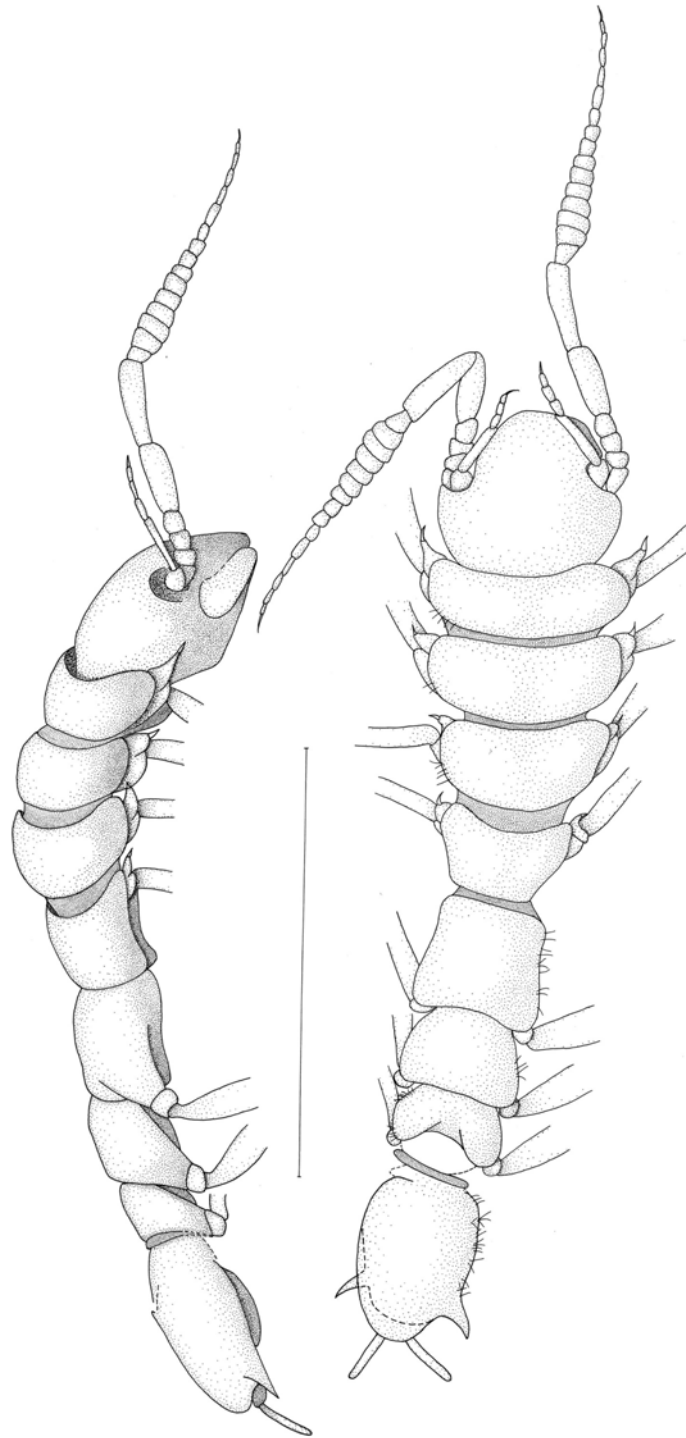
Pereopods II-IV (Fig. 109): Base about 6.2 times longer than wide. Lower margin proximal to ischium tipped with one strong terminal pointed seta. Base of PII on lower margin with one, on upper margin with two small setae. Ischium about 3.1 times longer than wide, on upper margin with one seta (PII strong terminally pointed, PIII-IV unequally bifid). Lower margin of PII with three small setae, PIII smooth, PIV with one unequally bifid seta. Merus about 1.3 times longer than wide.

PII-III with two terminally pointed setae, PIV with one simple seta. Upper margin of PII and PIV tipped with one simple seta, PIII smooth. Carpus about 4.3 times longer

### 3. Results

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than wide. Lower margins all with seven setae (PII: three setae next to propodus unequally bifid, PII showing most similarity to PI) PIV additionally with two small combs of fine hairs inserting in cuticular membrane.



**Fig. 108:** *Mirabilicoxa similipes* (Menzies & George, 1972), holotype male, (A) habitus lateral, (B) habitus dorsal; scale 1 mm

Distolaterally PII with four, PIII with five and PIV with four slender setae. Upper margin smooth, proximal to propodus tipped with one small seta. Propodus about 4.5 times longer than wide. PII: lower margin with one small unequally bifid seta and long cuticular membrane, partly fringed with fine hairs. Upper margin with five terminally pointed setae and two combs of fine hairs inserting in cuticular membrane, between last three setae of line. PIII: Lower margin with three slender setae, terminal tip spine-like produced, acute. Upper margin with five slender terminally pointed seta and line of several fine hairs. PIV: Lower margin with four setae (three of them small simple and one small unequally bifid, inserting next to slightly produced tip of lower margin). Upper margin with four slender terminally pointed setae and terminally with fine hairs inserting in cuticular membrane. Dactylus about 6.7 times longer than wide. PII with two small setae medially near claw in front of long conate seta of claw two small slender setae. Lower margin of dactylus of PIII strong, terminally pointed, two setae medially near claw in front of long conate seta of claw two small slender setae. Lower margin of dactylus of PIV smooth, upper margin fringed with fine hairs inserting in cuticular membrane, starting medially and becoming terminally a produced cuticular tip. Proximal to claw one small and one small slender seta. Claw out of one long conate terminally pointed seta.

Pereopods V-VII (Fig. 110): Base about 7.4 times longer than wide, upper and lower margins smooth, only PV medially with two broom setae. Ischium about 2.9 times longer than wide, smooth. Merus about 1.3 times longer than wide, lower margins of PV and PVII tipped with one small seta each, PVI smooth. Carpus about 5.5 times longer than wide, with seven (PV-VI) or five (PVII) long slender setae on lower margin. Upper margin of PV with two, of PVI with three and of PVII with one slender setae. Propodus about 5.7 times longer than wide, PV-VI with six long slender setae on lower margin, PVII with four slender setae.

Upper margin of PV with five, PVI with four (one unequally bifid) and PVII with three setae. Dactylus about 9.6 times longer than wide (of PVII broken off). PV margins smooth, PVI lower margin fringed with fine hairs inserting in cuticular membrane. Terminally three slender setae. Claw out of one long conate terminally pointed seta.

Pleopod 2 (operculum) (Fig. 110): nearly as wide as long, with eight small setae on proximal margin and numerous fine hairs on lower side.

Pleopod 3 (Fig. 110): Protopod rectangular, smooth margins. Endopod only with two distal long plumose setae.



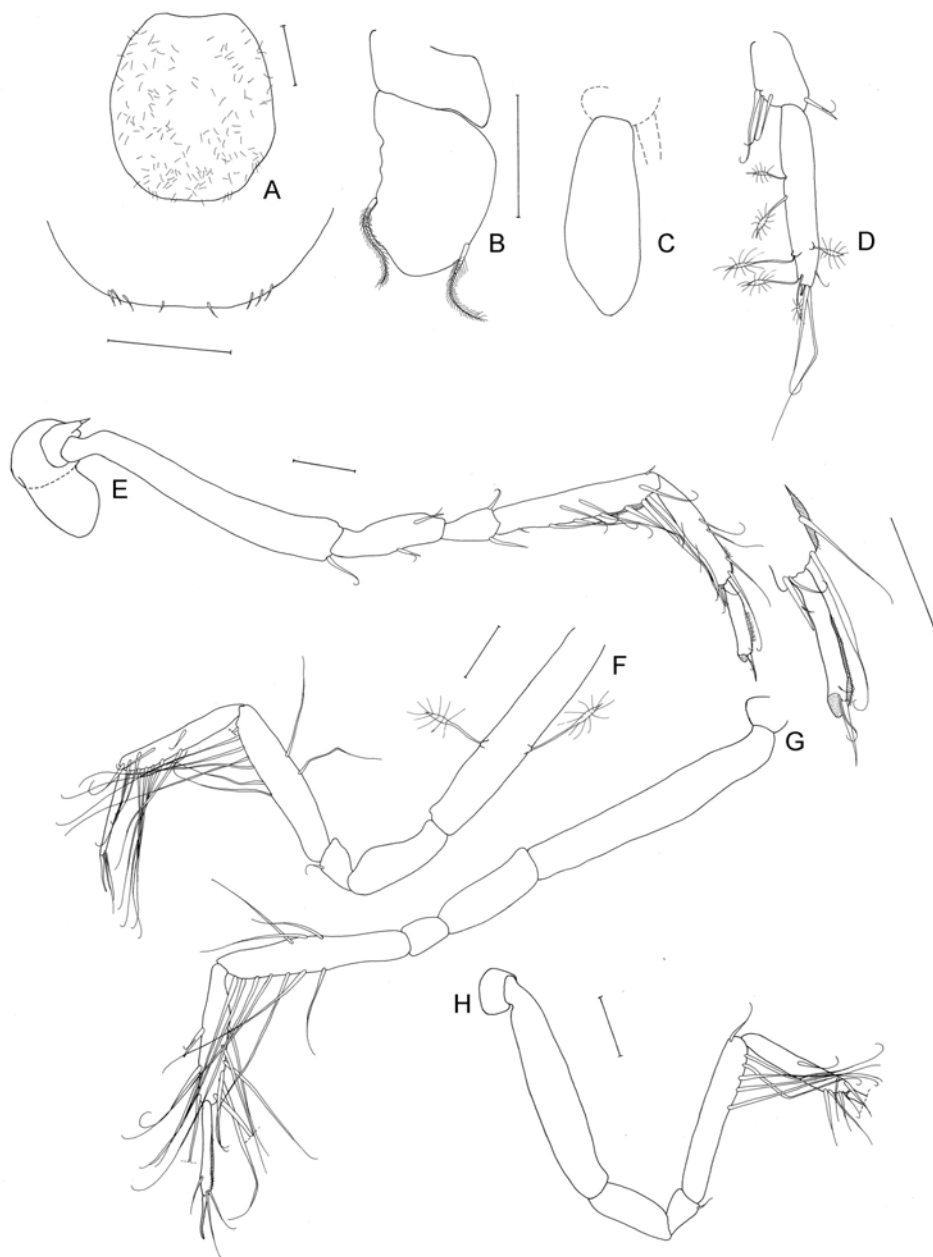
**Fig. 109:** *Mirabilicoxa similipes* (menzies & George, 1972), scale = 0.1 mm, Antenna (A), pereopod I (B detail b, pereopod II (C), III (D))

Pleopod 4 (Fig. 110): Protopod and exopod broken off. Endopod smooth, three times longer than wide.

Uropods (Fig. 110): uniramous, protopod with three simple setae (two at startingpoint of extremely reduced exopod) and terminally with one unequally bifid seta on inner margin. Endopod with six broom setae, one small and terminally two long slender setae, additionally one broken off.

#### Remarks

Allotype damaged.



**Fig. 110:** *Mirabilicoxa similipes* (Menzies & George, 1972), pereopods IV-VII, pleopods

### 3.2 Phylogeny

#### 3.2.1 List of characters used in the phylogenetic analysis

The detailed analysis of characters is part of the discussion (4.2.2.2). All 129 characters are binary coded and parsimony informative. Each character has a weight of 1. For complex patterns the number of details assigns the weight.

**Table 4:** List of characters used in the phylogenetic analysis

| number  | character           | character states  |  | weight<br>(number<br>of details)                   | CI<br>acctran/deltran |
|---------|---------------------|---|--|--|-----------------------|
|         |                     | apomorphy   | plesiomorphy   |  |                       |
| habitus |                     |   |  |  |                       |
| 1       | body                | Whole body serrated.  | [Not the whole body serrated.]                                       | 7  | 0.5/0.5               |
| 2       |                     | Only margins of pereonite 5-7 and pleotelson strongly serrate.            | [Not only margins of pereonite 5-7 and pleotelson strongly serrate.] |  | 1.0/1.0               |
| 3       |                     | Pereonites and pleotelson laterally expanding into flat marginal flanges. | [Pereonites and pleotelson not with flat lateral extensions.]        |  | 1.0/1.0               |
| 4       |                     | Body broad.   | [Body slender.]  |  | 0.5/0.5               |
| 5       |                     | Body anteriorly wide and posteriorly slender.                             | [Body not anteriorly wide and posteriorly slender.]                  |  | 0.143/0.125           |
| 6       |                     | Body elongated.   | [Body slender, but not elongated.]                                   |  | 0.167/0.2             |
| 7       |                     | Body cigar-like with straight body margins.                               | [Body not cigar-like with straight body margins.]                    |  | 1.0/1.0               |
| 8       | pereonites 1-3      | Close packing of pereonites 1-3.  | [Pereonites 1-3 not closely packed]                                  | 1  | 1.0/1.0               |
| 9       | pereonite 1         | Pereonite 1 not broad and half of size of pereonite 2 or smaller.         | [Pereonite 1 not broad nor half of size of pereonite 2 or smaller.]  | 6<br>(including 47-50 with a weight of 1 for each) | 0.25/0.2              |
| 10      |                     | Pereonite 1 broad and clearly smaller than pereonite 2.                   | [Pereonite 1 not broad and smaller than pereonite 2.]                |  | 0.5/0.5               |
| 11      | pereonite 2         | Pereonite 2 largest of pereonites 1-4.                                    | [Pereonites 1-4 subequal.]   | 1  | 0.2/0.25              |
| 12      | pereonites 1-4      | Pereonites 1-4 higher than pereonites 5-7.                                | [Pereonites 1-4 of same height as pereonites 5-7.]                   | 1  | 0.083/0.1             |
| 13      | pereonites 5-7      | Pereonites 5-7 enlarged.  | [Pereonites 5-7 not enlarged.]                                       | 1  | 0.333/0.333           |
| 14      | anterior pereonites | Pereonites 1-4 shorter than pereonites 5-7                                | [Pereonites 1-3 shorter than pereonites 4-7.]                        | 1  | 1.0/1.0               |
| 15      | pereonite 5         | Pereonite 5 clearly convex inflated lateral margins.                      | [Lateral margins of pereonite 5 not inflated.]                       | 3  | 0.167/0.167           |
| 16      |                     | Pereonite 5 inflated.   | [Pereonite 5 not inflated.]  |  | 0.5/0.5               |

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|               |                        |   |   |   |             |
|---------------|------------------------|---|---|---|-------------|
| 17            |                        | Pereonite 5 elongated.  | [Pereonite 5 similar in size to pereonite 6.]   |   | 0.333/0.333 |
| 18            | pleotelson             | Pleotelson enlarged.  | [Pleotelson not enlarged.]  | 1 | 0.5/0.5     |
| 19            | transverse section     | Body highly vaulted in transverse section especially in pleotelson.                 | [Body in transverse section axis not highly vaulted, lateral fields presenting a continuous profile.] | 1 | 0.333/0.333 |
| 20            | pereonites 4-7         | Pereonites 4-7 posteriorly acute.   | [Pereonites 4-7 not posteriorly acute.]   | 2 | 1.0/1.0     |
| 21            |                        | Posterior corners of the tergits of pereonites 4-7 tipped with one stout spine.     | [Posterior corners of the tergits of pereonites 4-7 without a stout spine.]                           |   | 1.0/1.0     |
| Cephalothorax |                        |   |   |   |             |
| 22            | cephalic keels         | Cephalic keels between antennular folds present.                                    | [Cephalic keels between antennular folds absent.]   | 1 | 0.5/0.5     |
| 23            | rostrum                | Cephalon with rostrum.  | [Cephalon without rostrum.]   | 1 | 1.0/1.0     |
| 24            | cephalic spine row     | Dorsal margin of antennular fold with row of spines resembling a rostral structure. | [Dorsal margin of antennular fold without any spines resembling a rostral structure.]                 | 1 | 1.0/1.0     |
| 25            | cephalic spine         | Margin of antennular fold with one anteriorly directed spine.                       | [Margin of antennular fold without distinct spine.]   | 1 | 0.2/0.2     |
| 26            | antennula              | Antennula consisting of 5 articles.   | [Antennula consisting out of 6 or more articles.]   | 1 | 0.077/0.077 |
| 27            | flagellum of antennula | Antennula with <i>specialized</i> distal articles.                                  | [Antennula with <i>unspecialized</i> distal articles.]  | 6 | 0.077/1.0   |
| 28            |                        | Flagellum with rounded bulbous last article.  | [Flagellum not with rounded bulbous last article.]  |   | 0.5/0.5     |
| 29            |                        | Antennula with bulbous and long terminal article (clearly longer than wide).        | [Terminal article of antennula not bulbous and long.]   |   | 1.0/1.0     |
| 30            |                        | Flagellar article 1 of antennula smallest.  | [Flagellar article 1 of antennula not smallest.]  |   | 1.0/1.0     |
| 31            |                        | Flagellar article 2 of antennula with elongation holding terminal bulbous article.  | [Flagellar article 2 of antennula without elongation holding terminal bulbous article.]               |   | 1.0/1.0     |
| 32            |                        | Terminal article of antennula bulbous and formed like a ball.                       | [Terminal article of antennula not bulbous and formed like a ball.]                                   |   | 1.0/1.0     |
| 33            | article 2 of antennula | Article 2 of antennula elongated (twice as long as first peduncular article).       | [Article 1 and 2 of antennula of the same size.]  | 3 | 0.5/0.5     |



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|            |                                       |  |  |  |             |
|------------|---------------------------------------|--|--|--|-------------|
| 34         |                                       | Article 2 of antennula distally with 3-4 joint articulated broom setae.                                    | [Broom setae sporadically present.]  |  | 1.0/1.0     |
| 35         |                                       | Article 2 of antennula distally with (just) two joint articulated broom setae.                             | [Article 2 of antennula with more than two joint articulated broom setae at distal end.] |  | 0.071/0.071 |
| 36         | antenna                               | Shortened and robust antenna, reaching only one quarter of the body length.                                | [Antenna long and slender, clearly longer than one quarter of the body length.]          | 1  | 1.0/1.0     |
| 37         | lacinia mobilis                       | Lacinia mobilis reduced to one small bulgelike tooth.  | [Lacinia mobilis with 3 to 5 teeth.]   | 1  | 0.333/0.333 |
| 38         | incisior process                      | Incisior process bent forward as one strong tooth.   | [Incisior process not bent forward as one strong tooth.]                                 | 4  | 1.0/1.0     |
| 39         |                                       | Incisior process simplified.   | [Incisior process with teeth.]   |  | 0.5/0.5     |
| 40         |                                       | Incisior process with strong shelf-like tooth.   | [Incisior process not shelf-like.]   |  | 0.5/0.5     |
| 41         |                                       | Incisior process enlarged.   | [Incisior process not enlarged.]   |  | 1.0/1.0     |
| 42         | mandibular palp                       | Mandibular palp absent.  | [Mandibular palp present.]   | 2  | 0.091/0.091 |
| 43         |                                       | Mandibular palp consisting out of two articles.  | [Mandibular palp not consisting out of two articles.]                                    |  | 0.333/0.333 |
| 44         | maxilliped                            | Retinaculae elongated: more than 3 times longer than width of stalk.                                       | [Retinaculae not elongated: about 2 times longer than width of stalk.]                   | 1  | 0.5/0.5     |
| 45         | mouthparts                            | Mouthparts extremely bent forward.   | [Mouthparts not bent forward.]   | 1  | 0.5/0.5     |
| pereonites |                                       |  |  |  |             |
| 46         | sensory seta                          | Stout sensory setae present <u>anteriorly</u> on tergites 1-4.   | [No sensory setae present <u>anteriorly</u> on tergites 1-4.]                            | 1  | 0.167/0.167 |
| 47         | pereonite 1                           | Pereonite 1 broader than pereonite 2.  | [Pereonite 1 not broader than pereonite 2.]  | 6<br>(including 9 and 10 with a weight of 1) | 0.167/0.167 |
| 48         |                                       | Pereonite 1 longer than pereonite 2 (midsagital length).   | [Pereonite 1 not longer than pereonite 2.]   |  | 0.125/0.143 |
| 49         |                                       | Pereonite 1 enlarged and clearly bigger (more than 2 times of midsagital length of pereonite 2).           | [Pereonite 1 not enlarged and clearly bigger than pereonite 2.]                          |  | 0.5/0.5     |
| 50         |                                       | Pereonite 1 shorter and not as broad as pereonite 2.   | [Pereonite not shorter than pereonite 2.]  |  | 0.083/0.083 |
| 51         | ventral elongations at pereonites 1-5 | Spine-like ventral elongations at pereonites 1 to 5 decreasing in length towards the posterior pereonites. | [Pereonites 1 to 5 without spine-like ventral elongations.]                              | 1  | 1.0/1.0     |
| 52         | anteriorly                            | Anteriorly directed  | [Pereonite 1 smooth  | 1  | 0.5/0.5     |

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|           |  |  |  |  |             |
|-----------|--|--|--|--|-------------|
|           | directed spine at pereonite 1            | spine at pereonite 1.  | ventrally.]  |  |             |
| 53        | ventral elongation at pereonites 6 and 7 | Spine-like ventral elongation at the fused pereonites 6 and 7, the elongation at pereonite 6 directed anteriorly, the one at pereonite 7 caudally. | [Pereonites 6 and 7 without fusion or spine-like elongation.]  | 1                                      | 1.0/1.0     |
| 54        | opercular spine                          | Ventral spine midway on the operculum.   | [Operculum without ventral spine.]                             | 4                                      | 0.5/1.0     |
| 55        |  | Caudally directed strong spine on pereonite 7.   | [Pereonite 7 smooth ventrally.]                                |  | 0.333/0.25  |
| 56        |  | Curved caudally directed spine located midway on the operculum.  | [Operculum without spine.]                                     |  | 1.0/1.0     |
| 57        |  | Straight, caudally directed spine positioned anteriorly on the operculum.  | [Operculum without spine.]                                     |  | 0.5/0.5     |
| 58        | fusion of posterior pereonites           | Pereonites 6 and 7 fused.  | [Pereonites free.]   | 3                                      | 0.2/0.2     |
| 59        |  | Pereonites 6 and 7 fused with pleotelson.  | [Pereonites and pleotelson free.]                              |  | 0.5/0.5     |
| 60        |  | Pereonite 7 and pleotelson fused.  | [Pereonites and pleotelson free.]                              |  | 1.0/1.0     |
| 61        | marginal flanges                         | Pereonites 6, 7 and pleotelson with marginal flanges.  | [Pereonites 6, 7 and pleotelson without marginal flanges.]     | 1                                      | 0.167/0.167 |
| pereopods |  |  |  |  |             |
| 62        | coxae                                    | Coxae 1-4 with anterolateral elongation  | [Coxae without anterolateral elongation.]                      | 3                                      | 0.333/0.333 |
| 63        |  | Coxae 1-4 anteriorly tipped with stout seta.   | [No stout seta present on anterior tip of coxae 1-4]           |  | 0.111/0.111 |
| 64        |  | Coxae produced anteriorly.   | [Coxae angular anteriorly, without projection.]                |  | 0.167/0.167 |
| 65        | pereopods III and IV                     | Pereopods I,II,VI and VII longer than pereopods III to V.  | [Pereopods of similar length.]                                 | 1                                      | 1.0/1.0     |
| 66        | posterior pereopods                      | Pereopods V to VII longer and more heavily built than pereopods II to IV.  | [Pereopods V to VII and pereopods II to IV of similar length.] | 3<br>(including 70 with a weight of 1) | 0.333/0.5   |
| 67        |  | Pereopods V-VII: Ischium elongated (over 5.5 times longer than wide).  | [Pereopods V-VII not with elongated ischium.]                  |  | 1.0/1.0     |
| 68        | pereopod III                             | Pereopod III dorsally bent.  | [Pereopod III not dorsally bent.]                              | 2                                      | 1.0/1.0     |
| 69        |  | Dactylus of PIII with row of long setae.   | [Dactylus of PIII without row of long setae.]                  |  | 1.0/1.0     |
| 70        | posterior pereopods                      | Ventral row of natatory setae at pereopods V to VII  | [Ventral row of natatory setae present.]                       | 3<br>(including 66 and 67)             | 0.25/0.25   |

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|    |              |   |   |                              |             |
|----|--------------|---|---|------------------------------|-------------|
|    |              | absent.   |   | with a weight of 1 for each) |             |
| 71 | pereopod VII | Basis of pereopod VII with long setae.  | [No long setae on basis of pereopod VII present.]   | 1                            | 1.0/1.0     |
| 72 | pereopod I   | Lower margin of carpus of pereopod I with composed robust setae in a row.                                 | [Lower margin of carpus of pereopod I not with composed robust setae in a row.]                                 | 35                           | 0.333/0.333 |
| 73 |              | Pereopod I: ventral row of setae on carpus reduced due to specialization.                                 | [Pereopod I: ventral row of setae on carpus not reduced due to specialization.]                                 |                              | 0.167/0.167 |
| 74 |              | Carpus of pereopod I dorsally bearing a row of long simple setae.   | [Carpus of pereopod I dorsally without a row of long simple setae.]   |                              | 0.333/0.333 |
| 75 |              | Pereopod I: dorsal row of setae on carpus reduced due to specialization.                                  | [Pereopod I: dorsal row of setae on carpus not reduced due to specialization.]                                  |                              | 0.111/0.125 |
| 76 |              | Enlargement of pereopod I concentrating on carpus.  | [Enlargement of pereopod I not concentrating on carpus.]  |                              | 0.2/0.25    |
| 77 |              | Enlargement of pereopod I concentrating on propodus.  | [Enlargement of pereopod I not concentrating on propodus.]  |                              | 0.25/0.333  |
| 78 |              | Pereopod I small and slender, but propodus enlarged.  | [Pereopod I not small and slender with enlarged propodus.]  |                              | 1.0/1.0     |
| 79 |              | Pereopod I as functional unit enlarged.   | [Pereopod I as functional unit not enlarged.]   |                              | 0.5/0.333   |
| 80 |              | Propodus of pereopod I ventrally with row of small stout unequally bifid setae.                           | [Propodus of pereopod I ventrally not with row of small stout unequally bifid setae.]                           |                              | 0.25/0.25   |
| 81 |              | Platformlike gap between propodus and distoventral seta on carpus present.                                | [Platformlike gap between propodus and distoventral seta on carpus absent.]                                     |                              | 1.0/1.0     |
| 82 |              | Carpus of pereopod I enlarged and tapering towards propodus.  | [Carpus of pereopod I not enlarged, not tapering towards propodus.]   |                              | 1.0/1.0     |
| 83 |              | Propodus of pereopod I ventrally fringed with fine hairs and setae breaking through a cuticular membrane. | [Propodus of pereopod I ventrally not fringed with fine hairs and setae breaking through a cuticular membrane.] |                              | 0.333/0.333 |
| 84 |              | Carpus of pereopod I enlarged and broadest at articulation to propodus.                                   | [Carpus of pereopod I not enlarged and not broadest at articulation of propodus.]                               |                              | 0.5/0.5     |
| 85 |              | Carpus distolaterally with "claw-seta".   | [Carpus distolaterally not with a "claw-seta".]   |                              | 0.5/1.0     |

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|     |  |  |  |  |             |
|-----|--|--|--|--|-------------|
| 86  |  | Carpus distolaterally produced.  | [Carpus distolaterally not produced.]  |  | 0.2/0.25    |
| 87  |  | Carpus of pereopod I with 1 composed seta midway.  | [Carpus of pereopod I not with 1 composed seta midway.]  |  | 0.5/1.0     |
| 88  |  | Ventral setae behind claw-seta small and simple or small and slender.                          | [Not with ventral setae behind claw-seta small and simple or small and slender.]                           |  | 0.25/0.5    |
| 89  |  | Carpus of pereopod I enlarged and with setae of irregular size.                                | [Carpus of pereopod I not enlarged, not with setae in irregular size.]                                     |  | 0.5/0.5     |
| 90  |  | Size of ventral setae on carpus irregular and of varying types.                                | [Size of ventral setae on carpus not irregular, of same type.]   |  | 1.0/1.0     |
| 91  |  | Setae behind claw-seta small, of similar size and type.  | [Carpus of pereopod I not with claw-setae and setae not behind claw-seta small, of similar size and type.] |  | 0.5/0.5     |
| 92  |  | Carpus distoventrally with claw-seta and penultimate seta.                                     | [Carpus not with claw-seta and penultimate seta.]  |  | 1.0/1.0     |
| 93  |  | Pereopod I robust, articles almost quadrangular.   | [Pereopod I not robust, articles not quadrangular.]  |  | 1.0/1.0     |
| 94  |  | Setae in ventral row on carpus of pereopod I increasing in length towards propodus.            | [Setae in ventral row on carpus of pereopod I not increasing in length towards propodus.]                  |  | 0.143/0.143 |
| 95  |  | Setae on carpus and propodus of pereopod I not composed.                                       | [Composed setae present on carpus and propodus of pereopod I]  |  | 0.143/0.143 |
| 96  |  | Distoventral seta on carpus of pereopod I shortest.  | [Distoventral seta of carpus of pereopod I not shortest.]  |  | 0.5/0.5     |
| 97  |  | Distoventral seta of carpus reaching full length of propodus.                                  | [Distoventral seta of carpus not reaching full length of propodus.]  |  | 0.25/0.25   |
| 98  |  | Second seta behind claw-seta of similar size.  | [Not with second seta behind claw-seta of similar size.]   |  | 1.0/1.0     |
| 99  |  | Pereopod I slender in comparison to pereopod II.   | [Pereopod I not slender in comparison to pereopod II.]   |  | 0.5/1.0     |
| 100 |  | Pereopod I slender and ventrally only slender setae present on carpus and propodus.            | [Pereopod I not slender and not only slender setae present on carpus and propodus.]                        |  | 1.0/1.0     |
| 101 |  | Pereopod I small in size, subchelate: propodus enlarged and dactylus folding against propodus. | [Pereopod I not small in size, not subchelate.]  |  | 1.0/1.0     |

### 3. Results

|     |             |   |  |   |             |
|-----|-------------|---|--|---|-------------|
| 102 |             | Propodus of pereopod I elongated in chela.  | [Propodus of pereopod I not elongated in chela.]   |   | 1.0/1.0     |
| 103 |             | Propodus of slender pereopod I elongated (over 3.5 times longer than wide).   | [Propodus of pereopod I not elongated.]  |   | 0.333/0.25  |
| 104 |             | Pereopod I slender: propodus between 4.1 and 5.2 times longer than wide, carpus about 4.5 times longer than wide.                                   | [Pereopod I not slender.]  |   | 1.0/1.0     |
| 105 |             | Pereopod I slightly attenuated: propodus of pereopod I between 6 and 9 times longer than wide and carpus between 5 and 7.2 times longer than wide). | [Pereopod I not slightly attenuated.]  |   | 1.0/0.5     |
| 106 |             | Pereopod I strongly attenuated (propodus 18.8 times longer than wide, carpus 15 times longer than wide), setae absent on propodus and carpus.       | [Pereopod I not strongly attenuated, setae present on propodus and carpus.]                    |   | 1.0/0.5     |
| 107 | pereopod II | Pereopod II robust, articles almost quadrangular.   | [Pereopod II not robust, articles, not quadrangular.]  | 6 | 0.5/0.5     |
| 108 |             | Propodus of pereopod II heavily built (carpus and propodus broad).  | [Propodus of pereopod II not heavily built.]   |   | 1.0/1.0     |
| 109 |             | Carpus of pereopod II bearing a ventral row of composed setae.  | [Setae on carpus of pereopod II not standing in ventral rows.]                                 |   | 0.5/0.5     |
| 110 |             | Propodus of pereopod II bearing a ventral row of composed setae.  | [Setae on carpus and propodus of pereopod II not standing in rows ventrally.]                  |   | 0.1/0.1     |
| 111 |             | Carpus and propodus of the pereopod II bearing dorsally a row of long setae.  | [Setae on carpus and propodus of pereopod II not standing in rows dorsally.]                   |   | 0.125/0.111 |
| 112 |             | Basis and ischium of pereopods II and III fringed with distally plumose setae.  | [Basis and ischium without this setal type.]   |   | 1.0/1.0     |
| 113 | pereopod IV | Pereopod IV folious, carpus and propodus paddle-like.   | [Pereopod IV not folious, carpus and propodus resembling carpus and propodus of pereopod III.] | 2 | 1.0/1.0     |
| 114 |             | Carpus and propodus surrounded (with dense row of) by numerous distally plumose setae.  | [Carpus and propodus not surrounded by numerous distally plumose setae.]                       |   | 1.0/1.0     |

### 3. Results

|            |                   |   |   |   |             |
|------------|-------------------|---|---|---|-------------|
| 115        | pereopod VII      | Ischium dorsally with anteriorly directed cuticular hook.   | [Ischium dorsally smooth.]  | 4 | 1.0/1.0     |
| 116        |                   | Propodus and carpus of pereopod VII with long setae dorsally.   | [No long setae dorsally of propodus and carpus of pereopod VII.]                        |   | 0.1/0.091   |
| 117        |                   | Propodus and carpus of pereopod VII with long setae dorsally.   | [No long setae dorsally of propodus and carpus of pereopod VII.]                        |   | 0.167/0.167 |
| 118        |                   | Basis of pereopod VII with long slender “swimming setae”.   | [Basis of pereopod VII without “swimming setae”.]                                       |   | 1.0/1.0     |
| pleotelson |                   |   |   |   |             |
| 119        | inflation         | Pleotelson dorsally inflated.   | [Pleotelson dorsally not inflated.]   | 1 | 0.25/0.333  |
| 120        | anus region       | Anus region separated and bilobed.  | [Anus region not separated and bilobed.]  | 1 | 1.0/1.0     |
| 121        | form              | Pleotelson vaulted in transverse section.   | [Pleotelson not vaulted in transverse section.]   | 1 | 0.333/0.25  |
| 122        | branchial chamber | Branchial chamber and operculum in relation to size of pleotelson small, operculum of oval shape and posterior part broadest. | [Branchial chamber and operculum covering nearly the whole ventral view of pleotelson.] | 2 | 1.0/1.0     |
| 123        |                   | Branchial chamber and operculum in relation to size of pleotelson small, rounded.   | [Branchial chamber not small and rounded.]  |   | 1.0/1.0     |
| 124        | uropods           | Uropods uniramous.  | [Uropods biramous.]   | 6 | 0.125/0.125 |
| 125        |                   | Uropodal sympod extremely elongated; styliform.   | [Uropodal sympod not elongated, shorter than endopod.]                                  |   | 1.0/1.0     |
| 126        |                   | Uropods cover anus valves.  | [Uropods not covering anus valves.]   |   | 0.167/0.167 |
| 127        |                   | Uropods short, not overlapping posterior margin of pleotelson.  | [Uropods overlapping posterior margin of pleotelson.]                                   |   | 0.5/0.5     |
| 128        |                   | Uropodal endopodite nearly bulbous.   | [uropodal endopodite clearly longer than wide.]   |   | 1.0/1.0     |
| 129        |                   | Uropodal exopod reduced to half of size of endopod or less.   | [Uropodal exopod not reduced to half of size of endopod or less.]                       |   | 0.143/0.125 |

#### **3.2.2 Consensus trees**

In total, 294 trees with a length of 405 steps were retained. The trees had a consistency index (CI) of 0.3185, a homoplasy index (HI) of 0.6815 and a retention index (RI) of 0.8182. As the strict consensus (Fig. 111), the 80 percent majority rule tree (Fig. 112) shows a high percentage of polytomy. The only differences to the strict consensus tree are that the position of Austroniscinae is resolved, *Hebefustis* is resolved as basal within Nannoniscinae and *Cryodesma* and *Pradesmosoma* are the first two genera behind the knot leading to the group of chelate genera. The 50 percent majority rule tree (Fig. 113) is best, but not completely resolved.

