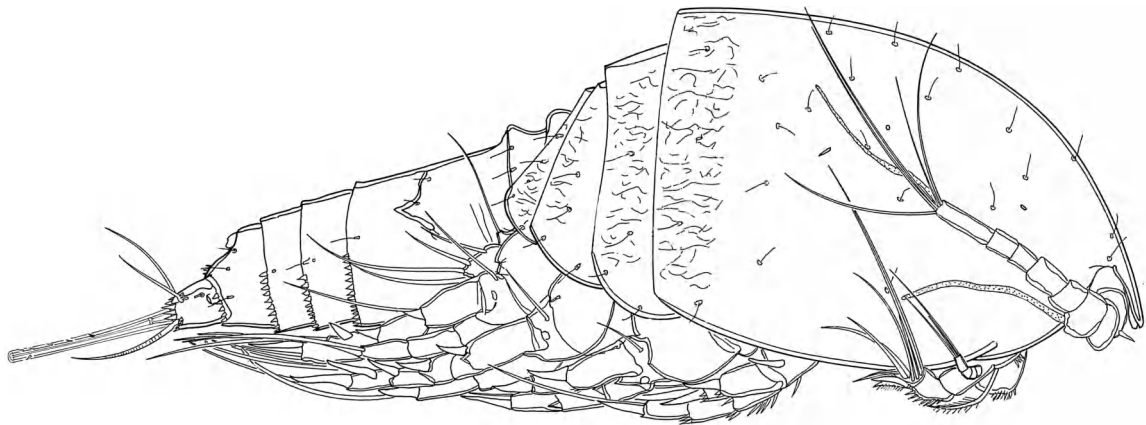


Phylogeny of Harpacticoida (Copepoda):  
Revision of  
“Maxillipedasphalea” and Exanechentera

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## 1. INTRODUCTION

Harpacticoida Sars, 1903 are small crustaceans of a size below one millimetre (Figs. 1 - 3). Wherever there is water or moisture they can be found. They are part of the marine plankton and inhabit all kinds of marine sediments. They live at hydrothermal vents, on muddy sediments in the deep sea, in sea ice, in estuaries, on algae and in the interstitial of sandy beaches. They are ubiquitous in freshwater lakes, groundwater, water bodies in caves, in puddles, rivers, streams, and moist moss. Some species of Harpacticoida are parasites, symbionts or commensals.

Harpacticoida live on anything their specific environment has to offer: bacteria, algae, and detritus; sometimes they are even carnivorous. Harpacticoids themselves serve as food for invertebrates, fish, and their larvae. Because of their specific ecological role, species of Harpacticoida have a fundamental impact on most aquatic ecosystems.

In the marine benthos, especially in the deep sea harpacticoids are the second largest meiofauna group after nematodes. They can reach a density of 500 individuals per 10 cm<sup>2</sup> sediment, sometimes even up to 4,000 individuals per 10 cm<sup>2</sup> sediment. It is still a matter of debate how many of them there are. By now, more than 3,000 species of Harpacticoida have been documented, but thousands of species remain to be discovered and described. For example, an estimation of the number of species of Harpacticoida in the deep-sea regions quickly leads to a five-digit number.

Despite this importance and their large numbers in respect to species and individuals, the taxon of Harpacticoida is not adequately known. As yet no phylogenetic system is available. The only comprehensive attempt, so far, to elucidate relationships within the whole Harpacticoida was undertaken by Lang (1944, 1948) including the revision of all species of Harpacticoida described at that time. Lang (1948) divided Harpacticoida into Polyarthra Lang, 1944 and Oligoarthra Lang, 1944 and split Oligoarthra into "Maxillipedasphalea" Lang, 1944, Exanechentera Lang, 1944, and Podogennonta Lang, 1944. The systematic changes and the taxa established by Lang (1944, 1948) were based on his phylogenetic system. To date, his system is outdated because it was founded not only on apomorphic but also on plesiomorphic characters. The present work is part of a project aiming at the revision of the system of Harpacticoida as a whole. One part of it is already finished (Willen, 2000); a second part is under way. These two parts concern the monophyletic taxon Podogennonta. The systematic revision of the remaining 868 described species of Harpacticoida (Polyarthra, "Maxillipedasphalea" Lang, 1944, Exanechentera Lang, 1944) is the subject of the present study.

During the past two decades, systematics went through a fundamental change. New ways to evaluate and validate hypotheses were opened up through methods delivered by computer-aided cladistics and molecular systematics. Working with morphological characters, it is a common practice today to generate phylogenetic hypotheses by applying the techniques of Phylogenetic Systematics sensu Hennig (i.e. Hennig, 1966, 1982; Ax, 1984, 1987; Wägele, 2000) and computer-aided cladistics. Both methods

have their strengths and weaknesses but the basis for both is that the phylogenetic relationships are based on apomorphies only. Apomorphies are evolutionary novelties evolved in the stem species of a monophylum.

As a first step, the supports for the hypothesis of the monophyly of Harpacticoida and Oligoarthra are presented and discussed (chapter 4.).

Then, the monophyly of 17 taxa of Harpacticoida was established on the basis of the adult morphology and the complete groundpatterns of all taxa were reconstructed. The groundpattern represents the hypothetical morphology of the members of the last common population of the species group in question (Wägele, 2000). The characterisation of the taxa contains the groundpattern, the autapomorphies, the diagnosis, a list of all taxa belonging to it, and the recent species number (chapter 4.).

Further, the phylogenetic relationships of Harpacticoida were established (chapter 3) by applying the techniques of Phylogenetic Systematics (i.e. Hennig, 1966, 1982; Ax, 1984, 1987; Wägele, 2000; chapter 5.1.4) and computer-aided cladistics (chapter 5.1.3). The analysis was made on the basis of the reconstructed groundpatterns of the terminal taxa. The methods used for the reconstruction of the groundpatterns and the phylogenetic analysis are described (chapter 2.) and discussed (chapters 4. and 5.2). The taxonomic changes that result from the analysis were deduced (chapter 3). First steps towards the characterisation of the evolution of Harpacticoida are made (chapter 5.1.6).

Then, the selection of characters, the homology of character states, their polarity, the irreversibility of character transformation, and the general oligomerization trend within Harpacticoida are discussed (chapter 5.2.1 - 5.2.6).

As last step, the complete groundpatterns, the autapomorphies and the diagnosis of the supraspecific taxa established by Lang (1944, 1948), that are verified by the present analyses and the new supraspecific taxa inferred from the phylogenetic system, were reconstructed (chapter 4).

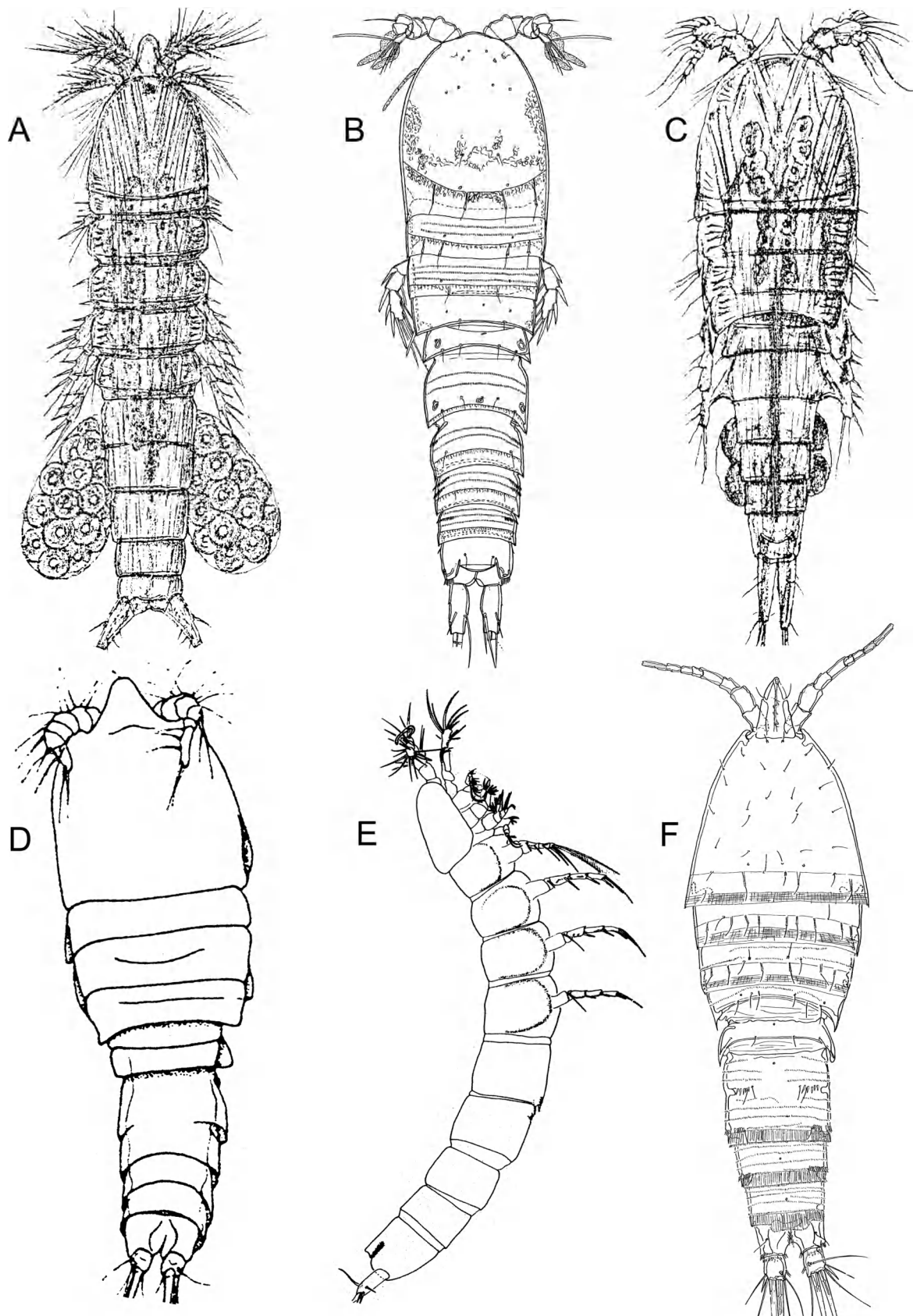


Fig. 1: Habitus of Harpacticoida. A. *Canuella perplexa* T. & A. Scott, 1893 (after Sars, 1903). B. *Romete spec.* C. *Eucanuella spinifera* T. Scott, 1901 (after Sars, 1903). D. *Marsteinia sarsi* (Bodin, 1968) (after Bodin, 1968). E. *Chappuisius singeri* Chappuis, 1940 (after Glatzel, 1989). F. *Paramphiascopsis spec.* (after Willen, unpublished).

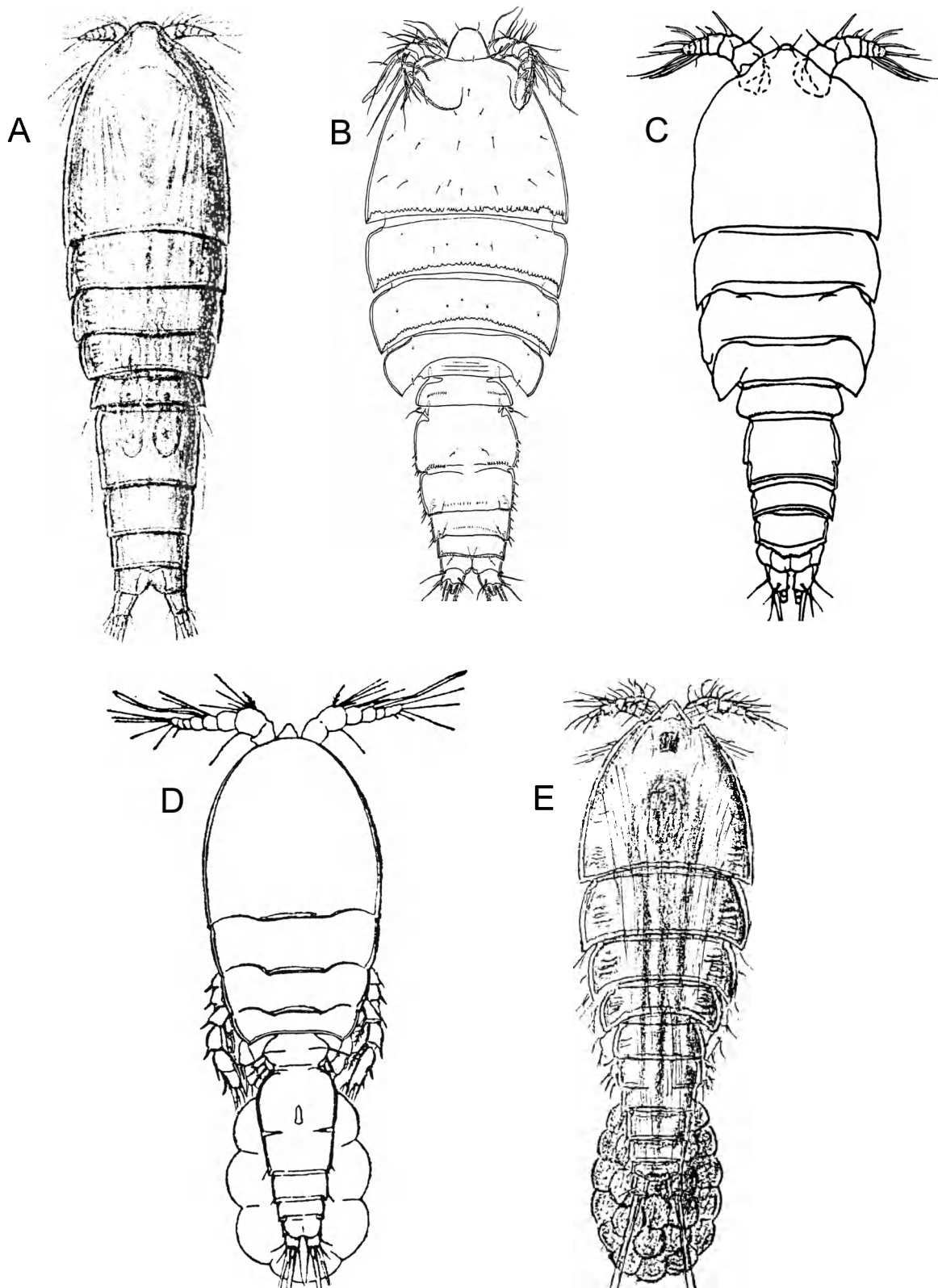


Fig. 2: Habitus of Harpacticoida. A. *Bradya macrochaeta* Sars, 1920 (after Sars, 1920). B. *Tachidiella kimi* Lee & Huys, 1999 (after Lee & Huys, 1999). C. *Zosime incrassata bathybia* Bodin, 1968 (after Bodin, 1968). D. *Diarthrodella psammophila* (Bocquet & Bozic, 1955) (after Bocquet & Bozic, 1955). E. *Tachidius discipes* Giesbrecht, 1881 (after Sars, 1909).