### 3. Results

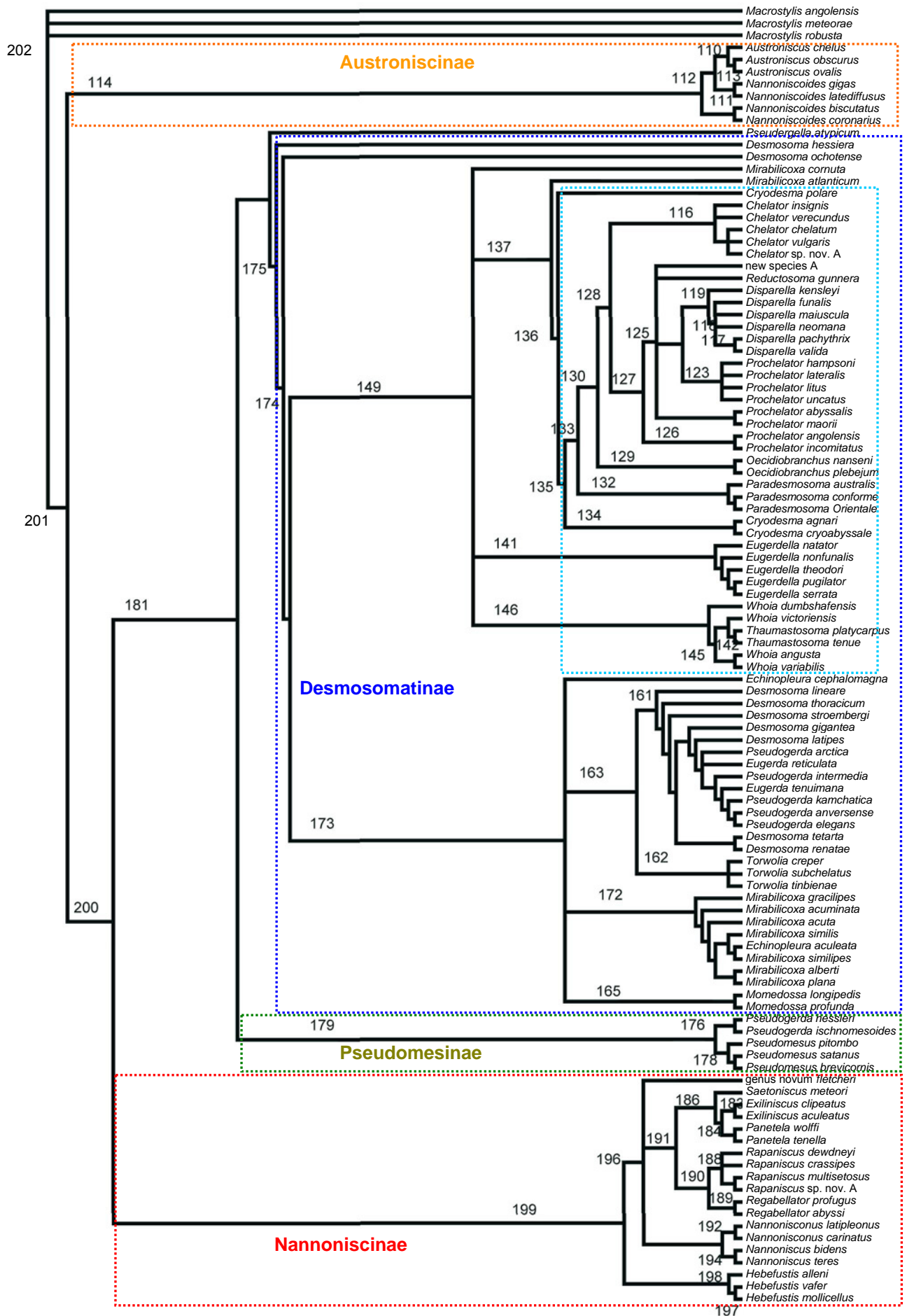
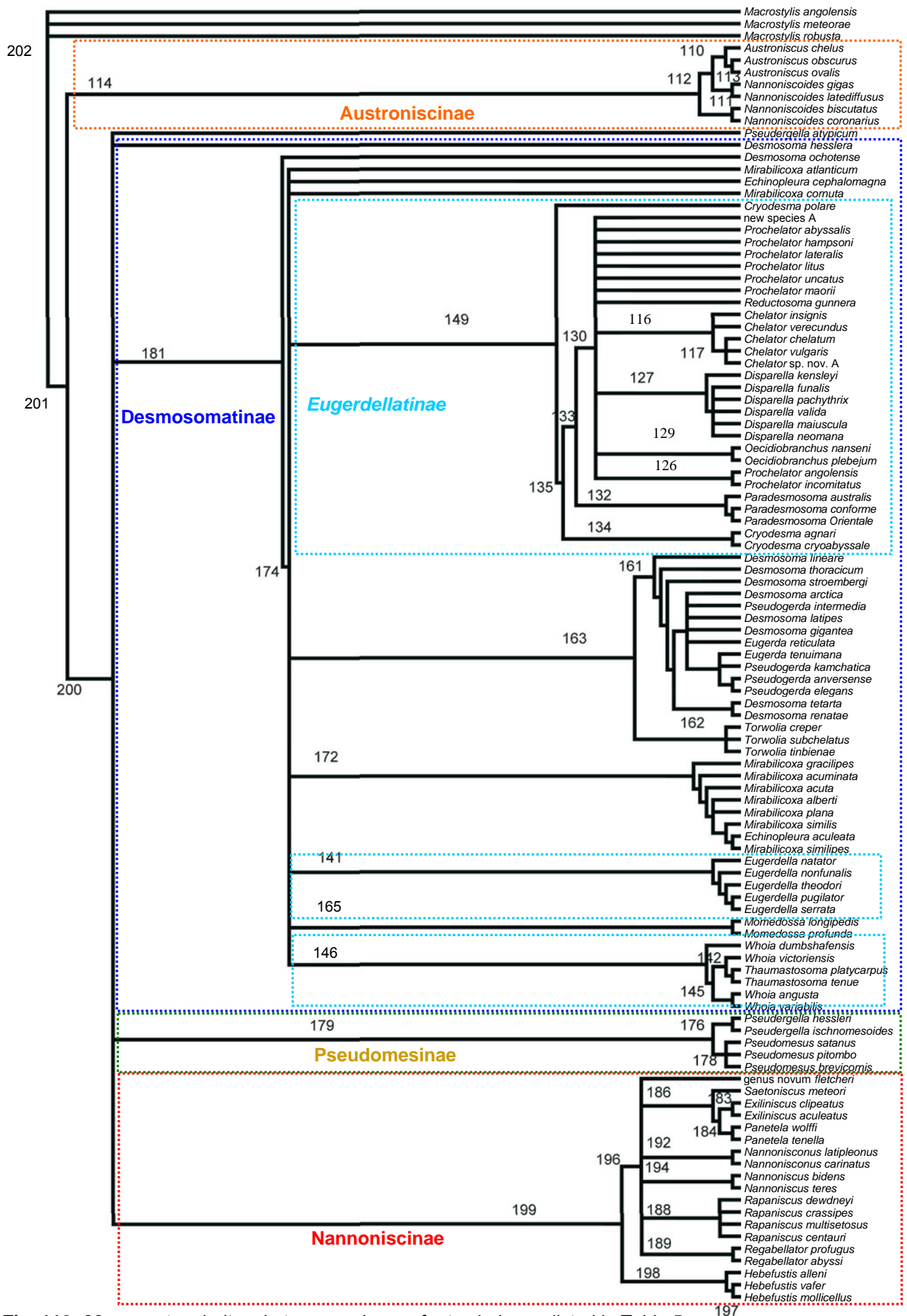


Fig. 111: 50 percent majority rule tree, numbers refer to clades as listed in Table 5



### 3. Results



**Fig. 112:** 80 percent majority rule tree, numbers refer to clades as listed in Table 5

### 3. Results

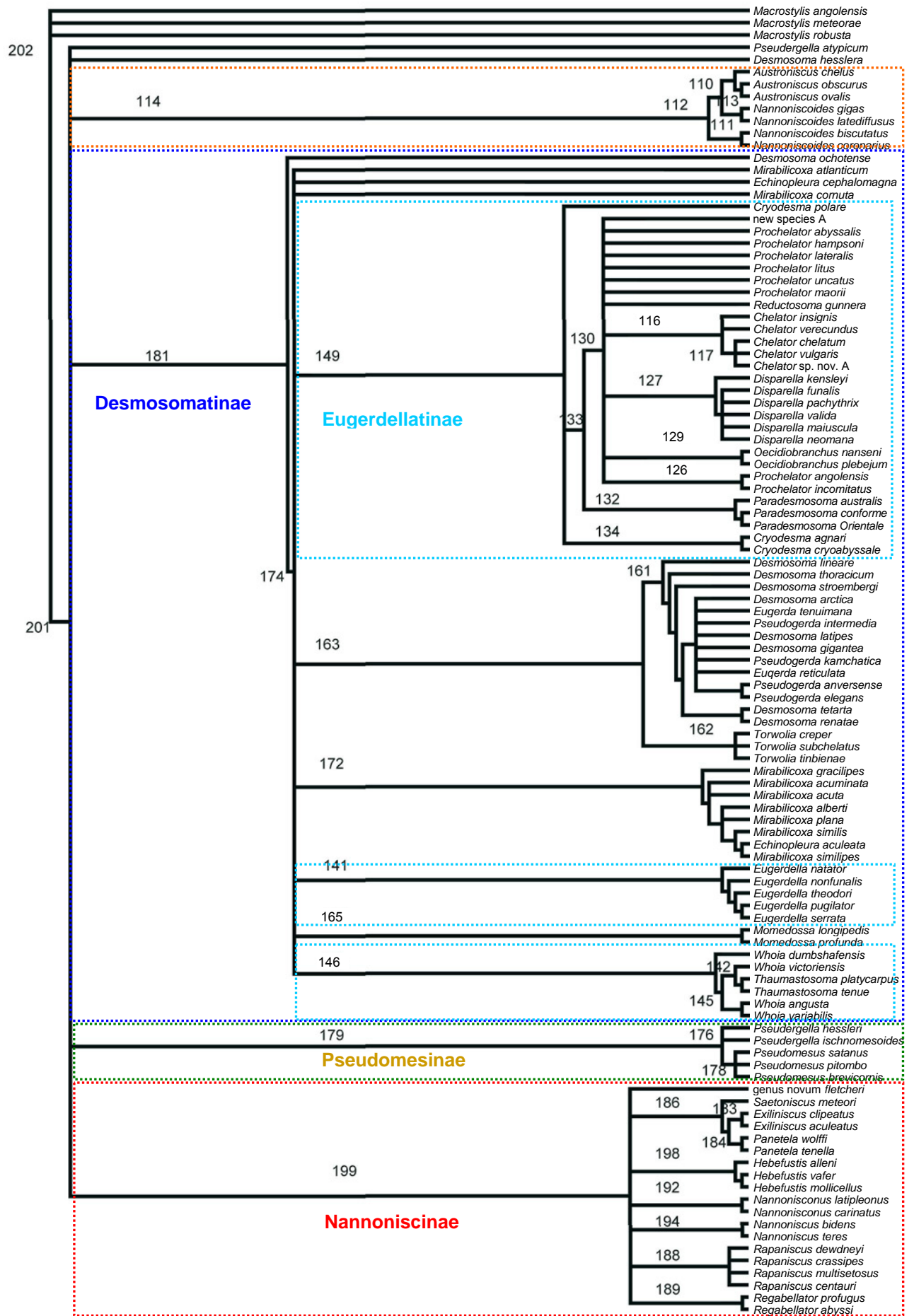


Fig. 113: strict consensus tree, numbers refer to clades as listed in Table 5

### 3.2.3 Character distribution in the trees

**Table 5:** Characters defining the branches

(+ indicates the presence of the node in the tree; - indicates a polytomy; for the comparison of the apomorphy list, the trees with the greatest distance were used, here: two trees with a distance of 68, numbers of nodes refer to tree 284)

| clade   | taxa  | character(s)  | strict consensus | majrule 80 | majrule 50 |
|---------|---|---|------------------|------------|------------|
|         |   | apomorphy list acctran trees 284/242  |                  |            |            |
| 202     | Macrostylidae   | 26 (1>2), 8 (2>1), 14 (1>2), 20 (2>1), 21 (2>1), 33 (1>2), 34 (1>2), 42 (2>1), 50 (1>2), 65 (2>1), 68 (2>1), 69 (2>1), 71 (2>1), 118 (2>1), 125 (2>1) | +                | +          | +          |
| 201→114 | Austroniscinae  | 4 (1>2), 10 (1>2), 22 (1>2), 95 (1>2)   | -                | +          | +          |
| 114→112 | <i>Austroniscus</i> , <i>Nannoniscoides</i>   | 3 (1>2)   | +                | +          | +          |
| 112→110 | <i>Austroniscus</i>   | 122 (1>2), 126 (1>2)  | +                | +          | +          |
| 110→    | <i>A. chelus</i>  | 35 (1>2)  | +                | +          | +          |
| 110→109 | <i>A. obscurus</i> , <i>A. ovalis</i>   | 95 (2>1)  | +                | +          | +          |
| 112→111 | <i>N. gigas</i> , <i>N. latipleonus</i>   | 28 (1>2), 29 (1>2), 58 (1>2)  | +                | +          | +          |
| 114→113 | <i>Nannoniscella</i>  | 25 (1>2)  | +                | +          | +          |
| 113→    | <i>N. biscutatus</i> , <i>N. coronarius</i>   | 35 (1>2)  | +                | +          | +          |
| 201→200 | Desmosomatidae without Austroniscinae   | 26 (1>2), 72 (1>2), 109 (1>2), 110 (1>2)  | -                | +          | +          |
| →181    | Desmosomatidae without Austroniscinae and Nannoniscinae   | 9 (1>2), 46 (2>1), 70 (2>1), 74 (1>2), 94 (1>2), 117 (1>2), 124 (1>2), 63 (1>2), 64 (1>2)   | -                | -          | +          |
| 200→199 | Nannoniscinae   | 28 (1>2), 58 (1>2), 126 (1>2)   | +                | +          | +          |
| 199→196 | Nannoniscinae without <i>Hebefustis</i>   | 27 (1>2), 30 (1>2), 31 (1>2), 32 (1>2)  | -                | +          | +          |
| 199→198 | <i>Hebefustis</i>   | 12 (1>2), 25 (1>2)  | +                | +          | +          |
| 198→197 | <i>H. vafer</i> , <i>H. mollicellua</i>   | 80 (1>2)  | +                | +          | +          |
| 198→    | <i>H. allenii</i>   | 50 (2>1)  | +                | +          | +          |
| 196→191 | <i>Saetoniscus meteori</i> , <i>Exiliniscus</i> , <i>Panetela</i> , <i>Rapaniscus</i> , <i>Regabellator</i> | 129 (1>2)   | -                | -          | +          |
| 191→186 | <i>Saetoniscus meteori</i> , <i>Exiliniscus</i> , <i>Panetela</i>   | 6 (1>2), 7 (1>2), 110 (2>1), 116 (1>2)  | +                | +          | +          |
| 186→185 | <i>Exiliniscus</i> , <i>Panetela</i>  | 46 (2>1), 58 (2>1)  | +                | +          | +          |

### 3. Results

|         |                                     |  |   |   |   |
|---------|-------------------------------------|--|---|---|---|
| 186→    | <i>Saetoniscus meteor</i>           | 57 (1>2), 70 (2>1), 111 (1>2), 117 (1>2), 119 (1>2), 127 (1>2)                                     | + | + | + |
| 185→183 | <i>Exiliniscus</i>                  | 23 (1>2), 33 (2>1), 36 (1>2), 42 (1>2)   | + | + | + |
| 183→    | <i>E. clipeatus</i>                 | 74 (1>2), 111 (1>2)  | + | + | + |
| 185→184 | <i>Panetela</i>                     | 35 (1>2), 50 (2>1), 72 (1>2), 95 (1>2), 109 (2>1)  | + | + | + |
| 184→    | <i>P. wolffi</i>                    | 15 (1>2), 70 (2>1)   | + | + | + |
| 184→    | <i>P. tenella</i>                   | 116 (2>1)  | + | + | + |
| 191→190 | <i>Rapaniscus, Regabellator</i>     | 12 (1>2)   | - | - | + |
| 190→188 | <i>Rapaniscus</i>                   | 50 (2>1), 55 (1>2), 76 (1>2), 79 (1>2), 80 (1>2), 82 (1>2)   | + | + | + |
| 188→    | <i>R. crassipes</i>                 | 63 (1>2)   | - | - | + |
| 188→187 | <i>R. multisetosus, R. centauri</i> | 54 (1>2)   | - | - | + |
| 187→    | <i>R. centauri</i>                  | 55 (2>1)   | - | - | + |
| 190→189 | <i>Regabellator</i>                 | 42 (1>2), 53 (1>2), 64 (1>2), 70 (2>1), 72 (2>1), 95 (1>2), 111 (1>2), 117 (1>2)                   | + | + | + |
| 189→    | <i>R. profugus</i>                  | 63 (1>2)   | + | + | + |
| 196→192 | <i>Nannonisconus</i>                | 18 (1>2), 22 (1>2), 58 (2>1), 60 (1>2), 120 (1>2)  | + | + | + |
| 192→    | <i>N. latipleonus</i>               | 48 (1>2), 50 (2>1)   | + | + | + |
| 192→    | <i>N. canalicatus</i>               | 47 (1>2)   | + | + | + |
| 196→194 | <i>Nannoniscus</i>                  | 4 (1>2), 10 (1>2), 22 (1>2), 111 (1>2)   | + | + | + |
| 194→    | <i>N. bidens</i>                    | 57 (1>2), 74 (1>2)   | + | + | + |
| 194→    | <i>N. teres</i>                     | 46 (1>2), 55 (1>2)   | + | + | + |
| 196→    | <i>Nymphodora fletcheri</i>         | 59 (1>2), 124 (1>2)  | + | + | + |
| 181→175 | Eugerdellatinae and Desmosomatinae  | 12 (1>2), 75 (1>2), 111 (1>2), 116 (1>2)   | - | - | + |
| →179    | Pseudomesinae                       | 6 (1>2), 35 (1>2), 74 (2>1), 119 (1>2), 9 (2>1), 17 (1>2), 18 (1>2), 70 (1>2), 94 (2>1), 110 (2>1) | + | + | + |
| 179→176 | <i>Pseudergella</i>                 | 67 (1>2), 96 (1>2), 117 (2>1)  | - | + | + |
| 176→    | <i>P. hessleri</i>                  | 15 (1>2), 16 (1>2), 50 (2>1), 110 (1>2), 119 (2>1)   | - | + | + |
| 176→    | <i>P. ischnomesoides</i>            | 12 (1>2), 26 (2>1), 111 (1>2)  | - | + | + |
| 179→178 | <i>Pseudomesus</i>                  | 115 (1>2), 126 (1>2), 127 (1>2), 128 (1>2)   | + | + | + |
| 178→177 | <i>P. satanus, P. brevicornis</i>   | 63 (2>1)   | - | - | + |
| 177→    | <i>P. brevicornis</i>               | 42 (1>2)   | - | - | + |
| 175→    | <i>Desmosoma ochotense</i>          | 43 (1>2), 73 (1>2), 95 (1>2)   | + | + | + |

### 3. Results

|         |  |  |   |   |   |
|---------|--|--|---|---|---|
| 175→174 | Desmosomatinae and Eugerdelatinae without <i>D. ochotense</i>                    | 5 (1>2), 9 (2>1), 26 (2>1)   | + | + | + |
| 174→149 | Eugerdelatinae (including <i>Mirabilicoxa cornuta</i> and <i>M. atlanticum</i> ) | 50 (2>1)   | - | - | + |
| 174→173 | Desmosomatinae (except for <i>Mirabilicoxa cornuta</i> )                         | 99 (1>2), 103 (1>2)  | - | - | + |
| →163    | <i>Torwolia</i> , <i>Desmosoma</i> , <i>Pseudogerda</i> , <i>Eugerd</i>          | 5 (2>1), 13 (1>2), 66 (1>2), 108 (1>2)   | + | + | + |
| 163→161 | <i>Desmosoma</i> , <i>Pseudogerda</i> , <i>Eugerd</i>                            | 12 (2>1), 61 (1>2), 100 (1>2)  | + | + | + |
| 163→162 | <i>Torwolia</i>  | 11 (1>2), 15 (1>2), 16 (1>2), 78 (1>2), 94 (2>1), 101 (1>2), 103 (2>1"), 116 (2>1) | + | + | + |
| →       | <i>Echinopleura cephalomagna</i>   | 1 (1>2), 37 (1>2), 39 (1>2), 45 (1>2), 73 (2>1)                                    | + | + | + |
| →165    | <i>Momedossa</i>   | 12 (2>1), 17 (1>2), 40 (1>2), 124 (2>1), 129 (1>2)                                 | + | + | + |
| 165→    | <i>M. profunda</i>   | 75 (2>1), 111 (2>1)  | + | + | + |
| 161→    | <i>Desmosoma lineare</i>   | 9 (2>1)  | + | + | + |
| 161→160 | <i>D. thoracicum</i> , <i>D. stroembergi</i> , <i>Eugerd</i>                     | 95 (1>2)   | + | + | + |
| 160→159 | <i>D. stroembergi</i> , <i>Eugerd</i>  | 73 (1>2), 94 (2>1)   | + | + | + |
| 159→    | <i>D. stroembergi</i>  | 26 (1>2)   | + | + | + |
| 159→158 | <i>Desmosoma</i> , <i>Pseudogerda</i> , <i>Eugerd</i>                            | 11 (1>2), 124 (2>1), 129 (1>2)   | + | + | + |
| 158→156 | <i>Pseudogerda</i> , <i>Eugerd</i>   | 104 (1>2)  | + | + | + |
| 156→154 | <i>Pseudogerda</i> , <i>Eugerd</i>   | 12 (1>2)   | + | + | + |
| 154→    | <i>Pseudogerda latipes</i>   | 43 (1>2)   | + | + | + |
| 154→153 |  | 105 (1>2)  | + | + | + |
| 153→152 |  | 13 (1>2), 26 (2>1), 66 (2>1)   | + | + | + |
| 152→150 |  | 61 (2>1)   | + | + | + |
| 150→    | <i>Pseudogerda elegans</i>   | 6 (1>2), 42 (2>1), 16 (2>1)  | + | + | + |
| 152→151 |  | 11 (2>1)   | + | + | + |
| 151→    | <i>Eugerd tenuimana</i>  | 26 (1>2), 106 (2>1), 116 (2>1), 117 (2>1)  | + | + | + |
| 151→    | <i>Pseudogerda kamchatica</i>  | 35 (1>2)   | + | + | + |

### 3. Results

|         |  |  |   |   |   |
|---------|--|--|---|---|---|
| 156→155 | <i>Eugerdella reticulata</i> ,<br><i>Desmosoma gigantea</i>      | 105 (1>2)  | + | + | + |
| 155→    | <i>Eugerdella reticulata</i>                                     | 106 (2>1)  | + | + | + |
| 158→157 | <i>Desmosoma tetarta</i> ,<br><i>Desmosoma renatae</i>           | 75 (2>1), 94 (1>2), 95 (2>1), 126 (1>2)            | + | + | + |
| 157→    | <i>Desmosoma tetarta</i>   | 12 (1>2), 73 (2>1)                                 | + | + | + |
| 173→172 | <i>Mirabilicoxa</i> (including<br><i>Echinopleura aculeata</i> ) | 42 (1>2), 61 (1>2)                                 | + | + | + |
| 172→171 | <i>Mirabilicoxa</i> (including<br><i>Echinopleura aculeata</i> ) | 62 (1>2), 110 (2>1)                                | + | + | + |
| 171→170 | <i>Mirabilicoxa</i> (including<br><i>Echinopleura aculeata</i> ) | 26 (1>2), 116 (2>1)                                | + | + | + |
| 170→168 | <i>Mirabilicoxa</i> (including<br><i>Echinopleura aculeata</i> ) | 61 (2>1)   | + | + | + |
| 168→167 | <i>Mirabilicoxa</i> (including<br><i>Echinopleura aculeata</i> ) | 62 (2>1)   | + | + | + |
| 167→    | <i>Echinopleura aculeata</i>                                     | 1 (1>2), 35 (1>2), 37 (1>2), 39 (1>2)              | + | + | + |
| 167→    | <i>Mirabilicoxa similipes</i>                                    | 42 (2>1)   | + | + | + |
| 170→169 |  | 50 (2>1)   | + | + | + |
| 169→    | <i>Mirabilicoxa alberti</i>                                      | 42 (2>1), 48 (1>2), 116 (1>2)                      | + | + | + |
| 169→    | <i>Mirabilicoxa plana</i>  | 35 (1>2)   | + | + | + |
| 171→    | <i>Mirabilicoxa acuminata</i>                                    | 225 (1>2), 35 (1>2)                                | + | + | + |
| →137    | clade of chelate genera  | 35 (1>2)   | + | + | + |
| →141    | <i>Eugerdella</i>  | 76 (1>2), 79 (1>2), 89 (1>2), 94 (2>1)             | + | + | + |
| →146    | <i>Whoia</i> ,<br><i>Thaumastosoma</i>                           | 15 (1>2), 107 (1>2), 121 (1>2), 126 (1>2)          | + | + | + |
| →       | <i>Mirabilicoxa cornuta</i>                                      | 25 (1>2), 61v, 62 (1>2), 76 (1>2)                  | - | - | + |
| 137→    | <i>Mirabilicoxa atlanticum</i>                                   | 103 (1>2), 124 (2>1), 129 (1>2)                    | - | - | + |
| 137→136 | clade of chelate genera  | 77 (1>2), 79 (1>2), 83 (1>2)                       | + | + | + |
| 141→    | <i>Eugerdella natator</i>  | 47 (1>2), 75 (1>2), 83 (1>2), 124 (2>1), 129 (1>2) | + | + | + |

### 3. Results

|         |  |  |   |   |   |
|---------|--|--|---|---|---|
| 141→140 | <i>E. nonfunalis</i> , <i>E. theodori</i> , <i>E. serrata</i> , <i>E. pugilator</i>          | 81 (1>2), 96 (1>2)   | + | + | + |
| 140→139 | <i>E. theodori</i> , <i>E. serrata</i> , <i>E. pugilator</i>                                 | 5 (1>2), 26 (1>2), 35 (1>2), 77 (1>2), 80 (1>2)  | + | + | + |
| 139→138 | <i>E. serrata</i> , <i>E. pugilator</i>  | 2 (1>2), 24 (1>2), 49 (1>2), 51 (1>2)  | + | + | + |
| 138→    | <i>E. pugilator</i>  | 47 (1>2), 75 (1>2), 116 (2>1)  | + | + | + |
| 138→    | <i>E. serrata</i>  | 110 (2>1), 111 (2>1)   | + | + | + |
| 146→145 | <i>Whoia</i> , <i>Thaumastosoma</i> without <i>W. dumbshafensis</i>                          | 93 (1>2), 97 (1>2), 110 (2>1)  | + | + | + |
| 145→143 | <i>Thaumastosoma</i> and <i>W. victoriensis</i>  | 15 (2>1), 124 (2>1), 129 (1>2)   | + | + | + |
| 143→142 | <i>Thaumastosoma</i>   | 6 (1>2), 38 (1>2), 44 (1>2), 45 (1>2), 46 (1>2), 47 (1>2), 55 (1>2), 56 (1>2), 61 (1>2), 107 (2>1), 117 (2>1), 121 (2>1) | + | + | + |
| 143→    | <i>Whoia victoriensis</i>  | 37 (1>2), 50 (1>2)   | + | + | + |
| 145→144 | <i>W. angusta</i> , <i>W. variabilis</i>   | 17 (1>2), 64 (2>1)   | + | + | + |
| 146→    | <i>Whoia dumbshafensis</i>   | 48 (2>1), 63 (2>1)   | + | + | + |
| 136→135 | clade of chelate genera without <i>Cryodesma polare</i>                                      | 75 (1>2), 85 (1>2), 97 (1>2)   | - | + | + |
| 135→134 | <i>C. agnari</i> , <i>C. cryoabyssale</i>  | 98 (1>2)   | + | + | + |
| 134→    | <i>C. cryoabyssale</i>   | 47 (1>2), 83 (2>1)   | + | + | + |
| 135→133 | clade of chelate genera without <i>Cryodesma</i>   | 5 (2>1), 26 (1>2), 48 (2>1), 84 (1>2)  | + | + | + |
| 133→132 | <i>Paradesmosoma</i>   | 43 (1>2), 63 (2>1), 89 (1>2), 90 (1>2), 97 (2>1), 112 (1>2), 113 (1>2), 114 (1>2)  | + | + | + |
| 133→130 | clade of chelate genera without <i>Cryodesma</i> and <i>Paradesmosoma</i>                    | 73 (1>2), 92 (1>2), 94 (2>1)   | + | + | + |
| 130→129 | <i>Oecidiobanchus</i>  | 19 (1>2), 42 (1>2), 50 (1>2), 121 (1>2), 123 (1>2)   | + | + | + |
| 130→128 | <i>Prochelator</i> , <i>Reductosoma</i> , new species A, <i>Chelator</i> , <i>Disparella</i> | 48 (1>2), 86 (1>2)   | - | - | + |
| 128→127 | <i>Prochelator</i> , <i>Disparella</i> , <i>Reductosoma</i> , new species A                  | 87 (1>2), 110 (2>1)  | - | - | + |

### 3. Results

|         |   |  |   |   |   |
|---------|---|--|---|---|---|
| 127→126 | <i>P. angolensis</i> , <i>P. incomitatus</i>  | 5 (1>2), 49 (1>2)  | - | - | + |
| 127→125 | <i>Prochelator</i> ,<br><i>Disparella</i> ,<br><i>Reductosoma</i> ,<br>new species A<br>without <i>P.</i><br><i>angolensis</i> and<br><i>P. incomitatus</i> | 124 (2>1), 129 (1>2)   | - | - | + |
| →116    | <i>Chelator</i>   | 121 (1>2)  | + | + | + |
| 116→115 | <i>C. vulgaris</i> , <i>C.</i><br><i>chelatum</i> and <i>C.</i><br><i>antarcticus</i>   | 91 (1>2)   | + | + | + |
| →119    | <i>Disparella</i>   | 5 (1>2), 25 (1>2), 40 (1>2),<br>97 (2>1), 102 (1>2), 124<br>(2>1), 129 (1>2)                     | + | + | + |
| 119→118 | <i>Disparella</i><br>without <i>D.</i><br><i>kensleyi</i>   | 41 (1>2), 86 (2>1), 91<br>(1>2)  | - | - | + |
| 118→117 | <i>D. funalis</i> , <i>D.</i><br><i>valida</i>  | 88 (2>1)   | - | - | + |
| →123    | <i>Prochelator</i><br>without <i>P.</i><br><i>angolensis</i> and<br><i>P. incomitatus</i>   | 116 (2>1)  | - | - | + |
| →       | <i>Reductosoma</i>  | 6 (2>1), 12 (2>1), 19 (1>2),<br>35 (2>1), 42 (1>2), 44<br>(1>2), 63 (2>1), 64 (2>1),<br>84 (2>1) | + | + | + |
| →       | new species A   | 58 (1>2), 59 (1>2)   | + | + | + |

In the following, the major clades of the ingroup are described. Accelerated (Acctran) and delayed transformation (Deltran) produced relatively similar results. The synapomorphy patterns produced by Acctran were a little bit more convincing for those characters known as synapomorphy for the genera (subfamilies), therefore these results are shown. In the following, numbers in square brackets refer to the character (Table 5).

Clade 114 consists of *Austroniscus* and *Nannoniscoides* (Austroniscinae) and is defined by following synapomorphies: body broad [4], pereonite 1 broad and clearly smaller than pereonite 2 [10], cephalon with cephalic keels [22] and ventral setae on carpus of pereopod I of "non-composed" seta-type [95]. *Austroniscus* (clade 110) is characterized by following synapomorphies: branchial chamber and operculum in relation to pleotelson small and posteriorly broadest [122], uropods not covering anus valves [126]. Clade 112 includes *Austroniscus* (clade 110) and species of *Nannoniscoides* (clade 113) and is the sistergroup to clade 111 (species of *Nannoniscoides*). Clade 113 is based on the apomorphy: margin of antennular fold



with one anteriorly directed spine [25]. Clade 111 is characterized by following apomorphies: flagellum of antennula with bulbous distal article [28], form of distal article elongated [29] and pereonites 6 and 7 fused [58].

Clade 200 (50 and 80 percent majority rule tree only) includes all Desmosomatidae except Austroniscinae based on following synapomorphies: antennula consisting of 5 articles [26], ventral margin of carpus of pereopod I with composed robust setae standing in a row [72], carpus of pereopod II ventrally with row of composed setae [109], propodus of pereopod II ventrally with a row of composed setae [110].

Clade 199 consists of all genera with a specialized antennula (*Hebefustis*, *Regabellator*, *Rapaniscus*, *Nannoniscus*, *Nannonisconus*, *Panetela*, *Saetoniscus* and genus novum *fletcheri*) and is defined by following synapomorphies: flagellum of antennula with bulbous distal article [28], pereonites 6 and 7 fused [58] and uropods covering anus valves [126]. In the 50 and 80 percent majority rule tree, *Hebefustis* (clade 198) is resolved as sistertaxon to all remaining genera of Nannoniscinae (clade 196) based on following synapomorphies: pereonites 1-4 higher than pereonites 5-7 [12] and margin of antennular fold with one anteriorly directed spine [25]. Clade 198 is defined by following synapomorphies: antennula with specialized distal articles [27], first article of flagellum of antennula smallest [30], second article of flagellum of antennula with elongation holding third bulbous article [31], distal article of flagellum bulbous and ball-shaped [32].

Clade 186 is defined by body elongated (more than five times longer than width of pereonite 2) [6], with straight, cigar-like body margins [6], propodus of pereopod II without setal row [110] and carpus and propodus of pereopod V dorsally with rows of long setae [116]. It includes the genera *Saetoniscus*, *Exiliniscus* and *Panetela*. *Panetela* (clade 184) and *Exiliniscus* (clade 183) are sistertaxa.

*Nannonisconus* (clade 192) is based on following synapomorphies: pleotelson enlarged [18], cephalon with cephalic keels [22], pereonites 6 and 7 not fused [58], pereonites 7 and pleotelson fused [60], anus region separated and bilobed [120]. *Nannoniscus* (clade 194) is defined by: body broad [4], pereonite 1 broad and clearly smaller than pereonite 2 [10], cephalon with cephalic keels [22], carpus and propodus of pereopod II bearing dorsal rows of setae [111].

*Rapaniscus* (clade 188) is defined by following synapomorphies: pereonite 1 not shorter than pereonite 2 [50], pereonite 7 with strong, caudally directed spine [55],

pereopod I concentrating in enlargement of the carpus [76], pereopod I as functional unit enlarged [79], propodus of pereopod I with ventral row of small stout setae [80], carpus of pereopod I enlarged and tapering towards the propodus [82].

*Regabellator* (clade 189) is characterized by: mandibular palp absent [42], pereonites 6 and 7 with anteriorly directed spine [53], coxae produced [64], natatory setae present on pereopods V-VII [70], lower margin of carpus of pereopod I without composed setae [72], ventral setae on carpus of pereopod I of not-composed seta type [95], carpus and propodus of pereopod II bearing dorsally rows of setae [111].

Clade 179 includes the genera *Pseudomesus* and *Pseudergella* (Pseudomesinae) and is defined by following synapomorphies: body elongated (more than five times longer than width of pereonite 2) [6], second article of antennula with only two articulated broom setae [35], carpus of pereopod I dorsally without a row of simple setae [74], pleotelson dorsally inflated [119], pereonite 1 not broad and half of size of pereonite 2 [9], pereonite 5 elongated [17], pleotelson enlarged [18], pereopods V-VII rows of natatory setae absent [70], setae on carpus of pereopod I not standing in a row and increasing in length towards the propodus [94], propodus of pereopod II ventrally without row of composed setae [110]. In the 50 percent majority rule tree Pseudomesinae are the sistertaxon to Desmosomatinae including *Pseudergella atypicum*, while *P. atypicum* is resolved to be the sistertaxon to all taxa included in Desmosomatinae and Eugerdellatinae (clade 175). In the 80 percent majority rule tree and the strict consensus *P. atypicum* branches polytom after clade 201. *Pseudergella* (without *P. atypicum*) (clade 176) is resolved in both majority rule trees and defined by following synapomorphies: ischium of pereopods V-VII elongated (over 3.5 times longer than wide) [67], distoventral seta in the ventral row on the carpus of pereopod I shortest [96], carpus and propodus of pereopod V without natatory setae [117]. *Pseudomesus* (clade 178) is based on following synapomorphies: ischium of pereopods V-VII with dorsal hook [115], uropods covering anus valves [126], uropods short, not overlapping posterior margin of pleotelson [127], uropodal endite bulbous [128].

The following synapomorphies define clade 181 (Desmosomatinae including Eugerdellatinae): pereonite 1 broad and half of size of pereonite 2 [9], tergites 1-4 anteriorly without sensory spines [46], at pereopods V-VII rows of natatory setae

present [70], carpus of pereopod I dorsally bearing a row of simple setae [74], ventral setae in row on carpus of pereopod I increasing in length towards propodus [94], carpus and propodus of pereopod V-VII ventrally with rows of long setae [117], uropods uniramous [124], coxae 1-4 anteriorly tipped with seta [63], coxae produced [64].

*Momedossa* (clade 165) is defined by following synapomorphies: pereonites 1-4 of same height as pereonite 5-7 [12], pereonite 5 elongated [17], incisor process shelf-like [40], uropods biramous [124], uropodal exopod reduced to half of size of endopod or less [129]. Clade 172 includes the *Mirabilicoxa* species, except *M. atlanticum* and *M. cornuta*, and *Echinopleura aculeata*. This clade is defined by: mandibular palp absent [42] and pereonites 6, 7 and pleotelson with marginal flanges [61].

The group *Torwolia*, *Desmosoma*, *Pseudogerda* and *Eugerdella* is united in clade 163 based on following synapomorphies: body not anteriorly wide and posteriorly slender [5], pereonites 5-7 enlarged [13], pereopods V-VII longer and more heavily built than pereopods I-IV [66], pereopod II heavily build, carpus and propodus broad [108]. *Torwolia* (clade 162) is characterized by: pereonite 2 largest of pereonites 1-4 [11], pereonite 5 with convex lateral margins [15], pereonite 5 inflated [16], pereopod I small and slender, but propodus enlarged [78], ventral setae on carpus of pereopod I composed [94], pereopod I much shorter than pereopod II [101], propodus of slender pereopod I not elongated [103], carpus and propodus of pereopod V without dorsal rows of natatory setae [116]. Clade 161 includes *Desmosoma*, *Pseudogerda* and *Eugerdella* and is based on following synapomorphies: pereonites 1-4 of same height as pereonites 5-7 [12], pereonites 6, 7 and pleotelson with marginal flanges [61], pereopod I slender and only slender setae on carpus and propodus [100].

In the 50 percent majority rule tree clade 149 consists of all Eugerdellatinae and is defined by following synapomorphy: pereonite 1 not shorter than pereonite 2 [50]. In the 80 percent majority rule tree and the strict consensus, the genera *Eugerdella* (clade 141, defined by: pereopod I not concentrating in enlargement of carpus [76], pereopod I as functional unit enlarged [79], carpus of pereopod I enlarged and with setae of irregular size [89], ventral setae on carpus of pereopod I not standing in a row and increasing in size [94]) and *Whoia* (clade 146, defined by: lateral margins of pereonite 5 convex [15], pereopod II robust (articles almost quadrangular) [107],

pleotelson vaulted in transverse section [121], uropods covering anus valves [126]) are not included in 149, but are polytom at the same node as clade 149.

Clade 134 is formed by *Cryodesma agnari* and *C. cryoabyssale* and inserts at a trichotome node next to *C. polare* and clade 133. The sisterspecies (clade 134) are united by following synapomorphy: penultimate seta in ventral row of the carpus of pereopod I as long as distoventral seta [98].

Clade 133 comprises all genera with a carpo-euchela except *Cryodesma* and is defined by following synapomorphies: body not anteriorly wide and posteriorly slender [5], antennula consisting of five articles [26], pereonite 1 not longer than pereonite 2 (in midsagittal length) [48], carpus of pereopod I enlarged and broadest at articulation towards propodus [84].

*Paradesmosoma* (clade 132) is the sistertaxon to clade 130 and based on following synapomorphies: mandibular palp of two articles [43], coxae 1-4 without seta on anterior tip [63], carpus of pereopod I enlarged and with setae of irregular size and type [89], ventral setae on the carpus of pereopod I composed [90], distal ventral setae not reaching full length of propodus [97], basis of pereopods II and III fringed with numerous distally plumose setae [112], pereopod IV folious, carpus and propodus paddle-like [113], carpus and propodus of pereopod IV surrounded by numerous distally plumose setae [114].

The relationships of the genera *Oecidiobanchus*, *Disparella*, *Chelator*, *Prochelator* and new species A as well as *Reductosoma* are not resolved (polytomy) in the 80 percent majority rule and the strict consensus tree.

Clade 129 includes the *Oecidiobanchus* species and is characterized by following synapomorphies: body in transverse section highly vaulted, especially in pleotelson [19], madibular palp absent [42], pereonite 1 shorter than pereonite 2 [50], pleotelson vaulted in transverse section [121], branchial chamber and operculum in relation to size of pleotelson small and rounded [123]. *Disparella* (clade 127) is defined by carpus of pereopod I with single composed seta midway [87], propodus of pereopod II ventrally with row of composed setae [110]. Clade 116 consists of species of the genus *Chelator* and is based on pleotelson vaulted in transverse section [121].

While two *Prochelator* species *P. angolensis* and *P. incomitatus* form a clade (126) based on body anteriorly wide and posteriorly slender [5], pereonite 1 enlarged and clearly bigger (in midsagittal length more than two times longer than pereonite 2) [49]. The remaining *Prochelator* species do not form a clade and branch polytom. In the 50

### 3. Results

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percent majority rule tree these *Prochelator* species form clade 123 based on the apomorphy: carpus and propodus of pereopod V dorsally without rows of natatory setae [116].

### 4 Discussion

#### 4.0 Zoogeographic aspects

In deep-sea study areas that are sampled for the first time, the fraction of species new to science ranges from 50 to 100% (Wilson 1980, Poore *et al.* 1994, Park 2000, Brenke & Wägele submitted). The DIVA-1 results for Nannoniscidae *sensu* Siebenhaller & Hessler (1981) and Wägele (1989) are presented in Brenke & Wägele (submitted). These results include also taxa with a questionable systematic position (chapter 4.1.1), e.g. *Thaumastosoma platycarpus* (chapter 4.2.1.3.11). For Desmosomatidae, the percentage of new species in the DIVA-1 samples is lower when Nannoniscidae are included in the family (instead of 93 %, 85,7 %). The taxonomy of new species which occur more frequently in the samples will be important for several other analyses (Brandt *et al.* 2005), e.g. phylogenetic studies and may lead to a better understanding of the phylogenetic relationships.

The Angola Basin represents a typical abyssal region of the world's oceans (chapter 1.2.1) without noticeable topographic influence from the surrounding ridges or the continental shelf. With 2718 specimens peracarid crustaceans represent a large group in the samples, Isopoda comprising 14% of the total samples (Brandt *et al.* 2005). In Janiroidea, Munnopsididae are the most dominant family, closely followed by Desmosomatidae. The fraction of species which occur in the North Atlantic or which are amphiatlantic is 46 %, only 5% of the species are native to the Southern Ocean (Brenke & Wägele submitted). Of all Janiroidea, 32 species were known. The main distribution of these species lies in the North Atlantic. This confirms the influence by the North Atlantic Deep Water on the fauna of the Angola Basin (chapter 1.2.1, Brandt *et al.* 2005, Brenke & Wägele submitted).

In the Angola Basin, the diversity of Desmosomatidae (10 genera, about 27 species) is comparable to that of Munnopsididae (eight genera, 27 species). The composition of the Isopod community with the dominant groups Munnopsididae and Desmosomatidae is typical for the deep sea (Kussakin 1973, Svavarsson *et al.* 1990, Brandt *et al.* 2004, 2005). Together, Desmosomatidae (10 genera, 28 species) and Nannoniscidae (six genera, eight species) are most diverse. An important factor for diversity is the age of the environment and the evolutionary time in which species can develop (Gaston & Chown 1999, Webb & Gaston 2000).

In the ANDEEP samples, Desmosomatidae *sensu* Hessler (1970), Wägele (1989) and Brandt (1992), excluding *Thaumastosoma* (48 species) are more divers than in the DIVA-1 samples (27 species), while their abundance in the deep Southern Ocean is lower than in the Angola Basin. Brenke & Wägele (submitted) compared DIVA-1 samples with samples from the deep Southern Ocean (ANDEEP stations 134-138) and found a slightly higher mean diversity in the Angola Basin. They concluded that the very homogeneous distribution of species and individuals in the Angola Basin, in contrast to the presumably heterogeneous and structurally rich Antarctic benthos can lead to a higher diversity at a lower total number of species. The pattern of species composition and distribution observed in the ANDEEP stations is patchy (Brandt *et al.* 2004). As for all Isopoda, the distribution of Desmosomatidae at the ANDEEP stations is found to be rather patchy and many species are rare (chapter 3.3.4).

The ANDEEP stations from the South Shetland Islands and those from the South Sandwich islands are quite different from each other in their species composition. Stations from the Weddell Sea show similarities in the species composition. The diversity is highest at stations 131 and 133. Brökeland (2004) described similar results for all Isopoda.

The differences between the sampling areas could be explained by the heterogeneity in grain size of the sediment, which enhances the diversity (Etter & Grassle 1992). The ANDEEP stations show high differences in the sediment size. Howe *et al.* (2004) and Diaz (2004) described strong variations in sediment size at the South Shetland stations and showed that sediment types and composition even varied between the relatively similar Weddell Sea stations. The South Sandwich stations varied not only in the species composition, they also had the widest depth range of all ANDEEP stations (Brökeland 2004).

The percentage of endemites in the Antarctic benthos is between 75% and 88% (Brandt 1991, 2000). In the South Atlantic benthos the percentage of endemites is clearly lower (Brenke & Wägele submitted). The fauna of the Angola Basin is not isolated. Consequently, the evolution of endemites was not encouraged. Furthermore, horizontal spreading along the constant water body of the NADW seems possible. Theoretically, it is possible that ancestors of the recent deep-sea Isopoda immigrated 140 million years ago from the Thetys into the abyssal plains of the Atlantic. This is possible because already at this time the Atlantic must have had a depth of approximately 4000 m (Brenke & Wägele submitted). Recent studies

confirm that the separation of Asellota and their deep-sea representatives occurred early in evolution (Wägele 1989, Wilson 1998, Raupach *et al.* 2004).

For Desmosomatidae, the percentage of potential endemites in the DIVA-1 samples is 33,3 %, in the ANDEEP samples 52 %. With the present knowledge, it is not possible to decide whether a species is endemic or not, because the density of stations in the deep sea is extremely low compared to the not sampled (unknown) area. Our knowledge about the distribution of deep-sea species is deficient. It may be hypothesized that the higher percentage of potential endemites in the Southern Ocean indicates the important role of the Southern Ocean deep-water production for the spreading of isopod taxa in the world's oceans.

Hessler & Thistle (1975) already pointed out that species with deep-sea origin lack eyes completely. Polar emergence had been postulated for Desmosomatidae and Nannoniscidae as well as for other families of Asellota (Brandt 1991, Wilson 1998, Hessler & Thistle 1975). The ANDEEP results support this hypothesis (Brökeland 2004). In Desmosomatidae, eight species were known from the shelf, the ANDEEP samples contained 48 species. Both, sub- and emergence can be observed simultaneously (Brandt 1991).

The bathymetric range of species from several Isopod families in the Southern Ocean is relatively large. For example, the newly described desmosomatid *Eugerdella serrata* sp. nov. is found at the deep-sea stations of ANDEEP II and occurs in samples from shallow waters in the Ross Sea (Madhumita Choudury pers. comm.). This supports the theory of enhanced eurybathy of Southern Ocean taxa, although it has to be considered that this depth range may be the result of sibling species (Held 2003, Held & Wägele 2005).

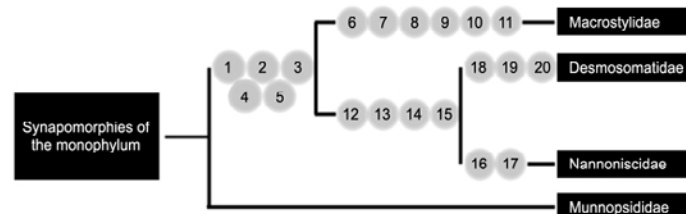
### **4.1 Are Desmosomatidae monophyletic?**

#### **4.1.1 Relationships of the families**

According to Hennig (1966, 1984) monophyletic groups are defined by synapomorphies, paraphyletic groups by symplesiomorphies and polyphyletic groups by homoplasies (characters may be convergently evolved). Using morphological characters Wägele (1989) hypothesized an ancestor of Macrostylidae, Nannoniscidae, Desmosomatidae and Munnopsididae, who was able to dig and swim with the posterior pereopods. The four families are postulated as a monophyletic



group. Macrostylidae do not have the ability to swim and neither do species of Nannoniscidae. In this chapter the apomorphies found in the literature are modified and summarized. Plesiomorphic character states are written in brackets behind the autapomorphic state.



#### Synapomorphies dividing the group Macrostylidae, Desmosomatidae and Nannoniscidae from the Munnopsididae:

- 1) flagellum of antennula short (3 or 4 articles) [flagellum of antennula long (consisting of more than 4 articles)]
- 2) pars molaris triangular without grinding plate [pars molaris strong, not triangular, with grinding plate]
- 3) no gap between setal row and base of pars molaris [gap between setal row and base of pars molaris]
- 4) pereonites with spinelike ventral elongations [pereonites without spine-like ventral elongations]
- 5) pereonites 1-4 higher and broader than pereonites 5-7 [pereonites 1-4 as high and as broad as pereonites 5-7]

#### **Remark**

Characters 4 and 5 are weak because they also occur in Munnopsididae; for example in Ilyarachinae, *Syneurocope* and *Munnopsis* (Marina Malyutina, pers. com.). For the ventral spines in Munnopsididae, Macrostylidae, Desmosomatidae and Nannoniscidae convergent evolution is hypothesized (chapter 4.2.2.2).

#### Macrostylidae are clearly separated from Desmosomatidae and Nannoniscidae by the following autapomorphies:

- 6) pleotelson with pair of statocysts [pleotelson without statocysts]

- 7) uropods uniramous with extremely elongated uropodal sympod [uropods biramous, sympod not elongated]
- 8) pereopods III to V shorter than remaining pereopods [all pereopods of almost the same length]
- 9) dactylus of pereopod III bent dorsally [dactylus of pereopod III ventrally directed]
- 10) dactylus of pereopod III with dorsal row of long setae [dactylus of pereopod III without dorsal row of long setae]
- 11) mandibular palp absent [mandibular palp present]

Synapomorphies of Nannoniscidae and Desmosomatidae are:

- 12) flagellum of antenna basally swollen in male [flagellum of antenna not basally swollen in male]
- 13) article 2 of antennula elongated [article 2 of antennula not elongated]
- 14) article 2 of antenna distally with 3-4 joint articulated broom setae [article 2 of antennula without a regular number of distal joint articulated broom setae]
- 15) ventral elongation of pereonites robust, caudally produced [ventral elongations of pereonites small (not robust) and straight]

Autapomorphies of Nannoniscidae are:

- 16) ventral row of natatory setae reduced at pereopods V to VII [ventral row of natatory setae present on pereopods V to VII]
- 17) uropods short, often cover anus valves [uropods overlapping distal margin of pleotelson, inserted at distolateral corners of pleotelson]

Autapomorphies of Desmosomatidae are:

- 18) carpus of pereopod I bearing a ventral row of enlarged composed setae and a dorsal row of long simple setae [carpus of pereopod I without ventral row of enlarged composed setae and no dorsal setae]
- 19) carpus and propodus of the pereopod II bearing a ventral row of enlarged composed setae and a dorsal row of long setae [carpus and propodus of the pereopod II without a ventral row of enlarged composed setae and no long setae dorsally]
- 20) article 2 of antennula with (only) two joint articulated broom setae [second article of antennula with more than 2 joint articulated broom setae]

#### 4.1.2 Molecular hints

Raupach *et al.* (2004) presented molecular data with a different position of Munnopsididae. In the clade of “munnopsid radiation”, the families Munnopsididae and Desmosomatidae are sistergroups. Both families are monophyla. Together they are the sistergroup to the Macrostylidae (trichotome split/knot together with the Janirellidae and Ischnomesidae).

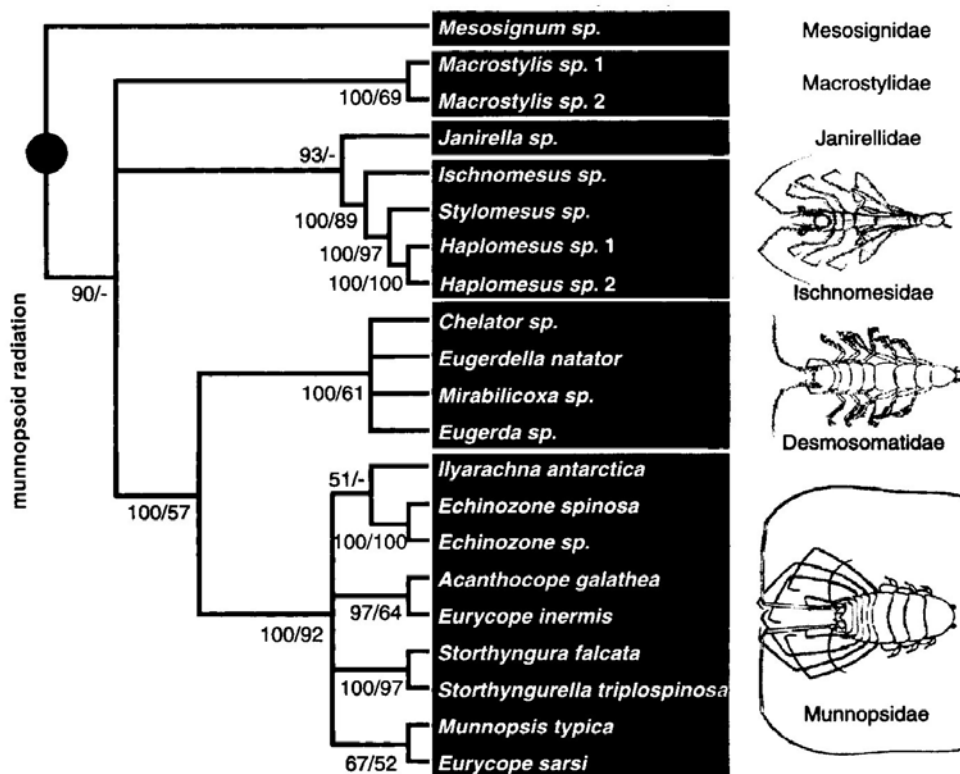


Fig. 115: Clade of “munnopsid radiation” within the tree presented by Raupach *et al.* (2004) based on sequences of the 18s gene (modified).

Unpublished nannoniscid sequences are basal to the knot of Desmosomatidae (Michael Raupach, pers. comm. 2005). These sequences are from species of *Austroniscus*, a genus discussed as basal in Nannoniscidae based on morphological characters (Siebenhaller & Hessler 1977, 1981; Kaiser 2005). Thus, there are differences in the relationships of the four families Munnopsididae, Macrostylidae, Desmosomatidae and Nannoniscidae comparing the molecular data and morphological data.

### 4.1.3 Two families or one?

In this study the question of the monophyly of Desmosomatidae is discussed based on morphological characters. The five synapomorphies that discriminate the group Macrostylidae, Desmosomatidae and Nannoniscidae from Munnopsididae are presented above.

The monophyly of Desmosomatidae and Nannoniscidae is based on four synapomorphies (12, 13, 14, 15) that characterize species of both families. There is no doubt about the close relationship between Desmosomatidae and Nannoniscidae as previously discussed in the literature (Hessler 1970, Siebenhaller & Hessler 1977, 1981, Wägele 1989), but they can only be distinguished by a few morphological characters. Wägele (1989) presented three characters (18, 19, 20) as autapomorphies of Desmosomatidae and two characters (16, 17) as autapomorphies of Nannoniscidae (Fig. 114).

Characters used to assign a species to Nannoniscidae are often not the apomorphies of the family. Instead species are classified by diagnostic characters as such whether there is a bulbous terminal article of the antennula, pereonites 6 and 7 are fused or a ventral spine on the operculum is present. However, these characters do not appear in all taxa. The question is: Can the sisterfamilies be clearly separated by their autapomorphies (12, 13, 14, 15)?

Since there are species that were described as Desmosomatidae and later re-assigned to Nannoniscidae due to diagnostic characters like the bulbous last article of the antennula and the fusion of pereonites, like genus novum *fletcheri* (Paul & George, 1975) (Kaiser 2005) or *Rapaniscus coalescus* (Menzies & George, 1972), the discussion of the autapomorphies is difficult (chapter 4.2.1.3.5). Actually, it has been repeatedly discussed if both families might be combined into one. Siebenhaller & Hessler (1977) saw a problem in differentiating Nannoniscidae from Desmosomatidae a problem and summarized that Hessler 's (1970) diagnosis of Desmosomatidae contains no character to exclude species of *Austroniscus* or *Nannoniscoides*, the genera regarded as basal in the Nannoniscidae. They concluded that the two families unquestionably are very closely related; although, if both families would be regarded as one family, they would divide into two subgroups. However, the taxonomic level describing a group of species defined as monophylum is not as important. A more important question is: are the groups monophyla, para- or polyphyla?

Unfortunately, Siebenhaller & Hessler (1977) present well-defined characters of these two subgroups. In their arguments a bulbous distal article on the antennula, fusion of pereonites 6 and 7 or a seta on the anterolateral corners of pereonites 2-4 are important characters. For example *Thaumastosoma* was moved to Nannoniscidae because of the presence of this last character. *Thaumastosoma platycarpus* Hessler, 1970 and *Thaumastosoma tenue* Hessler, 1970 possess “desmosomatid characters” such as a flagellum tapering to the tip with the second peduncular article bearing two joint articulated broom setae inserting in opposite to each other distally (20); although, a third short articulated broom seta is present (14). Natatory setae are present on the posterior pereopods as well as “nannoniscid characters” such as a midventral spine on pereonite 7 or the female operculum.

Originally, the autapomorphy regarding broom setae on the distal end of the second peduncular article of the antennula was defined as “only two broom setae inserting in opposite to each other” (20), while the plesiomorphic condition was defined as “second peduncular article distally with three to four long broom setae” (14) (Wägele 1989). Due to the presence of joint articulated long broom setae and smaller broom setae that may also be present but are not necessarily joint articulated in desmosomatid species, the definition of this autapomorphy of Desmosomatidae is not clear enough. Therefore, it is defined here as “two long joint articulated broom setae standing in opposite to each other”. However, even with this definition the apomorphy remains weak because there are also exceptions in Desmosomatidae.

The question about the systematic position of the genera *Pseudomesus* and *Thaumastosoma* is one of the most discussed systematic problems in the literature about Desmosomatidae and Nannoniscidae (chapter 4.2). The affiliation of both genera has been questioned more than once and by several authors (Hansen 1916; Gurjanova 1946; Kussakin 1965; Hessler 1970; Siebenhaller & Hessler 1977, Siebenhaller & Hessler 1981; Svavarsson 1984; Wägele 1989).

Wägele (1989) decided that a clear separation of both families is possible if *Pseudomesus* is transferred to Nannoniscidae. The argument that rows of composed setae (18, 19) on the carpus and propodus are not present and dorsal rows are absent is weak regarding the reduction of these rows in other desmosomatid genera like *Eugerdia*, *Desmosoma* or *Mirabilicoxa*. *Pseudomesus* Hansen, 1916 (see chapter 4.2.1.5.2) is a good example of the systematic difficulties in both families:

Species of this genus possess an antennula with a flagellum tapering to the end and, on the distal tip. Only two joint articulated broom setae are inserting in opposite to each other (20). Natatory setae on the carpi and propodi of pereopods V to VII are only developed in males, in females these are reduced (16). The coxae, not the tergites, bear spines anteriorly on the tip (desmosomatid character). The uropods are extremely short and inserting close to the anus valves (17). Thus, desmosomatid characters as well as nannoniscid characters are present in the genus.

The species *Rapaniscus multisetosus* (Brandt 2002b) was assigned to Nannoniscidae but, like the other two *Rapaniscus*-species (*R. crassipes* Hansen, 1916 and *R. sp. nov. A*), possesses a first pereopod with a setal row of composed setae on the propodus and carpus (autapomorphy Desmosomatidae). Although the shape of the robust pereopod I reminiscent of that of *Eugerdella* in Desmosomatidae. There are differences that lead to the hypothesis that the robust pereopod I evolved convergently in the two genera (chapter 4.2.1.3.5). However, the autapomorphy presented for Desmosomatidae obviously also occurs in species of Nannoniscidae. This leads to the conclusion that both families should be regarded as one family.

The apomorphy of setal rows on the first and second pereopods (18, 19) does not occur in all species of the Desmosomatidae (18, 19) does not occur in all species of this family (reduction in the slender forms of a specialized first pereopod). Reduction also occurs in Nannoniscidae. In the desmosomatid *Mirabilicoxa longispina* (Hansen, 1916), the dorsal row of setae on the carpus of pereopod I is absent and reduced on the carpus and propodus of pereopod II (only 2 setae on carpus); the dorsal row of natatory setae on the carpus of pereopod VII is absent, although a ventral row is present; and the uropods are inserting close to the anus valves (17).

#### Conclusion

Desmosomatidae and Nannoniscidae are not clearly separated by their autapomorphies. All characters presented as autapomorphies occur in species of both families. Thus, no clear classification is possible and the remaining characters are the synapomorphies of both families (12, 13, 14, 15). It is concluded that Nannoniscidae and Desmosomatidae together build a monophylum. Therefore, both families are treated as one in the phylogenetic analysis presented in this study. Desmosomatidae were erected by Sars in 1897; Nannoniscidae by Hansen in 1916. Thus, the valid family name is Desmosomatidae.

### 4.2 One family – five subfamilies

#### 4.2.1 Discussion of the subfamilies and genera

##### 4.2.1.1 *Austroniscinae* subfam. nov.

All three genera of this subfamily were assigned to *Nannoniscidae*. Their systematic position was regarded as basal within *Nannoniscidae* (Siebenhaller & Hessler, 1977, 1981) and now can be regarded as basal within *Desmosomatidae* (compare chapter 3.2.2 – 3.2.4). The genera *Nannoniscoides* Hansen, 1916 and *Nannoniscella* (Hansen, 1916) are discussed below. The genus *Austroniscus* Vanhöffen, 1914 is accepted as presented in the literature.

##### 4.2.1.1.1 *Nannoniscoides* Hansen, 1916

Type species: *Nannoniscoides angulatus* Hansen, 1916.

Siebenhaller & Hessler (1981) present a modified diagnosis of the genus with following characters:

- body broad (not more than 3 times longer than wide), depressed
- cephalon with cephalic keels
- antennula with 6 (rarely 7) articles
- pereopod I with thin setae ventrally on carpus and propodus except 1 distal composed seta on the carpus
- pleotelson with posterolateral spines
- operculum elongated, with concavity and calcareous fringe at midline of distal edge

This diagnosis is slightly modified in the present study: species of *Nannoniscoides* possess an antennula of 6 or 7 article and the last article is elongated and inflated. It is proposed to call this condition long and bulbous, since the last article never tapers to its distal tip, as being the case in an antennula that is regarded as unspecialized (as in *Desmosomatinae*, *Eugerdellatinae* and *Pseudomesinae*).

The close relationship of *Austroniscus* and *Nannoniscoides* was previously proposed by Siebenhaller & Hessler (1977, 1981). These two genera share the broad and depressed body form, an antennula of 6 or 7 articles, the flat laterally expanding flanges and the presence of sensory setae on the tergites of the anterior pereonites. They can be clearly distinguished by the size of the branchial chamber, the shape of

the operculum and the setation of pereopod I. While the branchial chamber in *Austroniscus* is very small in comparison to the size of the pleotelson the branchial chamber of *Nannoniscoides* is of normal size. Species of *Austroniscus* have composed setae on the ventral margins of the carpus and propodus of pereopod I, whereas species of *Nannoniscoides* possess thin setae at these margins except one composed seta inserting ventrodistally on the carpus.

### 4.2.1.1.2 *Nannoniscella* (Hansen, 1916)

Type species: *Nannoniscella biscutatus* (Siebenhaller & Hessler, 1977).

Originally, *Nannoniscella* was erected by Hansen (1916) and was later synonymized to *Austroniscus* (Birstein 1962; Siebenhaller & Hessler 1977, 1981). George (2001) presented *Nannoniscella* as new genus and transferred two species of *Nannoniscoides* to *Nannoniscella*: *N. biscutatus* (Siebenhaller & Hessler, 1977) and *N. coronarius* (Siebenhaller & Hessler, 1977). The following characters are presented in the generic diagnosis (George 2001):

- body broad
- pereonites free
- antennula composed of 6 or more articles
- cephalic keels “well developed or not”
- pleotelson with posterolateral spines

This diagnosis is not clear with regard to the presence or absence of cephalic keels. George (2001) included both species in *Nannoniscella*. They possess cephalic keels like species of *Nannoniscoides* and *Austroniscus*. George (2001) argued with diagnostic characters he took from the key presented by Siebenhaller & Hessler (1977), but not in a phylogenetic sense. *Nannoniscoides* sensu Siebenhaller & Hessler (1977, 1981) includes species with fused pereonites 6 and 7 and with free pereonites 6 and 7. The fusion of these pereonites is considered to be a phylogenetically informative character, although it occurs convergently in Nannoniscinae in different genera. Thus, the bulbous last article of the antennula is considered to be more informative than a fusion of the pereonites. Species of *Nannoniscoides* possess an elongated last article of the antennula that is clearly inflated in most species of the genus and regarded as long and bulbous (chapter



4.2.2), but not as round as in other Nannoniscinae. Additionally, the last article is not article 5 of the antennula as it is in all species included in Nannoniscinae, it is article 6 or 7.

A fusion of pereonites 6 and 7 occurs in different genera of Nannoniscinae and also in Eugerdellatinae (new species A). It is concluded that a separation of *N. biscutatus* and *N. coronarius* is not based on clear apomorphies. Within *Nannoniscoides*, the two species should be regarded as sistertaxa due to the fusion of pereonites 6 and 7, as both species have all characters that are presented in the diagnosis of *Nannoniscoides* (Siebenhaller & Hessler, 1981) such as the broad and flattened body, an antennula of 6 or 7 articles, an elongated last article of the antennula, robust sensory setae on the corners of pereonite 2, a pereopod I with thin setae on the ventral margins of carpus and propodus except for one distal composed seta on the carpus and an operculum with concavity and calcareous fringe. Therefore, *Nannoniscella* is rejected and *N. biscutatus* and *N. coronarius* re-transferred to *Nannoniscoides*.

### 4.2.1.2 **Desmosomatinae** Hessler, 1970

#### 4.2.1.2.1 ***Balbidocolon*** Hessler, 1970

Type species: *Balbidocolon atlanticum* Hessler, 1970.

According to Hessler (1970), the following apomorphies define the genus:

- pereonite 1 larger than pereonite 2
- pereopod I similar to pereopod II, only propodus somewhat slimmer
- carpus of PI with rows of setae dorsally and ventrally
- pleotelson three-lobed with diverging sides

Originally, the genus is defined by monotypy. Hessler (1970) hypothesized *B. atlanticum* to be most basal in Desmosomatidae due to the similarity of pereopods I and II. In *B. atlanticum*, only the propodus is “somewhat slimmer” (Hessler 1970). The similarity of pereopods is the plesiomorphic condition in the janioridean groundpattern. In *Balbidocolon*, the close similarity of the first two pairs of pereopods is presented as the main character distinguishing the genus from the other genera by Hessler (1970). Comparable relations of the first and second pereopod may be found in *Mirabilicoxa*, but in *Balbidocolon* a dorsal setal row on the carpus of pereopod I is

present while it is absent in most species of *Mirabilicoxa*, not in all. The characters of the pereopod I resemble the rather slender forms of pereopod I as also known in *Momedossa* and *Mirabilicoxa*. Although the strong unequally bifid distal seta in the carpal ventral row resembles already a claw-seta acting as antagonist to the fringed ventral margin of the propodus, the pereopod I of *B. atlanticum* is not chelate. The slightly enlarged pereonite 1 and the presence of a ventral row of composed setae on the carpus distinguish the species clearly from other members of the subfamily Desmosomatinae e.g. *Desmosoma* or *Eugerdia*. The coxal plates are faintly produced and tipped with small stout setae. A high similarity of pereopod I and II is also found in *Whoia*, but in *Whoia* the robust shape of the anterior pereopods is defined as an apomorphy. The propodus is elongated in *Balbidocolon* as in most species of *Mirabilicoxa*. There are no features of pereopod I that may distinguish *Balbidocolon* and *Mirabilicoxa*.

Hessler (1970) described also the three-lobed pleotelson as an important character distinguishing *B. atlanticum* from all other taxa that have a very similar pereopod I. The shape of the pleotelson as described in the diagnosis of Hessler (1970) is an apomorphy of the species, but not an apomorphy of a genus. The form of the pleotelson resembles members of *Mirabilicoxa*, although it differs in width and the position of the posterolateral spines. A rudimentary uropodal exopod as present in *Balbidocolon* occurs also in species of *Momedossa* and *Mirabilicoxa*. All autapomorphies of Desmosomatidae (chapter 4.1.1) are present in the species.

However, it is typological to define a monotypic genus by characters that show the plesiomorphic condition just because no apomorphies can be defined and the species can be distinguished from other species due to diagnostic characters. In the generic diagnosis of *Balbidocolon*, no “true apomorphies” are used to distinguish it from other genera. Thus, it is concluded that despite *B. atlanticum* definitely possesses apomorphies of the family, the genus cannot be characterized by clear autapomorphies. The only character may be the nearly fused two distal articles of the (still) 6-segmented antennula. All other characters also occur in other desmosomatid taxa. The nearly fused articles 5 and 6 of the antennula is an apomorphy of the species, but not an apomorphy of a genus.

*B. polare* Malyutina & Kussakin 1996 should be transferred to *Cryodesma* due to the characters of pereopod I. The condition of pereopod I is very similar to species of this genus (*C. agnari* and *C. cryoabyssale*). Malyutina & Kussakin (1996) had doubts to

assign this species to *Balbidocolon*, as it differs remarkably from *B. atlanticum* in the weakly developed setae on the carpus of pereopod I. The propodus of pereopod I resembles members of the genera *Prochelator*, *Chelator*, *Disparella* or *Oecidiobanchus* and resembles a chela folding with the dactylus as antagonist. The pleotelson is missing. A pereopod I more strongly developed than pereopod II does not fit into the diagnosis of *Balbidocolon* (Hessler 1970).

All apomorphies of *Mirabilicoxa* are found in *B. atlanticum*, while all apomorphies of *Cryodesma* are found in *B. polare*. Therefore, and since *Balbidocolon* is defined by plesiomorphies, the genus is rejected and *B. atlanticum* is transferred to *Mirabilicoxa*, *B. polare* to *Cryodesma*.

##### **4.2.1.2.2     *Desmosoma* Sars, 1864**

Type species: *Desmosoma lineare* (Sars, 1864)

Before 1970 Hessler's monograph was published most species of the family were described as *Desmosoma*, the type genus and only genus of the family until *Eugerdia* was erected by Meinert (1890). The next discussion of the genera of Desmosomatidae was published 75 years later by Kussakin (1965). Hessler's (1970) diagnosis of *Desmosoma* as Kussakin's (1965) followed the original one (Sars 1864) and was based on the inspection of literature (Hessler 1970). The following characters were presented in the diagnosis:

- pereonite 1 moderately to much smaller than pereonite 2
- pereopod I slightly reduced: carpus and propodus moderately attenuated, propodus devoid of setal rows, carpus without dorsal setal row, usually with ventral row of slender setae
- carpus of pereopod II broad, abundantly setose
- pleotelson without posterolateral spines, broadest anteriorly
- uropods uniramous, protopod may or may not be abundantly setose
- sexual dimorphism moderate to slight: in copulatory males pereonites 5 to 7 and pleotelson may be broader, coxae of pereopods I to IV stronger produced than in female

Hessler (1970) noted the similarity to *Echinopleura*. *Echinopleura*-species share all characters presented in the diagnosis of *Desmosoma*, but differ in the simplified incisor process and the serrated body margins (chapter 4.2.1.2.3). The difficulty Hessler (1970) dealt with was that the characters presented as apomorphies of *Desmosoma* were also found in other already existing genera of Desmosomatidae.

This problem was not solved by erecting more new genera that could be defined by clear autapomorphies. Still, there were species remaining in *Desmosoma* that clearly belonged to genera Hessler (1970) erected (chapter 3.1.5.4). Thus, after 1970, several species could be transferred from *Desmosoma* to the genera they fitted in, whereas the remaining species in the genus should be the “true *Desmosomas*”. Some species, including the type species *D. lineare*, are very similar to species of *Eugerdia* as defined by Hessler (1970) and the distinguishing characters remain weak (*D. lineare*, *D. thoracicum*, *D. stroembergi*, compare chapter 4.2.1.2.4). All three species have enlarged posterior legs with carpi and propodi that are broad and comprise rows of long natatory setae, marginal flanges are present from pereonite 5 to the pleotelson and pereopod I is slender, the propodus is elongated.