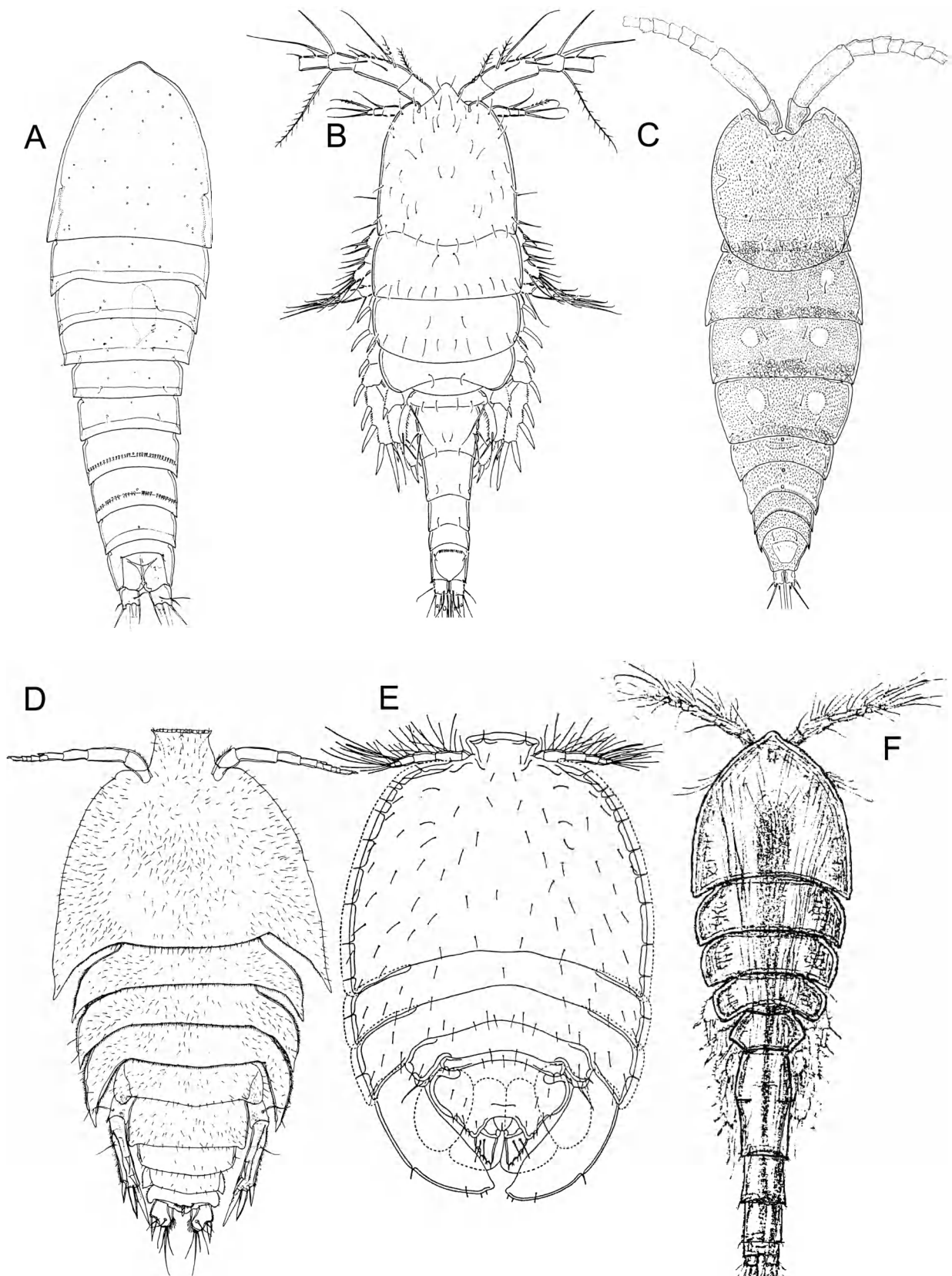


Fig. 3: Habitus of Harpacticoida. A. *Atergopedia vetusta* Martínez Arbizu & Moura, 1998 (after Martínez Arbizu & Moura, 1998). B. *Intercrusia problematica* Huys, 1996 (after Huys, 1996). C. *Rotundiclipeus canariensis* Huys, 1988 (after Huys, 1988a). D. *Eupelte villosa* (Brady, 1910) (after Dahms, 1992). E. *Porcellidium brevicaudatum* Thompson & A. Scott, 1903 (after Humes & Ho, 1969). F. *Tisbe tenella* Sars, 1911 (after Sars, 1911).



## 2. MATERIAL AND METHODS

### Taxonomy

All specimens were preserved in 5 % buffered formalin and subsequently transferred into glycerine. The dissected specimens were mounted on several slides in glycerine. Preparations were sealed with transparent nail varnish. All drawings have been prepared using a camera lucida on a Leitz Diaplan interference contrast microscope. The described and undescribed specimens are in the Copepod Collection of the AG Zoosystematik and Morphologie, Universität Oldenburg, Germany (see 8.1 Appendix I).

### Abbreviations and terminology used in the text and figures are:

- A1: antennule; A2: antenna; exp: exopod; enp: endopod; enp-1 (2, 3) proximal (middle, distal) segment of endopod; Aes: aesthetasc; Lb: labium; Lm: labium; Md: mandible; Mxl: maxillule; Mx: maxilla; Mxp: maxilliped; P1-P6: first to sixth legs.
- f: female; ff: females; m: male; mm: males; c: copepodid; cc: copepodids.
- AGT: Agassiztrawl; DRG: Dredge; GSN: Demersal trawl; MUC: Multicorer; GKG: Giant Boxcorer; SEM: Scanning electron microscopy; SMT: Seamount; TEM: transmission electron microscopy.
- A: apomorphy; P: plesiomorphy.

The descriptive terminology is adopted from Huys & Boxshall (1991). The setal formula notation applied here is the standard format throughout the whole Copepoda Milne Edwards, 1849 and is explained in Huys & Boxshall (1991).

The terms autapomorphy and synapomorphy are used as defined by Ax (1984, 1987). The term groundpattern is used in the sense of “Grundmuster” and represents the hypothetical morphology of the members of the last common population of the species group in question (Wägele, 2000).

“Oligoarthra segment” or “oligoarthran segment” refers to the respective homologous segment of oligoarthran groundpattern (see 4.3 Oligoarthra).

### Parsimony analysis and phylogeny

Two procedures to infer phylogeny on the basis of morphological characters of adult Oligoarthra were used and compared. First the methods of Phylogenetic Systematics were applied (i.e. Hennig, 1966, 1982; Ax, 1984, 1987; Wägele, 2000). In order to discern monophyletic taxa the study started at the species level. Calanoida Sars, 1903 and Misophrioida Gurney, 1933 were used as outgroups to polarise characters (Huys & Boxshall, 1991; chapter 5.2.2). Every group of species for which strong autapomorphies were found was recognized as a monophyletic group and its groundpattern was reconstructed. Sometimes, no single living taxon retained the full ancestral condition, so that the groundpattern had to be deduced from a comparison of all available species. Then, the sister taxon of the reconstructed taxon was ascertained on the basis of synapomorphies and both were united in a more inclusive monophyletic group. Subsequently, a groundpattern for this group was reconstructed and so on. The monophyly of taxa and the hypothesis of the phylogeny of Harpacticoida were tested with additional characters.

A computer based cladistic analysis was used as a second method to detect the relationships of species of Harpacticoida. An analysis on the basis of reconstructed groundpatterns was made with 16 monophyletic taxa of Oligoarthra, which are characterised by strong autapomorphies. The character states coded in the data matrix (especially the number of segments and setae in the groundpattern of the terminal taxa) were ascertained by additional computer based cladistic analysis within the terminal taxa (these analyses will be published elsewhere). When the maximum number of segments and setae is not regarded as the most plesiomorphic state within a taxon it is discussed in the chapter of the respective taxon (see chapters 4, 5.2.5, and 5.2.6). The data matrix was analysed and cladograms were generated on a Macintosh G4 (400 Mhz) with PAUP\* 4.0 beta 10 AltiVec (Swofford, 2003). Characters were examined with PAUP\* and MacClade, version 3.05 (Maddison & Maddison, 1992). All characters in this analysis were of type unordered and had equal weight. I used 'branch-and-bound' search under maximum parsimony to explore the data. Further 'branch-and-bound' settings were: addition sequence furthest, zero-length branches not collapsed, 'MulTrees' option in effect. Misophrioida and Calanoida (Huys & Boxshall, 1991; chapter 5.2.2) were used as outgroups to root the cladograms. Bootstrap and Bremer support values were estimated using the same 'branch-and-bound' settings described above using PAUP\*. For the discussion of the methods and settings see chapters 5.1.3, 5.2.1, 5.2.2, and 5.2.5. The results of the phylogenetic analysis according to Hennig (1966, 1982, chapter 5.1.4) and the cladistic analysis with PAUP\* (chapter 5.1.3) are compared in chapter 5.1.5. Additionally, an analysis was made with species selected from the over 3,000 species of Harpacticoida. This analysis will be published elsewhere.

### Systematics

The new phylogenetic system of Harpacticoida complies with the conventions of Phylogenetic Systematics (i.e. Hennig, 1966, 1982; Ax, 1984, 1987; Wägele, 2000). However, the convention of the International Code of Zoological Nomenclature (fourth edition) that every single species of Harpacticoida has to be a member of a "family" was always followed. According to the conventions of Phylogenetic Systematics, it is not necessary, to create a "family" for only one single species or one single genus (e.g. Ax, 1999). A new taxon name was given only if the monophyly of the respective taxon was well supported. Taxa named with N.N. followed by a number (e.g. N.N. 1) are probably monophyletic taxa but the monophyly of these taxa has to be confirmed. N.N. stands for *nomen nominandum* ("name to be given"). The subordinated taxa belonging to these taxa are listed in chapter 3.1. To guarantee continuity, as few taxa names as possible were changed for the new system of Harpacticoida. Sister taxa or more than two taxa which together represent a monophyletic taxon are connected with a dash (e.g. Tachidiidae - Palinarthra).

**Species of Copepoda examined for phylogenetic analysis.**

The available descriptions of all valid species of Harpacticoida (with the exception of several of Podogenmonta) and the undescribed species in Appendix I were used to reconstruct the groundpattern of the Harpacticoida taxa in question. It was not possible to analyse each individual specimen in every single detail. Only a part of the specimens in Appendix I were dissected. The specimens that showed interesting characters for the reconstruction of the phylogenetic relationships were analysed in detail. Some undescribed species of which characters were used for the groundpattern reconstruction of a taxon are and will be described completely elsewhere (Seifried & Schminke, 2003; see Appendix I). A survey of species that are part of museum collections is given in Appendix II.

### 3. SYSTEMATICS

#### 3.1 Hierarchical presentation of the phylogenetic system of Harpacticoida

Harpacticoida Sars, 1903

    Polyarthra Lang, 1944

        Longipediidae Sars, 1903

        Canuellidae Lang, 1944

    Oligoarthra Lang, 1944

        Aegisthoidea Giesbrecht, 1892

            Rometidae Seifried & Schminke, 2003

            Aegisthidae Giesbrecht, 1892

        Syngnatharthra Seifried & Schminke, 2003

            Neobradyidae Olofsson, 1917

        N.N. 1

            Podogennonta Lang, 1944

        N.N. 2

            Chappuisiidae Chappuis, 1940

        N.N. 3

            Ectinosomatidae Sars, 1903

            Exanechentera Lang, 1944

            Idyanthidimorpha tax. nov.

                Idyanthidae Lang, 1944

                Zosimidae fam. nov.

        N.N. 4

            Paramesochridae Lang, 1944

        N.N. 5

            Tachidiidae Sars, 1909

            Palinarthra tax. nov.

            Novocriniidimorpha tax. nov.

                Novocriniidae Huys & Iliffe, 1998

        N.N. 6

            Superornatiremidae Huys, 1996

            Rotundiclipeidae Huys, 1988

    Tisboidea Stebbing, 1910

        Peltidiidae Sars, 1904

        Tegastidae Sars, 1904

        N.N. 7

            Porcellidiidae Boeck, 1865

            Tisbidae Stebbing, 1910

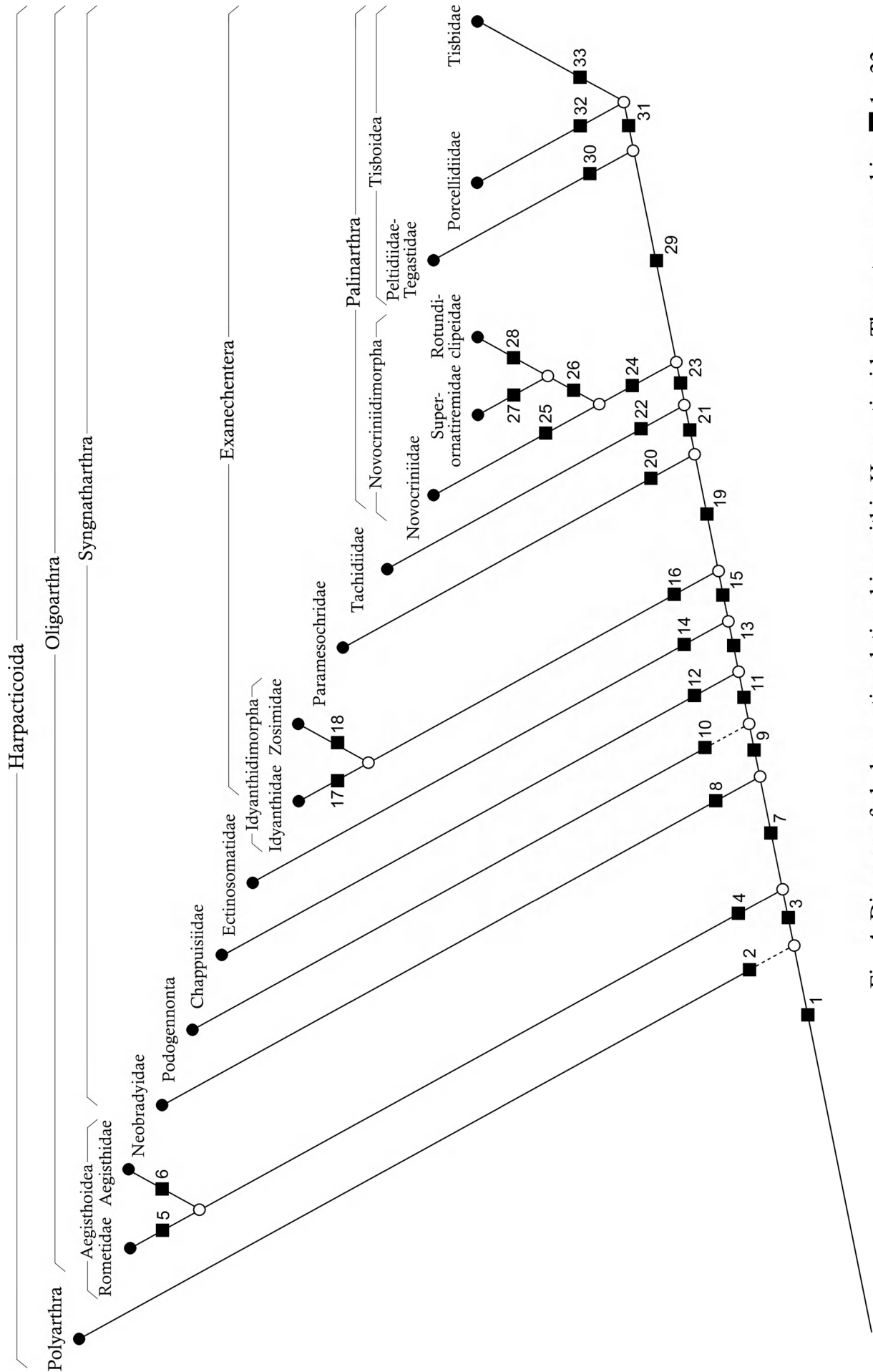


Fig. 4: Diagram of phylogenetic relationships within Harpacticoida. The autapomorphies ■ 1 - 33 are described in the text when treating the respective taxa (chapters 4.1 - 4.26 and 5.1.5).

The substantiation of the monophyletic taxa of Harpacticoida, their apomorphies, their groundpattern, the morphology of their species (chapter 4), and their relationships represented by the phylogenetic system of Harpacticoida (Fig. 4, chapter 5) are the main results of this investigation. The new systematics presented here (chapter 3.1 Hierarchical presentation of the phylogenetic system of Harpacticoida) is derived from substantiation of the monophyletic taxa and the phylogenetic system. For reasons of clarity the new systematics is applied from the beginning.

In the following, the autapomorphies supporting the phylogenetic relationships within Harpacticoida are summarized in character sets symbolized by black squares ■ followed by the branch number leading to the respective taxon (Fig. 4: e.g. ■ 3 represents the autapomorphies of Oligoarthra). Characters and their states according to the character list of the phylogenetic analysis and the character matrix (chapters 5.1.1 and 5.1.2) are marked in the text as follows: e.g. char. 1: 0→1 symbolizes the transformation of character 1 from character state 0 to character state 1. The character numbers of the character list (chapter 5.1.1) and the branch numbers (Fig. 4) are not the same.

### 3.2 Notes on changes and additions to harpacticoid systematics

Lang (1944, 1948), Bodin (1997) and all later articles that deal with the systematics of Harpacticoida (e.g. Seifried & Schminke, 2003) are the basis of the systematics presented above. The justifications of the systematic changes made here are given in the chapters dealing with the respective taxa. A new taxon name was given only if the monophyly of the respective taxon was well supported. Taxa named with N.N. followed by a number (e.g. N.N. 1) are probably monophyletic taxa but the monophyly of these taxa has to be confirmed. N.N. stands for *nomen nominandum* (“name to be given”). The subordinated taxa belonging to these taxa are listed in chapter 3.1. Sister taxa or more than two taxa which together represent a monophyletic taxon are connected with a dash (e.g. Tachidiidae - Palinarthra).

- “Maxillipedasphalea” Lang, 1944 is polyphyletic and therefore not maintained here (see Seifried & Schminke, 2003).
- *Brotskayaia* Huys, Møbjerg & Kristensen, 1997 is synonymized with *Expansicervinia* Montagna, 1981 (Aegisthidae Giesbrecht, 1892).
- *Neocervinia* Huys, Møbjerg & Kristensen, 1997 and *Pseudocervinia* Brodskaya, 1963, are synonymized with *Cervinia* Norman, 1878 (Aegisthidae).
- “Neobradyoidea” Olofsson, 1917 (Chappuisiidae, Darcythompsoniidae, Neobradyidae, Phyllognathopodidae) is polyphyletic and therefore not maintained here. Chappuisiidae is part of N.N. 1 (chapter 3.1). Darcythompsoniidae and Phyllognathopodidae are transferred to Podogennonta Lang, 1944.
- Neobradyidae is the sister taxon of Podogennonta - Chappuisiidae - Ectinosomatidae - Exanechentera Lang, 1944.
- Podogennonta is the sister taxon of Chappuisiidae - Ectinosomatidae - Exanechentera.
- *Paramesochra australis* Mielke, 1994 belongs to Ameiridae (Podogennonta) as

*Psammoleptomesochra australis* Mielke, 1994.

- Chappuisiidae is the sister taxon of Ectinosomatidae - Exanechentera.
- Ectinosomatidae is the sister taxon of Exanechentera.
- Ectinosomatoidea Sars, 1903 is synonymized with Ectinosomatidae, as both taxa enclose the same species.
- The monophyly of Exanechentera is confirmed. Thompsonulidae Lang, 1944 is excluded from Exanechentera and is transferred to Podogennonta Lang, 1944. Novocriniidae Huys & Iliffe, 1998, Paramesochridae Lang, 1944, Rotundiclipeidae Huys, 1988, and Superornatiremidae Huys, 1996 are integrated in Exanechentera.
- Idyanthidimorpha tax. nov. enclose Zosimidae fam. nov. and Idyanthidae Lang, 1944.
- Idyanthidimorpha is the sister taxon of Paramesochridae - Tachidiidae - Palinarthra.
- Lang (1944) established Idyanthinae Lang, 1944. Idyanthinae is excluded from Tisbidae Stebbing, 1910 *sensu strictu* and is raised to family rank.
- *Tachidiopsis* Sars, 1911 is excluded from Idyanthidae Lang, 1944 and is transferred to Neobradyidae Olofsson, 1917. *Tachidiopsis bozici* Bodin, 1968, *T. ibericus* Becker, 1974, *T. laubieri* Dinét, 1974, *T. parasimilis* Dinét, 1974, and *T. sarsi* Bodin, 1968 are moved to *Marsteinia* Drzycimski, 1968.
- Styracothoracidae Huys, 1993 is synonymized with Idyanthidae (Martínez Arbizu & Moura, in prep.).
- *Neoscutellidium* Zwerner, 1967 is excluded from Idyanthidae and is integrated in Cholidiinae Boxshall, 1979 (Tisbidae *sensu strictu*).
- *Zosime* Boeck, 1872, *Peresime* Dinét, 1974, and *Pseudozosime* Scott, 1912 are excluded from Idyanthidae and combined in Zosimidae fam. nov.
- *Dactylophia* Becker, 1974 together with *Idyanthe* Sars, 1909, *Idyella* Sars, 1906, *Idyellopsis* Lang, 1944, *Styracothorax* Huys, 1993, and *Tachidiella* Sars, 1909 represent the taxon Idyanthidae.
- Idyanthidae is the sister taxon of Zosimidae.
- Paramesochridae is the sister taxon of Tachidiidae - Palinarthra tax. nov.
- *Idyanthopsis psammophila* Bocquet & Bozic, 1955 belongs to Paramesochridae as *Diarthrodella psammophila* (Bocquet & Bozic, 1955).
- Tachidiidae is the sister taxon of Palinarthra.
- “Tachidioidea” Sars, 1909 is polyphyletic and therefore not maintained here, as Harpacticidae was transferred to Podogennonta (Willen, 2000).
- The monotypic Euterpinidae Brian, 1921 is synonymized with Tachidiidae Sars, 1909, as *Euterpina acutifrons* (Dana, 1848) belongs to Tachidiidae.
- Novocriniidimorpha tax. nov. (Novocriniidae Huys & Iliffe, 1998 - Superornatiremidae Huys, 1996 - Rotundiclipeidae Huys, 1988) and Tisboidea Stebbing, 1910 (Peltidiidae Sars, 1904 - Tegastidae Sars, 1904 - Porcellidiidae Boeck, 1865 - Tisbidae *sensu strictu* Stebbing, 1910) represent the taxon Palinarthra tax. nov.
- Peltidiidae - Tegastidae is the sister taxon of Porcellidiidae - Tisbidae *sensu strictu*.
- Clytemnestridae A. Scott, 1909 is synonymized with Peltidiidae Sars, 1904. The eight species of *Clytemnestra* Dana, 1847 and *Goniopsyllus* Huys & Conroy-Dalton, 2000 belong to an advanced taxon within Peltidiidae.
- Porcellidiidae is the sister taxon of Tisbidae *sensu strictu*.

#### 4. TAXA OF HARPACTICOIDA, THEIR AUTAPOMORPHIES AND GROUND PATTERN

As a first step, the supports for the hypothesis of the monophyly of **Harpacticoida** and **Oligoarthra** are presented and discussed (chapters 4.1 - 4.2). *Oligoarthra* is the ingroup of the phylogenetic analysis.

The characterisation of the remaining 24 taxa (chapters 4.3 - 4.26) is deduced either from the examination and substantiation of the monophyly of the terminal taxa of the phylogenetic analysis or from the phylogenetic analysis (chapter 5).

The methods of Phylogenetic Systematics were applied (i.e. Hennig, 1966, 1982; Ax, 1984, 1987, 1999; Wägele, 2000) for the **examination and substantiation of the monophyly of 17 taxa of Harpacticoida (terminal taxa)** on the basis of the adult morphology. Every group of species for which strong autapomorphies were found was recognized as a monophyletic group and its groundpattern and all autapomorphies were reconstructed (chapter 2). The groundpattern represents the hypothetical morphology of the members of the last common population of the taxon in question. This process was based on the study of the morphology of all taxa of Harpacticoida. Therefore, all available descriptions of over 3,000 species of Harpacticoida (apart from a number of Podogennonta) and the morphology of many undescribed species of Harpacticoida were analysed (see chapter 2 and Appendix I). The results from Huys & Boxshall (1991), Huys et al. (1996) and Willen (2000) are mostly not repeated in case their results are consistent with this study. If the results are conflicting they are referred and discussed. Supernumerary setae are always mentioned as additional setae to the oligoarthran groundpattern. The groundpattern characters of the terminal taxa were ascertained by additional cladistic analysis within the terminal taxa (these analyses will be published elsewhere)

In most cases, the traditional “families” of “Maxillipedasphalea” and Exanechentera could be confirmed as monophyla. These monophyletic taxa were recognized earlier mainly by striking complex and homologous characteristics and could therefore be verified in this analysis. In other cases, no autapomorphies for a “family” were found, because it was a paraphyletic or polyphyletic group of species. In the case of former Tisbidae four species groups were recognised. All species of *Marsteinia* and *Tachidiopsis* were integrated in Neobradyidae. The other three groups (Zosimidae fam. nov., Idyanthidae and Tisbidae *sensu strictu*) are monophyletic respectively. Four “families” (former Aegisthidae, Clytemnestridae, Euterpinidae, Styracothoracidae) contain only one or a few species that are derived members of another “family”. In these four cases these species were integrated in the respective taxa.