*Desmosoma atypicum* is transferred to *Pseudergerella* gen. nov. due to the characters of the habitus, pereonite 5, the pleotelson and the setation of pereopod I (chapter 4.2.1.5.1).

*D. ochotense* and *D. hesslera* show characters that are defined as apomorphies for *Eugerdia*, as in *Eugerdia* species, the posterior pereonites are enlarged and the limbs are heavily built. In *D. hesslera* pereonite 2 is the largest of the four anterior pereonites. As in *E. tetarta*, a row of long composed setae is present ventrally on the carpus of pereopod I. The only distinguishing character is the uniramous uropod. The exopod may have been reduced more than once in Desmosomatidae. Therefore, this character is too weak to base a genus definition on. If the genus definition is not clear, the uniramous uropod can be used as a distinguishing character at species level, not at generic level.

Due to the high similarity of species of *Desmosoma* and species included in group 1 and 2 of *Eugerdia* (chapter 4.2.1.2.4), it is proposed to transfer these species to *Desmosoma*, because this allows a generic diagnosis that distinguishes the genera. It is hypothesized that the species in group 1 and 2 of *Eugerdia* and those included in *Desmosoma* are closely related.

The tendency to an extremely elongated and attenuated pereopod I in *Eugerda* is discussed below (chapter 4.2.1.2.4). Species of group 3 are transferred to *Pseudogerda* (Kussakin, 1965); a modified diagnosis of this genus is presented in chapter 3.1.4.3.22.

### **4.2.1.2.3     *Echinopleura* Sars, 1897**

Type species *Echinopleura aculeata* (Sars, 1864)

According to Hessler (1970), the following characters define the genus:

- mandible with simplified incisor process
- margins of body strongly serrate
- pereonites 1 and 2 nearly equal in size
- pereopod I as large as pereopod II, propodus elongated (more than 3.5 times longer than wide) and without setae, carpus with row of ventral setae

Originally, the genus was designated by monotypy. In the present study *E. cephalomagna* sp. nov. is added. Hessler (1970) stated that the independence of this genus was based primarily on the aberrance of its only species (Sars 1899) and noted the similarity to the characters present in *Desmosoma*. A simplified mandible, a lacinia mobilis reduced to one short tooth and the strongly serrated body ornamentation is present in *E. cephalomagna* sp. nov. (chapter 3.1.5.2.7) as in *E. aculeata*. These characters are regarded as phylogenetically informative (chapter 4.2.2.2).

### **4.2.1.2.4     *Eugerda* Meinert, 1890**

Type species: *Eugerda tenuimana* (Sars, 1868)

Species descriptions since Hessler's monograph in 1970 present no modified diagnosis of the genus until George (2001) shortcuts Hessler's (1970) diagnosis presenting no better definition of autapomorphies. The genus defining characters according to Hessler (1970) are (comparison in Table 6):

- uropods biramous, exopod always well developed, protopod often abundantly setose distally
- pereonite 1 moderately to much smaller than pereonite 2
- pereopod I slightly to strongly reduced and attenuated; propodus without major setae; carpus without major setae except for primitive forms
- carpus of pereopod II broad, often with comb of small spines inserting distoventrally
- sexual dimorphism pronounced, in copulatory male, pereonites 5 to 7 and pleotelson with broad marginal flanges and coxae of pereopods I to IV produced anteriorly, with stout terminal setae
- Pleotelson without posterolateral spines.

According to George (2001), *Eugerda* is closely related to *Desmosoma*. There is a high similarity in the characters as discussed above (chapter 4.2.1.2.2). The intermediate forms show a trend towards an elongated and extremely slender pereopod I (see Table 6). Following the definition *sensu* Hessler (1970), the genera could not clearly be separated by the characters of pereopod I. Regarding the results of the character comparison (Table 6), a gradual transformation series is seen in *Eugerda sensu* Hessler (1970) in the form of the pereopod I in elongation and specialization. As result, the genus can be divided into four groups of species:

Group 1: *E. tetarta*, *E. renatae* sp. nov. and *E. zenkewitchki*; transferred to *Desmosoma* (chapter 4.2.1.2.2)<sup>4</sup>:

Pereopod I more slender than pereopod II, still rather heavily built. Propodus ventrally with few slender setae, on ventral margin of carpus row of unequally bifid setae present, dorsally on carpus row of slender setae present. Pereonite 1 still reaches 0.7 times the length of pereonite 2 while it reaches at most 0.6 times the length of pereonite 2 in all other species of *Eugerda*. The specialization of pereopod I as found

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<sup>4</sup> For some species, a missing pereopod I causes difficulties in clarifying their systematic position. In following species described in *Eugerda sensu* Hessler (1970) the main character (pereopod I) to distinguish *Eugerda* from *Desmosoma* is missing from the described specimens: *E. imbricata* Hessler, 1970; *E. pannosa* Hessler, 1970, *E. dubia* Malyutina & Kussakin 1996, *E. gurjanova* Malyutina & Kussakin 1996, *E. mandibulata* Malyutina & Kussakin 1996. In the case of *E. svavarssoni* George, 2001 it is not presented in the badly done description. *E. imbricata* and *E. pannosa* are transferred to *Desmosoma* because they have all apomorphies defined for *Desmosoma*. They are most similar to in the habitus to *E. renatae* sp. nov. and *E. tetarta*. Due to damage and incomplete description the systematic status of the four remaining species is uncertain and these species remain in *Eugerda* for the time being.

in group 1 is similar to the specialization found in *Desmosoma* e.g. in the type species *Desmosoma lineare* Sars, 1864, in *D. thoracicum* or *D. ochotense*.

Group 2: *E. gigantea* and *E. latipes*; transferred to *Desmosoma* (chapter 4.2.1.2.2):

Pereopod I slender, distinctly shorter than pereopod II, propodus with slender setae ventrally, carpus with finely serrated thin setae and small setae ventrally This condition of pereopod I is also present in *D. strombergi*. This kind of setation is found in *D. lobipes* although the carpus is not that elongated.

Group 3: *E. intermedia*, *E. elegans*, *E. arctica*, *E. anversense*, *E. kamchatica*, *E. fragilis* and *E. globiceps*<sup>5</sup>; transferred to *Pseudogerda* (chapter 4.2.1.2.7):

Pereopod I very slender, slightly attenuated (propodus about 9 times longer than wide, carpus about 5 times longer than wide), carpus and propodus ventrally and dorsally with few setae. Species of this group differ from the condition of pereopods found in *Desmosoma*. No species in *Desmosoma* shows this reduction of setae combined with the elongation of carpus and propodus. Although the diagnosis of *Pseudogerda* presented in this study (chapter 3.1.4.3.22) differs slightly from Kussakin's (1965) original one, his concept of *Pseudogerda* to exclude species that do not show the extremely attenuation of pereopod I from *Eugerda* is followed.

Group 4: *E. reticulata*, *E. fulcimandibulata* and the type species *E. tenuimana* (<sup>2</sup> see foot-note behind *E. globiceps*); remaining in *Eugerda*:

Pereopod I is strongly attenuated (propodus 15-19 times longer than wide, carpus 11-15 times longer than wide), setae are absent on propodus and carpus.

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<sup>5</sup> Hessler (1970) summarized the confusion about the status of the species *Eugerda tenuimana* and concludes that three valid species emerge from this confusion:

(1) *E. tenuimana* (Sars, 1868) including *E. globiceps* Meinert, 1890 and Sars, 1899 and *Desmosoma lobiceps* Blake, 1929;

(2) *E. filipes* (Hult, 1936) including *E. tenuimana* as described by Sars 1897;

(3) *E. intermedia* (Hult, 1936).

After working with the type material, it became obvious that *Desmosoma tenuimanum* as described by Sars in 1868 and refigured as *E. tenuimana* in 1897 is the same species (Sars 1868, 1897). A mistake was done by Hult (1936) by giving the species another name (*D. filipes*). The valid species name is *E. tenuimana* (Sars, 1868). Thus, this species as drawn by Sars (1897) is the type species of *Eugerda*. *E. globiceps* is considered to be a separate species after comparing Sars's (1868, 1897) and Meinert's (1890, Sars 1899) material. *D. lobiceps* Blake, 1929 is a synonym of *E. globiceps* (compare Hessler 1970). Thus, following species are valid:

(1) *E. tenuimana* (Sars 1868) (Sars 1897; described as *D. filipes* by Hult (1936));

(2) *E. globiceps* Meinert, 1890 (described by Sars (1899) and synonym with *D. lobiceps* Blake, 1929);

(3) *E. intermedia* (Hult, 1936).

The diagnosis presented by Hessler (1970) combines the genera *Eugerdia* Meinert, 1890 and *Pseudogerdia* Kussakin, 1965 to one genus. Hessler (1970) put *Pseudogerdia* into *Eugerdia* as a junior synonym. Unlike Kussakin's (1965) diagnoses of the genera he included species in *Eugerdia* that have a rather robust than extremely attenuated first pereopod. The absence of the mandibular palp was ignored as character. Kussakin (1965) erected *Pseudogerdia* for some species of *Eugerdia* and distinguished the genus by a narrow pereonite 1, a slender pereopod I and a mandibular palp of three articles.



#### 4. Discussion

**Table 6 : *Eugerda* Meinert, 1890: comparison of characters according to Hessler (1970)** (Only completely described species are used.)

| <i>species</i>   | posterolateral spines at pleotelson                      | uropodal exopod well developed, protopod abundantly setose | pereonite 1 moderately to much smaller than pereonite 2 (midsagittal length)            | trend of specialization of pereopod I: slightly to strongly attenuated?                 | PI: setae on propodus  | PI; setae on carpus  | carpus of pereopod II broad (length to width ratio)    | carpus of PII: setation? | carpus of PII: comb of small spines distoventrally | body: setose?   |
|--|--|--|---|---|--|--|--|--------------------------|--|-----------------|
| <i>E. anversense</i> (Schultz , 1979) preparatory female | (pleotelson is missing from the only available specimen) | missing  | Pereonite 1 0.25 of length of pereonite 2 (pereonite 2 4 times longer than pereonite 1) | Slender, propodus about 6 times longer than wide, carpus about 7 times longer than wide | 1 distal dorsal seta, 1 midventral seta and 2 distal ventral setae, no "major setae" | 2 simple slender setae ventrally (one midway, one distal) as well as 2 simple slender seta in the same position dorsally | About 2.8 times (estimated! 3.6:1.3) longer than wide  |                          | absent   | Slightly setose |
| <i>E. arctica</i> Svavarsson , 1988 preparatory female   | Absent in both sexes                                     | Half of size of endopod                                    | 0.6 times of length of pereonite 2  | Slender, propodus 6.5 times longer than wide, carpus 5.6 times longer than wide         | Absent (only 2 distal small setae)   | Absent (only small setae)  | Yes (broader than propodus) 2.9 times longer than wide |                          | absent   | smooth          |
| <i>E. elegans</i> Kussakin , 1965                        | Absent in female drawn                                   | Half of length of endopod                                  | About 0.5 of midsagittal length of pereonite 2  | Slender, propodus about 9 times longer than wide, carpus 5 times longer than wide       | No setae   | Absent, only 1 small distal ventral seta and 1 dorsal distal seta  | Carpus about 2 times longer than wide                  |                          | absent   | smooth          |

#### 4. Discussion

|  |   |   |  |   |   |   |  |  |         |                 |
|--|---|---|--|---|---|---|--|--|---------|-----------------|
| <i>E. intermedia</i><br>(Hult, 1936)<br>(drawings in Hessler 1970)   | Absent in female, if present in male ?    | One third (0.34 times) of length of endopod         | Pereonite 2 1.5 times longer than pereonite 1                          | <b><u>slender</u></b> , propodus 8.6 times longer than wide; carpus 7.2 times longer than wide                            | Absent (only 5 small setae)                                 | Absent (only 1 small seta)  | 2.9 times longer than wide, clearly broader than carpus of pereopod I.       |  | present | Setose (?)      |
| <i>E. latipes</i><br>(Hansen, 1916) (after drawings in Hessler 1970) | Absent in female and male                 | Exopod 0.48 length of endopod                       | 0.43 of length of pereonite 2  | <b><u>Reduced and slender</u></b> , propodus 5.2 times longer than wide; carpus 4.8 times longer than wide                | Absent (few small distal setae and 1 midventral small seta) | 2 slender setae, 2 small setae dorsally resembling in their position a reduced dorsal row               | 1.9 times longer than wide, clearly broader than carpus of pereopod I.       |  | absent  | smooth          |
| <i>E. fulcimandibulata</i> Hessler, 1970                             | Absent in female and male                 | 0.2 times of length of endopod                      | 0.6 of length of pereonite 2   | <b><u>Extremely attenuated</u></b> , propodus 15.2 times longer than wide; carpus 11.8 times longer than wide             | No setae  | No setae  | Carpus 2.8 times longer than wide, more than clearly broader than pereopod I |  | present | Slightly setose |
| <i>E. gigantea</i> Park, 1999  | Absent in holotype female, no males known | Exopod slightly longer than half of size of endopod | Narrower and shorter than pereonite 2<br>Length 1:0.8<br>Length 2: 1.3 | <b><u>Slender, distinctly shorter than PII</u></b> ; propodus 4.1 times longer than wide; carpus 4 times longer than wide | Five "major setae" (slender setae) ventrally                | Five major finely serrated thin setae and further small setae (may this condition be defined as row???) | Not broader than PI: 4.4 times longer than wide                              |  | absent  | smooth          |

#### 4. Discussion

|   |   |  |  |   |   |  |  |  |         |   |
|---|---|--|--|---|---|--|--|--|---------|---|
| <i>E. kamtschatica</i> Kussakin , 1965  | Absent in female drawn  | Slightly longer than half of length of endopod | About 0.45 of length of pereonite 2                            | Slender, propodus about 9.5 times longer than wide, Carpus about 4 times longer than wide                   | No major setae, bunch of small distal setae ventrally and 2 small setae distaldorsally      | No major setae, on midventral simple seta and 1 distal dorsal small seta   | Carpus clearly broader, about 1.9 times longer than wide |  | absent  | smooth  |
| <i>E. reticulata</i> (Gurjanova , 1946) (Preparatory female in Svavarsson 1988) | In female absent, in male present as well as marginal flanges at pleotelson | Smaller than 1/3 of size of endopod            | Around 0.6 times of length of pereonite 2                      | <b><u>Strongly attenuated.</u></b> Propodus 18.8 times longer than wide, carpus 15 times longer than wide   | Absent (no setae)   | Absent (no setae)  | Not really broad... 4.2 times longer than wide           |  | absent  | smooth  |
| <i>E. tetarta</i> Hessler , 1970  | Absent in female and male   | One third of length of endopod                 | 0.78 of length of pereonite 2                                  | <b><u>Rather heavily built.</u></b> Propodus 5.2 times longer than wide; carpus 3 times longer than wide.   | Ventrally fringed, row of 3-4 "major setae" terminating distally in a tuft of 3 small setae | Ventral row of robust unequally bifid setae increasing in size (length) towards propodus and dorsal row of 5-6 slender setae | Carpus 3.1 times longer than wide                        |  | absent  | smooth  |
| <i>E. zenkewitschi</i> (Gurjanova , 1946)                                       | Absent in drawings of original species description                          | Nearly half of length of endopod               | Much smaller than pereonite 2: one third of midsagittal length | <b><u>Rather heavily built.</u></b> propodus 2 times longer than wide and carpus 1.9 times longer than wide | 1 midventral long slender seta, dorsally a row of 3 long slender setae                      | Ventral row of 4 composed setae; dorsally a row of 4 long setae  | missing  |  | missing | Seems to be smooth (as estimated from drawings) |

### 4.2.1.2.5 *Mirabilicoxa* Hessler, 1970

Type species: *Mirabilicoxa gracilipes* (Hansen, 1916)

The genus was erected by Hessler (1970). George (2001) presented a modified diagnosis of the genus, but used Hessler's (1970) words. This did not clarify the apomorphies. The most important apomorphy seems to be the sexual dimorphism as already stated in Hessler's (1970) original diagnosis. The following characters were presented in the generic diagnosis (Hessler 1970):

- body presenting a continuous profile
- coxae of pereopods I to IV in females moderately produced, in copulatory males enormously produced
- pereopod I moderately reduced and attenuated, propodus without major setae, carpus with row of major ventral setae, rarely with dorsal setae
- carpus of PII slender, with few setae
- pleotelson with posterolateral spines

All other characters presented in the diagnosis do also occur in other genera of Desmosomatinae. The diagnosis was not clear concerning the characters of pereopod I. The question remains how species of *Mirabilicoxa* can be distinguished from species of *Desmosoma* (chapter 4.2.1.2.2) or *Momedossa* (chapter 4.2.1.2.6). Pereopod I and II are of similar shape, while pereopod I is slightly more slender in all species of the genus except in *Mirabilicoxa coarctata* (chapter 4.2.1.3.5). Thus, the species does not clearly fit into the genus, although it shows all other characters. In *Mirabilicoxa* the propodus of pereopod I lacks setae; a ventral row of long composed setae increasing in length towards the propodus is present on the carpus. Dorsal setae on the carpus occur sporadically.

Hessler (1970) explained the questionable value of the presence or absence of the mandibular palp with examples of the genus *Mirabilicoxa*. Only two of the eleven species he included into the genus bear a palp (*M. longispina* and *M. palpata*). The character mostly used to distinguish species of this genus from species of *Eugerdia*, *Desmosoma* or *Momedossa* are the enormous projections of the coxae as they occur in male individuals. In females this character is not that obvious.

To distinguish females of *Mirabilicoxa* from females of *Momedossa* Hessler (1970) uses the length of the pereopods (chapter 4.2.1.2.7). *Momedossa* can be clearly distinguished by characters of pereopod I and the mandible (chapter 4.2.1.2.7).

The pronounced sexual dimorphism as described by Hessler (1970) e.g. the enormous projections of the coxae on pereopods I to IV and the conspicuous marginal flanges on pereonites 5 to 7, cannot be regarded as apomorphy. Marginal flanges occur also in *Desmosoma* or *Eugerdia* or in males of *Chelator*. If the pronounced elongations of the coxae also occur in males of other genera is not clear, because males are not known for every described species. In most species the coxae of males are more produced than those of females. Thus, this apomorphy of *Mirabilicoxa* is weak. Only the combination of the presence of produced coxal elongations and the presence of a row of long composed setae ventrally on the carpus of pereopod I allows to characterize the genus.

### 4.2.1.2.6 *Momedossa* Hessler, 1970

Type species: *Momedossa profunda* Hessler, 1970

According to Hessler's (1970) diagnosis of the genus, the only distinguishing character to *Mirabilicoxa* are the long pereopods, all other characters are also found in *Mirabilicoxa*:

- incisor process large, shelf-like
- pereonites 1 and 2 subequal
- pereopods long in relation to the length of the animal
- pereopod I slender, carpus and propodus somewhat attenuated, propodus without setal rows, carpus with row of composed setae ventrally
- pleotelson with posterolateral spines
- uropods biramous (exopod reaching less than one third of endopod length)

The genus is very similar to *Mirabilicoxa*, but differs from *Mirabilicoxa* in the characters of the mandible. In *Momedossa* the incisor process is large and formed shelf-like. To distinguish females of *Mirabilicoxa* from females of *Momedossa* Hessler (1970) uses the length of the pereopods. Both species of *Momedossa* have very long pereopods and the pereopods are setose (carpi with more than 15 setae in the ventral and dorsal rows). To describe the length in ratios does not clarify the terminus "long". The pereopods are long in relation to the length of the animal compared to species of *Mirabilicoxa*. *Momedossa* can be clearly distinguished by characters of pereopod I: the setae in the ventral row on carpus of pereopod I are of nearly similar

length slightly increasing towards the propodus and the distal setae in clearly longer than the rest.

### **4.2.1.2.7     *Pseudogerda* Kussakin, 1965**

Type species: *Pseudogerda filipes* Kussakin, 1965

The genus is re-established based on the characters of pereopod I that show the tendency to attenuation, but not as found in species of *Eugerdia* (chapter 4.2.1.2.4). Characters presented in Kussakin's (1965) original diagnosis are:

- mandibular palp of 3 articles
- pereonite 1 short, about half as long as pereonite 2
- pereopod I slender, carpus and propodus elongated, carpus with few ventral setae
- pereopods V-VII modified for swimming, carpi and propodi expanded, with many long setae

The main difference between the original diagnosis (Kussakin 1965) and the diagnosis presented here is, that species with a slender but rather heavily built pereopod I are excluded and are regarded as members of *Desmosoma* as discussed in chapter 4.2.1.2.2.

### **4.2.1.2.8     *Torwolia* Hessler, 1970**

Type species: *Torwolia creper* Hessler, 1970

Hessler (1970) explained that the condition of pereopod I is well documented by a series of intermediate types except for the subchelate condition found in *Torwolia*. In contrast to most diagnoses presented by Hessler (1970) the diagnosis of *Torwolia* is very clear presenting following characters:

- pereonite 1 reduced
- pereopod I small, subchelate, carpus broad, but short, propodus enlarged and elongated, dactylus reflected downward and opposing ventral margin of propodus
- pereonite 2 and pereopod II enlarged

In the groundpattern of Janiroidea (chapter 3.1.2) the pereopods are subchelate in the plesiomorphic condition. Thus, an evolution back from a non-subchelate condition

to a subchelate condition as proposed by Wägele (1989) would need two evolutionary steps. This may lead to the conclusion that the condition of the pereopod I as found in the species of *Torwolia* is more plesiomorph than the condition found in *Balbidocolon* although Hessler's (1970) arguments seem to be trustworthy. This is not the case, because the subchela in *Torwolia* is correlated with a reduction of size of this limb and pereonite 1. Additionally, pereopod I is slender except the modified propodus. The subchela must be a result of loss of setation and an specialization of the propodus, the elongated propodus indicates a former walking condition of the limb (Wilson 1987). Due to the characters of the posterior pereopods and the reduction in size of pereopod I a close relationship to *Desmosoma*, *Pseudogerda* and *Eugerdia* is postulated.

The remarkable enlargement of pereonite 2 correlating to the specialization of pereopod II is found in most, but not all, species of *Eugerdia*, *D. hessleri* and also in *Torwolia*. Somehow the enlargement of pereonite 2 may correlate with specializing and reducing the "size" of the first limb, using the second limb in a different, but important way.

Since 1970 the genus is treated as a subfamily *incertae sedis*, because Hessler (1970) preferred to leave the subfamilial affinities open; no clear position of the genus is found in the literature. Following the arguments presented above, *Torwolia* is regarded as member of Desmosomatinae.

### **4.2.1.3 Eugerdellatinae Hessler, 1970**

The difference between the original diagnosis of this subfamily and the diagnosis presented in this study (chapter 3.1.4.2.3) is that all species with a robust pereopod I are included. According to Hessler (1970) only the species with a chelate or raptorial pereopod I belonged to this subfamily. Here, *Thaumastosoma* and *Whoia* are assigned to Eugerdellatinae as discussed below (chapter 4.2.1.3.11 and 4.2.1.3.12).

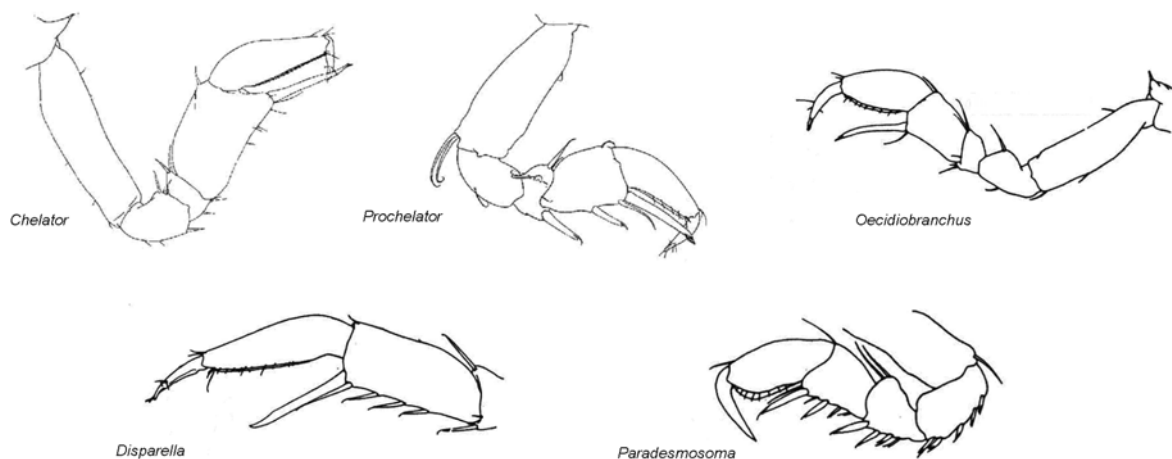
#### **4.2.1.3.1 Chelator Hessler, 1970**

Type species: *Chelator insignis* (Hansen, 1916)

Hessler (1970) presented the following characters in the original diagnosis of the genus:

- first pereopod large, chelate
- claw formed by large distoventral seta on the carpus
- carpus enlarged
- carpus distinctly produced at base of claw
- ventral margin of carpus with small setae (behind claw-seta)
- pleotelson without posterolateral spines in female
- uropods uniramous

Strong emphasis was laid on the comparison with *Prochelator* as also done in the diagnoses of *Disparella* and *Oecidiobanchus* (Hessler 1970). The carpus in species of *Chelator* is enlarged and distinctly produced at the base of the claw-seta. None of the ventral small setae is defined as “accessory seta”, a terminus Hessler (1970) used for the unequally bifid seta and the slender seta proximal to the claw-seta in the species of *Prochelator*. In all chelate forms, not only in *Chelator*, the claw is formed by a large distoventral seta on the carpus and the propodus. Apomorphies of *Chelator* are the production of the carpus at the base of the claw and the presence of only small setae behind the claw-seta. For a comparison of *Chelator* and *Prochelator* see chapter 4.2.1.3.9. Characters that distinguish *Disparella* from *Chelator* are the elongated propodus of pereopod I, the distinct spine at the margin of the antennular fold, a lacinia mobilis with 4 or 5 teeth and the biramous uropods.



**Fig. 116:** Pereopod I of the genera *Chelator*, *Prochelator*, *Oecidiobanchus*, *Disparella* and *Paradesmosoma*: differences in the setation on the ventral margin of the carpus.

Pereopod I is enlarged in *Chelator* as in all Eugerdelatinae (*sensu* Hessler 1970). The character confirming the close relationship to *Disparella* is the type of setation on



the ventral margin of the carpus: setae behind claw-seta small, of similar size and type. This kind of setation is not found in *Prochelator* although two species (*P. incomitatus* and *P. angolensis*) have a small seta behind the midventral seta that is defined as apomorphy for species of the genus *Prochelator*. These two species also possess extremely small posterolateral spines at the pleotelson. This is an intermediate condition “between” the genera *Chelator* and *Prochelator*. To define the absence of posterolateral spines in species of *Chelator* as apomorphy is weak because males may have posterolateral spines. It is true that all species of *Chelator* have uniramous uropods, but uniramous uropods do also occur in two species of *Prochelator* (*P. angolensis* and *P. incomitatus*) and *Oecidiobranchus*; members of *Disparella* have always biramous uropods with well developed exopods. As clear apomorphies of *Chelator* remain the characters of pereopod I.

##### **4.2.1.3.2     *Chelibranchus* Mezhov, 1986**

Type species: *Chelibranchus canalicatus* Mezhov, 1986

The existence of this monotypic genus with the species *Chelibranchus canalicatus* Mezhov, 1986 is questioned. Mezhov (1986) presented following characters in the generic diagnosis:

- body more than 4 times longer than wide,
- pereonites subequal in width
- frontal projection of head concave
- pereonite 1 longer than pereonite 2
- pereonites 3, 5 and 6 subequal or pereonite 6 slightly longer than 5
- anterolateral margins of pereonite 5 rounded
- coxae of pereopods I to IV subequal in size (angular, not produced)
- pleotelson of rounded-pentagonal shape without posterolateral spines
- flagellum of antennula with partially fused articles
- pereopod I with elongated articles: carpus more than 2 times longer than wide, distoventral seta almost as long as propodus (chela), propodus 1.5 times longer than dactylus
- operculum broadened distally, distal margin deeply concave
- uropods uniramous, protopod extending beyond distal margin of pleotelson, endopod broad

Although Mezhov (1986) described characters in the text, they were not visible in the drawings or they were completely missing in the described specimen. The drawings of the only species of this genus are insufficient, no pereopod is presented completely. Mezhov (1986) documented only 2 female specimens, both without pereopods. No information is given about the developmental stage of the holotype. Due to the importance of the first pereopod, it is impossible to define a genus without describing the characters of this first pereopods. When Mezhov (1986) described the genus he used an example of another species for some characters e.g. pereopod I *Chelator brevicaudus* (Menzies & George, 1972).

Mezhov (1986) suggested to put *Desmosoma lineare* G.O. Sars, 1864 into *Chelibranchus*, which is irritating, because this species is the type species of *Desmosoma*. Furthermore, the characters of pereopod I of *Desmosoma lineare* are totally different from those of the species with a chelate pereopod I.

Kussakin (1999) added *Nymphodora fletcheri* (Paul & George, 1975) to *Chelibranchus*. This is noteworthy, because this species is definitely a nannoniscid as redescribed by Kaiser (2005). This underlines the impression that *Chelibranchus* is badly defined due to missing characters.

The differences in the body shape to other desmosomatid genera are not remarkable enough to define a new genus. Only the strongly concave dorsal margin of the operculum differs from all other Desmosomatidae. However, this may be a result of describing a juvenile. This remains guessing without having a look at the type material. The whole definition of *Chelibranchus* as a new genus as done by Mezhov (1986) is based on speculation. Thus, *Chelibranchus* is not accepted as a genus and is rejected. As the species description does not allow an allocation to one of the other genera, the genus becomes *incertae sedis*.

##### **4.2.1.3.3     *Cryodesma* Svavarsson, 1988**

Type species: *Cryodesma agnari* Svavarsson, 1988

*Cryodesma* was designated by monotypy with the only species *C. agnari* by Svavarsson (1988). The following characters were presented in the generic diagnosis:

- pereonite 1 larger than pereonite 2
- pereopod I more strongly developed than pereopod II

- pereopod I: propodus broad with convex ventral margin without major setae, carpus with ventral row of composed setae, most distal seta as long as penultimate one
- carpus of pereopod II abundantly setose<sup>6</sup>, ventral setae stout
- uropods uniramous
- pleotelson with posterolateral spines, widest at position of spines
- sexual dimorphism pronounced in pleotelson shape, in males coxa of pereopod I produced and more setae on posterior pereopods than in females

Svavarsson (1988) hypothesized a close relationship of *Cryodesma* and *Eugerdella* due to a stout pereopod I that bears a row of composed ventral setae on the carpus while the dorsal margin of the carpus has nearly no setae. Most similar to *C. agnari* is *E. minutula* possessing no short but a distal seta that is the longest of all irregular ventral setae on the carpus. According to Svavarsson (1988) *C. agnari* shows also affinity to *Mirabilicoxa atlanticum* Hessler, 1970 and *Momedossa profunda* Hessler, 1970. The female individuals of the species are wide anteriorly and very slender posteriorly. Both species bear posterolateral spines on the pleotelson. The first pereopod of *M. profunda* and *M. atlanticum* differs clearly in having a slender propodus. In *Momedossa*, the carpus is 3.3 times longer than wide, clearly longer than in *M. atlanticum* (2.1 times longer than wide) or *C. agnari* (1.8 times longer than wide).

Furthermore, *C. polare* Malyutina & Kussakin, 1996 resembles *C. agnari* in the characters of the first pereopod. The species is transferred to *Cryodesma* (chapter 4.2.1.2.1). In *C. agnari*, the two distal setae of the carpus ventral row are of similar length. In *C. polare*, the most distal seta is slightly longer and a row of dorsal setae is present on the carpus, which is absent in *C. agnari*. Although the pleotelson is missing in *C. polare*, the dorsal view of the body resembles much *C. agnari* regarding the form and shape of the pereonites. The elongated incisor process of the mandible represents a distinguishing character, possessing two teeth in *C. agnari*, while it is more stout and possesses three teeth in *C. polare*. The condition of a chelate pereopod I as found in species of *Cryodesma* may show a condition “between” the development of an enlarged claw-seta and a large distal seta in the ventral setal row

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<sup>6</sup> The terminus “setose” is difficult to define (chapter 4.2.2.1). How many setae must be present to describe the condition of a limb as setose? Here, the species possesses more than 10 setae in the setal rows on the carpus.

with setae increasing in length towards the propodus (see also chapter 4.2.1.2.1). This condition is found in *C. polare*.

### 4.2.1.3.4 *Disparella* Hessler, 1970

Type species: *Disparella valida* Hessler, 1970

Three species of the genus were known: *Disparella valida* Hessler, 1970, *D. pachythrix* Hessler, 1970 and *D. longimana* (Vanhoeffen, 1914). To these two species are transferred: *Desmosoma neomana* (Menzies & George, 1972) and *Desmosoma funalis* (Menzies & George, 1972). *Disparella maiuscula* was described recently including a detailed discussion of species of the genus (Kaiser & Brix 2005). *Disparella kensleyi* sp. nov. is described in the present study (chapter 3.1.5.3.6). The characters Hessler (1970) gave most weight in the original diagnosis were:

- cephalic spines lateral to antennae
- shelf-like incisor tooth
- carpus of pereopod I not produced at base of claw, ventrally with row of small setae behind claw-seta

Cephalic spines occur also in members of *Prochelator*. In comparison with members of *Prochelator*, *Disparella* possess longer cephalic spines. Furthermore, the modifications of the mouthparts, especially the shelf-like incisor tooth and the lacinia mobilis with 4 or 5 teeth differ clearly from *Prochelator*. Due to the similarity to other “chelate genera” Hessler (1970) hypothesized a common ancestor of this group. (For a discussion of the ventral setae on the carpus of pereopod I see chapter 4.2.1.3.1.) In this study a monophyly of all chelate species is hypothesized, as already presented by Wägele (1989). The genus is clearly to distinguish from *Prochelator* and *Chelator* by the elongated propodus of pereopod I (chapter 4.2.1.3.1). *Disparella* and *Chelator* share the presence of a row of small setae behind the claw-seta. While in *Chelator* this row may be absent (or represented by a single small seta as for example in *Chelator verecundus*), the row is always well developed in species of *Disparella* (except *Disparella kensleyi* sp. nov.).

### 4.2.1.3.5 *Eugerdella* Kussakin, 1965

Type species: *Eugerdella natator* (Hansen, 1916)

Hessler (1970) modified the diagnosis of the genus in a way that nearly no similarities to the original diagnosis of Kussakin (1965) remain. The inclusion of *E. armata* Sars, 1864 (the type species of Kussakin's 1965 genus *Desmosomella*) and *E. coarctata* Sars, 1899 in *Eugerdella* caused major changes in the generic diagnosis. Hessler's (1970) diagnosis is not clear in the following characters:

- pereopod I similar in size and shape to pereopod II or much more powerfully developed;
- pereonite 1 larger, as large as or smaller than pereonite 2;
- pleotelson with or without anterolateral spines;
- transverse ridge on frons and frons clypeal furrow may or may not be present.

Table 7 (comparison of characters) shows examples of the variability in *Eugerdella*. Interestingly, the robust shape of the first pereopod correlates with the body form. The genus may be divided into 4 groups based on the characters of the first pereopod and the presence of ventral spines on the first 5 pereonites:

- group 1: *E. serrata* and *E. pugilator*
- group 2: *E. ischnomesoides* and *E. hessleri*, species are transferred to *Pseudergella* gen. nov. as discussed below (chapter 4.2.1.5.1)
- group 3: *E. natator* and *E. coarctata*
- group 4: *E. theodori*, *E. rotunda*, *E. polita*, *E. ordinaria*, *E. nonfunalis*, *E. minutula* and *E. falklandica*

Transferring the species *E. cornuta* Hessler, 1970 into *Mirabilicoxa*, Kussakin (1999) was the first in trying to clarify the generic composition of *Eugerdella*. Previously Svavarsson (1984) mentioned the need to discuss the characters in this genus. When transferring *Pseudomesus* into Desmosomatidae because of its high similarity to *E. ischnomesoides* Hessler, 1970 (now *Pseudergella*, chapter 4.2.1.5.1) Svavarsson (1984) explained the need to re-examine the genus *Eugerdella* to obtain a better understanding of evolutionary trends within Desmosomatidae.