The taxa of which the monophyly is well founded and that are therefore used as terminal taxa in the following phylogenetic analysis are **Polyarthra, Rometidae, Aegisthidae, Neobradyidae, Podogennonta, Chappuisiidae, Ectinosomatidae, Idyanthidae, Zosimidae tax. nov., Paramesochridae, Tachidiidae, Novocriniidae, Superornatiremidae, Rotundiclipeidae, Peltidiidae - Tegastidae, Porcellidiidae, and Tisbidae sensu strictu**. The supporting arguments for the hypothesis of the



monophyly of the terminal taxa are presented and discussed in this chapter and in Seifried & Schminke (2003).

The supraspecific taxa inferred from the phylogenetic analysis (chapter 5) are either the **supraspecific taxa established by Lang (1944, 1948)** that are verified by the phylogenetic analysis or **new supraspecific taxa** inferred from the phylogenetic analysis (see chapter 5 and Seifried & Schminke, 2003). These taxa are: **Oligoarthra**, **Aegisthoidea**, **Syngnatharthra**, **Exanechentera**, **Idyanthidimorpha tax. nov.**, **Palinarthra tax. nov.**, **Novocriniidimorpha tax. nov.**, and **Tisboidea**. The supporting arguments for the hypothesis of the monophyly of these taxa are presented and discussed in chapter 5 and in Seifried & Schminke (2003).

As **result** the following description and characterisation of a taxon contains:

- a list of all taxa belonging to it
- the recent species number
- the autapomorphies
- the diagnosis
- the groundpattern

The **discussion** of the results can be found under “remarks on the systematics and morphology” of the respective taxon.

Not all recognised morphological differences between single taxa were considered here as **characters** for the phylogenetic analysis (see chapter 5.2.1). Characters that have a very high rate of evolution are not suitable for a systematic analysis above species level. The number of segments and setae of the antennal exopod, for example, is highly variable within Oligoarthra. The exopod of an antenna can differ among sister species and is therefore only a useful character to infer relationships between species or genera. Characters with an extremely high rate of evolution are thus not considered as autapomorphies for the terminal taxa and are not included in the list of characters (chapter 5.1.1). Only characters with a very high likelihood of being autapomorphies are so listed for a given taxon.

The **autapomorphies** supporting the phylogenetic relationships within Harpacticoida are summarized in character sets symbolized by black squares (■) followed by the branch number leading to the respective taxon (e.g. ■ 3 in Fig. 4 represents the autapomorphies of Oligoarthra; see 4.3). The characters and their states according to the character list and the character matrix (chapters 5.1.1 and 5.1.2) are marked in the text as follows: e.g. char. 1: 0→1 symbolizes the transformation of character 1 from character state 0 to character state 1.

The autapomorphies of the 17 terminal taxa are mainly inferred from the examination of the monophyly of the harpacticoid taxa. However, in the phylogenetic analysis based on the terminal taxa, some additional autapomorphies for the terminal taxa were deduced. For the phylogenetic analysis only informative characters are chosen, i.e. characters that appear in the groundpattern of more than one terminal taxon. As shown by the phylogenetic analysis, some of these characters are convergences. It was also

shown, that some of the evolved characters are reduced in advanced taxa. The convergently evolved characters and the reductions are additional autapomorphies of the terminal taxa. They are marked in the list of autapomorphies of the respective taxon (e.g. char. 1: 0→1 or char. 1: 1→0).

In general, the autapomorphies can also be found in the respective figure of the groundpattern of a taxon or in drawings of some single appendages, marked by asterisks (\*). The arrows (→) in drawings of single appendages indicate characters discussed in the text.

In the **diagnoses** of a taxon only the autapomorphies of the respective taxon are given. There, the autapomorphies are marked by **bold type**. The **groundpattern** is a combination of all plesiomorphies and all apomorphies of a taxon.

#### 4.1 Harpacticoida Sars, 1903

##### Taxa belonging to Harpacticoida

Oligoarthra Lang, 1944, Polyarthra Lang, 1944.

##### Diagnosis: Autapomorphies of Harpacticoida (Fig. 4: ■ 1; Fig. 5)

*Female* with **2 egg-sacs** (char. 4: 0→1). Antennule **9-segmented**. Mandible endopod with **3 setae** on enp-1, enp-2 with **9 setae**. Praecoxal arthrite of maxillule bearing **12+2 setae**. **Claw-like appearance of the basal seta II (seta "D")** of maxilla. Endopod of maxilliped **2-segmented**, enp-1 representing segments 1-5 and enp-2 segment 6 of Copepoda; syncoxal formula of maxilliped: **1, I+1, I+3, I+2, three elements transformed to spines**. P1 enp-2 with **only 1 inner seta**; P2 exp-3 with **only 2 inner setae**; P1+P2 formula of armature:

	coxa	basis	exopod	endopod
P1	0-1	1-I	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-3
P2	0-1	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-3

Exopod P5 **1-segmented, as long as wide** (char. 60: 0→1).

*Male*. Antennule **14-segmented**.

##### Groundpattern of Harpacticoida (Fig. 5)

*Female*. **Major body articulation** between fourth and fifth pedigerous somites (podoplean position), without difference in width between prosome and urosome. **Nauplius eye** present. **Rostrum** delimited at base. **Prosome** consisting of cephalosome and 4 free pedigerous somites; first pedigerous somite completely separated from dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 2 egg-sacs, 2 copulatory pores, 2 seminal receptacles, 2 gonopores. **Anal somite** not divided longitudinally, anus located dorsally covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented. **Antenna** comprised of coxa, basis, 3-segmented endopod and 8-segmented exopod; coxa without seta; basis with 1 inner seta; proximal endopod segment with 2 setae, middle endopod segment with 5 and distal endopod

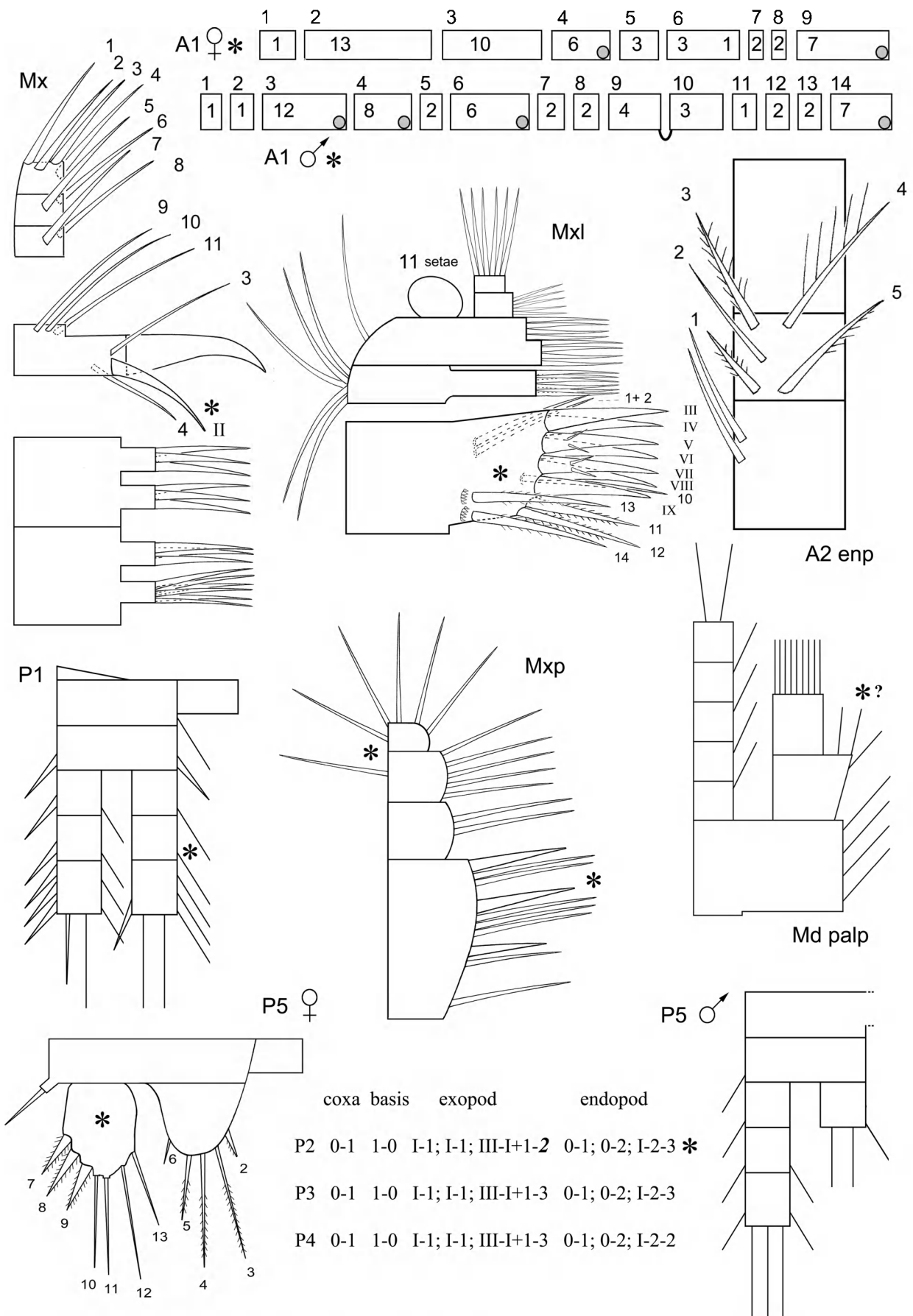


Fig. 5: Groundpattern of Harpacticoida. Asterisks mark autapomorphies of Harpacticoida.

segment with 7 distal setae; exopodal segments 1 to 7 representing segments II to VIII of Copepoda, segment 8 representing segments IX - X of Copepoda, setal formula 1, 1, 1, 1, 1, 1, 4 setae. **Labrum** an undivided muscular lobe. **Paragnaths** separate. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at dorsal corner; palp comprising basis, endopod and exopod; basis with 4 setae on inner margin; endopod 2-segmented with 3 setae on enp-1, enp-2 with 9 setae; exopod 5-segmented with 1, 1, 1, 1, 2 setae. **Maxillule** consisting of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in the outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III - IX, at least 2 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: 2, VII, 1, 2, 2; coxa with single endite bearing 6 setae, and vestigial epipodite incorporated into segment, bearing 5 setae; basis with 1 seta on outer margin representing exite, 2 closely set endites, proximal endite well developed, with 4 setae, distal endite largely incorporated into segment, represented by 4 setae; endopod 2-segmented, setal formula (3, 2) 6; exopod 1-segmented, with 11 setae. **Maxilla** 6-segmented, composed of praecoxa, coxa, allobasis, and 3-segmented endopod; praecoxa and coxa each with 2 endites, endite formula 6, 3, 3, 3; basis with well-developed endite; accessory armature of the fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II) and 1 seta (3) on anterior surface, and 1 seta (4) on posterior surface; accessory armature of fused endopod segment of 2 setae on anterior surface (9, 10) and 1 seta on posterior surface (11); endopod 3-segmented with armature formula: 2, 2, 4. **Maxilliped** 4-segmented, consisting of syncoxa with 1 incorporated praecoxal endite and 3 incorporated coxal endites, basis and 2-segmented endopod; syncoxal formula 1, I+1, I+3, I+2, three elements transformed to spines; basis with 2 setae on inner edge; endopod setal formula 5 + 1, 5. **P1-P4** biramous with 3-segmented rami; praecoxa present; members of leg pairs joined by intercoxal sclerite; formula of armature:

	coxa	basis	exopod	endopod
P1	0-1	I-I	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-3
P2	0-1	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-3
P3	0-1	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-1	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** with intercoxal sclerite joining the coxae; praecoxa absent; basis bearing 1 outer seta; endopod 1-segmented with 5 setae: 2 inner setae, 2 terminal setae, 1 outer seta; exopod 1-segmented with 7 setae: 2 inner setae, 2 terminal setae, 3 outer spines. **P6** with 3 setae.

*Male.* Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, comprising somite bearing P5 and 4 abdominal somites; posterior border of genital somite with strong spiniform projection, 2 spermatophores. **Antennule** haplocer with 14 segments. **P5** composed of intercoxal sclerite, coxa, basis, endopod and exopod; endopod 1-segmented with 3 setae; exopod 3-segmented with 1-0, 1-1, 1-3-1 setae. **P6** symmetrical, with 3 setae.