The high morphological variability puts the monophyly of the genus in question. In Hessler's (1970) diagnosis, strong emphasis was placed on the carpus of pereopod I and the most distal ventral seta that is shorter than the penultimate one. He stated that this character is the only one he is able to see as a synapomorphy of this genus.

In fact, every member of *Eugerdella* possess such a seta, but even this seta may vary in size and form. There is no relation presented. Consequently, *Eugerdella* must be considered a paraphylum.

**Table 7** : Examples of character variability in *Eugerdella*

| species  | pereopod I in comparison to pereopod II  | type, size (length in relation to penultimate seta) of distal seta in ventral row on carpus | platform-like gap | pereonite 1 in comparison to pereonite 2 from dorsal                         | ventral elongations on pereonites 1 to 5     |
|--|--|---|-------------------|--|--|
| <i>E. serrata</i> sp. nov.<br><b>group 1</b>   | enlarged, carpus and propodus twice as broad as in pereopod II                                       | unequally bifid, one third to and half of length of penultimate seta                        | present           | pereonite 1 much longer and slightly broader than pereonite 2                | present                                      |
| <i>E. pugilator</i> Hessler, 1970<br><b>group 1</b>                                    | enlarged, carpus and propodus twice as broad as in pereopod II                                       | unequally bifid, one third to half of length of penultimate seta                            | present           | pereonite 1 much longer and slightly broader than pereonite 2                | present                                      |
| <i>E. hessleri</i> Just, 1980<br><b>group 2 (transferred to Pseudergella)</b>          | not enlarged, slightly more robust than pereopod II, capus of nearly similar shape as in pereopod II | unequally bifid, much smaller than penultimate seta (not reaching 1/3 of length)            | absent            | slightly smaller in length, but of similar width as pereonite 2              | absent                                       |
| <i>E. ischnomesoides</i> Hessler, 1970<br><b>group 2 (transferred to Pseudergella)</b> | not enlarged, similar in shape to pereopod II  | unequally bifid, much smaller than penultimate seta (not reaching 1/3 of length)            | absent            | smaller in length and slightly smaller in width                              | absent                                       |
| <i>E. coarctata</i> (Sars, 1899) <sup>7</sup><br><b>group 3</b>                        | ? <sup>8</sup> , but pereopod I seems to be enlarged   | Distal setae nearly as long as penultimate one according to drawings in Kussakin (1999)     | absent            | of nearly similar size   | absent                                       |
| type: <i>E. natator</i> (Hansen, 1916)<br><b>group 3</b>                               | carpus of pereopod II longer and not as broad as carpus of pereopod I                                | unequally bifid, slightly longer than half of length of penultimate seta                    | absent            | wider and longer than pereonite 2 although from lateral nearly equal in size | absent                                       |
| <i>E. minutula</i> Mezhov, 1986<br><b>group 4</b>                                      | enlarged, carpus more stout and nearly 3 times   | Distal seta biggest in row forming chela together with                                      | absent            | pereonite 1 slightly broader and longer than pereonite 2                     | no lateral view of the animal in description |

<sup>7</sup> This species was synonymized with *E. natator* by Hult 1936 and 1941; according to Hessler (1970), these are two separate species because of the different shapes of pereonite 5.

<sup>8</sup> Pereopod II is missing in the drawings, the holotype needs to be inspected for details.

#### 4. Discussion

|  |  |   |                       |   |  |
|--|--|---|-----------------------|---|--|
|  | broader than in pereopod II <sup>9</sup>                         | propodus <sup>10</sup> .  |                       |   |  |
| <i>E. nonfunalis</i> sp. nov.<br><b>group 4</b>              | enlarged, carpus and propodus twice as broad as in pereopod II   | unequally bifid, half of length of penultimate seta                                       | present               | pereonite 1 as broad, but longer than pereonite 2                 | absent                                       |
| <i>E. ordinaria</i> Mezhov, 1986<br><b>group 4</b>           | enlarged, carpus nearly twice as broad as in pereopod II         | unequally bifid, much smaller than penultimate seta (not reaching 1/3 of length)          | absent                | pereonite 1 slightly longer than pereonite 2                      | no lateral view of the animal in description |
| <i>E. polita</i> (Hansen, 1916)<br><b>group 4</b>            | enlarged, carpus nearly twice as broad as in pereopod II         | unequally bifid   | present <sup>11</sup> | pereonite 1 wider and longer than pereonite 2                     | no lateral view of the animal in description |
| <i>E. falklandica</i> (Nordenstam, 1933)<br><b>group 4</b>   | enlarged, carpus twice as broad as in pereopod II                | unequally bifid, reaching half of length of penultimate seta                              | present               | of nearly similar size  | absent                                       |
| <i>E. rotunda</i> (Menzies & George, 1972)<br><b>group 4</b> | enlarged, capus and propodus clearly broader than in pereopod II | unequally bifid, half of length of penultimate seta                                       | present               | bigger <sup>12</sup>  | absent                                       |
| <i>E. theodori</i> sp. nov.<br><b>group 4</b>                | enlarged, capus and propodus clearly broader than in pereopod II | unequally bifid, much smaller than penultimate seta (not reaching 1/3 of length)          | present               | bigger  | absent                                       |
| <i>E. armata</i> (Sars, 1864)<br><b>group 4</b>              | enlarged, carpus twice as broad as in pereopod II                | type? <sup>13</sup> , but much smaller than penultimate seta (not reaching 1/3 of length) | present               | pereonite 1 slightly broader and longer than pereonite 2 (bigger) | no lateral view of the animal in description |

Excluding species of group 2, it is hypothesized that the genus becomes a monophylum, because the remaining species in the genus are of slender, but not

<sup>9</sup> This species possesses an unusual pereopod II, which is much more slender than pereopod I and ventral rows of setae present on carpus, propodus and dactylus.

<sup>10</sup> This character excludes the species from *Eugerdella* following the diagnosis presented by Hessler (1970)!

<sup>11</sup> Both characters are not completely discernable from the drawings of Hansen 1916 and Gurjanova 1932.

<sup>12</sup> Relation in length and width from original drawing and damaged holotype is not clear.

<sup>13</sup> No clear definition possible from the original drawings.

elongated body form (like species of group 2). Pereonite 1 is bigger than pereonite 2 in all species of the genus and pereopod I is clearly enlarged, the ventral setal row always bearing large robust composed setae of irregular size.

Most species (group 1 and group 4) have a platform-like gap between the insertion of the propodus and the above mentioned short distal ventral seta. This platform functions as antagonist to the propodus. Some species, like the type species *E. natator*, lack this gap. Thus, the function of the propodus as antagonist to the carpus may be somehow different from species that possess a platform-like gap. The presence of this gap correlates with the enlargement of the carpus. In species with a gap the carpus is larger (broader) than in species without a gap. It may be possible that a pereopod I with a platform-like gap is the more derived form.

Interestingly, the two species (*E. serrata* and *E. pugilator*) with the most robust pereopod I additionally possess a serrated pleotelson, spine-rows at the cephalon and spine-like ventral elongations at pereonites 1 to 5. These characters do not occur in any other species of the genus.

The ventral setal row on carpus of pereopod I is consisting of large robust composed setae of irregular size distal seta between one third and one half of length of penultimate seta (except *E. minutula*, here: distal seta longest; and *E. coarctata*, here: distal setae nearly as long as penultimate one), platform-like gap present between insertion of propodus and distal seta in *E. armata*, *E. falklandica*, *E. nonfunalis*, *E. polita*, *E. pugilator*, *E. rotunda*, *E. theodori* and *E. serrata*. Pereonite 1 longer than pereonite 2 (corresponding to the enlargement of pereopod I).

*E. minutula* is very similar to *Cryodesma agnari* in possessing no short but a distal seta that is the longest of all irregular ventral setae on the carpus. Thus, the most important generic character of *Eugerdella* does not occur in this species (according to the drawings in Mezhov 's (1986) species description). Svavarsson (1988) noted, that the relatively small penultimate seta in the ventral row indicates a relationship of *E. minutula* to species of the genus *Prochelator* as also hypothesized by Mezhov (1986). While in *Eugerdella* (as in *E. minutula*) the setae of the ventral row are of irregular size, this condition is not present in *Prochelator*.



### 4.2.1.3.6 *Leutziniscus* George, 2001

Type species: *Leutziniscus jebamoni* George, 2001

The only species of this genus *Leutziniscus jebamoni* George, 2001 is remarkable due to the antennula that consists of 11 articles. This is unusual for Desmosomatidae and Nannoniscidae. George (2001) presented following characters in the diagnosis of *Leutziniscus*:

- pereonites free, body not flat or broad
- antennula with 11 articles
- pleotelson with posterolateral spines
- operculum lacking spine
- uropods biramous

The characters of this diagnosis are characters that distinguish the species/genus from other nannoniscid genera, but no true apomorphies. If the antennula really consists of 11 articles is questioned because in the drawing presented in the species description the basal articles of the antenna and the antenna seem to be interchanged. If the antennula really consists of 11 articles, *Leutziniscus* should not be a Desmosomatidae, because members of this family do possess an antennula of 5-7 articles and not more. The synapomorphy of all species included in the family is that the second peduncular article is twice as long as the first one. In *Leutziniscus* the second article is elongated, as well as the third one, then followed by 8 articles that are clearly shorter. This is typical for the antenna, not for the antennula. Thus, it is supposed that George (2001) did a mistake in his species description interchanging the antenna and the antennula. The presence of the characteristic setal rows on pereopods I and II lead to the conclusion that the species belongs to Desmosomatidae.

*L. jebamoni* belongs to Eugerdelatinae due to the robust pereopod I. Most characters of *Thaumastosoma* (as far as presented in the drawing) are present. The species description of *L. jebamoni* is incomplete, for the mouthparts nothing can be said and no lateral drawing is presented. George (2001) himself mentioned a high similarity of *L. jebamoni* to *T. platycarpus* due to the quadrangular shape of pereonite 4 and 5. He mentioned that an opercular spine is absent in *Leutziniscus*. Possibly George (2001) did not see the ventral spine on the operculum. Like in *Thaumastosoma*-species the

pereopod I bears ventrally and dorsally on carpus and propodus rows of setae, the ventral setae on the carpus are robust composed setae increasing in length towards the propodus. Like in *Thaumastosoma* the pleotelson is slightly quadrangular and the uropods are of the same shape. Unfortunately, no lateral or ventral drawing is presented by George (2001).

The species shows characters defined for *Thaumastosoma* (except for the ventral spine on the operculum). Clear apomorphies to define the genus *Leutziniscus* are not present. Thus, the genus is rejected here. The species is transferred to *Thaumastosoma* for the time being. A detailed study of the holotype and a redescription of the species is necessary.

### 4.2.1.3.7 *Oecidiobanchus* Hessler, 1970

Type species: *Oecidiobanchus plebejum* (Hansen, 1916)

The main apomorphy of *Oecidiobanchus* is the small branchial chamber and operculum. Following characters were presented in the generic diagnosis (Hessler 1970):

- pereopod I large, chelate: dactylus and enlarged specialized propodus acting in opposition to the large claw-seta distoventrally on the carpus, carpus enlarged, not produced at base of claw, no small seta distally to base of claw, row of ventral setae may or may not be present
- pereonite 1 and 2 subequal
- pleotelson without posterolateral spines
- branchial chamber and operculum relatively small to size of pleotelson
- uropods uniramous
- lacinia mobilis and maxilliped as in *Prochelator*
- face of cephalon with transverse ridge on frons and frons-clypeal furrow

The characters of the left mandible and the maxilliped seem to be apomorphies of the whole group of chelate species, describing the characters just with “as in *Prochelator*” (Hessler 1970) which is the same description as in the generic diagnosis of *Chelator* (Hessler 1970). Complex characters containing phylogenetic information are the features of pereopod I and the pleotelson namely the small branchial chamber. The pleotelson seems to be inflated (transverse axis vaulted), it is as high or slightly higher than pereonite 5 (in *O. nanseni*, *O. plebejum* and *O. slopei*; in *O. glacialis* the

specimen is damaged, so that this feature can only be guessed and in *O. polare* no lateral view is presented in the species description).

The dactylus of pereopod I folds in all species against the ventral margin of the propodus although a “claw-seta” is present. The propodus is more enlarged than the carpus in all species. No ventral setae except one slender seta next to the claw seta are present on the ventral margin in *O. polare* and *O. glacialis*; *O. nanseni* and *O. plebejum* possess a small simple seta midway and *O. slopei* possesses a row of 3 additional slender distally setulate setae on the fringed ventral margin.

### **4.2.1.3.8                    *Paradesmosoma* Kussakin, 1965**

Type species: *Paradesmosoma conforme* Kussakin, 1965

Hessler (1970) supposed a close relationship of the species of this genus to species of the genus *Eugerdella* based on the row of irregular setae at the ventral margin of the specialized carpus of pereopod I. Hessler’s (1970) diagnosis followed Kussakin (1965) presenting the following characters:

- pereopod I chelate, propodus not tapering to distal end, ventral margin of carpus with row of composed setae of irregular size, single very slender setae distal to claw
- pereopod IV at all articles except base and dactylus with dense rows of setae which have sturdy bases and abruptly slender flexible tips (distally plumose setae)
- pereopod II and III developed like in other desmosomatids, but with the same setae as pereopod IV on the Ischium
- mandible with reduced palp

Already Kussakin (1965) mentioned the similarity to *Eugerdella* and described the carpus of *Paradesmosoma* as less developed, the propodus as less narrowing distally. He described the most distal seta in the ventral row of irregular sized setae of the carpus as longest and stout. This is the case regarding only the robust and stout setae on the carpus, but there are slender setae between these robust setae, the most distal seta being a long slender one.

The most important autapomorphy of the genus is the extremely modified fourth pereopod, a character which distinguishes the species of the genus from all other

Desmosomatids. Carpus and propodus of pereopod IV are surrounded by numerous distally plumose setae, this type of setae is unique to the species of this genus and occurs also on the other anterior pereopods. The characters of pereopod IV are so complex, that convergent evolution of such a character seems to be impossible. The long distally plumose setae occurring on the ischium, but not on carpus and propodus of pereopods I to III are described by Kussakin (1965) as swimming setae. Swimming setae on the anterior pereopods are unusual within the Desmosomatidae and setae of this type are known in species of *Paradesmosoma* only.

### **4.2.1.3.9                    *Prochelator* Hessler, 1970**

Type species: *Prochelator lateralis* (Sars, 1897)

The characters presented in the generic diagnosis are also characters presented in the generic diagnosis of *Chelator*. According to Hessler (1970) following characters characterize the genus:

- pereonite 1 as large or larger than pereonite 2
- pereopod I large, chelate, specialized propodus acting as antagonist to large distoventral seta on the carpus, carpus usually not produced at base of claw, ventral margin of carpus behind claw-seta with two additional setae: one composed seta located midway and one slender seta located at the base of the claw
- pleotelson with posterolateral spines

It is necessary to distinguish between diagnostic characters and apomorphies. The main character shared by *Prochelator* and *Chelator* is the chela. Based on the ventral projection at the base of the claw seta *Chelator* can be distinguished from *Prochelator*. This projection is the only distinguishing character that remains comparing the generic diagnoses of both genera (Table 8). Morphologically the two genera may be regarded as one until true apomorphies are defined.

#### 4. Discussion

**Tab. 8 :** Comparison of characters used in the generic diagnoses of *Prochelator* and *Chelator* on species level

| characters<br>species         | Prn1 to Prn2: midsagittal length, lateral view                         | Lm: number of teeth, lp: number of teeth and form, lm-like structure of left Md?                          | Coxae: form (angular or produced)                         | Height of Prn1 in comparison to Prn5 (ventral body spines or smooth?) | Prn5 to Plt  | Plt: lateral margins | Plt: spines (present, absent, location, anus region)  | Exopod: if present length in relation      | Type of penultimate seta to claw-seta, produced or not?, number of setae and type on ventral margin of carpus                                   | Setation of pereopod II, length to width ratios of carpus and propodus   | Transverse ridge on frons, frons-clypeal furrow                    |
|-------------------------------|--|---|---|---|--|----------------------|---|--|---|--|--|
| <i>Prochelator angolensis</i> | Prn1 <u>1.6</u> times longer than prn2, this also visible from lateral | Lm: <u>3</u> ; lp: 3 strong teeth surrounding lm, lm-like structure serrated on distal margin (8 "teeth") | <u>Slightly produced</u> and tipped with small stout seta | Prn1 <u>2.1</u> times <u>higher</u> than Prn5, smooth                 | Plt as high as Prn5                                      | straight             | Present, at height of distal margin of branchial chamber, not visible from dorsal, no separation of anus region visible | <u>absents</u>                             | <u>Slender</u> , <u>0.5</u> of length of claw-seta, <u>plus 1 small distally setulate</u> midway and <u>1 very small</u> simple seta proximally | Pll slender: <u>carpus: 4.8</u> , <u>propodus: 4.5</u> times longer than wide; Carpus: ventral row of <u>6 long</u> <u>unequally bifid</u> setae and dorsal row of 5 long simple setae | Neither ridge nor furrow present                                   |
| <i>Prochelator abyssalis</i>  | Prn1 <u>1.2</u> times longer than prn2, this also visible from lateral | Lm: <u>4</u> ; lp: 3 teeth of comparable shape of lm, lm-like structure of MdR not described              | <u>Produced</u> and tipped with small stout setae         | Prn1 <u>1.5</u> times <u>higher</u> than Prn5, smooth                 | <u>Slightly flattening</u> , Plt. nearly as high as Prn5 | convex               | Present, located 0.78 of pleotelson length, anus region behind spines, "separation visible"                             | Exopod <u>0.42</u> times of endopod length | <u>Distally setulate</u> , reaching 0.6 of length of claw-seta, somewhat <u>produced</u> , <u>plus 1</u> <u>unequally bifid</u> seta            | Pll "slender": <u>carpus: 3.4</u> , <u>propodus: 4.2</u> times longer than wide; Carpus: ventral row of <u>5 stout</u> <u>unequally</u>  | Transverse ridge slightly developed, frons-clypeal furrow not deep |

#### 4. Discussion

|                                       |   |  |  |  |  |                                 |   |                                      |   |   |   |
|---------------------------------------|---|--|--|--|--|---------------------------------|---|--------------------------------------|---|---|---|
|                                       |   |  |  |  |  |                                 |   |                                      |   | bifid setae and dorsal row of 6 slender setae   |   |
| <b><i>Prochelator hamptoni</i></b>    | Prn1 <u>1.4</u> times longer than Prn2, also visible from lateral | Lm: <u>3</u> , lp: 3 teeth only slightly stronger than lm, lm-like structure of MdR not described    | <u>Not produced</u> , tipped with small stout seta | Prn1 with anteriorly curved ventral elongation, measured without elongation <u>1.8 times of height of</u> Prn5 | Slightly <u>flattening</u> , Plt. nearly as high as Prn5 | straight                        | <u>Present</u> , located 0.81 of pleotelson length, anus parallel to position of spines, no separation visible            | Exopod <u>0.23</u> of endopod length | <u>Distally setulate</u> , <u>0.3</u> times of length of claw-seta, <u>not produced</u> , <u>plus 1 small unequally bifid seta</u> midway                     | Pll "more robust than slender": <u>carpus: 3</u> , <u>propodus: 3.9</u> times longer than wide; Carpus: ventral row of <u>13 robust setae</u> , <u>distal setae of row unequally bifid</u> and dorsal row of up to 18 slender setae | No transverse ridge, frons-clapeal furrow present                       |
| <b><i>Prochelator incomitatus</i></b> | Prn <u>1.2</u> times longer than prn 2, also visible from lateral | Lm: <u>3</u> , lp: with 3 small dosal teeth, lm-like structure serrated on distal margin (7 "teeth") | <u>Not produced</u> , tipped with stout small seta | Prn1 <u>2.4</u> times <u>higher</u> than Prn5, smooth  | Plt somewhat higher than Prn5                            | Straight converging posteriorly | Very small spines located at <u>0.82</u> of pleotelson length, anus parallel to position of spines, no separation visible | absent                               | <u>Slender and distally setulate</u> , <u>0.6</u> of length of claw-seta, <u>not produced</u> , <u>plus 1 small distally setulate seta</u> midway and 1 small | Pll "slender": <u>carpus: 2.9</u> , <u>propodus: 3.2</u> times longer than wide; Carpus: ventral row of <u>6 large stout unequally bifid setae</u> and dorsal   | Transverse ridge slightly present, frons-clypeal furrow clearly visible |

#### 4. Discussion

|                                     |   |  |   |   |                   |  |   |  |  |  |  |
|-------------------------------------|---|--|---|---|-------------------|--|---|--|--|--|--|
|                                     |   |  |   |   |                   |  |   |  | simple seta posteriorly, fringed   | row of 9 long slender setae  |  |
| <b><i>Prochelator lateralis</i></b> | Prn1 <u>1.4</u> times longer than Prn2, this also visible from lateral view | Lm: <u>3</u> ; lp: 3 teeth, lm-like structure of MdR not described | <u>Not produced</u> , tipped with a small simple seta | Prns 1-4 <u>with ventral elongations</u> , Prn1 measured without ventral elongation <u>1.3 times higher</u> than Prn5 | <u>flattening</u> | Slightly <u>convex</u> until spines                                      | <u>Spines</u> located on height of distal margin of branchial chamber, <u>0.74</u> of pleotelson length anus region with distal part of pleotelson after spines smallest: " <u>separation visible</u> " | <u>Exopod 0.4</u> of endopod length    | <u>Long slender</u> (may be distally setulate), <u>0.7</u> times of length of claw-seta, <u>plus 1 large stout unequally bifid seta</u> midway | PII "robust": <u>carpus: 2.2, propodus: 4.1</u> times longer than wide; Carpus: ventral row of 4-5 <u>robust unequally bifid setae</u> and dorsal row of 3 slender setae | Transverse ridge possibly present, but no frons-clypeal furrow |
| <b><i>Prochelator litus</i></b>     | Prn1 1.3 times longer than Prn2, this also from lateral view                | Lm: 3; lp: 3 teeth, lm-like structure of MdR not described         | Blunt, not produced, but tipped with small stout seta | Prn1 2.1 times higher than Prn5, smooth   | flattening        | Tendency to convex with a concave curve behind the posterolateral spines | Spines located at 0.68 of pleotelson length, anus behind spines (smallest part of the pleotelson, but no clear separation due to the  | Exopod 0.26 times of length of endopod | Distally setulate, 0.4 of length of claw-seta, carpus not produced (but more produced than in the following species...), plus 1 small distally | PII "slender": carpus: 3.7, propodus: 4 times longer than wide; Carpus: ventral row of 5 robust unequally bifid setae and dorsal row of 4-5                              | Transverse ridge not present, but a clear frons-clypeal furrow |

#### 4. Discussion

|                                   |  |   |                                       |  |  |                             |  |                                |   |   |   |
|-----------------------------------|--|---|---------------------------------------|--|--|-----------------------------|--|--------------------------------|---|---|---|
|                                   |  |   |                                       |  |  |                             | form)  |                                | setulate seta more anteriorly located than midway   | slender setae   |   |
| <b><i>Prochelator sarsi</i></b>   | Midsagittal length 1.2 times of Prn2, from lateral view Prn1 slightly longer than Prn2 | Lm: lp: ?, damaged, lm-like structure of MdR not described              | Angular, (more rounded than produced) | Smooth, Prn1 higher than Prn5, due to damage no exact measurement possible | Plt seems to be more flattened than Prn5, but: posterior part of body damaged! | Seem to be convex (damaged) | Present, but due to damage location can only be guessed, anus located behind spines  | Present, 0.5 of endopod length | Distally setulate, carpus not produced at base of claw-seta, plus stout distally setulate seta midway | PII "slender": carpus: 3.4, propodus: 2.7 times longer than wide; ventral row of 5 unequally bifid setae and dorsal row of 4 slender setae plus 1 unequally bifid distal seta | No ridge, but deep frons-clypeal furrow                             |
| <b><i>Prochelator uncatus</i></b> | Midsagittal length 0.9 of Prn2, from lateral view Prn 1 longer than Prn2               | Lm: 4; lp: 3 short dorsal teeth, lm-like structure of MdR not described | Angular (more rounded than produced)  | Prn1 2.2 times higher than Prn5, smooth                                    | Plt somewhat higher than Prn5  | straight                    | Small spines present, located at distal end of branchial chamber (0.6) of pleotelson length, anus within the distal part of pleotelson | Present, 0.5 of endopod length | Distally setulate, base of claw-seta not produced, plus 1 stout unequally bifid seta midway           | PII "robust": carpus: 2, propodus: 3 times longer than wide; ventral row of 4 long robust unequally bifid setae and 2 slender dorsal  | Transverse ridge not obvious, frons-clypeal furrow slightly present |



#### 4. Discussion

|  |   |  |  |  |  |  | behind<br>spines  |  |   | setae  |  |
|--|---|--|--|--|--|--|---|--|---|--|--|
| <b><i>Prochelato<br/>r kussakini</i></b>           | Midsagital<br>length<br>about 3<br>times<br>longer than<br>Prn2, no<br>lateral view<br>presented<br>in species<br>description | ???<br>mandibles<br>not drawn<br>in species<br>description                                   | Angular<br>(production<br>seems to<br>be<br>rounded)             | No lateral<br>view<br>presented<br>in species<br>description | No lateral<br>view<br>presented<br>in species<br>description | straight   | Present,<br>but very<br>small and<br>only visible<br>from lateral<br>view, anus<br>within the<br>distal part,<br>no<br>separation<br>within form<br>of<br>pleotelson<br>visible     | Present,<br>about half<br>of length of<br>exopod<br>(measured<br>from the<br>drawings<br>within the<br>species<br>description) | Slender,<br>0.7 of<br>length of<br>claw-seta,<br>carpus not<br>produced<br>as base of<br>claw-seta        | PII:<br>carpus:,<br>propodus:<br>times<br>longer than<br>wide;<br>ventral row<br>of setae<br>and dorsal<br>row of<br>setae | ? no lateral<br>view<br>presented<br>in species<br>description |
| <b><i>Prochelato<br/>r serratum</i></b>            | Midsagital<br>length 1.6<br>of Prn2, in<br>lateral view<br>as long as<br>prn2   | Lm:  | Angular<br>(production<br>rounded,<br>not tipped)                | smooth   |  | Slightly<br>convex,<br>serrated,<br>serration<br>fluently<br>going over<br>into<br>posterolater<br>al sines? | Present in<br>a serration<br>of the<br>whole<br>pleotelson,<br>no<br>separation<br>of anus<br>region in<br>the form of<br>the<br>pleotelson<br>from the<br>anterior<br>part visible | present  |   | PII:<br>carpus:,<br>propodus:<br>times<br>longer than<br>wide;<br>ventral row<br>of setae<br>and dorsal<br>row of<br>setae |  |
| <b><i>Prochelato<br/>r maorii<br/>sp. nov.</i></b> | Midsagital<br>length 1.5<br>times of<br>prn2, in<br>lateral view<br>longer than<br>prn2                                       | Lm: 3, Ip: 3<br>teeth as<br>strong as<br>lm, lm-like<br>structure of<br>MdR not<br>described | Produced<br>and tipped<br>with small<br>stout<br>sensory<br>seta | Prn1 1.3<br>times<br>higher than<br>Prn5,<br>smooth          | flattening   | Convex<br>with<br>concave<br>curve in<br>front of<br>spines  | Present in<br>both sexes,<br>located on<br>height of<br>distal<br>margin of<br>branchial<br>chamber at<br>0.6 of  | Exopod<br>reaching<br>0.6 times of<br>endopod<br>length  | Slender<br>(0.4 of<br>length of<br>claw seta),<br>plus 1 short<br>distally<br>setulate<br>seta<br>midway, | PII<br>"slender":<br>carpus: 4.3,<br>propodus:<br>5.1 times<br>longer than<br>wide;<br>Carpus:<br>ventral row              | Both<br>present  |

#### 4. Discussion

|                                    |                                   |  |  |  |                            |   |  |               |   |  |  |
|------------------------------------|-----------------------------------|--|--|--|----------------------------|---|--|---------------|---|--|--|
|                                    |                                   |  |  |  |                            |   | pleotelson length, anus behind spines, (smaller than anterior part of pleotelson), somehow separated                                   |               | carpus not produced at base of claw seta  | of 12 distally setulate (dital unequally bifid) setae and dorsal row of 18 slender setae   |  |
| <b><i>Chelator brevicaudus</i></b> | Prn1 slightly longer than Prn2    | MdL not described, lm-like structure of MdR triangular and serrated on distal margin (8 "teeth") | In male slightly produced and tipped with small stout seta | Prn1 higher than Prn5, exact measurement possible from drawings?, smooth | Plt as high as Prn5        | Convex giving the pleotelson a rounded form | Present in male (no females known) at distal "corners" of pleotelson, no separation of anus region visible, spines located behind anus | absent        | Short slender distally setulate, 0.34 of length of claw-sea, plus 2 short slender distally setulate setae, carpus ventrally fringed between setae, slightly produced at base of claw-seta | Pll "slender": carpus: 4.1, propodus: 4.9 times longer than wide; ventral row of 7 distally setulate (distal two of row unequally bifid) setae and dorsal row of 7 slender distally setulate setae | Due to damage not clearly to distinguish: a transverse ridge may be present, the frons-clypeal furrow is visible |
| <b><i>Chelator chelatum</i></b>    | Prn1 <u>1.3</u> times longer than | Lm: <u>3</u> , lp: 3 strong teeth, lm-   | <u>produced</u> and tipped with small                      | Prn1 <u>1.7</u> times <u>higher</u> than                                 | Plt <u>as high as</u> Prn5 | straight                                    | <u>Absent</u> , no separation of anus  | <u>absent</u> | <u>Slender</u> , <u>0.3</u> of length of  | Pll "more robust than slender":  | Transverse ridge and deep frons-   |

#### 4. Discussion

|                                 |  |  |  |  |  |          |  |        |   |  |   |
|---------------------------------|--|--|--|--|--|----------|--|--------|---|--|---|
|                                 | Prn2, from lateral view subequal                 | like structure of MdR not described                        | stout sensory seta                                 | Prn5   |  |          | region visible, rounded distally                               |        | claw-seta, <u>plus 4 small slender setae</u> , carpus slightly <u>produced</u> at base of claw-seta             | carpus: 3.3, propodus: 2.5 times longer than wide; <u>ventral row of 10 long unequally bifid setae</u> and dorsal row of 9 slender distally setulate setae               | clypeal furrow present                                  |
| <b><i>Chelator insignis</i></b> | Prn1 1.2 rimes longer than Prn2                  | Lm: 3, lp: 3 teeth, lm-like structure of MdR not described | Produced and tipped with small stout setae         | Prn1 1.3 times higher than prn5, smooth          | Plt as high as Prn5                              | straight | Absent, no separation of anus region visible, rounded distally | absent | Slender, 0.3 of length of claw-seta, plus 4 irregular small slender setae, carpus produced at base of clae-seta | PII "more slender than robust": carpus: 1.6, propodus: 3.3 times longer than wide; ventral row of 10-13 stout unequally bifid setae and dorsal row of 7-11 slender setae | No clear transverse ridge, frons-clypeal furrow present |
| <b><i>Chelator stellae</i></b>  | Prn1 shortest, 0.8 of midsagittal length of Prn2 | Lm: 4; lp: 3 acute teeth, lm-like structure of MdR not     | Slightly produced and tipped with small stout seta | No lateral view presented in species description | No lateral view presented in species description | straight | Absent, no separation of anus region visible, rounded          | absent | Slender, 0.28 of length of claw-seta, no other ventral  | PII: carpus: 2.4, propodus: 2.4 times longer than wide;  | No drawing from lateral view presented in description:  |

#### 4. Discussion

|                                   |  |   |   |  |  |   |   |        |  |  |  |
|-----------------------------------|--|---|---|--|--|---|---|--------|--|--|--|
|                                   |  | described   |   |  |  |   | distally  |        | setae, carpus not produced at base of claw-seta  | Carpus: ventrally 2 unequally bifid setae and dorsal row of 3 long setae | ?  |
| <b><i>Chelator striatus</i></b>   | Prn1 larger than prn2, no exact measurement possible due to drawings in species description and the damaged holotype | Lm: 3 (plus a extremely small fourth), lp: shelflike with no clear separation of the 3 or 4 teeth, lm-like structure of MdR not described | Produced and tipped with a stout seta   | No lateral view presented in species description | No lateral view presented in species description | straight  | Absent, no separation of anus region visible, sides parallel, rounded distally                            | absent | PI is missing in the only specimen (holotype female)   | Not described  | No drawing from lateral view presented in description: ?   |
| <b><i>Chelator verecundus</i></b> | Prn1 and Prn2 subequal   | Lm: 3, lp: 3 strong teeth, lm-like structure of MdR not described   | Slightly produced, tipped with small stout seta, coxae 2-4 with small simple seta | Prn1 1.3 times higher than Prn5, smooth          | Plt as high as Prn5                              | Straight, in male a spinelike posterolateral projection present on height of distal margin of the branchial chamber | Absent in female, in male located at 0.8 of pleotelson length, no clear separation of anus region visible | absent | Slender, 0.3 of length of claw-seta, plus 2 small slender setae (1 on high of penultimate seta, 1 somehow midway), carpus slightly produced at base of claw-seta | PII "slender", more unknown in female                                    | Transverse ridge not obvious, frons-clypeal furrow present |

#### 4. Discussion

|                                 |                                 |   |  |   |                     |  |  |        |  |  |   |
|---------------------------------|---------------------------------|---|--|---|---------------------|--|--|--------|--|--|---|
| <b><i>Chelator vulgaris</i></b> | Prn1 1.4 times longer than Prn2 | Lm: 4, Ip: 3 teeth (third tooth very small), Im-like stricture of MdR three-lobed distally, distal "tooth" serrated | Acute projections tipped with slender seta | Prn1 1.5 times higher than Prn5, smooth | Plt as high as Prn5 | Slightly convex, in male more straight with acute posterolateral corners | Absent in female, in male with poaterolateral corners (spines?) located 0.8 of pleotelson length, no clear separation of anus region visible | absent | Small slender, 0.2 of length of claw-seta, plus 6 irregular small simple setae, strongly produced at base of claw-seta | Pll "more robust": carpus: 3.8, propodus: 3.7 times longer than wide; ventral row of 20 stout distally setulate setae and dorsal row of up to 21 slender setae | Transverse ridge present and a clear frons-clypeal furrow |
|---------------------------------|---------------------------------|---|--|---|---------------------|--|--|--------|--|--|---|

The ventral setae on the carpus of pereopod I were so uniform in species Hessler (1970) assigned to the genus *Prochelator* that they had been given the formal designation “accessory setae”. Hessler (1970) used this term not only for the genus *Prochelator*. Due to his hypothesis of relationships between *Prochelator* and *Chelator* he describes the ventral row of small setae within species of *Chelator* as row of setae, of which none can be labeled as “accessory seta”. The terminus “accessory seta” is confusing and may be synonymized with the terminus “major seta”. Both termini are not used in this thesis; instead the setal types on the articles of the pereopods are described, because homologizing the setae on the ventral margin of the carpus is not possible.

If the characters of pereopod I contain significant apomorphies, it may be possible to distinguish the genera. Difficulties are caused by the intermediate forms such as in *P. incomitatus* and *P. angolensis*. Hessler (1970) already mentioned that the evolutionary steps within the Desmosomatidae are connected through intermediate forms. According to Hessler (1970) the prefix “Pro-“ refers to the fact, that species of *Chelator* are probably derived from species of *Prochelator*. To access the taxonomic position of *Prochelator* and *Chelator* a detailed discussion of all characters (possible apomorphies) is necessary. This comparison is presented in Table 9 listing those characters that were used for distinguishing the genera until 1970

**Table 9:** Comparison of the characters of *Prochelator* and *Chelator* as presented in the diagnoses (Hessler 1970)

|  | <b>Md</b>                    | <b>Mxp</b>                         | <b>Pl</b>   | <b>Prn1</b>                           | <b>Coxae</b> | <b>Plt</b>                                   | <b>Ur</b>             |
|--|------------------------------|------------------------------------|---|---------------------------------------|--------------|--|-----------------------|
| <b><i>Prochelator</i></b><br>Hessler, 1970 | lacinia mobilis with 3 teeth | article 3 with long lateral margin | ventral margin with 2 setae <sup>14</sup> ; carpus not produced at base of claw | as large or larger than Prn2          | produced     | with spines, which are sometimes obscure     | biramous or uniramous |
| <b><i>Chelator</i></b><br>Hessler, 1970    | lacinia mobilis with 3 teeth | article 3 with long lateral margin | ventral margin with small setae; carpus produced at base of claw                | smaller, as large or larger than Prn2 | produced     | Absent in females, in males spines may occur | uniramous             |

<sup>14</sup> A short, stout, unequally bifid seta located midway (fig. 7) and a long slender seta located basally to the claw. The claw-seta is not counted although this seta can be homologized with the distal seta in the carpal ventral row of setae of other desmosomatid species.

While in species of *Prochelator* the posterior pereonites and the pleotelson are flattening, in species of *Chelator* the pleotelson is as high as pereonite 5, the rounded pleotelson form giving the body line a more compact look than in *Prochelator*. In *Chelator* the first four body segments are more compact than in species of *Prochelator* (first pereonite in *Chelator* twice as high as pereonite 5).

Other desmosomatid species with a chelate pereopod I can be distinguished from *Prochelator* and *Chelator* by clear apomorphies. Species included in *Oecidiobanchus* possess a propodus more enlarged than the carpus, a “slender” claw-seta and a dactylus folding against the ventral margin of the propodus. Thus, a chelate pereopod I, which combines the sub- and the carpo-euchela. Most important is the small branchial chamber that is occurring in *Oecidiobanchus* (chapter 4.2.1.3.7).

*Disparella*-species possess a large cephalic spine at the insertion of the antennula. Such a cephalic spine is also found in species of *Prochelator* (*P. lateralis*, *P. uncatus*), but not in species of *Chelator*. The apomorphy of *Disparella* distinguishing the genus from *Prochelator* is the elongated slender propodus (more than 3.5 times longer than wide) and the setation on the ventral margin of the carpus of pereopod I. Species of *Disparella* possess a well defined row of setae behind the claw-seta. Such a row is found in any species of *Prochelator* or *Chelator*. Worth to note is that the pereopods II-IV of *Disparella*-species are obviously setose (carpus > 20, propodus > 8 in adult, respectively) while in *Prochelator* the carpi of the anterior pereopods comprise not more than 10 setae in a row (except *P. hampsoni*).

Although the comparison of characters in table 8 shows that species of *Prochelator* and *Chelator* are very similar and most characters occur in species of both, *Prochelator* and *Chelator* should be treated as separate genera due to following difficulties:

- It is not possible to homologize the setae on the ventral margin of the carpus of pereopod I and no transformation series can be postulated explaining how the midventral setae and the few small setae originated;
- the uniramous uropod in *P. incomitatus* and *P. angolensis* may have evolved convergently because the loss of the exopod is documented for many species of Desmosomatidae belonging to different genera;

- the body form of females differs clearly between the two genera, while species of *Chelator* are more compact and the pereonites are rounded, species of *Prochelator* have a different profile from lateral view;
- posterolateral spines at the pleotelson are always present in females of *Prochelator* while in females of *Chelator* these posterolateral spines are absent.

It is concluded that the presence of only small setae behind the claw-seta together with the produced ventral margin at the base of the claw are apomorphies to define *Chelator* and distinguish the genus from *Prochelator*.

##### **4.2.1.3.10    *Reductosoma* Brandt, 1992**

Type species: *Reductosoma gunnera* Brandt, 1992

The species differs in many characters from other Desmosomatidae as there are the reduced number of articles of the maxilliped palp and the elongated coupling hooks (although not as elongated as in *Thaumastosoma*). Following characters were defined in the diagnosis (Brandt 1992):

- pereonite 1 slightly longer than pereonite 2
- mandibel without palp
- maxilliped palp out of (only) 4 articles
- pereopod I large and chelate: dactylus and propodus forming a grab organ acting in opposition to the carpal claw formed by a large sensory seta

The reduction of mouthparts is visible in the loss of the mandibular palp and the fifth article of the maxilliped palp. The species shares synapomorphies with other desmosomatid species, which indicate a close relationship to *Prochelator* (Brandt 1992) due to the characters of pereopod I. The species shares the typical enlarged distal seta ("claw-seta") acting as antagonist to the movable propodus, building together the carpo-euchela (Wägele 1989).

##### **4.2.1.3.11    *Thaumastosoma* Hessler, 1970**

Type species: *Thaumastosoma platycarpus* Hessler, 1970

Following characters were presented in the diagnosis of *Thaumastosoma* by Hessler (1970):



- mouthparts produced forward conspicuously
- mandible elongated, incisor process bent forward, lacinia mobilis membranous, palp well developed
- maxilliped with unusually elongated coupling hooks, palp segments 2-4 produced forward medially
- basal endite of second maxilla less than half the length of the other lobes
- pereopod I robust, much like pereopod II, but stouter, carpus much shorter
- pereonite 1 somewhat larger than pereonite 2
- coxa of pereopods I slightly produced and tipped with stout seta; coxae of pereopods II-IV not produced and without seta
- corners of tergites of pereonites 2-4 acute, tipped with stout seta
- pleotelson without posterolateral spines.

Hessler (1970) erected the genus, described two new species of *Thaumastosoma* in his monograph about Desmosomatidae and transferred *Desmosma distinctum* Birstein, 1963 to *Thaumastosoma*. The argument for the allocation of the genus to Desmosomatidae is the ventral row of enlarged robust composed setae on carpus of pereopod I. In contrast the presence of stout setae on the tergites is described as character of Nannoniscidae (Siebenhaller & Hessler 1977).

In 1977, Siebenhaller & Hessler transferred *Thaumastosoma* into Nannoniscidae. The change was based on the presence of anterolateral setae on the tergites (pereonites 2-4), spine-like ventral elongations on pereonite 7, and on the operculum in female. In 1981, Siebenhaller & Hessler modified the generic diagnosis adding the following characters to distinguish this genus from the other nannoniscid genera:

body slender, not depressed; cephalon without rostrum; pereonites 6 and 7 as well as pleotelson with small lateral flanges; pereonites 6 and 7 not fused; pereonite 7 venter with medial spine; operculum with midventral posteriorly directed spine; males with posterolateral spines on pleotelson, in female spines absent or clearly smaller than in male; antennula with 6 articles, unspecialised distal articles and pereopod I stouter than pereopod II.

In Nannoniscidae these ventral elongations are known at pereonite 7 and at the operculum only (compare chapter 4.2.2.2). In *Thaumastosoma distinctum* (Birstein, 1963) no ventral spines are drawn in the original species description (Birstein 1963).

No desmosomatid species bears any spine-like ventral elongations on pereonites 6 and 7 or on the operculum (for discussion see chapter 4.2.2.2).

Wägele (1989) transferred the genus back to Desmosomatidae because of the characters of pereopods I and II, especially the ventral row of composed setae on the carpus of pereopod I. Species of *Thaumastosoma* have ventral rows of robust composed setae and dorsal rows of long setae, both characters are used as a apomorphy of Desmosomatidae (Wägele 1989, chapter 4.1.1). In his opinion the synapomorphies of Nannoniscidae are not present in *Thaumastosoma*. There are “nannoniscid characters” present in *Thaumastosoma*: the uropods are inserting very close to the anus, particularly overlapping the valves. The uropods are longer than in most nannoniscids, but there are species of Nannoniscidae known with uropods of comparable length to other genera (for example in *Nannoniscus acanthurus* or *Nannoniscella biscutatus*) and only few swimming setae on the posterior pereopods are present.

Kaiser (2005) returned the genus to Nannoniscidae following the opinion of Siebenhaller & Hessler (1977) because “nannoniscid characters” outnumber the “desmosomatid characters”. This is still problematic because the synapomorphy “natatory setae absent at pereopods V to VII” (chapter 4.1.1) is not present in all three species of this genus.

Here, a close relationship to species of *Whoia* is hypothesized due to the characters of pereopod I: in species of both genera pereopod I is robust and bears large robust composed setae. Thus, it is proposed here that *Thaumastosoma* belongs to Eugerdelatinae and the “nannoniscid characters” e.g. the spine on the operculum are evolved convergently in *Thaumastosoma* and species of Nannoniscinae.

### **4.2.1.3.12    *Whoia* Hessler, 1970**

Type species: *Whoia angusta* (Sars, 1899)

Originally the genus was allocated to Desmosomatinae. For the “not-chelate” species in Eugerdelatinae sensu Hessler (1970) e.g. *Paradesmosoma* and *Eugerdella* an origin from a “*Eugerdella*-like condition” was hypothesized. The question, if the condition of pereopod I as found in *Whoia* could be a “*Eugerdella*-like” condition is addressed. Characters presented in the original diagnosis (Hessler 1970) were:

- pereonite 1 somewhat inflated, larger than pereonite 2
- pereopods I and II robust
- pereopod I as large as pereopod II (only propodus slimmer than in pereopod II), carpus with ventral and dorsal row of setae<sup>15</sup>, propodus without dorsal row of setae, ventrally fringed, single or few small composed setae present, merus comprising ventrally 2 or 3 robust large composed setae
- coxae of pereopods I-IV not produced
- pleotelson highly vaulted in transverse section

Most of the characters may be regarded as plesiomorphies e.g. pereopod I as large as pereopod II, coxae not produced (chapter 3.1.2). Hessler (1970) regarded the lack of specialization of pereopod I as primitive. No clear apomorphies were defined, although species of *Whoia* have phylogenetic informative characters. Svavarsson (1988) presented no modified diagnosis although the species he describes (*Whoia dumbshafensis*) shows characters that are not compatible with the original diagnosis: pereonite 1 and 2 subequal, the long unequally setae on carpus are more slender than in the other members of the genus and the whole pereopod I is smaller and more slender than pereopod II, the pleotelson is not highly vaulted in the transverse section, instead the body is flattening from pereonite 5 to the distal tip of the pleotelson.

The lateral margins of pereonite 5 are convex in most species, inflated laterally and elongated in *Whoia variabilis* resembling the condition found in *Pseudergella ischnomesoides* and *P. hessleri* (chapter 4.2.1.5.1). The other three species of *Whoia* possess convex lateral margins of pereonite 5, but no extrem elongation of this body segment, although pereonite 5 is the longest segment of the whole body.

The most important character for a generic diagnosis of *Whoia* are the characters of the pereopod I especially the enlargement of the merus comprising ventrally 2 or 3 robust large unequally bifid setae (in *W. dumbshafensis* only 1 unequally bifid seta present and also the dorsal row of distally setulate seta on the carpus reduced on 2-3 slender seta). The carpus is always stout, the propodus always slightly elongated. The condition of pereopod I may be regarded as “*Eugerdella*-like” because the limb is robust and comprises large composed setae. Although the setae are not irregular in

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<sup>15</sup> Hessler (1970) uses here the terminus “major seta” describing the seta in the carpal rows. The meaning for species of *Whoia* is: large unequally bifid setae ventrally and slender distally setulate setae dorsally.

size and the carpus is not enlarged, it might be hypothesized that such a pereopod I could have led to the evolution of a pereopod I as found in *Eugerdella*. Robust pereopods with rows of large composed setae are found in species of *Whoia* and *Thaumastosoma*. Thus, both genera are included in Eugerdellatinae, not in Desmosomatinae.

### 4.2.1.4 Nannoniscinae (Hansen, 1916)

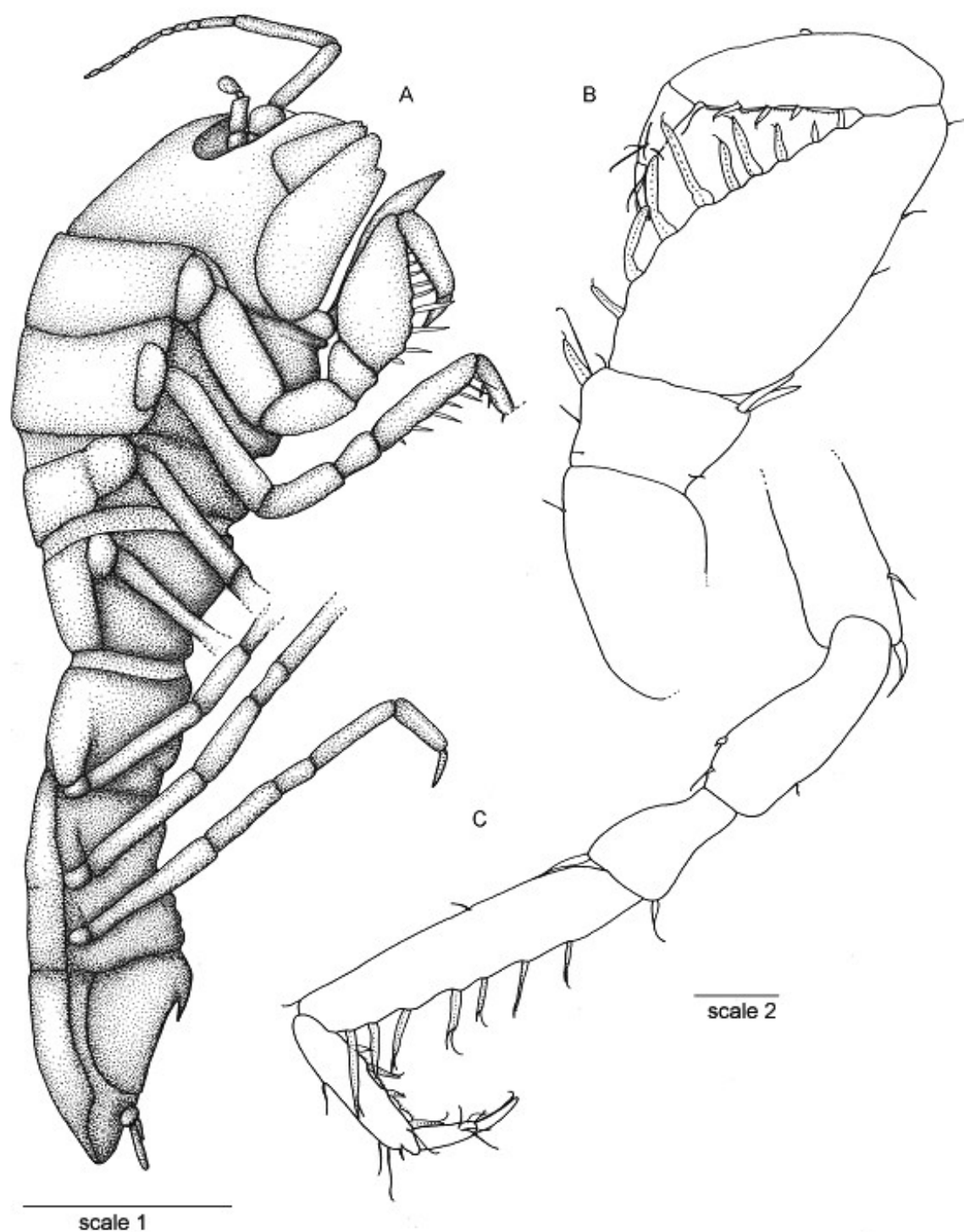
The genera of Nannoniscinae are accepted as presented in the literature (*Exilinisca* Siebenhaller & Hessler 1981; *Hebefustis* Siebenhaller & Hessler 1977; *Micromesus* Birstein, 1963; *Nannonisconus* Schultz, 1966; *Nannoniscus* Sars, 1870; *Nymphodora* Kaiser, 2005; 1970; *Panetela* Siebenhaller & Hessler 1981; *Rapaniscus* Siebenhaller & Hessler 1981; *Saetoniscus* Brandt, 2002b). Only *Rapaniscus* is discussed due to its high similarity in the characters of pereopod I to *Eugerdella* (compare chapter 4.1).

#### ***Rapaniscus*** Siebenhaller & Hessler 1981

Type species: *R. dewdneyi* Siebenhaller & Hessler, 1981

This genus belonged to Nannoniscidae. Species of *Rapaniscus* Siebenhaller & Hessler (1981) possess a first pereopod very similar to the robust forms in *Eugerdella* (Kussakin 1965). The difference lies in the shape of the carpus, which tapers towards the propodus. Following characters were presented in the diagnosis of *Rapaniscus* (Siebenhaller & Hessler 1981):

- body length about 3.4 times of the tergal width of pereonite 2
- pereonites 6 and 7 fused medially
- antennula consisting of 5 articles, last article bulbous, fourth article with shelf-like process
- pereopod I massive: carpus broad bearing long robust setae, carpus and propodus of approximately equal length
- pereopods II – VII slender
- females with large, strongly curved spine on the operculum or venter of preopercular segments



**Fig. 117:** *Rapaniscus* sp. nov. A, female, habitus lateral (A), pereopod I (B), pereopod II (C), scale 1 = 1 mm, scale 2 = 0.1 mm (drawing: Stefanie Kaiser)

The ventral row of robust composed setae, presented by Wägele (1989) as an autapomorphy of Desmosomatidae, is present in *Rapaniscus*. As in *Eugerdella* the most distal seta is the shortest of the row, but in the length of the setae in the row of forms an arc, slowly decreasing in size towards the propodus. This is in contrast to the big difference in the size of the penultimate seta in *Eugerdella*.

The first pereopod of *R. sp. nov. A* (Fig. 117) is most similar to the one of *R. multisetosus* Brandt 2002b. Both species possess the “typical nannoniscid” spine on the operculum and the bulbous last article of the antennula and therefore are clearly distinguishable from species of the genus *Eugerdella*, although the lateral and dorsal shape of the habitus is very similar.

Also note that the form and setation of the first pereopod of *Nannoniscus coalescus* (Menzies & George 1972) closely resembles *Rapaniscus*. Additionally, the species shares the bulbous last article of the antennula. After examining the holotype, the species is transferred into *Rapaniscus* due to these characters as well as the medial fusion of pereonites 6 and 7. The holotype is too damaged to examine the spine on the operculum, but this spine is most probably present.

From the generic diagnoses of *Eugerdella* and *Rapaniscus*, it is clear that species of both genera differ in the “typical nannoniscid” characters as there is the bulbous last article of the antennula, the spine on the operculum and the fusion of the pereonites. It may be hypothesized that a robust pereopod I is a result of convergent evolution. This is supported by the shape of the carpus, which tapers towards the propodus in species of *Rapaniscus*.

### 4.2.1.5 Pseudomesinae (Hansen, 1916)

#### 4.2.1.5.1 *Pseudergella* gen. nov.

Type species: *Pseudergella ischnomesoides* (Hessler, 1970)

Four species are transferred to *Pseudergella*: *Eugerdella ischnomesoides* Hessler, 1970 *Eugerdella hessleri* Just, 1980, *Desmosoma atypicum* Fresi & Schiecke, 1969 and *Pseudomesus bispinosus* Chardy, 1974. Following characters are regarded as apomorphies of *Pseudergella* gen. nov.:

- body elongated (about 6 times longer than width of pereonite 2)
- pereonite 1 smaller than pereonite 2
- pereonite 5 elongated with convex inflated lateral margins

- pleotelson enlarged, slightly inflated dorsally, lateral margins convex (curved) in front of posterolateral spines
- pereopod I slightly stouter than pereopod II, carpus with row of 3 or 4 robust composed setae ventrally, dorsally without setal row, propodus lacking setae
- ischium of posterior pereopods elongated (about 5 times longer than wide)

The most similar species to *Pseudergella ischnomesoides* (Hessler, 1970) is *P. hessleri* (Just, 1980). Both species have a slender elongated body, an elongated pereonite 5 and share the almost complete lack of long natatory setae on pereopods V to VII, which is unique within Desmosomatidae (Just 1980). Just (1980) questions if the two species represent a common unique line of evolution in *Eugerdella* or if the slender, elongated body and particularly the elongated pereonite 5 have evolved more than once. If the elongated pereonite 5 is regarded as a synapomorphy of the two species, Just (1980) argued that it is possible to establish a separate genus for them. Such an elongation combined with strongly convex lateral margins does not occur in any other species of *Eugerdella*; additionally the pereopod I in *Eugerdella* is enlarged, especially the carpus, and the ventral setae of the carpus are of irregular size. These characters do not occur in *P. ischnomesoides* and *P. hessleri*.

Bilateral bulges on the cephalon as described as sexual dimorphism in *Pseudomesus* (chapter 4.2.1.5.2) also occur in the copulatory male of *P. hessleri*. The natatory setae on pereopods V to VII are located dorsally, ventrally on carpus and propodus relatively long stout unequally bifid setae are present. In both species, the most distal setae of the row is shortest as defined in the generic diagnosis of *Eugerdella* (chapter 4.2.1.3.5), while in *P. bispinosus* the distal seta of the row is longest. The shape of the uropods of *P. hessleri* resembles that of *P. bispinosus*. All three species possess an elongated pereonite 5 with convex inflated lateral margins. *P. atypicum* (Fresi & Schiecke, 1969) is transferred to *Pseudergella* due to the enlarged pleotelson, the convex inflated and elongated pereonite 1 and the ventral setal row of short composed setae on the carpus. As in *P. bispinosus*, in *P. atypicum* the ventral setae on pereopod I are increasing in length towards the propodus.

Species of *Pseudergella* and *Pseudomesus* share the elongated body form, the enlarged dorsally inflated pleotelson and are very similar in the characters of pereopod I. In *Pseudergella* the ischium of the posterior pereopods is elongated, it is not in *Pseudomesus*. Species of *Pseudomesus* have a different form of pereonite 5, it may be elongated, but never inflated with convex lateral margins. While in

*Pseudomesus* the uropod is specialized with a nearly bulbous and extremely short endopod, the uropods in *Pseudergella* are clearly longer than wide and an extremely reduced exopod may occur (e.g. in *P. ischnomesoides*).

### 4.2.1.5.2 *Pseudomesus* Hansen, 1916

Type species: *Pseudomesus brevicornis* Hansen, 1916

The history of the genus *Pseudomesus* may best be described as “*systematic odyssey*“, a title that reflects the ambiguity of the characters resulting in this genus “*falling between two stools*“, namely, the families Nannoniscidae and Desmosomatidae. The question about the systematic position of *Pseudomesus* is one of the most discussed problems in the systematic literature of Desmosomatidae and Nannoniscidae.

Hansen (1916) first described *Pseudomesus brevicornis* as type species and genus of? a separate family, Pseudomesidae. Gurjanova (1933) downgraded it to the subfamily Pseudomesini within the family Macrostylidae. Menzies (1962) and Birstein (1963) redefined the family Pseudomesidae and transferred *Pseudomesus* back into Pseudomesidae together with the genus *Micromesus*.

In 1984, *Pseudomesus* was moved to Desmosomatidae by Svavarsson . Describing the male of *Pseudomesus brevicornis* Hansen, 1916, he discussed its characters and found them to be most similar to *Eugerdella ischnomesoides*, a desmosomatid. The only distinguishing character according to Svavarsson (1984) between *Eugerdella* and *Pseudomesus* are the extremely short uropods, while both species share obvious similarities in the setation of the first and second pereopods, in the habitus, and in the pleopods. Hessler (1970) had already mentioned these similarities but still followed Menzies (1962) and Birstein (1963) in leaving *Pseudomesus* in Pseudomesidae. Svavarsson (1984) argued that even within Desmosomatidae the uropods may be uniramous or biramous on a generic level. Hessler (1970) shared the opinion that the uropodal exopod may be reduced more than once. Furthermore, this character is also variable in Nannoniscidae.

*P. bispinosus* is transferred to *Pseudergella* (chapter 4.2.1.5.1) due to the characters of the uropod. Like the other three species transferred to *Pseudergella*, *P. bispinosus* possesses uropods that are clearly longer than wide, while in species of *Pseudomesus* the endopod is bulbous and extremely short. In *Pseudomesus* the uropod is specialized in a unique way. A bulbous endopod is regarded as



phylogenetically informative character. The unique shape of the bulbous short uropods is present in all remaining species of the genus.

Wägele (1989) placed the genus into Nannoniscidae arguing that the short uropods, their insertion close to the anus valves and the absence of natatory setae at pereopods V to VII were regarded as synapomorphies of Nannoniscidae (chapter 4.1.1). These characters occur in all described species of the genus. However, the desmosomatid species *Mirabilicoxa longispina* (Hansen 1916) possesses a uniramous uropod that is inserted very close to the anus valves and overlaps them. Kaiser (2005) concluded that although the systematic position of the genus is uncertain, *Pseudomesus* fits best in Nannoniscidae. The absence or presence of a mandibular palp is discussed by Svavarsson (1984). *P. pitombo* Kaiser, 2005 and *P. satanus* sp. nov. have a mandibular palp. Originally, the absence of a mandibular palp was presented as an autapomorphy of the genus. In agreement with Kaiser (2005), the absence of a mandibular palp cannot be regarded as a plesiomorphic condition nor as autapomorphy of *Pseudomesus*. A phylogenetic discussion of the characters is presented in chapter 4.2.2.

### 4.2.2 Discussion of characters used in phylogeny

The DELTA matrix concentrates on highly complex characters, which are hypothesized to be phylogenetically informative. Macrostylidae are used as outgroup (Macrostylidae are closely related representatives of Janioridea). The outgroup is defined by 12 characters (8, 14, 20, 21, 42, 65, 68, 69, 71, 118, 124, 125). Of these characters, only the uniramous uropod (124) and the loss of the mandibular palp (42) occur also in Desmosomatidae and Nannoniscidae. All other characters that are apomorph in Desmosomatidae and Nannoniscidae are plesiomorph in Macrostylidae.

Furthermore, the phylogeny of deep-sea Asellota presented in Raupach *et al.* (2004), based on molecular data, shows Macrostylidae (together with Janirellidae and Ischnomesidae, (Fig. 115) to be the sister taxon to Munnopsididae and Desmosomatidae. Comparing molecular data with morphological data, there are different relations of the four families Munnopsididae, Macrostylidae, Desmosomatidae and Nannoniscidae found by the two methods. However, both

results show that Macrostylidae are clearly outside Desmosomatidae and Nannoniscidae (Wägele 1989, Raupach *et al.* 2004, Michael Raupach pers. comm.).

Characters of Nannoniscidae and Desmosomatidae are treated equally. Both families are analysed as one group. All characters are discussed on the background of the principles of a phylogenetic analysis *sensu* Hennig (1966, 1984) and Wägele (2000, 2004). Plesiomorphic character states are shown in brackets behind the autapomorphic state. This implies that the plesiomorphy is relevant for all other taxa. Characters of sexual dimorphism are not used within the phylogenetic analysis because males and females are not known for all species. For the phylogenetic analysis, only species with a detailed description of adult or preparatory females are used or, alternatively, material that could be borrowed from museum collections.

Genera defined by monotypy are included (except for *Chelibranchus*, see chapter 4.2.1.3.2 and *Micromesus*) because they support groups of related taxa. For all other genera, a minimum number of two species (type species plus an additional species) is used for the phylogenetic analysis.

### 4.2.2.1      **Setation**

Hessler (1970) described the setation as conservative. Within a series of setae, such as the ventral row on the carpus, the range of variation generally does not exceed one or two setae (Hessler 1970). The data he gathered for his comparison of individuals showed that in *Desmosoma tetarta* (Hessler, 1970), the range of variation is low, whereas it is high in *Whoia variabilis* Hessler, 1970. Further, a species may show a low standard variation at one locality, but it may still vary from place to place (Hessler 1970). There are clear differences in the number of setae within the setal rows on the carpus and the propodus between species. Therefore. Utilisation of the setal number for phylogenetic analysis becomes critical. One reason not to use numbers of setae is the necessity to determine the intraspecific variation for each species used for the phylogenetic analysis. In many cases the available number of individuals of a species is too low for statistical comparison. Additionally, setal numbers may vary between different developmental stages as seen in *Desmosoma tetarta* (Hessler, 1970). This does not affect the phylogenetic analysis presented in this thesis because only adult or preparatory females are used. However, in order to

avoid numerical mistakes, this character matrix concentrates on the presence of setal types, not on numbers of setae.

Hessler (1970) concluded that the presence of many kinds of setae is highly conservative such that setae fulfil a specific sensory function. Without doubt, every seta fulfils a certain function. Nevertheless, the question is if setae at specific positions can be homologised *a priori*. Some setae are not only constant in numbers in a species but are present in all members of the family at the same position (an example is article 2 of the first antenna carrying 3-4 distomedial broom setae). Hessler (1970) hypothesized that such characters, although minute, may serve for the family diagnosis unless they are constant in other asellote families as well. Hessler's hypothesis about the broom setae was used by Wägele (1989) when he defined *two big broom setae inserted opposite to each other* as an autapomorphy of Desmosomatidae (character 20 chapter 4.1.1).

### 4.2.2.2 Characters

In the following, a discussion of each single character used for the phylogenetic analysis is presented. The characters discussed here are the same as defined in the DELTA-matrix (Appendix). They are numbered the same way. An O marks a character that is defined as "ordered" and the direction of evolution is defined before the computer analysis using PAUP; a U marks a character that is defined as "unordered". The taxa for which the synapomorphies, autapomorphies and plesiomorphies are defined are shown in brackets behind the plesiomorphy.

### Body

1) O **Whole body serrated. [Not the whole body serrated.]** (*Echinopleura* species and *Prochelator serratum*)

Not only the two *Echinopleura* species have a completely serrated body. *Prochelator serratum* also possesses serrated body segments and a serrated pleotelson. *Eugerdella serrata* (chapter 4.2.1.3.5) and *Prochelator serratum* show most probably convergent evolution. Nevertheless, the character confirms the relationship of the *Echinopleura* species.

**2)    O    Only margins of pereonite 5-7 and pleotelson strongly serrated.**

**[Not only margins of pereonite 5-7 and pleotelson strongly serrated.]**

(*Eugerdella serrata* and *E. pugilator*)

Serration, including body segments 5 to 7 and the pleotelson, is found in both species *Eugerdella serrata* sp. nov. and *E. pugilator*. This character is limited to the posterior part of the body and due to the large differences found in *Eugerdella* species convergent evolution is hypothesized. Therefore, serration of the posterior body part is defined as apomorphy.

**3)    O    Pereonites and pleotelson laterally expanding into flat marginal extensions. [Pereonites and pleotelson not with flat lateral extensions.]**

(“nannoniscid character”: *Austroniscus*, *Nannoniscoides* and some species of *Nannoniscus*<sup>16</sup>)

This character was presented by Siebenhaller & Hessler (1981) to distinguish *Thaumastosoma* from other nannoniscid genera. In Nannoniscidae, *Austroniscus* species in particular have a depressed body with an oval shape. The pereonites and pleotelson expand laterally into flat marginal flanges, doubling the real width of the body and extending posteriorly. This condition must have evolved secondarily, because the flattened shape of the body of other Isopoda includes whole body segments, not only lateral extensions. The lateral extensions are regarded as an autapomorphy of *Austroniscus* by Siebenhaller & Hessler (1981).

**4)    O    Body broad (between 2 times and 3.5 times longer than tergal width of pereonite 2). [Body slender (between 3.5 and 5 times longer than tergal width of pereonite 2).] (*Austroniscus*, *Nannoniscoides* and species of *Nannoniscus*)**

According to Wägele (1989), nannoniscids have a broader body than desmosomatids. This is true for the genera *Austroniscus*, *Nannoniscoides* and for some species of *Nannoniscus*. Species of other nannoniscid genera are very similar to the body shape found in desmosomatids: slender and a body length more than three times the width of pereonite 2. Species of some genera that were assigned to Nannoniscidae are of a cigar-like body shape (*Panetela*, *Exilinisca*). According to

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<sup>16</sup> Remark: The monophyly of *Nannoniscus* is questioned due to the high variability of shapes within the genus. Some species of *Nannoniscus* are flattened. Nevertheless, they are not included in the phylogenetic analysis, because of the lack of many details in the description that are necessary for the phylogenetic analysis.

Wägele (1989), this may be regarded as secondarily evolved. The elongated body shape of *Pseudomesus* may also be secondarily evolved like in some other species of Desmosomatidae (*Pseudergella ischnomesoides*, *E. hessleri*) (chapter 4.2.1.3.5). The wide range of body shapes makes it difficult to present possibly homologous characters. The slender body shape is regarded as plesiomorphy while a depressed body is hypothesized to be an apomorphy. The broad body shape of *Austroniscus* results from a secondarily evolved lateral extension of the tergites, not from whole body segments.

**5)    U    Body anteriorly wide and posteriorly slender. [Body not anteriorly wide and posteriorly slender.]** (“desmosomatid character”)

Originally, this character was presented in the generic diagnosis of *Balbidocolon* (Hessler 1970). Later this body shape was discussed as typical desmosomatid body shape (Siebenhaller & Hessler 1977, 1981; Svavarsson 1984). Thus, it is defined as an apomorphy for species belonging to Desmosomatidae.

**6)    O    Body elongated (more than 5 times longer than tergal width of pereonite 2). [Body slender, but not elongated (between 3.5 and 5 times longer than tergal width of pereonite 2).]** (*Pseudergella* and *Pseudomesus*)

In Desmosomatidae a body more than five times longer than the tergal width of pereonite 2 occurs in *Pseudergella hessleri* Just, 1980 (6.8 times the tergal width of pereonite 2) and *E. ischnomesoides* Hessler, 1970 (6.1 times the tergal width of pereonite 2). These two species also bear an elongated segment 5 with convex margins. The elongation of pereonite 5 is the main difference in body shape to distinguish the two *Eugerdella* species from species of *Pseudomesus*. All species of *Pseudomesus* are about six times longer than wide (tergal width of pereonite 2). Therefore, the elongate body shape is discussed as a phylogenetically useful character since the similarity in the body shape correlates with similarities in the characters of pereopod I that are considered to be highly phylogenetically informative.

**7)    O    Body cigar-like with straight body margins (all pereonites of similar width). [Body not cigar-like with straight body margins.]** (*Exilliniscus*, *Panetela*)

“Cigar-like and with straight body margins” is the characteristic body shape for the nannoniscid genera *Exilniscus* and *Panetela*. In *E. clipeatus* Siebenhaller & Hessler, 1981 and *E. aculeatus* Siebenhaller & Hessler, 1981, pereonites 3 and 4 are of similar size and shape as pereonites 5 and 6. Pereonite 1 is smallest. In *Panetela wolffi* Siebenhaller & Hessler, 1981, pereonites 4 and 5 are the longest and 1 and 2 are nearly the same size and the smallest. This body shape is regarded as apomorphy for the species of these two genera.

**8)    Q    Close grouping of pereonites 1-3. [Pereonites 1-3 clearly separated by intersegmental skin, not closely grouped]** (“macrostylid character”)

Macrostylidae are easily distinguished from Nannoniscidae and Desmosomatidae by their distinctive body shape as diagnostic character. The terminus “distinctive” is presented as a distinguishing feature from desmosomatids and nannoniscids by Siebenhaller & Hessler 1981. One feature to clarify “distinctive” is the close grouping of pereonites 1-3, while the first three pereonites are usually clearly separated by intersegmental gaps. The close grouping of the first three pereonites occurs in all Macrostylidae. Therefore, it is hypothesized to be homologous within this family and considered to be an apomorphy of Macrostylidae.

**9)    Q    Pereonite 1 not broad and half of size of pereonite 2 or smaller. [Pereonite 1 not broad nor half of size of pereonite 2 or smaller.]** (*Desmosoma* species, *Echinopleura cephalomagna*, *Eugerdia* species, *Torwolia* species)

This character is typical for desmosomatids that have a specialized slender pereopod I e.g. *Torwolia* species, *Desmosoma* species and *Eugerdia* species as well as *Echinopleura cephalomagna*. Thus, the character is defined as an apomorphy while a pereonite similar in size to the following pereonites is hypothesized as plesiomorphic condition.

**10)   Q    Pereonite 1 broad and clearly smaller than pereonite 2. [Pereonite 1 not broad and smaller than pereonite 2.]** (*Austroniscus*, *Nannoniscoides* species, some *Nannoniscus* species)

In Nannoniscidae, a group of species have a small pereonite 1. In Nannoniscidae, the small pereonite 1 correlates with a broad body shape while in Desmosomatidae, there seems to be a correlation to the specialization of pereopod I. In Nannoniscidae,

pereopod I is not specialized in species which have this character. Thus, convergent evolution is hypothesized in this case. A small pereonite 1 is thought to be a separate apomorphy for this group of nannoniscids.