### Remarks on the monophyly of Harpacticoida

The hypothesis that Harpacticoida is monophyletic has been criticised. Tiemann (1984) analysed Lang's (1948) diagnosis of Harpacticoida in detail applying the criteria of Phylogenetic Systematics according to Hennig (1966, 1982) and did not find a single autapomorphy. Tiemann (1984) concluded that the Polyarthra should be separated from Harpacticoida and placed as a basic taxon near the roots of Copepoda. As a consequence Oligoarthra would be synonymous with Harpacticoida. Dahms (1990) questions the monophyly of Harpacticoida on the basis of naupliar characters. He found no synapomorphies linking Polyarthra and Oligoarthra. On this basis he suggested that Polyarthra should be removed from Harpacticoida. Huys & Boxshall (1991) listed some characters supporting the monophyly of Harpacticoida. Willen (2000) analysed these characters and showed that the fusion pattern of segments of female and male antennules of Polyarthra probably differs from the interpretation of Huys & Boxshall (1991). The groundpattern of the antennule of Polyarthra has to be reconstructed to clarify, whether or not the segmentation of the short antennule is an autapomorphy of Harpacticoida. The segmentation of the maxilliped as interpreted by Huys & Boxshall (1991) results from an analysis of species of Polyarthra only and has to be confirmed for Oligoarthra (Willen, 2000). Willen (2000) added some autapomorphies for Harpacticoida resulting from analyses of the mandible, maxillule and maxilla of Thalestridimorpha Lang, 1944. The "12+2" pattern of setae of the praecoxa of the maxillule in contrast to the "13+2" pattern of Misophrioida and the unique claw-like appearance of the basal seta II of the maxilla are also autapomorphies of Harpacticoida. The "3+9" pattern of endopod mandible was not explained so that it is not clear why this character could be an autapomorphy of Harpacticoida (Willen, 2000). This character has to be compared with the mandible morphology of the outgroups of Harpacticoida. The three spines on the coxa of maxilliped (syncoxal formula 1, I+1, I+3, I+2) are also a synapomorphy linking Polyarthra and Oligoarthra, as species of both taxa show these three spines, as indicated here. Species of Calanoida and Misophrioida have only setae on the (syn-) coxa. However, the coxal elements of other copepod species have to be examined in detail. As Willen (2000; p. 195) concludes: "A comprehensive analysis of the whole Copepoda will be necessary to decide on the monophyly of Harpacticoida". Pending the re-examination of the phylogeny of the Copepoda as a whole the best-supported hypotheses remain: Harpacticoida is monophyletic and Polyarthra is the sister taxon of Oligoarthra as proposed by Lang (1948). In the present analysis of phylogeny, Oligoarthra is the ingroup and Polyarthra is used only as outgroup.

### Remarks on the homology

#### **Anal somite**

A telson should not be named a somite. However, the term "anal somite" is established among copepodologists (Huys & Boxshall, 1991) and will therefore be used until clarification, whether or not the telson is fused with additional abdominal somites.

#### **Maxillula**

The setae of the praecoxa of maxillule are homologised and numbered (Fig. 5). An armature formula is established to describe the different setation patterns of Harpacticoida species. The formula of armature of Harpacticoida groundpattern is 2,

VII, 1, 2, 2. The setae are counted beginning with seta 1 on the anterior surface and ending with seta 14 on the posterior surface (Fig. 5: 1 + 2, III - VIII, 10, 11 + 12, 13 + 14).

### **Maxilla**

Willen (2000) and Huys & Boxshall (1991) did not number all setae of maxilla basis and endopod of Harpacticoida. The numbering of basis setae begins here with the big claw, followed by the anterior and posterior setae. The endopod setae are numbered beginning with the distal segment (enp-3) and the anterior setae, continued with the posterior setae and the more proximal segments (enp-2, enp-1) (Fig. 5; Table 1). The proximal segment of the endopod of groundpattern of Copepoda (“enp-0”) is always fused with the basis in Harpacticoida (see below), but the setae are still counted as endopodal setae.

### **Paragnaths**

In Crustacea the term labium is used to describe a bilobed structure also named paragnaths. Huys & Boxshall (1991; p. 343) regard “the medial fusion of the paragnaths to form a labium as the derived state” and restrict the term labium to “a median lobe formed by fusion of the paragnaths”. This is followed here.

### **P5 of female**

The numbering of setae (Fig. 5) is adopted from Willen (2000). Willen (2000) described the setation groundpattern of the female P5 of *Podogennonta* Lang, 1944. This setation pattern, i.e. the number of 6 endopodal (setae 1 - 6) and 8 exopodal (setae 7 - 14) setae is not plesiomorphic within Harpacticoida (see below).

### Remarks on the morphology of Harpacticoida

Boxshall (1979) reported 9 elements on the **caudal rami** of *Bathyidia remota* Farran, 1926 (*Tisbidae sensu strictu*) and two closely related genera. Re-examination revealed the basic 7 elements plus several conspicuous tube pores (Huys & Boxshall, 1991). Lang (1948) reported additional armature on the caudal rami of *Canuella perplexa* (Canuellidae) but only the basic 7 elements are present.

The **antennular** groundpattern of Polyarthra still requires reconstruction. Antennule structure appears to be quite different between Oligoarthra and Polyarthra (Willen, 2000). The groundpattern of the antennule of Harpacticoida remains unclear especially for the females, until that one of Polyarthra has been completely reconstructed (Willen, 2000).

The lateral armature of the second endopod segment of **antenna** of Novocriniidae consists of 1-2 setae and a setoid tuft. This tuft is a transformed setal element homologous with one lateral seta (Huys & Iliffe, 1998, Martinez & Moura, 1998).

Some species of Ectinosomatidae, *Neobradya pectinifera* T. Scott, 1892 (Neobradyidae), *Antarcticobradya tenuis* (Brady, 1910) (Neobradyidae) and some *Podogennonta* have 2 proximal setae on the cutting edge of **mandible**. Huys & Boxshall (1991) describe without comment 2 setae on the proximal (dorsal) side of the coxal gnathobase as the ancestral state of mandible of copepods. This is debatable. Some copepods have 1 seta (e.g. Calanoida, Misophrioida); others have 2 setae (e.g. Platycopioidea Fosshagen, 1985; some Cyclopoida Burmeister, 1835). Anyhow, the comparison with outgroups does not help in identifying the plesiomorphic state for Harpacticoida, as long as the sister taxon of Harpacticoida is not known. All

Table 1: The numbering of basis and endopod setae of maxilla for Harpacticoida.

segment	Present account Fig. 5	Willen, 2000 Fig. 37	Huys & Boxshall, 1991, Fig. 3.10.1
enp-3	seta 1	seta 4	—
enp-3	seta 2	seta 5	—
enp-3	seta 3	seta 6	—
enp-3	seta 4	—	—
enp-2	seta 5	seta 3	—
enp-2	seta 6	—	—
enp-1	seta 7	seta 2	—
enp-1	seta 8	seta 7	—
“enp-0”	seta 9	seta 1?	seta III
“enp-0”	seta 10	seta 9?	seta IV
“enp-0”	seta 11	seta 8	seta I
basis	claw I	claw A	claw A
basis	spine II	spine D	spine D
basis	seta 3	seta C	seta C
basis	seta 4	seta B	seta B
basis	tube pore	tube pore	—

Harpacticoida with a more plesiomorphic morphology have 1 seta on the proximal side of the cutting edge of mandible. Only few advanced species of some taxa have 2 setae. This is a secondary phenomenon that has evolved more than once within Harpacticoida. Mielke (1984) describes a fourth minute seta for *Diarthrodelta neotropica* Mielke, 1984 (Paramesochridae) on the proximal endopod segment of the mandible. It is unclear, whether this is a seta or a setule.

The arrangement and shape of the setae and spines of the praecoxal arthrite of the **maxillule** (above all the 2 neighbouring surface-setae 1 + 2) can be relocated in Misophrioidea, which possess 15 praecoxal setae altogether (e.g. *Arcticomisophria bathylaptevensis* Martínez Arbizu & Seifried, 1996). In all other Podoplea fewer setae are present. Willen (2000) emphasized the fact that 4 apical posterior spines show an additional pair of “double-spinules”, each of which she interpreted as a novelty and therefore as autapomorphic for Podogennonta. Species of Polyarthra, Aegisthidae, *Romete bulbiseta* Seifried & Schminke, 2003 (Rometidae), and other species of Oligoarthra that do not belong to Podogennonta have 2 or 3 apical posterior spines showing an additional pair of “double-spinules” each. Species of Misophrioidea (e.g. *Arcticomisophria bathylaptevensis*) have 1-2 apical posterior spines with an additional pair of “double-spinules”. “Double-spinules” are interpreted here as plesiomorphic for Harpacticoida. Only species of Miraciidae Dana, 1846 (synonym of Diosaccidae Sars, 1906 after Willen, 2002) have 4 apical posterior spines with an additional pair of

“double-spinules”. The number of 4 apical posterior spines with a pair of “double-spinules” appears to be apomorphic for Miraciidae and not for Podogennonta.

Huys & Boxshall (1991) reported in the text that in *Tachidiopsis cyclooides* Sars, 1911 (Neobradyidae) (Sars Collection, Oslo, F20350) the proximal endopod segment of the **maxilla** is not fused with the basis, but with the next endopod segment. This may lead to the conclusion that a 4-segmented endopod is the ancestral state for Oligoarthra and Harpacticoida. The drawings in Huys & Boxshall (1991, fig. 2.4.15 B + C) are unclear. Moreover, there is an allobasis in *Tachidiopsis cyclooides* specimen from Sars' material in Oslo (F20350) and *Tachidiopsis* spec. from the Antarctic. The plesiomorphic condition in Oligoarthra is an allobasis and a 3-segmented endopod. This condition is found in all species of Harpacticoida and in all Copepoda apart from some Calanoida.

The strong claw (I) of the maxilla is not fused with the endite of the basis in some species of Neobradyidae, Ectinosomatidae, Idyanthidae, Zosimidae, and in some outgroup-taxa like species of Calanoida. This character state is probably the plesiomorphic state of Harpacticoida, rather than the fused claw that can be found in most Oligoarthra.

Willen (2000) describes a seta that inserts at the border between allobasis and enp-1 (her seta 1) of the maxilla (Table 1). It is possible that this seta is seta 9 and belongs to the fused endopod segment (seta 9 of “enp-0”). It is also possible that this seta is an additional seta of enp-1 in the groundpattern of Harpacticoida. The ancestral state for Harpacticoida would then be: allobasis with 4 basis setae and 2 setae from fused endopod segment and endopod with 3, 2, 4 setae. This hypothesis has to be confirmed first. The ancestral state for the endopod of maxilla in Copepoda is 4, 3, 2, 4 (Huys & Boxshall, 1991). Seta 10 seems to be displaced in *Rhynchothalestris helgolandica* (Claus, 1863) (Huys, 1990; Willen, 2000). In many species of Oligoarthra (e.g. *Romete bulbiseta*) a tube pore is situated at the same position as seta 10 in *Rhynchothalestris helgolandica*. When the tube pore is long and slender as in *Romete bulbiseta*, it is sometimes very difficult to distinguish this tube pore from a hyaline seta. However, the additional seta in *Rhynchothalestris helgolandica* (Podogennonta) is unipinnate. This seta is probably the displaced seta 10.

Willen (2000) and Huys & Boxshall (1991) supposed a (incompletely) separated **maxillipedal** praecoxa in the groundpattern of Harpacticoida and not a syncoxa. In *Neobradia pectinifera* and some Aegisthidae the praecoxa is only incompletely fused to the coxa (see chapters 4.6 and 4.8). Praecoxa and coxa of maxilliped are still completely separated in some species of Thalestridimorpha (Willen, 2000). A praecoxa in the groundpattern of Harpacticoida could only be explained with many independently evolved fusions of praecoxa and coxa (at least seven). The praecoxa of some Podogennonta is therefore interpreted here as secondary. The incompletely separated praecoxa evolved within Neobradyidae and Aegisthidae.

The three spines of the maxillipedal syncoxa are visible in all basal Harpacticoida (syncoxal formula 1, I+1, I+3, I+2). Species of Polyarthra, Rometidae, Aegisthidae, and Neobradyidae have these spines. In Syngnatharthra the spines do not exist, as the respective elements are reduced. No outgroup species have three spines on the syncoxa of maxilliped, because all elements are developed as setae. In the groundpattern of Calanoida the endite formula is 1, 2, 4, 4 and that of Misophrioida 1, 2, 4, 3 (Huys &



Boxshall, 1991).

In *Scottopsyllus langi* Mielke, 1984, *S. robertsoni* (T. & A. Scott) and *S. pararobertsoni* Lang, 1965 (Paramesochridae) a secondary increase occurred in the number of inner basal setae on the **P1**. Superornatiremidae show also additional setae as compared to the oligoarthran groundpattern on the P1. This can be regarded as apomorphic within Harpacticoida.

The examination of the type material showed that *Hastigerella scheibeli* Mielke, 1975 (Ectinosomatidae) is armed with an additional seta as compared to the oligoarthran groundpattern on the posterior surface of proximal segments of **P2-P4**, respectively (compare also Mielke, 1975). These hyaline setae are probably a duplication of the inner setae, displaced to the proximal surface.

Many Copepoda have a biramous **female P5** with a 3-segmented exopod and a demarcated endopod. The 1-segmented exopod is an autapomorphy of Harpacticoida (char. 60: 0→1) and the baseoendopod is assumed to be an autapomorphy of Oligoarthra (char. 59: 0→1; chapter 5.2.3; chars 59 and 60).

The maximal numbers of setae in Copepods are 8 endopodal and 12 exopodal setae (Huys & Boxshall, 1991). The numbers of 6 endopodal (setae 1 - 6) and 8 exopodal (setae 7 - 14) setae described for Podogennonta by Willen (2000) are not plesiomorphic within Harpacticoida. It is highly probable that only 5 endopodal (setae 2 - 6) and 7 exopodal (setae 7 - 13) setae are plesiomorphic within Harpacticoida. Only some species of *Mesochra* Boeck, 1865, *Cletocamptus* Schmankevitch, 1875 and Louriniidae Monard, 1927 (all Podogennonta) have 6 setae on the endopod of P5 and some species of Parastenheliidae and *Antiboreodiosaccus* Lang, 1944 (Podogennonta) have 8 exopodal setae (Willen, 2000). The most parsimonious hypothesis is that setae 1 and 14 evolved secondarily within Podogennonta or within the ancestor line to Podogennonta. To suppose that setae 1 and 14 are part of the groundpattern of Harpacticoida would mean that both setae were reduced at least six times within Harpacticoida. The report of 6 endopodal setae in *Eupelte villosa* Dahms, 1992 and Tegastidae (counted by Willen, 2000) is erroneous. The species of Peltidiidae - Tegastidae never have more than 5 setae (2 - 6) on the endopodal lobe of female P5 and 1 outer basal seta that is sometimes slightly displaced. The displaced outer basal seta can easily be counted as an endopodal seta. The exopod of most Podogennonta is developed as a foliated ramus (Fig. 19). This form of the exopod of the female P5 is interpreted here as an autapomorphy of Podogennonta or a more derived group within Podogennonta. The reconstructed exopod of the female P5 of the hypothetical ancestor of Harpacticoida (Fig. 5) resembles the exopod of the P5 of *Marsteinia bozici* (Bodin, 1968) (Neobradyidae). Drzycimski (1968) described the P5 of the female of *Marsteinia similis* Drzycimski, 1968 with discrete coxa, basis, exopod, and endopod. This is a very unlikely morphology for a female P5 of Harpacticoida. The type material of this species is inaccessible, since it has not been returned to the Zoological Museum of the University of Bergen (see Appendix II).

*Romete* spec. has 3 distal setae on proximal exopod segment of the **P5 of male**. No other Harpacticoida shares this plesiomorphic state. The males of Harpacticoida usually have 2 setae on the endopod; some males of Podogennonta species have 3 setae. Only *Novocrinia trifida* Huys & Iliffe, 1998 (Novocriniidae) and an undescribed male in Huys & Boxshall (1991) have 4 setae. *Nitocra hibernica* (Brady, 1880)

(Podogennonta) has 5 setae. In these three unrelated species the number of setae is identical in both sexes. It is therefore probable that 4 and 5 setae on the male P5 endopod are a secondary phenomenon (see also Huys & Iliffe, 1998).

## 4.2 Polyarthra Lang, 1944

Taxa belonging to Polyarthra (60 species in 18 genera)

Canuellidae Lang, 1944, Longipediidae Sars, 1903.

Diagnosis: Autapomorphies of Polyarthra (Fig. 4: ■ 2; Fig. 6)

*Female.* Exopod of antenna 4-segmented with 1, 1, 1, 3 setae, **two distal segments of Harpacticoida groundpattern not separated.** Anterior surface of maxillular praecoxa in the outer half with 2 neighbouring setae (1 + 2), apically 7 spines (III - IX) as well as 1 plumose seta (11), 1 smaller, flexible seta (10) inserting on anterior surface; **subapical inner margin with 2 setae (12 + 14), posterior surface with 1 subapical seta (13)** (formula of armature: 2, VII, 1, 2, 2). Accessory armature of fused endopod segment maxilla of 1 seta on anterior (9) surface and **2 setae on posterior surface (10? + 11): posterior seta (11) of fused endopod segment displaced to fusion zone of strong claw (I), seta 10 displaced from anterior to posterior side (?).** Exopod P5 female with 6 setae, **seta 13 lacking; endopod with 2 setae.**

*Male.* Coxa of P5 **not separated from basis** (char. 70: 0→1); exopod **1-segmented.**

Groundpattern of Polyarthra (Fig. 6)

*Female.* **Body** without difference in width between prosome and urosome. **Nauplius eye** present. **Rostrum** defined at base. **Prosome** consisting of cephalosome and 4 free pedigerous somites; first pedigerous somite completely separated from dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 2 egg-sacs (?), 2 copulatory pores, 2 seminal receptacles, 2 gonopores. **Anal operculum** developed. **Caudal rami** with 7 setae. **Antennule** indistinctly 6-segmented. **Antenna** composed of coxa, basis, 3-segmented endopod and 8-segmented exopod; basis with 1 seta; proximal endopod segment with 2 setae, middle endopod segment with 5 setae and distal endopod segment with 7 setae; setation of middle endopod segment composed of 1 short proximal seta (1), 1 long proximal seta (5), 2 long distal setae (3 + 4) and 1 bare slender seta (2); seta 2 inserting between seta 1 and seta 3; exopodal segments 1 to 7 representing segments II to VIII of Copepoda, segment 8 representing segments IX-X of Copepoda, setal formula 1, 1, 1, 1, 1, 1, 1, 4 setae. **Labrum** not prominent. **Paragnaths** separate. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at dorsal corner; palp comprising basis, endopod and exopod; basis with 2 setae; endopod 2-segmented with 3 setae on enp-1, enp-2 with 9 setae; exopod 4-segmented with 1, 1, 1, 3 setae, two distal segments of Harpacticoida groundpattern not separated. **Maxillule** comprising praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in the outer half with 2 neighbouring setae (1 + 2), apically with 7 spines (III - IX) as well as 1 plumose seta (11), 1 smaller, flexible seta (10) inserting on anterior surface; subapical inner margin with 2 setae (12 + 14), posterior surface

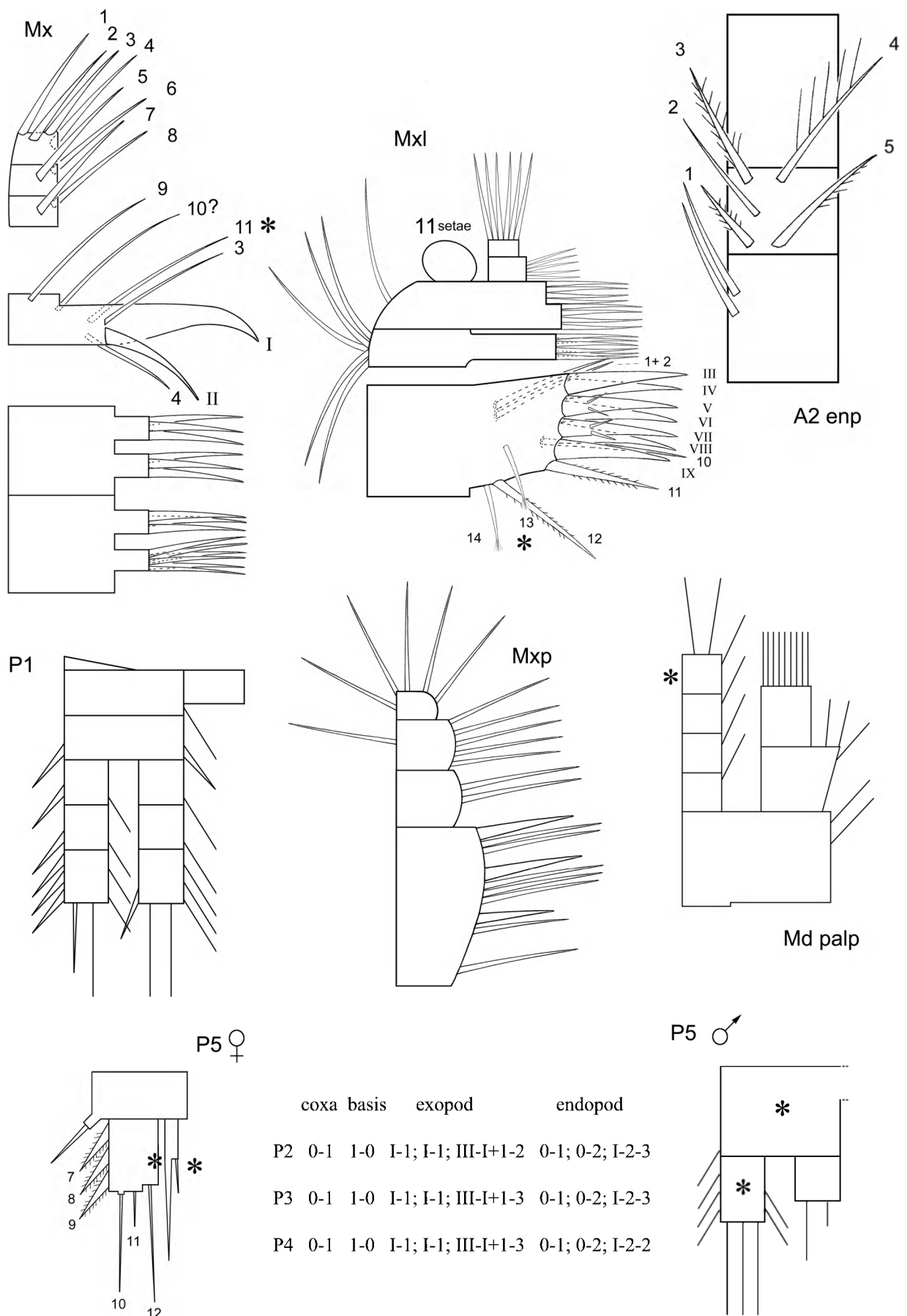


Fig. 6: Groundpattern of Polyarthra. Asterisks mark autapomorphies of Polyarthra.

with 1 subapical seta (13) (formula of armature: 2, VII, 1, 2, 2); coxa with single endite bearing 6 setae, and vestigial epipodite incorporated into segment, bearing 5 setae; basis with 1 seta on outer margin representing exite, 2 closely set endites, proximal endite well developed, with 4 setae, distal endite largely incorporated into segment, represented by 4 setae; endopod 2-segmented, setal formula (3, 2) 6; exopod 1-segmented, with 11 setae. **Maxilla** 6-segmented comprising praecoxa, coxa, allobasis, and 3-segmented endopod; praecoxa and coxa each with 2 endites, endite formula 6, 3, 3, 3; basis with well developed endite; accessory armature of fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II) and 1 seta (3) on anterior surface and 1 seta (4) on posterior surface; strong claw (I) fused with endite of basis; accessory armature of fused endopod segment of 1 seta on anterior (9) surface and 2 setae on posterior surface (10? + 11): posterior seta (11) of fused endopod segment displaced to fusion zone of strong claw (I), seta 10 displaced from anterior to posterior side (?); endopod 3-segmented with armature formula: 2, 2, 4. **Maxilliped** 4-segmented, consisting of syncoxa with 4 endites, basis and 2-segmented endopod; syncoxal formula 1, I+1, I+3, I+2; basis with 2 setae on inner edge; endopod setal formula 5 + 1, 5. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; formula of armature:

	coxa	basis	exopod	endopod
P1	0-1	I-I	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-3
P2	0-1	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-3
P3	0-1	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-1	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** basis bearing 1 outer seta; exopod 1-segmented with 6 setae: 3 outer setae, 2 terminal setae, 1 inner seta, setae 13 lacking; endopod 1-segmented with 2 setae. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, comprising somite bearing P5 and 4 abdominal somites; posterior border of genital somite with strong spiniform projection, 2 spermatophores. **Antennule** 6-segmented **P5** fused medially; coxa not separated from basis; basis bearing 1 outer seta; exopod 1-segmented with 8 setae: 3 outer setae, 3 terminal setae, 2 inner setae; endopod 1-segmented with 2 setae. **P6** symmetrical with 3 setae.

#### Remarks on the monophyly of Polyarthra

The monophyly of Polyarthra is rather badly supported. The antennular morphology seems to be a rewarding character complex for understanding the evolution of Polyarthra. Nauplii of Polyarthra are significantly different from those of Oligoarthra (Dahms, 1990). An analysis of all Copepoda will be necessary in order to find out, whether Polyarthra are monophyletic. In the present phylogenetic analysis Oligoarthra is the ingroup and Polyarthra is used as one outgroup.

#### Remarks on the morphology of Polyarthra

The number of **egg-sacs** in the groundpattern of Polyarthra is probably 2, as in Canuellidae and many other copepod taxa. The production of 1 egg-sac obviously was convergently evolved in the ancestor line of Oligoarthra and Longipediidae. (chapter 5.2.3; char. 4).

The antennula groundpattern of Polyarthra still requires reconstruction. The structure of the **antennule** appears to be quite different between Oligoarthra and Polyarthra (Willen, 2000).

The number of 14 setae on the praecoxal arthrite of **maxillule** is found in Polyarthra (e.g. *Longipedia minor* T. & A. Scott, 1893 in Huys & Boxshall, 1991, fig. 2.4. 12 B) and Oligoarthra. However, compared with Oligoarthra and Misophrioida, setae 12, 13, and 14 of praecoxal arthrite are displaced in Polyarthra. Seta 12 inserts further proximally and not beneath seta 11, seta 14 inserts on the proximal border of the arthrite, and seta 13 inserts subapically and not beneath seta 14.

The accessory armature of the fused endopod segment of the **maxilla** is unclear. Seta 9 inserts on the anterior surface near the border to the endopod like in Oligoarthra. Seta 11 is displaced to the fusion zone of the strong claw (I) with the basal endite. The third seta of the fused endopod segment lies posteriorly and not anteriorly near seta 9. This may be either seta 10 of Oligoarthra displaced from the anterior to the posterior or the additional 4th seta of the groundpattern of Copepoda (compare Huys & Boxshall, 1991, fig. 1.5.5). There are no arguments in favour of one of these possibilities. A tube pore on the anterior surface is lacking.