**11)    Q      Pereonite 2 largest of pereonites 1-4. [Pereonites 1-4 subequal.]**  
(*Torwolia*, species of *Eugerda*, *Desmosoma hesslera*)

The enlargement of pereonite 2 reflects the enlarged and robust pereopod 2 in the genera *Torwolia* and *Eugerda* as well as in *Desmosoma hesslera*. Characters 11 and 12 are often combined in species of both genera. Although, not all species that have one character also have the other. Both characters are regarded to be apomorphic.

**12)    U      Pereonites 1-4 higher than pereonites 5-7. [Pereonites 1-4 of same height as pereonites 5-7.]** (“desmosomatid character”)

The typical body shape of a desmosomatid in lateral view is flattening from the cephalothorax/pereonite 1 towards the posterior pereonites. The anterior pereonites are always higher than the posterior ones. The same condition is found within some groups of Nannoniscidae (for example in species of *Regabellator*, *Rapaniscus*, *Thaumastosoma* or *Pseudomesus*), but not within Macrostylidae. In Munnopsididae the body shape is highly variable. Within the groundpattern, all body segments are hypothesized to be of the same height (chapter 3.1.2). Therefore, this character state is used as apomorphy.

**13)    Q      Pereonites 5-7 enlarged. [Pereonites 5-7 not enlarged.]** (species of *Desmosoma*, *Eugerda*, *Pseudogerda*, *Torwolia*)

The enlargement of the posterior pereopods is probably the result of the swimming life-style of those species. The posterior pereonites hold strong muscles for these enlarged limbs that carry rows of long natatory setae on carpi and propodi. The enlargement of the limbs is correlated with this character, but not necessarily. Thus, the enlargement of the posterior pereonites is treated as a separate character and defined as an apomorphy.

**14)    Pereonites 1-4 shorter than pereonites 5-7 [Only anterior 3 pereonites shorter than pereonites 4-7.]** (“macrostylid character”)

Originally, pereonites 1-3 were shorter than the following pereonites (as in Macrostylidae, compare chapters 3.1.2; 4.1.1; 4.1.2). The adaptation of the fourth

pereonite, which more closely resembles one of pereonites 1-3 in Desmosomatidae and Nannoniscidae, is regarded as apomorphy.

**15)    Q      Pereonite 5 with clearly convex lateral margins. [Lateral margins of pereonite 5 not convex.]** (*Pseudomesus atypicum*, *Pseudergella hessleri*, *Panetela wolffi*)

(see character 17)

**16)    Q      Pereonite 5 inflated. [Pereonite 5 not inflated.]** (*Torwolia*, *Pseudergella hessleri*)

(see character 17)

**17)    Q      Pereonite 5 elongated. [Pereonite 5 similar in size to pereonite 6.]** (*Pseugerdella*, *Pseudomesus pitombo*, *Whoia* species, *Momedossa* species)

Character 15 distinguishes *Pseudergella hessleri* from species of the genus *Pseudomesus*. In *Pseudomesus* pereonite 5 is elongated, but the lateral margins are not convex. Inflation also occurs in species of *Torwolia*, but is not correlated with strongly convex lateral margins. Elongation seems to have evolved more than once in Desmosomatidae and occurs also in *Momedossa* and *Whoia*. Hence, elongation of pereonite 5 (17), an inflation (16) and strongly convex lateral margins (15) are regarded as apomorphies.

**18)    Q      Pleotelson enlarged. [Pleotelson not enlarged.]** (*Pseudomesus* species, *Nannonisconus* species, *Pseugerdella*)

Enlargement of the pleotelson is defined as an apomorphy regardless of the shape of the pleotelson.

**19)    U      Body highly vaulted in transverse section, especially in pleotelson. [Body in transverse section axis not highly vaulted, lateral fields presenting a continuous profile.]** (*Chelator*, *Oecidiobanchus*, *Reductosoma*)

The plesiomorphic condition is found for example in species of *Mirabilicoxa* and is presented as a character in the diagnosis of this genus (Hessler 1970). Highly vaulted bodies are found in *Chelator*, *Oecidiobanchus* and *Reductosoma*. This may indicate convergent evolution. For species of *Chelator* and *Oecidiobanchus*, a close relationship is hypothesized due to the characters of pereopod I. Therefore, this



character might be phylogenetically informative within a monophyletic group of species with a chelate pereopod I.

**20)    Q     Pereonites 4-7 posteriorly acute. [Pereonites 4-7 not posteriorly acute.]** (“macrostylid character”)

In Macrostylidae, the first three pereonites are closely grouped and clearly differ from pereonites 4-7. Additionally, these pereonites are posteriorly acute. This condition is not found in Desmosomatidae and Nannoniscidae and may be regarded as an autapomorphy of Macrostylidae.

**21)    Q     Posterior angles of the tergites of pereonites 4-7 with one stout spine. [Posterior angles of the tergites of pereonites 4-7 without a stout spine.]** (“macrostylid character”)

Pereonites 4-7 of Macrostylidae are acute and the posterior angles of the tergites are tipped with a stout spine. This condition is neither found in Desmosomatidae nor in Nannoniscidae and may be regarded as an autapomorphy of Macrostylidae.

#### **Cephalothorax**

**22)    O     Cephalic keels between antennular folds. [Cephalic keels between antennular folds absent.]** (“nannoniscid character”: *Austroniscus*, *Nannoniscoides*, *Nannonisconus*, *Nannoniscus*)

These bilateral rostral-like structures are very similar in species of nannoniscid genera with a broad body and do not occur in nannoniscids with a slender body shape. Thus, this character is regarded as an apomorphy of this group of taxa.

**23)    O     Cephalon with rostrum. [Cephalon without rostrum.]** (autapomorphy *Exciliniscus*)

The janiroidan groundpattern does not include a rostrum (chapter 3.1.2). Species of the nannoniscid genus *Exciliniscus* bear a rostrum between the insertion of the antennae. Therefore, the presence of a rostrum is regarded as an autapomorphy of this genus (Siebenhaller & Hessler 1981). It is hypothesized that other generic characters also confirm the monophyly of the genus such as a robust antenna, loss of the mandibular palp (although discussed as weak character), and a uniform body shape.

No desmosomatid species bears a rostrum. Likewise, in Macrostylidae, no rostrum is known. There are desmosomatid species such as *Eugerdella pugilator* Hessler, 1970 and *E. serrata* sp. nov. which possess cephalic spines that resemble a rostral structure. However, these rows of spines must have evolved independently due to their position at the dorsal margin of the antennular fold where the antennulae and antennae are inserted (character 24).

**24) O     Dorsal margin of antennular fold with row of spines resembling a rostral structure. [Dorsal margin of antennular fold without any spines resembling a rostral structure.]** (*Eugerdella pugilator*, *E. serrata*)

This spine row on the cephalon is found in *Eugerdella pugilator* Hessler, 1970 and *E. serrata* sp. nov. but in no other desmosomatid species. With regard to the high similarity of characters of pereopod I (character 81), these two species may form a group within *Eugerdella*. This relationship is confirmed by the presence of the spine row.

**25) O     Margin of antennular fold with one anteriorly directed spine. [Margin of antennular fold without distinct spine.]** (*Disparella*, *Mirabilicoxa cornuta* and *M. acuminata*, *Hebefustis*, *Nannoniscoides*, *Prochelator lateralis* and *P. uncatus*)

A pronounced anteriorly directed spine on the antennular fold occurs in species of different genera in Desmosomatidae, especially in *Mirabilicoxa cornuta* (Hessler, 1970), *Prochelator* and all species of *Disparella*. For *Disparella*, such a projection (cephalic spine) is presented in the generic diagnosis (Hessler 1970). The character appears to be weak, but is used in the phylogenetic analysis due to its possible value in characterizing a subgroup (*Disparella*) within a group of species that were previously defined by highly weighted characters like the chela of pereopod I. As such a cephalic spine also occurs in Nannoniscidae, it may have evolved convergently, but seems to be useful in defining small groups of taxa.

#### Antennula

**26) O     Antennula consisting of 5 articles. [Antennula consisting of 6 or more articles.]**

Only in the genera *Austroniscus* and *Nannoniscoides*, some species are included that possess an antennula with 7 articles. The reduction to five articles instead of six or more is regarded as an apomorphic condition. The possibility of convergent reduction restricts the phylogenetic use of this character. Although it appears to be weak, it may be useful in a group that is clearly defined as a monophylum when the ventral number of antennular articles may be used as apomorphic character state. The number of articles becomes important with regard to the evolution of the specialized antennulae with a bulbous last article (discussed below).

**27) O    Antennula with *specialized* distal articles. [Antennula with *unspecialized* distal articles.]** (“nannoniscid character”)

The specialized antennula includes more than one character. The specialization may include only the last article which is bulbous (*Hebefustis* and *Nannoniscoides*) or involve also an elongation of the previous article holding the last bulbous one. Character 27 is used to distinguish between a last bulbous article only (characters 28 and 29) or a character complex that depends on patterns of the previous articles (characters 30 to 32). The specialization of the antennula as defined in characters 30 to 32 is hypothesized to have evolved only once. Therefore, defining a large group of species, the “true Nannoniscidae” (Stefanie Kaiser pers. comm.), while a bulbous last article alone may have evolved twice as defined in characters 28 and 29.

Whether the reduction of the flagellar articles from 4 to 3 proceeds the specialization of the distal articles is crucial in understanding the evolution of the distal antennula. If the reduction to three articles is followed by this specialization, this evolution needs a minimum of two steps and must be the apomorphy while the bulbous last article as the fourth flagellar article evolved convergently.

In some species of *Nannoniscus*, the elongation holding the last bulbous article is located at the first flagellar segment according to drawings of Menzies & George (1972). For example, in *Nannoniscus ovatus* and *Nannoniscus muscarius* there is no true elongation, and in *Nannoniscus perunis* there are two. Possibly there are mistakes in the drawings. The type material was not studied to clarify the questionable descriptions. However, the monophyly of *Nannoniscus* is questioned, as only plesiomorphies define the genus and species of this genus show a high variability.

**28)    Q     Flagellum with rounded bulbous last article. [Flagellum not with rounded bulbous last article.]** (“nannoniscid character” occurring in species of *Exilinisculus*, *Nannonisconus*, *Nannoniscus*, gen. nov. *fletcheri*, *Panetela*, *Rapaniscus*, *Regabellator*, *Saetoniscus* and *Hebefustis*)

Although the bulbous terminal article of the antennula seems to be a conservative condition, there are exceptions in the features of this character. The bulbous article is only one of the characters regarded as phylogenetically informative (character 27). It is hypothesized that a bulbous last article evolved from a fusion of distal articles or an inflation of the distal article (except for the condition found in *Nannoniscoides*). This probably was followed by an elongation of flagellar article 2 which holds the third bulbous article and the bulbous form became more pronounced. The flagellar article 1 was reduced with further functional specialization of flagellar articles 2 and 3. Species of the genus *Hebefustis* bear a bulbous terminal article, but no elongation at the flagellar article 2. This is considered as a plesiomorphic condition within the evolutionary steps necessary for the specialized antennula.

**29)    Q     Antennula with bulbous and long terminal article (clearly longer than wide). [Terminal article of antennula not bulbous and long.]** (*Nannoniscoides*)  
(see character 27 and 28)

**30)    Q     Flagellar article 1 of antennula smallest. [Flagellar article 1 of antennula not smallest.]** (“nannoniscid character” occurring in: *Exilinisculus*, *Nannonisconus*, *Nannoniscus*, *Panetela*, *Rapaniscus*, *Regabellator*, *Saetoniscus*)

The features of the flagellar articles have to be regarded as a complex character. It is difficult to decide if the features of the antennulae with a terminal bulbous flagellar article are homologous or convergently evolved<sup>17</sup>.

**31)    Q     Flagellar article 2 of antennula with elongation holding terminal bulbous article. [Flagellar article 2 of antennula without elongation holding terminal bulbous article.]** (see character 27 and 28)

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<sup>17</sup> Flagellar article 4 as last bulbous article occurs in *Micromesus* Birstein, 1963, a monotypic genus with the species *Micromesus nannoniscoides* Birstein, 1963, which is excluded from the phylogenetic analysis due to an incomplete species description and a questionable systematic position in Nannoniscidae (Siebenhaller & Hessler 1981, Wägele 1989, Kaiser 2005). Therefore, this character is not defined here.

**32)    Q     Terminal article of antennula bulbous and ball-shaped. [Terminal article of antennula not bulbous and ball-shaped.]**

(see character 27 and 28)

**33)    Q     Article 2 of antennula elongated (twice as long as first peduncular article). [Article 1 and 2 of antennula of the same size.]** (character 13 in chapter 4.1.1")

This character state was used as a synapomorphy for the sistergroups Desmosomatidae and Nannoniscidae by Wägele (1989). In members of both families, the second peduncular article is the longest article of the antennula. In Macrostylidae, the first peduncular article of the antennula is the largest. It is used in the phylogenetic analysis to separate Macrostylidae from the sistergroups Desmosomatidae and Nannoniscidae.

**34)    Q     Article 2 of antennula distally with 3-4 joint articulated broom setae. [Broom setae sporadically present.]** (character 14 in chapter 4.1.1)

In Macrostylidae, broom setae are sporadically present on the second peduncular article while in Nannoniscidae and Desmosomatidae the number of joint articulated broom setae is constant. The constant presence of broom setae is not known in the closest related group, Munnopsididae. Therefore, the constant number of three or four articulated broom setae is regarded as an apomorphy according to Wägele (1989).

**35)    Q     Article 2 of antennula distally with (just) two joint articulated broom setae. [Article 2 of antennula with more than two joint articulated broom setae at distal end.]** (character 20 in chapter 4.1.1)

This character is presented as an autapomorphy for Desmosomatidae by Wägele (1989). A question to be raised with regard to the original definition of this character is: what kind of broom setae may be included in the definition. In the present analysis, the character means joint articulated broom setae only. Broom setae with a simple cuticular articulation are not included.

##### **Antenna**

**36)    Q     Shortened and robust antenna, reaching only one quarter of the body length. [Antenna long and slender, clearly longer than one quarter of the body length.] (*Exiliniscus*)**

This character state is presented in the generic diagnosis of *Exiliniscus* and is regarded as an autapomorphy of this genus (Siebenhaller & Hessler 1981).

##### **Mandible**

**37)    Q     Lacinia mobilis reduced to one small tooth. [Lacinia mobilis with 3 to 5 teeth.] (*Echinopleura*, *Whoia victoriensis*)**

Both species of *Echinopleura* possess a lacinia mobilis that is only one small tooth. This character state occurs also in *Whoia victoriensis*. It is regarded as an apomorphy of *Echinopleura*.

**38)    Q     Incisior process bent forward as one strong tooth. [Incisior process not bent forward as one strong tooth.] (*Thaumastosoma*)**

This character is one of the features of the mandible that is influenced by the anteriorly directed production of the mouthparts in *Thaumastosoma*. Thus, it is regarded as an autapomorphy of the genus. The incisior process is also bent forward in *Cyodesma agnari* but not so strongly and with two distal teeth.

**39)    Q     Incisior process without teeth. [Incisior process with teeth.] (*Echinopleura*)**

Simplified mandibles are presented as a character in the generic diagnosis of *Echinopleura* (Sars 1864, Hessler 1970). The mouthparts in general are complex structures adapted to the lifestyle and feeding mechanisms of the species. Thus, the characters of the mandible are regarded to be phylogenetic informative. Specializations of mandibular structures (here a simplified incisior process) are correlated with other features as in *Echinopleura* where the lacinia mobilis is reduced to a small tooth (character 37).

**40)    Q     Incisor process with strong shelf-like tooth. [Incisior process not shelf-like.] (*Disparella*, *Momedossa*)**

In this kind of incisior process, the teeth seem to be fused into one extremely strong enlarged shelf-like tooth, which is regarded as the apomorphic character state.

**41)    Q      Incisor process enlarged (almost twice as long as lacinia mobilis).  
[Incisor process not enlarged.]** (*Disparella*)

This may be regarded as apomorphy of *Disparella*, as such an enlargement of the incisor process is unique for species of this genus.

**42)    Q      Mandibular palp absent. [Mandibular palp present.]** (character 11 in chapter 4.1.1)

The presence or absence of the mandibular palp is a weak character in the families Desmosomatidae and Nannoniscidae; although the *absence of the mandibular palp* is presented as an autapomorphy of Macrostylidae by Wägele (1989). According to Wägele (1989), the presence of the mandibular palp is the plesiomorphic condition in Desmosomatidae and Nannoniscidae. In both families there are genera that include species with and without a mandibular palp (in *Mirabilicoxa* some species possess a palp and some do not, whereas in *Exiliniscus* no species possesses a palp).

**43)    Q      Mandibular palp consisting of two articles. [Mandibular palp not consisting of two articles.]** (*Paradesmosoma*, *Desmosoma latipes*, *D. ochotense*)

A reduced third article of the mandibular palp occurs in all species of *Paradesmosoma*. Therefore, it is hypothesized that the reduction is an apomorphy of the genus although the third article is reduced, most possibly convergently, in other species of Desmosomatidae as well.

#### **Maxilliped**

**44)    Q      Retinaculae elongated: more than 3 times longer than width of stalk. [Retinaculae not elongated: about 2 times longer than width of stalk.]** (*Thaumastosoma*, *Reductosoma*)

Such an elongation of the retinaculae is known only for the genus *Thaumastosoma*. No other desmosomatid, nannoniscid or macrostylid species possesses such long retinaculae. In *Reductosoma gunnera* Brandt, 1992, the retinaculae are longer than usual, but not as elongated as in *Thaumastosoma*. Species of *Thaumastosoma* have extremely highly specialized mouthparts and the elongated retinaculae are one of the complex patterns of this specialization.

**45)    Q     Mouthparts extremely bent forward. [Mouthparts not bent forward.]**  
(*Thaumastosoma*, *Echinopleura cephalomagna*)

From a lateral view, the cephalothorax tapers to the tip of the maxilliped palp, covering the mouthparts. It is difficult to decide what the plesiomorphic condition of the position of the mouthparts is. In *Thaumastosoma* the head is characterized by the mouthparts bent extremely forward, forming a “tip” from lateral view. This condition is also found in *Echinopleura cephalomagna*, most possibly as the result of convergent evolution. However, the extremely modified mouthparts are a complex character that include more than one phylogenetically informative character.

#### **Pereonites**

**46)    Q     Stout sensory setae present anteriorly on tergites 1-4. [No sensory setae present anteriorly on tergites 1-4.]** (“nannoniscid character”)

Most nannoniscid species possess spines on the tergites. Such spines on the tergites do not occur in Desmosomatidae or Macrostylidae. The anteriorly directed spines on the tergites may be an autapomorphy of a group of species in Nannoniscidae *sensu* Siebenhaller & Hessler 1981.

**47)    Q     Pereonite 1 broader than pereonite 2. [Pereonite 1 not broader than pereonite 2.]** (“desmosomatid character”)  
(see character 48)

**48)    Q     Pereonite 1 longer than pereonite 2 (midsagittal length). [Pereonite 1 not longer than pereonite 2.]** (Eugerdellatinae)

The enlargement of pereonite 1 is dependent on the need of musculature for a modified robust pereopod. Most species with a robust or chelate first pereopod possess an enlarged pereonite 1. When in the evolution of the families Nannoniscidae and Desmosomatidae was a robust or chelate first pereopod developed? The similar size of the pereonites is here regarded as a plesiomorphy as well as in the following character (49).

**49)    Q     Pereonite 1 enlarged and clearly bigger (more than 2 times of midsagittal length of pereonite 2). [Pereonite 1 not enlarged and clearly bigger than pereonite 2.]** (*Eugerdella* species group 1)



The extreme enlargement of pereonite 1 is found in *Eugerdella* species (group 1: chapter 4.2.1.3.5). It is regarded as an autapomorphy for this group.

**50)    Q      Pereonite 1 shorter and not as broad as pereonite 2. [Pereonite not shorter than pereonite 2.]** (species of *Eugerdella*, *Pseudogerdella* and *Desmosoma*)

The reduction or attenuating of pereopod I is often combined with a reduction in size of pereonite 1 (species of *Eugerdella*) although this dependence is not always given (species of *Pseudogerdella* and *Desmosoma*). Thus, equal size of pereonite 1 and 2 is the plesiomorphic state, which also relates to the groundpattern of Janiroidea.

**51)    Q      Spine-like ventral elongations at pereonites 1 to 5 decreasing in length towards the posterior pereonites. [Pereonites 1 to 5 without spine-like ventral elongations.]** (*Eugerdella pugillator* and *E. serrata*)

The presence or absence of a ventral elongation at the pereonites should be treated as single character for each pereonite. If a common ancestor of Macrostylidae, Nannoniscidae and Desmosomatidae is hypothesized to have ventral elongations at the pereonites, the absence of the elongations is a reduction. Here it is postulated that the common ancestor did not possess ventral elongations. Although, the presence of ventral elongations at the pereonites is regarded as synapomorphy of the three families by Wägele (1989). (character 15, chapter 4.1.1)

When comparing the ventral elongations which occur in all three families, it becomes obvious that they are located at different pereonites and that their shape varies: the nannoniscid species *Regabellator profugus* and *R. abyssi* possess ventral elongation at the fused pereonites 6 and 7 (character of the generic diagnosis of *Regabellator*), the elongation at pereonite 6 is directed anteriorly, the one at pereonite 7 caudally. The nannoniscids *Rapaniscus dewdneyi*, *R. crassipes* and *R. multisetosus* possess a caudally directed strong ventral elongation on pereonite 7, but not at the dorsally fused pereonites 6 and 7. *R. centauri* and *R. multisetosus* possess a ventral spine on the operculum. In addition to these characters, all three *Rapaniscus* species possess a specialized antennula with a bulbous last article. *Nannoniscus teres* possesses a caudally directed strong spine on pereonite 7, *N. analis* a curved caudally directed spine on the operculum and *N. bidens* and *N. antennaspinis* a straight, but caudally directed spine on the operculum. Within *Nannoniscus*, species with and without opercular spine are grouped together. *Saetoniscus meteori* possesses an opercular

spine. In *Thaumastosoma*, a straight spine on pereonite 7 and a strong midventral spine on the operculum are present. The spines of *Nannoniscus* are more anteriorly positioned on the operculum as they are in *Saetoniscus meteori*.

Opercular spines also occur in Macrostylidae. *Macrostylis longipedis* possesses a straight opercular spine tapering to the posterior part of the operculum, a short straight ventral spine on pereonite 1, and a slightly curved caudally directed spine on pereonite 2. In *M. abyssalis*, ventral caudally directed elongations are present at pereonites 5 and 6 and in *M. longispinis* at pereonites 6 and 7. However, the elongation on pereonite 7 is stronger than the one on pereonite 6.

The desmosmatid species *Prochelator lateralis* and *P. hampsoni* possess an anteriorly directed spine at pereonite 1. In *P. lateralis* ventral caudally directed spines also occur on pereonite 2-4. *Disparella kensleyi* sp. nov. bears an anteriorly directed ventral elongation at pereonite 5 and the *Eugerdella* species *E. pugilator* and *E. serrata* possess anteriorly directed ventral elongation at pereonites 1-5 which decrease in length towards the posterior pereonites.

With regard to the differences in the families, one might homologize the ventral elongations present in Desmosomatidae at pereonites 1-5 (with the exception of *Disparella kensleyi*), a second group of ventral elongations at the pereonites in Nannoniscidae, a third group of ventral elongations at the operculum and - as a fourth group - the ventral elongations occurring in Macrostylidae. In the present analysis, it is decided to treat each type of spine or involvement of ventral elongations in a character complex as a single character (characters 51 to 57). For the macrostylid spines, no characters are defined because they were previously defined as an outgroup due to 10 other characters. Further, the spines occurring in Macrostylidae seem to have evolved convergently compared to those found in Nannoniscidae and Desmosomatidae.

**52) Q Anteriorly directed spine at pereonite 1. [Pereonite 1 smooth ventrally.]** (*Prochelator lateralis* and *P. hampsoni*, *P. uncatus*)

(see character 51)

**53) Q Spine-like ventral elongation at the fused pereonites 6 and 7, the elongation at pereonite 6 directed anteriorly, the one at pereonite 7 caudally. [Pereonites 6 and 7 without fusion or spine-like elongation.]** (*Regabellator* species: *R. profugus* and *R. abyss*)

(see character 51)

**54) Q Ventral spine midway on the operculum. [Operculum without ventral spine.]** (*Rapaniscus centauri* and *R. multisetosus*)

(see character 51)

**55) Q Ventral caudally directed strong spine on pereonite 7. [Pereonite 7 smooth ventrally.]** (*Nannoniscus teres*, *Thaumastosoma platycarpus* and *T. tenue*, *Rapaniscus dewdneyi*, *R. crassipes* and *R. multisetosus*)

(see character 51)

**56) Q Ventral curved caudally directed spine located midway on the operculum. [Operculum without spine.]** (*Nannoniscus analis*, *Thaumastosoma platycarpus* and *T. tenue*)

(see character 51)

**57) Q Ventral straight, caudally directed spine positioned anteriorly on the operculum. [Operculum without spine.]** (*Nannoniscus antennaspinis*, *N. bidens*, *Saetoniscus meteor*)

(see character 51)

**58) Q Pereonites 6 and 7 fused. [Pereonites free.]** (“nannoniscid character” *Saetoniscus*, *Rapaniscus*, *Regabellator*, *Nannoniscus*, *Hebefustis*, *Nannoniscoides*, *Gen. nov.*, new species A)

The fusion of the pereonites is a character occurring in Nannoniscidae and can be regarded as an apomorphy, while free pereonites are the plesiomorphic condition in the asellotan groundpattern and in closely related groups.

**59) Q Pereonites 6 and 7 fused with pleotelson. [Pereonites and pleotelson free.]** (“nannoniscid character”, gen. nov. *fletcheri*, new species A)

This character state occurs in gen. nov. *fletcheri* (Paul & George 1975; Kaiser 2005). In no other nannoniscid species the posterior two pereonites (6 and 7) and the pleotelson are fused. This character is regarded as an autapomorphy and may have evolved out of a fusion of pereonites 6 and 7 only, secondarily involving the pleotelson or from a fusion of the pleotelson with pereonite 7, secondarily involving

pereonite 6. Since the pleotelson contains fused pleonites, it is hypothesized that the fusion first included pereonite 7 and the pleotelson at first and then pereonite 6.

**60)    Q        Pereonite 7 and pleotelson fused. [Pereonites and pleotelson free.]**  
(“nannoniscid character” *Nannonisconus*)

Only pereonite 7 and the pleotelson are fused in species of *Nannonisconus*. The character is regarded as an apomorphy of this genus.

**61)    Q        Pereonites 6, 7 and pleotelson with marginal flanges. [Pereonites 6, 7 and pleotelson without marginal flanges.]** (*Mirabilicoxa*, *Eugerdia*, *Desmosoma*, *Thaumastosoma*)

Marginal flanges occur in different genera of Desmosomatidae representing a character also known as sexual dimorphic and occurs in females and males. Therefore, it is difficult to decide whether it evolved convergently or not. Although the character appears to be weak, it is used in the analysis. It is hypothesized that the marginal flanges may be used as apomorphy to define a subgroup within a genus.

#### **Pereopods**

**62)    Q        Coxae 1-4 with anterolateral elongations [Coxae without anterolateral elongations.]** (*Mirabilicoxa*)

In the generic diagnosis of *Mirabilicoxa* presented by Hessler (1970), the produced coxae are regarded as an autapomorphy of the genus. This is probably true, because they do not known for any other genus of Desmosomatidae. In females, the projections are not as strong as in males. In Nannoniscidae and Macrostylidae, such coxal projections are absent.

**63)    Q        Coxae 1-4 anteriorly tipped with stout seta. [No stout seta present on anterior tip of coxae 1-4]** (“desmosomatid character”)

The presence of setae on the tip of the coxal projections is regarded as a desmosomatid character (contrary to character 39). The presence of a sensory spine is defined as apomorphy. Taxa without a projection usually posses a seta on the angular anterior tip of the coxa.

**64) O Coxae produced anteriorly. [Coxae angular, without projection.]**

(“desmosomatid character”)

In the janioridean groundpattern, coxae are not produced anteriorly. Such a projection is regarded as an apomorphy.

**65) Q Pereopods I, II, VI and VII longer than pereopods III to V. [Pereopods of similar length.]** (“macrostyliid character”)

This character was considered to be a macrostyliid character in the literature (e.g. Siebenhaller & Hessler 1981). In most nannoniscid species all pereopods are of similar length. Species of *Thaumastosoma* and *Pseudomesus* in addition to most Desmosomatidae possess posterior swimming legs that are slightly longer than the anterior pereopods.

**66) Q Pereopods V to VII longer and more heavily built than pereopods II to IV. [Pereopods V to VII and pereopods II to IV of similar length.]** (*Eugerdia*, *Pseudogerdia Torwolia*, *Desmosoma*)

The plesiomorphic condition is a similar length of the pereopods. A difference in strength (length) is regarded as apomorphy.

**67) Q Pereopods V-VII: Ischium elongated (more than 5.5 times longer than wide). [Pereopods V-VII not with elongated ischium.]** (*Pseudergella hessleri*, *P. ischnomesoides*)

Such an elongation of the ischium occurs in no other species of Desmosomatidae or Nannoniscidae. This characterizes these two species as sistertaxa.

**68) Q Pereopod III dorsally bent. [Pereopod III not dorsally bent.]** (“macrostyliid character” 9, chapter 4.1.1)

When comparing the pereopod III of macrostyliid species with pereopods of desmosomatid or nannoniscid species, the macrostyliid dactyli are dorsally bent (and the dorsal margin has long setae). This is regarded as an autapomorphy of Macrostylidae (Wägele 1989).

**69) Q Dactylus of pereopod III with row of long setae. [Dactylus of pereopod III without row of long setae.]** (“macrostyliid character” 10, chapter 4.1.1)

This character is an autapomorphy of Macrostylidae according to Wägele (1989).

**70)    U        Ventral row of natatory setae at pereopods V to VII absent. [Ventral row of natatory setae present.]** (“nannoniscid character” 16, chapter 4.1.1)

Ventral rows of setae were presented as an autapomorphy of Desmosomatidae by Wägele (1989). Thus, Nannoniscidae are regarded as a more derived group. Consequently, the presence of ventral rows of setae in some nannoniscid species (for example at carpus and propodus of pereopod VII in the *Pseudomesus* and *Thaumastosoma* species) leads to the hypothesis of a reduction of these setae in Nannoniscidae. It may also be possible, that the group of species without natatory setae on the posterior limbs is the group that has the plesiomorphic condition. Consequently, natatory setae evolved once in Nannoniscidae and Desmosomatidae regarding the two families as one group. In this case, the species with the ability to swim would be more derived (most desmosomatids).

**71)    O        Basis of pereopod VII with long setae. [No long setae on basis of pereopod VII present.]** (“macrostylid character”)

The “swimming setae” at the basis of pereopod VII in Macrostylidae do not occur in Desmosomatidae and Nannoniscidae (Brandt 2004). In contrast to these two families, Macrostylidae possess robust setae on propodus and carpus. This kind of setation may be regarded as an apomorphy, which distinguishes Macrostylidae from Desmosomatidae, Nannoniscidae and other Janiroidea.

#### **Pereopod I\***

**72)    U        Ventral margin of carpus of pereopod I with composed robust setae in a row. [Ventral margin of carpus of pereopod I not with composed robust setae in a row.]** (“desmosomatid character” 18, chapter 4.1.1)

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\* The functional unit of the propodus and carpus as well as the setation of the ventral margin of the carpus on pereopod I is a complex character. Each sub-character (pattern) is coded separately. The “claw-seta” can be homologized with the distal seta of the ventral row. The composed (unequally bifid) seta is regarded as a plesiomorphic condition, while distally setulate or slender setae are hypothesized to be reductions of the originally composed seta, because composed setae are not only present in Desmosomatidae, but also in Nannoniscidae and Macrostylidae. The characters of pereopod I are mainly defined to distinguish between the related groups in Desmosomatidae because ventral and dorsal rows are not present in most species of Nannoniscidae. However, there are exceptions (character 18 chapter 4.1.1).

This character is one of the apomorphies of Desmosomatidae as presented by Wägele (1989) Setae standing in a row means more than three setae inserting very close and in regular distances to each other increasing in size towards the distal setae of the article. Hessler (1970) used the term “major setae”. Composed robust setae are present in Macrostylidae, but are not lined-up in clear rows. In some Nannoniscidae, composed robust setae are lined-up in a row (for example on the carpus and propodus of the robust pereopod I of the three *Rapaniscus* species). In Desmosomatidae these rows tend to be reduced in the genera *Desmosoma*, *Eugerdia*, *Pseudogerdia* and *Mirabilicoxa* as well as in those genera where pereopod I has a chela (*Chelator*, *Prochelator*, *Disparella*, *Oecidiobanchus*). These reductions are regarded as apomorphies of the single groups, while within Desmosomatidae composed setae lined-up in rows are the plesiomorphic condition (defined in character 73). In Desmosomatidae the setae tend to be composed and long while in Nannoniscidae, if present, the setae in the row are composed and short.

**73) Q Pereopod I: ventral row of setae on carpus reduced due to specialization. [Pereopod I: ventral row of setae on carpus not reduced due to specialization.]** (“desmosomatid character”)

(see character 72)

**74) Q Carpus of pereopod I with a row of long simple setae dorsally. [Carpus of pereopod I without a row of long simple setae dorsally.]** (“desmosomatid character” 18, chapter 4.1.1).

Reduction of this dorsal row is present in desmosomatid species depending on the specialization of pereopod I. These reductions are defined as an apomorphy in character 75.

**75) Q Pereopod I: dorsal row of setae on carpus reduced due to specialization. [Pereopod I: dorsal row of setae on carpus not reduced due to specialization.]** (“desmosomatid character”)

(see character 74)

**76) Q Enlargement of pereopod I concentrating on carpus. [Enlargement of pereopod I not concentrating on carpus.]** (*Prochelator*, *Chelator*, *Disparella*,

*Eugerdella* species, *Mirabilicoxa cornuta*, new species A, *Paradesmosoma*, *Reductosoma*, *Rapaniscus*)

The enlargement of pereopod I correlates with the enlargement of the carpus. This occurs in the group of species possessing a carpo-euchelate or a raptorial pereopod I. A heavy carpus seems to be essential in both forms. Thus, the concentration on the enlargement of the carpus is defined as apomorphy for this group of species.

**77) Q Enlargement of pereopod I concentrating on propodus. [Enlargement of pereopod I not concentrating on propodus.]** (*Eugerdella* species, *Paradesmosoma*, *Prochelator*, *Reductosoma*, *Oecidiobranchus*, new species A, *Cryodesma*)

This character is defined as apomorphy for the species possessing a raptorial pereopod I due to the hypothesis, that its function makes the evolution of the enlarged propodus necessary.

**78) Q Pereopod I small and slender, but propodus enlarged. [Pereopod I not small and slender with enlarged propodus.]** (*Torwolia*)

In *Torwolia* the propodus is modified to form a subchela and differs in form and shape from the kind of enlargement found in other desmosomatids. Furthermore, the other articles and specialization of pereopod I in *Torwolia* resembles more the trend found in *Eugerdella*, *Pseudogerdella* and some *Desmosoma* species (chapter 4.2.1.2.4).

**79) Q Pereopod I as functional unit enlarged. [Pereopod I as functional unit not enlarged.]** (Eugerdellatinae, *Rapaniscus* species)

Eugerdellatinae are regarded as a monophyletic group due to the enlargement of pereopod I leading to different forms of specialization in this subfamily. Thus, this character is regarded to be an apomorphy for all species included in Eugerdellatinae. In some species of Nannoniscidae an enlarged pereopod I evolved convergently, which is clearly distinguishable by characters of the carpus and propodus as discussed in chapter 4.2.1.3.5.

**80) U Propodus of pereopod I ventrally with row of small stout unequally bifid setae. [Propodus of pereopod I ventrally not with row of small stout unequally bifid setae.]** (*Eugerdella* species, *Hebefustis*, *Nannoniscus*, Gen. nov., *Rapaniscus*)



Within species possessing a raptorial pereopod small stout unequally bifid setae occur on the ventral margin of the propodus. This is regarded as an apomorphy related to the function of the limb, as such a row does not occur in any other of the five forms of pereopod I. Since the apomorphic character state also occurs in some nannoniscid genera, it may be possible, that such a row evolved more than once. The character is defined “unordered” due to the possibility of convergent evolution or reduction of the row.