### 4.3 Oligoarthra Lang, 1944

#### Taxa belonging to Oligoarthra

Adenopleurellidae Huys 1990, Aegisthidae Giesbrecht, 1892, Ameiridae Monard, 1927, Ancorabolidae Sars, 1909, Argestidae Por, 1986, Balaenophilidae Sars, 1910, Cancrincolidae Fiers, 1990, Canthocamptidae Sars, 1906, Chappuisiidae Chappuis, 1940, Cletodidae T. Scott, 1905, Cletopsyllidae Huys & Willems, 1989, Cristacoxidae Huys, 1990, Dactylopusiidae Lang, 1936, Darcythompsoniidae Lang, 1936, Ectinosomatidae Sars, 1903, Harpacticidae Sars, 1904, Huntemanniidae Por, 1986, Idyanthidae, Lang, 1944, Laophontidae T. Scott, 1905, Laophontopsidae Huys & Willems, 1989, Latiremidae Bozic, 1969, Leptastacidae Lang, 1948, Leptopontiidae Lang, 1948, Louriniidae Monard, 1927, Metidae Sars, 1910, Miraciidae Dana, 1846, Neobradyyidae Olofsson, 1917, Normanellidae Lang, 1944, Novocriiniidae Huys & Iliffe, 1998, Orthopsyllidae Huys, 1990, Paramesochridae Lang, 1944, Parastenheliidae Lang, 1944, Parastenocarididae Chappuis, 1933, Peltidiidae Sars, 1904, Phyllognathopodidae Gurney, 1932, Porcellidiidae Sars, 1904, Pseudotachidiidae Lang, 1936, Rhizothricidae Por, 1986, Rhynchothalestridae Lang, 1948, Rometidae Seifried & Schminke, 2003, Rotundiclipeidae Huys, 1988, Superornatiremidae Huys, 1996, Tachidiidae Sars, 1909, Tegastidae Sars, 1904, Tetragonicipitidae Lang, 1944, Thalestridae Sars, 1905, Thompsonulidae Lang, 1944, Tisbidae Stebbing, 1910 *sensu strictu*, Zosimidae fam. nov.; taxa incerta et incertae sedis: Ismardiidae Leigh-Sharpe, 1936, *Dactylopina* Brady, 1910, *Flavia* Brady, 1899, *Goffinella* Wilson, 1932, *Ismardis* Leigh-Sharpe, 1936, *Mawsonella* Brady, 1918, *Pyroclotodes* Coull, 1973, *Tisemus* Monard, 1928.

Diagnosis: Autapomorphies of Oligoarthra (Fig. 4: ■ 3; Fig. 7)

*Female* with **1 egg-sac** (char. 4: 1→2); genital double-somite with **1 copulatory pore**. Antennule **9-segmented**; **armature formula: 1, 13, 10, 6 + aes, 3, 4, 2, 2, 6 + acrothek**; segments of Copepoda: 1-I, 2-(II-VIII), 3-(IX-XIV), 4-(XV-XVIII), 5-(XIX-XX), 6-(XXI-XXIII), 7-XXIV, 8-XXV, 9-(XXVI-XXVIII). Antenna with **2-segmented endopod due to the fusion of 2 distal endopod segments of Polyarthra** (char. 8: 0→1); enp-1 with **1 seta**; enp-2 with **4 subterminal setae** (char. 9: 0→1); subterminal setation of enp-2 consisting of **1 short proximal spine (I)** (char. 11: 0→1), **1 longer distal spine (III)** (char. 12: 0→1), **1 distal geniculate seta (4)** and **1 bare slender seta (2)**, inserted between spine I and spine III; **seta 5 of Polyarthra lacking**; exopod **4-segmented, armature formula: 2, 1, 1, 3** (char. 14: 0→1). Mandible endopod **1-segmented due to fusion of enp-1 and enp-2** (char. 17: 0→1); endopod with **3 proximal lateral setae** (from enp-1), and **3 + 2 + 2 apical setae** (char. 20: 0→1), **each group of apical setae basally fused**; exopod **4-segmented due to the fusion of two proximal segments of Polyarthra** (char. 21: 0→1), with **2, 1, 1, 2 setae**. Epipodite of maxillular coxa represented by **4 setae**; basis without outer seta; endopod **1-segmented** (char. 29: 0→1) with **6 setae** (char. 32: 0→1); exopod with **4 setae** (char. 32: 0→1). Maxilla with **syncoxa** (char. 33: 0→1) with 4 endites with **5, 3, 3, 3 setae**; allobasis bearing **1 tube pore on anterior surface** (char. 38: 0→1). Maxilliped **syncoxa without praecoxal seta** and with incorporated coxal endites represented from proximal to distal by **I+1, I+2, I+1 spines and setae (X - 16)**; basis with **1 seta (9)** and **1 spine (VIII)**; endopod with **3, II + 2 setae and spines (1 - 7)**. P1-P4: coxae without inner seta (char. 51 + 57: 0→1); enp-3 of P1 and P2 with **2 inner setae**; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-2
P2	0-0	I-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	I-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	I-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

P5 basis and endopod fused to baseoendopod (char. 59: 0→1).

*Male*. Antennule **haplocer with 14 segments**; **armature formula: 1, 1, 12 + aes, 8 + aes, 2, 6 + aes, 2, 2, 4 / 3, 1, 2, 2, 6 + acrothek, aesthetasc on segment 6 fused at base with 1 seta, segments 1 and 2 with 1 seta each**; segments of Copepoda: 1-I, 2-(II), 3-(III-VIII), 4-(IX-XII), 5XIII, 6-(XIV-XVI), 7-XVII, 8-XVIII, 9-(XIX-XX), 10-(XXI-XXII), 11-XXIII, 12-XXIV, 13-XXV, 14-(XXVI-XXVIII).

Groundpattern of Oligoarthra (Fig. 7)

*Female*. **Body** without difference in width between prosome and urosome. **Nauplius eye present**. **Rostrum** delimited at base. **Prosome** consisting of cephalosome and 4 free pedigerous somites; first pedigerous somite completely separated from dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; **1 egg-sac, 1 copulatory pore, 2 seminal receptacles, 2 gonopores**. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; **armature formula: 1, 13, 10, 6 + aes, 3, 4, 2, 2, 6 + acrothek, characteristic**

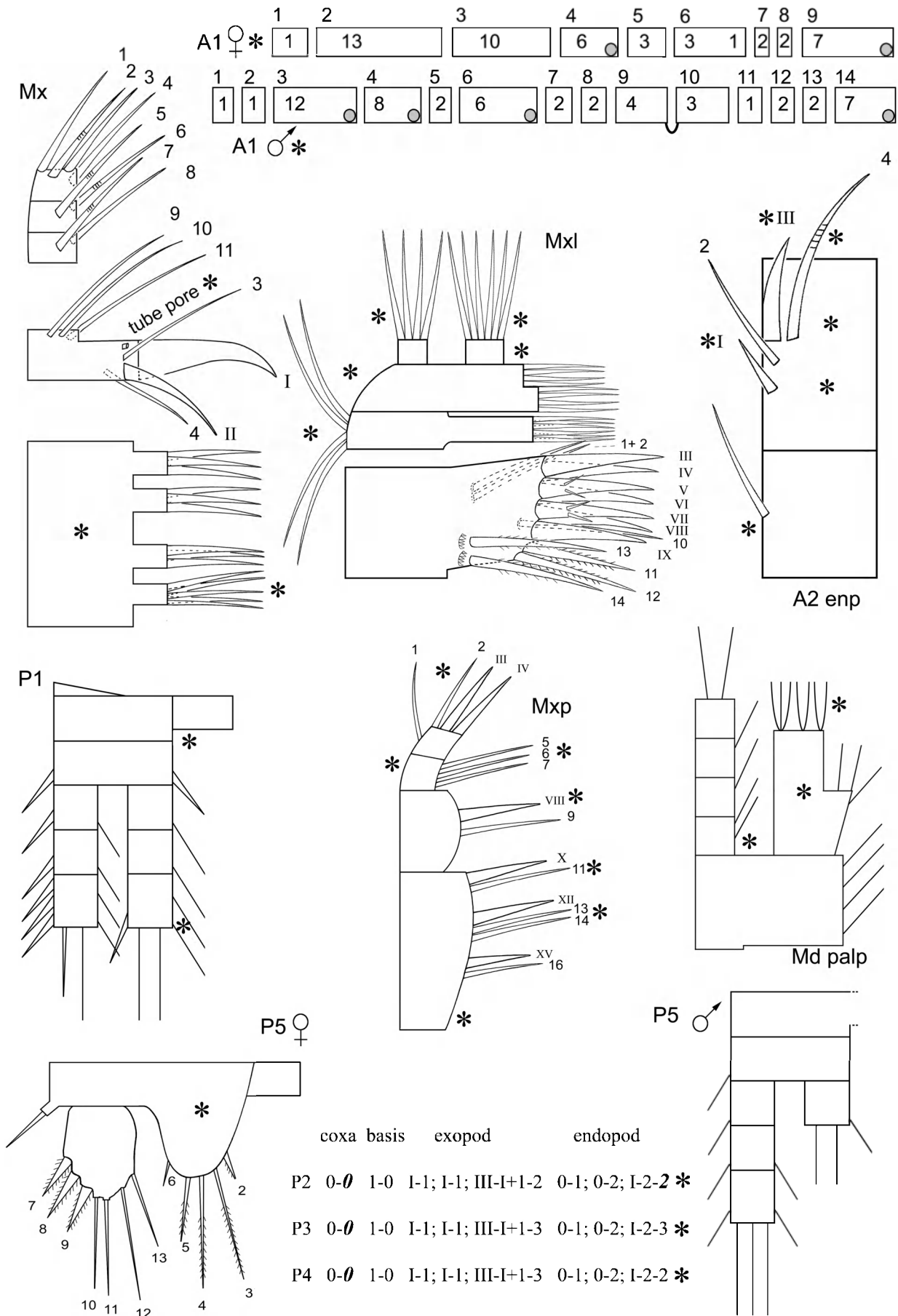


Fig. 7: Groundpattern of Oligoarthra. Asterisks mark autapomorphies of Oligoarthra.

arrangement and shape of setae, paedomorphic female antennule; segments of Copepoda: 1-I, 2-(II-VIII), 3-(IX-XIV), 4-(XV-XVIII), 5-(XIX-XX), 6-(XXI-XXIII), 7-XXIV, 8-XXV, 9-(XXVI-XXVIII). **Antenna** composed of coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 4 subterminal and 7 distal setae; subterminal setation of enp2 consisting of 1 short proximal spine (I), 1 longer distal spine (III), 1 distal geniculate seta (4) and 1 bare slender seta (2), seta 5 of Polyarthra lacking; seta 2 inserting between spine I and spine III; exopod with 2, 1, 1, 3 setae. **Labrum** not prominent. **Paragnaths** separate. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at dorsal corner; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented due to fusion of enp-1 and enp-2; endopod with 3 lateral setae (from enp-1) and 3 + 2 + 2 apical setae, each group of apical setae basally fused; exopod 4-segmented with 2, 1, 1, 2 setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in the outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III - IX, at least 2 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: 2, VII, 1, 2, 2; coxa with 6 setae, epipodite represented by 4 setae; basis with 4 + 4 setae; endopod 1-segmented with 6 setae; exopod 1-segmented with 4 setae. **Maxilla** 5-segmented consisting of syncoxa, allobasis, and 3-segmented endopod; syncoxa with 4 endites with 5, 3, 3, 3 setae; basis with well-developed endite; accessory armature of the fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II), 1 setae (3) and 1 tube pore on anterior surface and 1 seta (4) on posterior surface; accessory armature of fused endopod segment of 2 setae on anterior surface (9, 10) and 1 seta on posterior surface (11); endopod 3-segmented with armature formula: 2, 2, 4: proximal segment with geniculated seta anteriorly (7), middle segment with 2 geniculated setae (5, 6), distal segment with only 1 geniculated seta (2). **Maxilliped** 4-segmented, syncoxa, basis and 2-segmented endopod; syncoxa without praecoxal seta and with incorporated coxal endites represented from proximal to distal by I+1, I+2, I+1 spines and setae (X - 16); basis with 1 spine (VIII) and 1 seta (9) on the inner edge; endopod with 3, II+2 setae and spines (1-7). **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-1	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-2
P2	0-0	I-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	I-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	I-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** with intercoxal sclerite joining the coxae; praecoxa absent; baseoendopod with 1 outer basal seta, endopodal lobe with 5 setae (2 - 6): 2 inner setae, 2 terminal setae, 1 outer seta; exopod with 7 setae (7 - 13): 2 inner setae, 2 terminal setae, 3 outer spines.

**P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; posterior border of genital somite with strong spiniform projection, 2 spermatophores. **Antennule** haplocer with 14 segments; armature formula: 1, 1, 12 + aes, 8 + aes, 2, 6



+ aes, 2, 2, 4 / 3, 1, 2, 2, 6 + acrothek, characteristic arrangement and shape of setae, aesthetasc on segment 6 fused at base with a seta; segments of Copepoda: 1-I, 2-(II), 3-(III-VIII), 4-(IX-XII), 5XIII, 6-(XIV-XVI), 7-XVII, 8-XVIII, 9-(XIX-XX), 10-(XXI-XXII), 11-XXIII, 12-XXIV, 13-XXV, 14-(XXVI-XXVIII). P5 composed of intercoxal sclerite, coxa, basis, endopod with 3 setae and 3-segmented exopod with 1-0, 1-1, 1-3-1 setae. **P6** symmetrical, with 3 setae.

#### Remarks on the monophyly of Oligoarthra

The monophyly of Oligoarthra is a hypothesis well supported by many autapomorphies (see also Dahms, 1990; Martínez Arbizu & Moura, 1998; Willen, 2000). However, Huys et al. (1996, p. 32) state: “The Oligoarthra, however, are polyphyletic and the term has no strict taxonomic significance but, at the moment, is the only one available to cover the remaining families.” The authors give no evidence in support of this assertion. It remains unclear which other taxon of Copepoda could be related to subtaxa of Oligoarthra, or which apomorphies are shared. As recognised by Lang (1948), Oligoarthra is a monophyletic taxon and the present analysis supports this.

#### Remarks on the homologisation

##### **Antennule of female and male**

The homologisation of setae (Fig. 7) is adopted from Willen (2000). The terms haplocer, subchirocer, and chirocer are used according to Willen (2000) to characterise male antennules of Oligoarthra.

##### **Maxilliped**

Willen (2000) numbers only three setae of the endopod of maxilliped. All setae and spines of the maxilliped are homologised and numbered here (Fig. 7; Table 2). The numbers of the setae and spines begin with the outer seta of the distal endopod segment ending at the most proximal seta of the coxa.