**81)    Q     Platform-like gap between propodus and distoventral seta on carpus present. [Platform-like gap between propodus and distoventral seta on carpus absent.]** (*Eugerdella serrata*, *E. pugilator*, *E. theodori*, *E. nonfunalis*)

This platform-like gap occurs in the extremely enlarged forms of a raptorial pereopod I only and seems to act as a stopping mechanism for the movement of the propodus. Thus, it is regarded as an apomorphy.

**82)    Q     Carpus of pereopod I enlarged and tapering towards propodus. [Carpus of pereopod I not enlarged, not tapering towards propodus.]** (*Rapaniscus*)

An enlarged carpus tapering towards the propodus is the result of convergent evolution of the enlarged pereopod I within Nannoniscidae. This form of the carpus is regarded as apomorphy defining the *Rapaniscus* species (chapter 4.2.1.4).

**83)    Q     Propodus of pereopod I ventrally fringed with fine hairs and setae connected by a cuticular membrane. [Propodus of pereopod I ventrally not fringed with fine hairs and setae connected by a cuticular membrane.]** (all species with a carpo-euchelate pereopod I)

A fringed ventral margin occurs in all species possessing a carpo-euchela. Thus, it is hypothesized, that there is a functional need of such a structure for the function of the chela. The character state is defined as apomorphic for this group of species. In some species belonging to *Momedossa*, *Desmosoma* or *Pseudogerda* the ventral margin of the propodus may be fringed with a cuticular membrane, but there are no setae breaking through this membrane as defined for this character.

**84) Q Carpus of pereopod I enlarged and broadest at articulation to propodus. [Carpus of pereopod I not enlarged and not broadest at articulation of propodus.]** (new species A, *Paradesmosoma*, *Oecidiobanchus*, *Prochelator*, *Chelator*, *Disparella*)

In the specialized pereopod I forming a carpo-euchela, the width of the carpus gives the propodus more room at the articulation and the propodus is wider at its posterior articulation than at its anterior articulation with the dactylus. The carpus being broadest anteriorly is defined as an apomorphic character state.

**85) Q Carpus distolaterally with “claw-seta”. [Carpus distolaterally not with a “claw-seta”.]** (*Oecidiobanchus*, *Prochelator*, *Chelator*, *Cryodesma*, *Disparella*, new species A, *Paradesmosoma*, *Reductosoma*)

The distal seta of the ventral row of the carpus is extremely enlarged reaching the full length of the ventral margin of the propodus or is even slightly longer than this. The claw-seta acts as an antagonist to the propodus forming a grasping organ. The evolution of these patterns is so complex, that it is most likely, that such a structure evolved only once. Consequently, the group of species possessing a carpo-euchela can be defined as a monophyletic group.

**86) Q Carpus distolaterally produced. [Carpus distolaterally not produced.]** (species of *Chelator*, *Prochelator* and *Disparella*, *Reductosoma gunnera*)

In some species of the carpo-euchelate genera the carpus is produced at the base of the claw-seta. This may support the function of the claw-seta and is therefore defined as apomorphic character state. However, this character appears to be weak, as it is difficult to distinguish between a production and only a bulge due to the insertion of the large claw-seta, but was presented in the generic diagnosis of *Chelator* (Hessler 1970).

**87) Q Carpus of pereopod I with one composed seta midway. [Carpus of pereopod I not with one composed seta midway.]** (*Prochelator*, new species A, *Reductosoma*)

The composed midventral seta is presented as character within the generic diagnosis of *Prochelator* (Hessler 1970). Some species of the genus possess a composed seta midway, others a distally setulate seta, which is also described as “accessory seta”

by Hessler (1970). Such a midventral seta occurs not only in species of the genus *Prochelator*, but also in *Reductosoma gunnera* and new species A. It may be regarded as an apomorphy of this group of species.

**88)    Q    Ventral setae behind claw-seta small and simple or small and slender. [Not with ventral setae behind claw-seta small and simple or small and slender.]** (*Chelator*, *Disparella*)

This combination of characters does only occur in species of *Chelator* and *Disparella*. It is regarded to be an apomorphy of this group of species.

**89)    Q    Carpus of pereopod I enlarged and with setae of irregular size. [Carpus of pereopod I not enlarged, not with setae of irregular size.]** (*Paradesmosoma*, *Eugerdella*)

The apomorphy was used for the generic diagnoses of *Eugerdella* modified by Hessler (1970) and *Paradesmosoma* as presented by Kussakin (1965). The species of these two genera are the only species possessing setae of irregular size. Thus, this is regarded as an apomorphy of *Paradesmosoma* and a group of species within *Eugerdella* (chapter 4.2.1.3.5).

**90)    Q    Size of ventral setae on carpus irregular and of varying types. [Size of ventral setae on carpus not irregular, of same type.]** (*Paradesmosoma*)

This character distinguishes the species of *Paradesmosoma* from the *Eugerdella* species. No other desmosomatid or nannoniscid species has this character. It clearly defines the group of species united within *Paradesmosoma*. Size of ventral setae on carpus irregular and of varying types is regarded as an apomorphy of the genus.

**91)    Q    Setae behind claw-seta small, of similar size and type. [Carpus of pereopod I not with claw-setae and setae not behind claw-seta small, of similar size and type.]** (some *Disparella* species, *Chelator* species)

This combination of setae defines a group of species in *Chelator* and *Disparella*. The regular size combined with the claw-seta is unique for this group of species and therefore can be regarded as apomorphic character state.

**92) Q Carpus distoventrally with claw-seta and penultimate seta. [Carpus not with claw-seta and penultimate seta.]** (*Prochelator*, *Chelator*, *Oecidiobanchus*, *Reductosoma*, *Disparella* and new species A)

This apomorphy characterizes the group of species with a carpo-euchela and supports the monophyly of this group.

**93) Q Pereopod I robust, articles almost quadrangular. [Pereopod I not robust, articles not quadrangular.]** (*Whoia*, *Thaumastosoma*)

Species of *Whoia* and *Thaumastosoma* possess limbs very similar to the form hypothesized for the janioridean groundpattern, but the limbs are more robust and bear rows of large composed setae. This robust form of the limb is regarded as an apomorphy.

**94) U Setae in ventral row on carpus of pereopod I increasing in length towards propodus. [Setae in ventral row on carpus of pereopod I not increasing in length towards propodus.]** (“desmosomatid character”)

In most species the setae in the ventral row are increasing in length towards the propodus. This condition is not found in nannoniscids. Thus, it is regarded as desmosomatid character, although in many species these rows are reduced. Due to this fact, the character is defined as “unordered”.

**95) Q Setae on carpus and propodus of pereopod I not composed. [Composed setae present on carpus and propodus of pereopod I]** (*Desmosoma*, *Eugerdella*, *Austroniscus*, *Regabellator*, *Nannoniscoides*)

The composed setae may have been reduced several times in both families. Therefore, this is defined as apomorphic character state.

**96) Q Distoventral seta on carpus of pereopod I shortest. [Distoventral seta of carpus of pereopod I not shortest.]** (*Eugerdella* species, *Pseudergella*, *Mirabilicoxa cornuta*)

This character defines the genus *Eugerdella* as presented by Hessler (1970), but the genus can be regarded as paraphyletic. It is quite possible that a short distal seta evolved convergently. However, here it is used as apomorphic character state, because it is hypothesized that this may clarify the relationship in terminal taxa and

support the relationship between sistertaxa (for example *Pseudergella* gen. nov., chapter 4.2.1.5.1, and *Pseudomesus*, chapter 4.2.1.5.2).

**97) Q     Distoventral seta of carpus reaching full length of propodus. [Distoventral seta of carpus not reaching full length of propodus.]** (all species with a carpo-euchelate pereopod I as well as *Cryodesma*, *Whoia angusta* and *Thaumastosoma platycarpus*)

This apomorphy defines species with enlarged distal setae and the group of species bearing a carpo-euchelate pereopod I. It is hypothesized, that the large size of the distal setae evolved first and therefore is the plesiomorphic condition for the species bearing a carpo-euchela.

**98) Q     Second seta behind claw-seta of similar size. [Not with second seta behind claw-seta of similar size.]** (*Cryodesma*)

Species included in *Cryodesma* bear a ventral row of long composed setae on the carpus of pereopod I as well as a seta very similar to a claw-seta. The similarity in size of the setae in the row is regarded as an apomorphy of the genus (Svavarsson, 1988).

**99) Q     Pereopod I slender in comparison to pereopod II. [Pereopod I not slender in comparison to pereopod II.]** (*Desmosoma*, *Echinopleura*, *Eugerdia*, *Pseudogerdia*, *Mirabilicoxa*, *Torwolia*)

Here, the specialization of pereopod I with the trend to an attenuated condition is described. A slender pereopod I is defined as apomorphic character state.

**100) Q     Pereopod I slender and ventrally only slender setae present on carpus and propodus. [Pereopod I not slender and not only slender setae present on carpus and propodus.]** (*Desmosoma*, *Eugerdia*, *Pseudogerdia*)

This condition is only found in species of *Desmosoma* and *Eugerdia* and is defined as an apomorphy for this group of species. The composed setae are hypothesized to be reduced.

**101) Q     Pereopod I small in size, subchelate: propodus enlarged and dactylus folding against propodus. [Pereopod I not small in size, not subchelate.]** (*Torwolia*)

A subchela is unique for species of *Torwolia*. Thus, this condition is defined as an apomorphy of the genus.

**102) Q Propodus of pereopod I elongated in chela. [Propodus of pereopod I not elongated in chela.] (*Disparella*)**

An elongation of the propodus in the carpo-euchela of pereopod I is only found in species of *Disparella* and is defined as an apomorphy of the genus.

**103) Q Propodus of slender pereopod I elongated (over 3.5 times longer than wide). [Propodus of pereopod I not elongated.] (*Desmosoma* species, *Echinopleura*, *Eugerdia* *Pseudogerdia*, *Mirabilicoxa*)**

This character defines a group of species in the subfamily Desmosomatinae. For the species characterized by this apomorphy a close relationship is hypothesized. The elongation of the propodus leads to a transformation series that ends in an extremely attenuated pereopod I (chapter 4.2.1.2.4, here: characters 104-106).

**104) Q Pereopod I slender: propodus between 4.1 and 5.2 times longer than wide, carpus about 4.5 times longer than wide. [Pereopod I not slender.] (*Desmosoma*)**

*Desmosoma gigantea* propodus 4.1 times longer than wide; carpus 4 times longer than wide, *D. latipes* propodus 5.2 times longer than wide; carpus 4.8 times longer than wide. For discussion see character 103 and chapter 4.2.1.2.4.

**105) Q Pereopod I slightly attenuated: propodus of pereopod I between 6 and 9 times longer than wide and carpus between 5 and 7.2 times longer than wide). [Pereopod I not slightly attenuated.] (*Pseudogerdia*)**

*Pseudogerdia intermedia* propodus 8.6 times longer than wide; carpus 7.2 times longer than wide. *P. elegans* propodus about 9 times longer than wide, carpus about 5 times longer than wide, *P. arctica* propodus 6.5 times longer than wide, carpus 5.6 times longer than wide, *P. anversense* propodus about 6 times longer than wide, carpus about 7 times longer than wide. For discussion see character 103 and chapter 4.2.1.2.4.

**106) Q Pereopod I strongly attenuated (propodus 18.8 times longer than wide, carpus 15 times longer than wide), setae absent on propodus and carpus.**

**[Pereopod I not strongly attenuated, setae present on propodus and carpus.]**  
(*Eugerdia*)

*Eugerdia reticulata* (propodus 18.8 times longer than wide, carpus 15 times longer than wide), *Eugerdia fulcimandibulata* (propodus 15.2 times longer than wide, carpus 11.8 times longer than wide). For discussion see character 103 and chapter 4.2.1.2.4.

#### **Pereopod II**

**107) Q Pereopod II robust, articles almost quadrangular. [Pereopod II not robust, articles, not quadrangular.]** (*Whoia*)

In species of *Whoia* pereopod II is as robust as pereopod I. The first two limbs resemble (compare character 93) each other so much that the similarity was presented in the generic diagnosis by Hessler (1970). Such a robust pereopod II occurs in no other species of Desmosomatidae or Nannoniscidae. It is regarded here as an apomorphy of the genus.

**108) Q Propodus of pereopod II heavily built. (carpus and propodus broad). [Propodus of pereopod II not heavily built.]** (*Torwolia*, *Eugerdia*, *Pseudogerdia*, *Desmosoma*)

In some species of *Desmosoma* and *Eugerdia* pereopod II is specialized to a an enlarged and strong limb. This correlates with the reduction of size of pereopod I and sometimes with an enlargement of pereonite 2, e.g. in *Torwolia*. A heavily built pereopod II is defined as an apomorphy.

**109) Q Carpus of pereopod II bearing a ventral row of composed setae. [Setae on carpus of pereopod II not standing in ventral rows.]** (desmosomatid character 19 chapter 4.1.1)

This character is part of a complex autapomorphy presented by Wägele (1989). The other parts are defined in characters 110 and 111. Composed setae occur on pereopod II in Macrostylidae, Desmosomatidae and Nannoniscidae. The presence of composed setae can be regarded as a plesiomorphy. In Macrostylidae these setae are not standing in a row. In most species of Nannoniscidae, these setae are not sanding in a row. The presence of a row has to be defined as an apomorphy.

**110) Q Propodus of pereopod II bearing a ventral row of composed setae. [Setae on carpus and propodus of pereopod II not standing in rows ventrally.]** (see character 109, second part of the autapomorphy.)

**111) Q Carpus and propodus of the pereopod II bearing dorsally a row of long setae. [Setae on carpus and propodus of pereopod II not standing in rows dorsally.]** (see character 109, third part of the autapomorphy.)

**112) Q Basis and ischium of pereopods II and III fringed with distally plumose setae. [Basis and ischium without this setal type.]** (compare characters 113 and 114, *Paradesmosoma*) This type of seta occurs only in the genus *Paradesmosoma*.

#### **Pereopod IV**

**113) Q Pereopod IV folioid, carpus and propodus paddle-like. [Pereopod IV not folioid, carpus and propodus resembling carpus and propodus of pereopod III.]** (*Paradesmosoma*)

The species of the genus *Paradesmosoma* possess a very specialized pereopod IV – a character, which distinguishes the species of the genus from all other desmosomatids and nannoniscids. Hessler (1970) described the fourth pereopod to be unique for this genus and suggested an origin separate from that of the chelate forms.

**114) Q Carpus and propodus surrounded by (with a dense row of) numerous distally plumose setae<sup>18</sup>. [Carpus and propodus not surrounded by numerous distally plumose setae.]** (*Paradesmosoma*)

This type of seta (see character 112) occurs only within the species of the genus *Paradesmosoma*. The setae are surrounding the propodus and carpus so characteristically, that this can be defined as an apomorphy of the genus. The plesiomorphic character state is a ventral and dorsal row of setae (composed or

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<sup>18</sup> Ventral margins of ischium, merus, capus and propodus with setae having sturdy long bases, being abruptly more slender with flexible tips possessing fine hairs (Figure 7).



slender setae) as in other desmosomatid species which bear a pereopod IV that resembles pereopod III.

#### **Pereopod VII**

**115) Q Ischium dorsally with anteriorly directed cuticular hook. [Ischium dorsally smooth.] (*Pseudomesus*)**

The dorsal hook on the ischium is a cuticular structure appearing in the species of *Pseudomesus* only and can therefore be regarded as an autapomorphy of this genus.

**116) Q Propodus and carpus of pereopod VII with long setae dorsally. [No long setae dorsally of propodus and carpus of pereopod VII.] (“desmosomatid character”)**

The evolution of natatory setae on the carpi and propodi of the posterior pereopods is presented as an autapomorphy of Desmosomatidae in the literature (Hessler 1982, Wägele 1989). While some species possess a condition “between” like *Thaumastosoma platycarpus* or *Pseudomesus satanus* sp. nov. or the natatory setae are completely absent in other nannoniscid species. Wägele (1989) hypothesized a common ancestor of Munnopsididae, Macrostylidae, Desmosomatidae and Nannoniscidae that was able to dig and swim with the posterior pereopods. Consequently, Macrostylidae lost the natatory setae, while in Desmosomatidae the natatory setae evolved as a row and these rows were reduced in Nannoniscidae, the most derived group according to Wägele (1989). Regarding the relationships of the families in figure 115 based on molecular data (Raupach *et. al.* 2004), an other hypothesis could be that Macrostylidae never had swimming setae and these setae have evolved in Munnopsididae and Desmosomatidae (including Nannoniscidae, compare chapter 4.1.1).

**117) Q Propodus and carpus of pereopod VII with long setae dorsally. [No long setae dorsally of propodus and carpus of pereopod VII.] (“desmosomatid character”, see character 116)**

**118) Q Basis of pereopod VII with long slender “swimming setae”. [Basis of pereopod VII without “swimming setae”.] (“macrostylid character”)**

According to Brandt (2004), the presence of these setae is regarded as a macrostylid autapomorphy.

#### **Pleotelson**

**119) Q Pleotelson dorsally inflated. [Pleotelson dorsally not inflated.]**  
(*Pseudomesus*)

The dorsal inflation of the pleotelson is the most typical feature of *Pseudomesus* species next to the extremely short uropods. It is probably an apomorphy of the genus.

**120) Q Anus region separated and bilobed. [Anus region not separated and bilobed.]** (*Nannonisconus*)

This shape of the anus region is unique for species of this genus. Thus, it is defined as its apomorphy.

**121) Q Pleotelson vaulted in transverse section. [Pleotelson not vaulted in transverse section.]** (*Chelator*, *Oecidiobanchus*, *Whoia* species)

This condition was defined as generic character of *Oecidiobanchus* by Hessler (1970). It also occurs in *Chelator antarcticus* sp. nov. and some *Whoia* species. In *Oecidiobanchus* there may be a correlation of the form of the pleotelson and the small opercular chamber (character 123). This form of the pleotelson may indicate a close relationship of *Oecidiobanchus* and *Chelator*. Both genera possess a carpo-euchela on pereopod I.

**122) Q Branchial chamber and operculum in relation to size of pleotelson small, operculum of oval shape and posterior part broadest. [Branchial chamber and operculum covering nearly the whole pleotelson ventrally.]**  
(*Austroniscus*)

This condition of the branchial chamber in *Austroniscus* (Nannoniscidae) differs from the form of a small branchial chamber as it occurs in *Oecidiobanchus* (character 123); in *Austroniscus* the branchial chamber is small with regard to the flat lateral body extension. This is unique for species of this genus and therefore defined as apomorphy.

**123) O      Branchial chamber and operculum in relation to size of pleotelson small, rounded. [Branchial chamber not small and rounded.]**

(*Oecidiobranchus*)

A very small operculum occurs also in species of *Austroniscus*, which are defined by other autapomorphies like the lateral elongation and the flattening of the tergites. In *Oecidiobranchus*, the size of the branchial chamber is small in comparison to the body without regard to any flanges. Therefore, it is possible, that a small branchial chamber evolved convergently within these two taxa. Here, both character states are presented as an apomorphy due to the different shapes of the branchial chamber and the operculum (character 122). It is considered to be useful to define the systematic position of the species of the two genera.

**124) O      Uropods uniramous. [Uropods biramous.]**

Macrostylidae possess very characteristic uropods: uniramous with elongated articles. In most cases, the uropods are much longer than the length of the pleotelson. It is hypothesized that the reduction of the exopod took place first, and then the elongation followed as evolutionary step. Reduction of the exopod occurs frequently within Desmosomatidae while most Nannoniscidae possess biramous uropods (exception: *Pseudomesus*, *Nannoniscus ovatus* and *N. perunis*). Reduction of the exopod is not a phylogenetically useful character. The uniramous condition with the extreme elongation found in Macrostylidae can be regarded as a macrostylid autapomorphy (character 125).

Hessler (1970) described five stages of reduction and presented examples from different species. In his opinion, the species possessing a reduced exopod indicate how this structure might have got lost. The loss of the exopod cannot be regarded as a transformation series, as long as species with a reduced exopod are not characterized by any other synapomorphy. The description of different „stages of reduction“ is most possibly a description of convergent evolution. The phylogenetic information of these reductions is doubtful, but the reduction may serve well as diagnostic character. In Desmosomatidae, the uropodal exopod does never reach the full length of the endopod.

**125) Q Uropodal sympod extremely elongated; styliform. [Uropodal sympod not elongated, shorter than endopod.]** (“macrostylid character” 7 chapter 4.1.1)

This character is presented as an autapomorphy for Macrostylidae by Wägele (1989). The very characteristic uropods are described above (character 124).

**126) U Uropods cover anus valves. [Uropods not covering anus valves.]** (“nannoniscid character” 17 chapter 4.1.1)

Wägele (1989) presented this character as an autapomorphy for Nannoniscidae. The question is, how much of the anus valves are covered by the uropods or whether a very close insertion to the anus valves is the same. This character state is scored when the uropods are partly overlapping the anus valves (due to a close insertion next to them). The plesiomorphic state is given, if the uropods are inserting near the distal ends of the pleotelson. Within the phylogenetic analysis, groups may be defined by this character although it occurs also in some desmosomatid species, not only in Nannoniscidae (chapter 4.1).

**127) Q Uropods short, not overlapping posterior margin of pleotelson. [Uropods not short, overlapping posterior margin of pleotelson.]** (“nannoniscid character” 17 chapter 4.1.1)

For using the apomorphic character state that was presented as an autapomorphy of Nannoniscidae by Wägele (1989), “uropods short” has to be defined clearly. The terminus “short” is defined here as not overlapping the terminal margin of the pleotelson (for example species of *Pseudomesus*). Thus, the plesiomorphic condition is that the uropods overlap the posterior margin of the pleotelson. However, the definition of this character remains weak. To define the length of the uropod, as morphometric relation its extension beyond the posterior margin of the pleotelson was used.

**128) Q Uropodal endopod bulbous. [uropodal endopod clearly longer than wide.]** (*Pseudomesus*)

An extremely shortened, bulbous uropodal endopod occurs within species of *Pseudomesus*. This is regarded as an apomorphic condition while in the plesiomorphic state the uropodal endopod is longer than wide.

**129) Q Uropodal exopod reduced to half of size of endopod or less.  
[Uropodal exopod not reduced to half of size of endopod or less.]**

For this character, convergent evolution is hypothesized in many taxa. Although this character appears to be weak, the reduction of the exopod is used as apomorphic state because it may solve the relationship in terminal clades.

### **4.3 Results of phylogenetic analysis**

Desmosomatidae are a difficult group for systematic research because of the high variability of forms and many intermediate forms of characters. The number of undescribed species that have interesting and possibly phylogenetically informative characters is extremely high. Describing more species may clarify the relationships indicated by intermediate forms. The present knowledge does not completely dissolve the relationship of all taxa. A hypothesis about the phylogeny and evolution in Desmosomatidae is presented.

#### **4.3.1 Topology and tree data**

The consistency index of the trees found in the phylogenetic analysis is low. Consequently, the homoplasy index is high. The retention index (0.8182) is thought to be not distorted by autapomorphies and symplesiomorphies (Wägele 2001). This index is distinctly higher than the homoplasy index (0.6815). In total, 49 apomorphies were found only once in the trees, 27 apomorphies twice, while the rest occurred more than twice.

Although the resulting trees seem not to reproduce the data in a satisfying way and difficulties were obtained during the branch swapping, the strict consensus trees of all PAUP runs had the same result. The difficulties were probably obtained 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. Due to these difficulties, bootstrap values are not shown. Although three consensus trees are presented as a result in the present study, the phylogenetic relationships of Desmosomatidae are still problematic. The 50 percent majority rule tree may give an idea about evolution in Desmosomatidae. However, it has to be doubted that a better resolution can be found by morphological means alone.

### 4.3.2 Results compared to previous phylogenetic studies

All three consensus trees support the five subfamilies as defined in chapter 3.1.4.2 and discussed in chapter 4.2.1. Austroniscinae (clade 114) and Nannoniscinae (clade 199) are monophyla in all three trees, Pseudomesinae (clade 179 without *Pseudergella atypicum*) are a monophyletic group. The position of *P. atypicum* resolved in the 50 percent majority-rule tree, while in the 80 percent majority-rule tree and the strict consensus the position of *P. atypicum* is not resolved.

Desmosomatinae (clade 174) can be regarded as monophyletic group, while Eugerdellatinae (clade 149) are weakly supported and are only completely resolved as monophyletic group in the 50 percent majority rule tree (clade 149). They may be regarded as a derived group of species. Their monophyly, previously discussed as “group C” by Wägele (1989) is confirmed in the 50 percent majority rule tree, while in the 80 percent majority rule tree and the strict consensus tree the subfamily seems to be paraphyletic because *Whoia* and *Eugerdella* branch off in a polytomy. Within Eugerdellatinae, a robust pereopod I (*Whoia*, *Eugerdella*, compare discussion in chapters 4.2.1.3.5 and 4.2.1.3.12) develops to a chela (clade 135). The synapomorphy of clade 149 in the 50 percent majority rule tree “pereonite 1 not shorter than pereonite 2” appears to be weak because the branches collapse in the 80 percent majority rule tree and the strict consensus tree.

The *Whoia-Thaumastosoma* clade (146) and the “true *Eugerdella* species” (clade 141; see discussion in chapter 4.2.1.3.5) are defined by clear apomorphies. The position of *Mirabilicoxa atlanticum* and *M. cornuta* is problematic, because both species do not possess a robust pereopod I. The systematic position of *M. cornuta* has been previously discussed by Kussakin (1999), who decided to transfer this species from *Eugerdella* to *Mirabilicoxa* although it does not fit into the genus completely (compare chapter 4.2.1.2.5 and 4.2.1.3.5). The result of the phylogenetic analysis confirms the fact that the systematic position of this species is not clear to distinguish. The same difficulty occurs regarding *M. atlanticum* (discussion in chapter 4.2.1.2.1).

In contrast to Eugerdellatinae, Desmosomatinae *sensu* Hessler (1970) were regarded as “collection-group ” of taxa (Wägele 1989). Although most genera could be proved to be monophyletic in the present phylogenetic analysis, the relationship between the genera could not completely solved. Some groups of species are well defined by apomorphies e.g. clade 165 (*Momedossa*) and clade 163 (*Torwolia*,

*Desmosoma*, *Pseudogerda* *Eugerd*). The relationships of *Desmosoma*, *Pseudogerda* and *Eugerd* (clade 161) are discussed in chapters 4.2.1.2.2, 4.2.1.2.4 and 4.2.1.2.8. While it seems that *Desmosoma* species are basal within this clade (50 and 80 percent majority rule trees), the relationship of species of *Pseudogerda* and *Eugerd* are not completely clear.

In the 80 percent majority rule tree and the strict consensus tree, Desmosomatinae (clade 174) are clearly resolved, while *Whoia* and *Thaumastosoma* (clade 165), *Eugerdella* (clade 141), branch off polytom together with *Mirabilicoxa atlanticum*, *M. cornuta*, clade 172 (species of *Mirabilicoxa* and *Echinopleura cephalomagna*), *Momedossa* (clade 165), clade 163 (see above) and clade 149 (all genera with a chelate pereopod I).

*Torwolia* (clade 162) was treated as subfamily *incertae sedis* (Hessler 1970, Wägele 1989). The present study can show that this genus belongs to the subfamily Desmosomatinae and is closely related to *Desmosoma*, *Pseudogerda* and *Eugerd* (clade 161).

### 4.3.3 Problematic characters and clades and their plausibility

The two species of the genus *Echinopleura* do not occur as a monophyletic group in the trees. *E. aculeata* stands as sisterspecies to *Mirabilicoxa similis* in the clade of most of the *Mirabilicoxa* species (clade 172). The systematic position of *E. cephalomagna* is not clearly resolved in all three trees. The synapomorphies of the genus *Echinopleura* (chapter 3.1.4.3.6) are not supported in the trees, although the modifications of the mouthparts are regarded as phylogenetically informative in the character discussion (chapter 4.2.2). In regard to the geographical distance of these two *Echinopleura* species, the result of the phylogenetic analysis is not surprising. While *E. aculeata* was found in the northern hemisphere (Sars 1897), *E. cephalomagna* sp. nov. was collected from the South Australian continental slope. Maybe, the two species evolved similar characters due to convergent evolution in a similar environment.

In general, distribution or depth does not seem to influence the result of the phylogenetic analysis. The terminal clades contain deep-sea species and species which were sampled in shallow waters grouped together in a monophylum, for example Pseudomesinae (clade 179), clade 161 (*Desmosoma*, *Pseudogerda*, *Eugerd*) or *Paradesmosoma* (clade 132). In contrast to the genus *Echinopleura*, in

*Paradesmosoma* the two species known from arctic waters group together with the species from the South Australian continental slope (*P. australis* sp. nov.). This is somehow surprising, but the apomorphies of the genus *Paradesmosoma* are well supported in all trees. It is worth to note, that species of *Paradesmosoma* were whether found in the DIVA-samples nor in the ANDEEP samples.

Although *Austroniscus* species which are included into this analysis show a distribution in shallow waters, the genus is recorded from the deep sea (Table 3). *A. ovalis* is known from East Antarctica in a depth between 70 and 385 m. *A. chelus* and *A. obscurus* were sampled from the Antarctic shelf in the Weddell Sea in up to 910 m depth (Kaiser submitted).

In *Nannoniscoides*, only *N. latediffusus* has a distribution shallower than 1000 m (584 m), but this seems to have no influence on the result. Important is the fusion of pereonites 6 and 7 [58]. Due to the presence of this apomorphy in *Nannoniscoides gigas* and *N. latediffusus*, *Nannoniscoides* splits into two clades (111 and 113). Clade 111 includes *N. biscutatus* and *N. coronarius*, the two species that were assigned to *Nannoniscella* by George (2001) as discussed in chapter 4.2.1.1.2; clade 113 contains *N. gigas* and *N. latediffusus*, the two species without a fusion of pereonites. The high variability of forms in *Nannoniscoides* indicates that the phylogenetic relationships of species within this genus need further analysis. Not all species of the genus were included in the present study. The systematic position of *N. biscutatus* and *N. coronarius* may be discussed anew. This discussion should be based on a more detailed analysis of all characters and species of this genus.

Together, *Whoia* and *Thaumastosoma* are a monophyletic group and are regarded as separate genera (chapters 4.2.1.3.12 and 4.2.1.3.11). Lateral margins of pereonite 5 convex [15] and pereopod II robust (articles almost quadrangular) are apomorphies that occur only in species of this clade and support their relationship. Interestingly, *Thaumastosoma* species form the sistergroup to *Whoia victoriensis* sp. nov. from the Australian continental slope (clade 143). Both *Thaumastosoma* species are known from the northern hemisphere and *T. platycarpus* was recorded in the DIVA-1 samples from the Angola Basin (Brandt 2002, Kaiser 2005, Brenke & Wägele submitted). Following synapomorphies support this grouping: lateral margins of pereonite 5 not convex inflated [15], uropods biramous [124] and uropodal exopod reduced to half of size of endopod or less [129]. Thus, the uropods are important to define this clade. This is not convincing because the reduction of the exopod



happened more than once independently and clade 146 is defined by uniramous uropods [129].

Although most genera are well supported and grouped together, the relationships within the genera are not resolved. This problem may be solved if apomorphies of single species could be treated as phylogenetically informative. For example, *Reductosoma gunnera*, the only species of the genus, possesses a maxilliped differing completely from the form usually found in Desmosomatidae. The palp consist of four articles instead of five and the shape and form of the articles are elongated. *Reductosoma gunnera* is the only species with these apomorphies. They were not included in the computer analysis because PAUP would have treated them, occurring in one taxon only, as phylogenetically uninformative. However, the specialization of the mouthparts in *Reductosoma* are regarded as informative enough to hold the status of a genus (Brandt 1992; see chapter 4.2.1.3.10). In addition, the close relationship of *Reductosoma* to the other genera possessing a carpo-euchelate pereopod I as proposed by Brandt (1992) could be confirmed, although the species branches off in a polytomy.

New species A (chapter 3.1.5.3.1) has to be fully described before any decision about the systematic position is made. Nevertheless, the species is included in the phylogenetic analysis due to the unique combination of following apomorphies: fusion of pereonite 6, 7 and the pleotelson [59], antennula consisting of 5 articles [26] and unspecialized [27], pereopod I carpo-euchelate [85] and uropods biramous [124], overlapping anus valves [126]. The carpo-euchelate pereopod I confirms the relationship to the other genera included in clade 135. This proofs that also in Desmosomatidae a fusion of pereonites can evolve, although fusion of pereonites were previously discussed as “nannoniscid character” (chapter 4.2.2).

It has to be regarded, that the assumption about evolution within Desmosomatidae of this phylogenetic analysis is based on unambiguous results. Despite all problems discussed above, a general idea about evolution within the family can be gained.

### 5 Outlook

Our knowledge about the distribution of many species depends on sampling activity. The distribution of Desmosomatidae worldwide correlates with sampling data of previous projects and expeditions. The international project CeDAMar (Census of the Deep Abyssal Marine Life) was created to gain a more detailed picture about benthic life in the deep sea. DIVA is one of the projects under the umbrella of CeDAMar and the work with the samples of DIVA-2 are under progress.

The present study yields the morphological and taxonomic background for further analyses of the DIVA samples. Using molecular methods seems to be necessary to access a better understanding of the relationships in Desmosomatidae. Yet, the molecular work depends on fresh material for DNA extraction.

During DIVA-2, DNA of over 300 isopods was extracted, 97 extract from Desmosomatidae (including Nannoniscidae). Until now, the 18s gene of 13 species was sequenced and 21 sequences of COI could be obtained including two species of the most discussed genus *Pseudomesus*. The next aim is to compare results of a molecular analysis with the phylogenetic ideas gained out of the morphological analysis of the family Desmosomatidae.

The species composition of the deep-sea basins of the East South Atlantic will be compared and species occurring at stations of DIVA-1 and DIVA-2 will be described. Although the description of new species is a time consuming work, it is important for all future analyses.

The question is if there are sibling species in the Atlantic and may species turnover along the latitudinal gradient from North to South be morphologically visible? What is found to be a single species, may represent in reality a number of very similar species. Recently, the problem of sibling species became more and more obvious (Wilson 1983, Held 2003, Held & Wägele 2005). A detailed study of the *Mirabilicoxa* species by morphological and molecular methods may help to understand the reasons for the development of the high diversity of benthic deep-sea invertebrates.

### 6 References

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## 8. Appendix

**Table 10: Character matrix (DELTA) of 107 species and 129 characters used in the phylogenetic analysis**

[illegible]

## 8. Appendix

[illegible]

## 8. Appendix

[illegible]

8. Appendix

|                                  |   |
|----------------------------------|---|
| <i>Thaumastosoma platycarpus</i> | 00000100000101000000000000000000011?001000001111100000011000010110000000101000000000000000001100100000000000101000010000000001001 |
| <i>Thaumastosoma tenue</i>       | 000001000001010000000000000000000110001000001111100000011000010110000000101000000000000000001100100000000000101000010000000001001 |
| <i>Torwolia creper</i>           | 000000001011111100000000000000000111000000000000001000000000000110100000101100100000000000000000001010000001111000001000000100000 |
| <i>Torwolia subchelatus</i>      | 000000001011111100000000000000000111000000000000001000000000000110100000101100100000000000000000001010000001111000001000000100000 |
| <i>Torwolia tinbieniae</i>       | 000000001011111100000000000000000111000000000000001000000000000110100000101100100000000000000000001010000001111000001000000100000 |
| <i>Whoia angusta</i>             | 0000000000010110100000000000000001100000000000001000000000000100000000101000000000000000001100100000000010101000011000100101000   |
| <i>Whoia dumbshafensis</i>       | 0000000000010110000000000000000001100000000000000000000000000100000001010000000000000000100000000000010111000011000100101000      |
| <i>Whoia variabilis</i>          | 0000000000010110100000000000000001100000000000001000000000000100000000101000000000000000001100100000000010101000011000100101000   |
| <i>Whoia victoriensis</i>        | 000000000001010000000000000000000110?10000000000101000000000001100000001010000000000000000110010000000001010100001100010000?001   |



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December 15, 2005

To whom it may concern:

This is to certify that the quality of the English employed in the Ph.D. thesis submitted by the candidate Saskia Brix entitled „Evolution, Systematics and Distribution of the Desmosomatidae (Isopoda, Peracarida, Crustacea) in the Deep Sea“ is of a standard sufficient to fulfill the language requirements of the University of Hamburg.

Prof. Dr. Patricia Nevers  
(native speaker of the English language)

*Patricia Nevers*

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