##### **P5**

The homologisation of setae (Fig. 7) is adopted from Willen (2000). For the number of setae see chapter 4.1.

#### Remarks on the morphology of Oligoarthra

Within Oligoarthra, all females of Miraciidae sensu Willen (2002) and some of *Huntemannia* Poppe, 1884 (Huntemaniidae) produce 2 **egg-sacs**. It is very likely that this is a secondary phenomenon. Assuming that the production of 2 egg-sacs is part of the groundpattern of Oligoarthra would mean, that the production of only one egg-sac evolved many times (chapter 5.2.3; char. 4).

Willen (2000) reconstructed the groundpattern of **antennule** of Oligoarthra. She reanalysed data published by Huys & Boxshall (1991; Boxshall & Huys, 1998) and proposed a new autapomorphy for Oligoarthra: “Thus the segmentation and setation of the male antennule, without the compound segments due to sexual dimorphism, are interpreted here as the oligoarthran groundpattern. The heterochronic events leading to the pedomorphic female antennule are considered here as an autapomorphy of the Oligoarthra” (Willen, 2000).

The copepodids I of *Tisbe gracilis* (T. Scott, 1895) and *Ectinosoma melaniceps* Boeck,

Table 2: The numbering of coxa, basis and endopod setae of maxilliped for Oligoarthra.

segment	Present account Fig. 7	Willen, 2000 Fig. 46
enp-2	seta 1	—
enp-2	seta 2	—
enp-2	spine III	—
enp-2	spine IV	—
enp-1	seta 5	claw 3
enp-1	seta 6	claw 2
enp-1	seta 7	seta 1
basis	spine VIII	—
basis	seta 9	—
coxa	spine X	—
coxa	seta 11	—
coxa	spine XII	—
coxa	seta 13	—
coxa	seta 14	—
coxa	spine XV	—
coxa	seta 16	—

1865 have 3 setae on the first segment of antennule, but the adults have only 1 (Dahms, 1989).

At least three species of Aegisthidae (*Cervinia brevipes* Brodskaya, 1963, *C. langi* Montagna, 1979, *Expansicervinia glaceria* Montagna, 1981) have 2 aesthetascs on segment 3 of the female antennule. The second aesthetasc is secondary. In *Cerviniopsis muranoi* Itô, 1983 there are 2 other secondary aesthetascs: one on segment 4 and one on the last segment. Some species of Tegastidae and Peltidiidae have additional aesthetascs on male antennule and some species of Tegastidae have additional aesthetascs on female antennule. This is also secondary (see chapter 4.24). Some species of Tisbidae *sensu strictu*, e.g. *Drescheriella glacialis* Dahms & Dieckmann, 1987 have additional setae on the antennule of the female oligoarthran segment 2 and the male oligoarthran segment 3. The more plesiomorphic species of Tisbidae *sensu strictu* and the species of all outgroups do not have these additional setae. It is highly probable that these additional setae of both sexes were added during the evolution within Tisbidae.

Compared to the oligoarthran groundpattern many species of Tisbidae *sensu strictu* have 2 additional setae on the oligoarthran segment 6 of **male antennule**, as have species of Paramesochridae, Peltidiidae - Tegastidae and *Atergopedia vetusta*. Otherwise these additional setae are not described for the male antennule of Exanechentera, but this is probably due to incomplete description of the antennule of

the males. It is very likely that these additional setae are more widespread within Exanechentera and that they are an autapomorphy of this taxon or of N.N. 4 (Tachidiidae - Palinarthra; chapters 2, 3.1 and 4.2.6).

The aesthetasc on segment 6 of the male antennule is not basally fused with a seta in Rometidae, Neobradidae gen. spec. 1, and *Tachidiopsis* spec. Species of Aegisthidae and most Syngnatharthra have an aesthetasc on the homologous segment fused to a seta. The fused aesthetasc on Oligoarthra segment 6 male antennule is interpreted here as an autapomorphy of Oligoarthra as suggested by Willen (2000). The free aesthetasc in some taxa is assumed to be secondarily separated.

Neobradidae gen. spec. 1 has in the middle of the distal segment of the exopod **antenna** a row of spinules, which looks like the rows that mark the distal ends of the exopodal segments. If there were a segmental articulation in the ancestor at this position, the groundpattern of Oligoarthra would be a 5-segmented exopod with 2, 1, 1, 0, 3 setae. The antenna of *Atergopedia vetusta* suggests a 5-segmented exopod, because the distal segment is indistinctly subdivided (Martínez Arbizu & Moura, 1998).

The 4 lateral setae of the distal endopod segment antenna are derivable from the 5 setae of the middle endopod segment of Polyarthra (Figs. 6 - 7). A homologous modification of the 4 subterminal setae of proximal endopod segment antenna is found in most Oligoarthra. The setation consists of 1 short proximal spine (I), 1 longer distal spine (III), 1 distal geniculate seta (4) and 1 bare slender seta (2) (Willen, 2000). Seta 5 of Polyarthra is lacking (chapter 5.2.3; chars 9 to 12).

Willen (2000) reconstructed a 5-segmented exopod of **mandible** for the oligoarthran groundpattern. She referred to Dactylopusiidae, which have “a 2-segmented exp with 1, 4 setae and 1 additional seta located directly on the basis”. Willen (2000, p. 93) suspected that “the proximal segment is fused with the basis and represented only by 1 seta, so that an original separation of the 2 proximal segments can be assumed.” A fusion of the proximal segment of the exopod with the basis could not be observed in other species of Harpacticoida. As long as there is no indication from e.g. the postembryonic development, to help explain that an additional seta inserts on the basis, the astonishing morphology of the mandible exopod of Dactylopusiidae is interpreted as derived.

Willen (2000) also reconstructed 10 setae for the (fused) distal endopod segment of mandible as groundpattern of Oligoarthra and Podogennonta. However, this is obviously a secondary phenomenon. The ancestor of Oligoarthra had no more than 7 distal setae on the (fused) distal endopod segment of mandible (chapters 5.2.3 and 5.2.4; char. 20).

Willen (2000) recognized the groups of fused apical setae of the mandible endopod (3 + 2 + 2) as an autapomorphy of Oligoarthra.

The endopod of *Drescheriella glacialis*, *Novocrinia trifida*, and some species of Paramesochridae is 2-segmented. However, the 1-segmented endopod is an autapomorphy of Oligoarthra (chapter 5.2.3; char. 17: 1→0).

The setation of exopod and basis of **maxillule** assumed for the groundpattern of Oligoarthra is questionable. Huys (1988a) described the proximal endite of maxillular basis of *Rotundiclipeus canarensis* with 2 setae and the distal one with 5. The drawing of the setae of the maxillular basis does not enable this setation to be confirmed. It is

likely that the proximal endite bears 3 and the distal one 4 setae. Martínez Arbizu & Moura (1998) and Willen (2000) reported 5 setae for the maxillular exopod, but this is erroneous.

Only the two species of Rometidae, *Marsteinia* spec. 5 and *Marsteinia* spec. 8 have a maxillule with 4 setae representing the epipodite of the coxa (Fig. 10). *Neobradya pectinifera* and *Antarcticobradya tenuis* have 3 setae. All other described Oligoarthra have no more than 2 setae representing the epipodite of coxa.

As indicated in the figure and the text, Bodin (1968) counts 2 inner setae on the distal exopod segment of **P1** of the only existing specimen of *Marsteinia sarsi*. All other Oligoarthra have 1 or no inner seta. However, the P2 of the type specimen of *Marsteinia sarsi* is not drawn and the exp-3 is lost so that the setae number is not known. The P1 of *Marsteinia sarsi* in Bodin's description (1968) rather looks like the typical P2 of *Marsteinia* species. The exp-3 of P2 of *Marsteinia* species is normally rectangular and two times longer than wide and the exp-3 of P1 is not much longer than wide and more oval than rectangular (e.g. *Marsteinia bozici*). As the exp-3 of described P1 of *Marsteinia sarsi* is rectangular and two times longer than wide, it is possible that Bodin (1968) described the P2 of this only existing specimen instead of the P1. However, as *Marsteinia sarsi* is a species with a very plesiomorphic morphology within Oligoarthra, it is possible that the P1 has indeed 2 inner setae and look like the P2 of other *Marsteinia* species. Polyarthra, Misophrioida, and Calanoida have 2 or more inner setae on the distal exopod segment of P1. Therefore, 2 inner setae on the distal exopod segment of **P1** have to be assumed for the groundpattern of Oligoarthra until a redescription of the P1 and P2 of *Marsteinia sarsi* can be made.

#### 4.4 Aegisthoidea Giesbrecht, 1892

##### Taxa belonging to Aegisthoidea

Aegisthidae Giesbrecht, 1892 (77 species in 16 genera), Rometidae Seifried & Schminke, 2003 (1 species in 1 genus).

##### Changes in systematics

For recent changes in systematics see Seifried & Schminke (2003).

##### Diagnosis: Autapomorphies of Aegisthoidea (Fig. 4: ■ 2; Figs. 8 + 9)

*Female*. Endopod of mandible with 1 spine and 2 setae laterally (char. 19: 0→1). **Basis and endopod of maxillule fused, fused segment of characteristic rectangular shape, all setae at distal edge** (Fig. 9; char. 30: 0→1). Endopodal armature of maxillar allobasis consisting of **displaced seta 10 between anterior and posterior surface** (char. 40: 0→1), **an additional seta closely set to seta 10** (char. 41: 0→1), **displaced seta 9 inserting near seta 10 but on anterior surface**, and seta 11 on posterior surface. P5 exopod **more than twice as long as wide** (char. 60: 1→2).

*Male*. P5 basis **not separated from coxa** (char. 70: 0→1) **nor from endopod** (char. 71: 0→1).

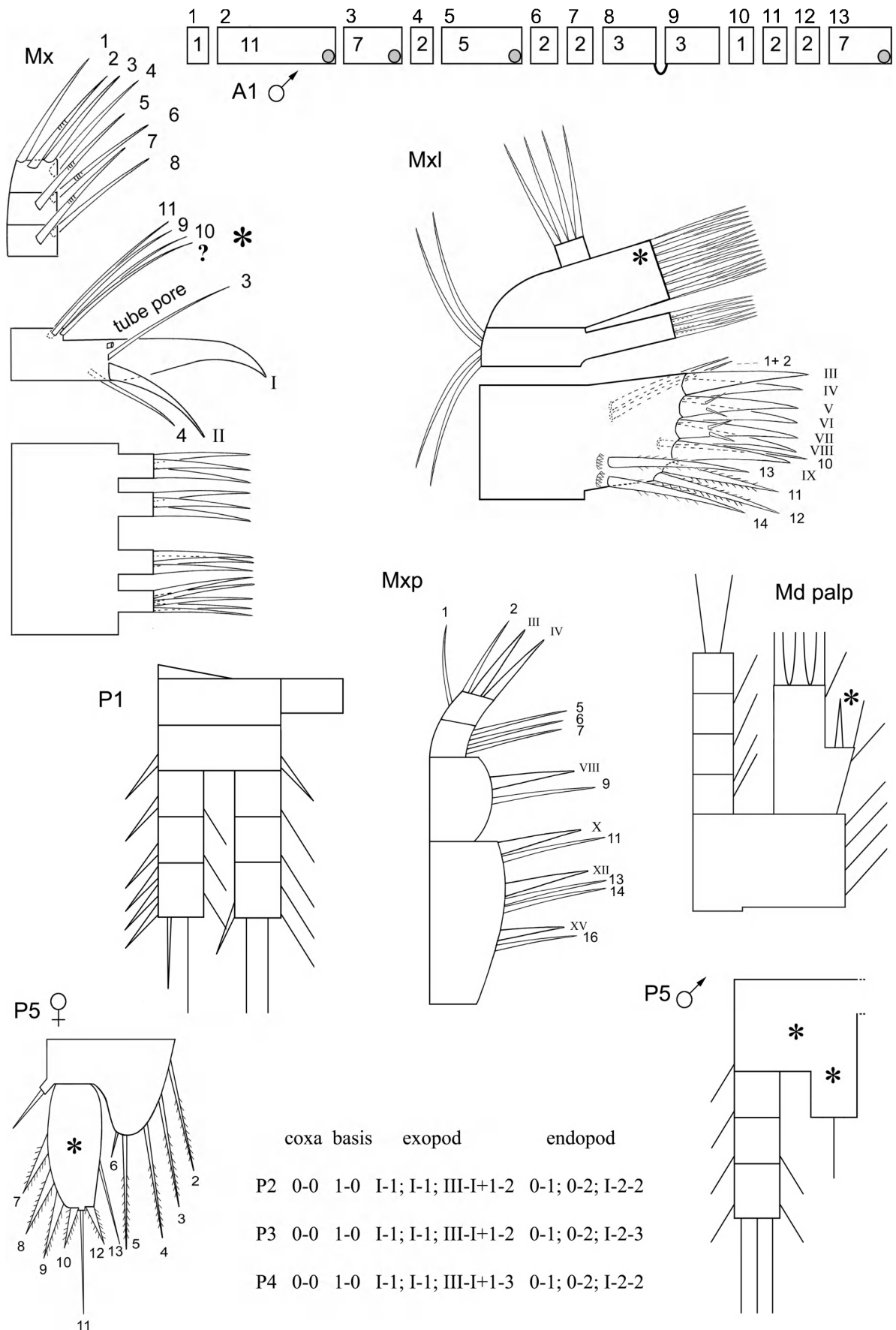


Fig. 8: Groundpattern of Aegisthoidea. Asterisks mark autapomorphies of Aegisthoidea.

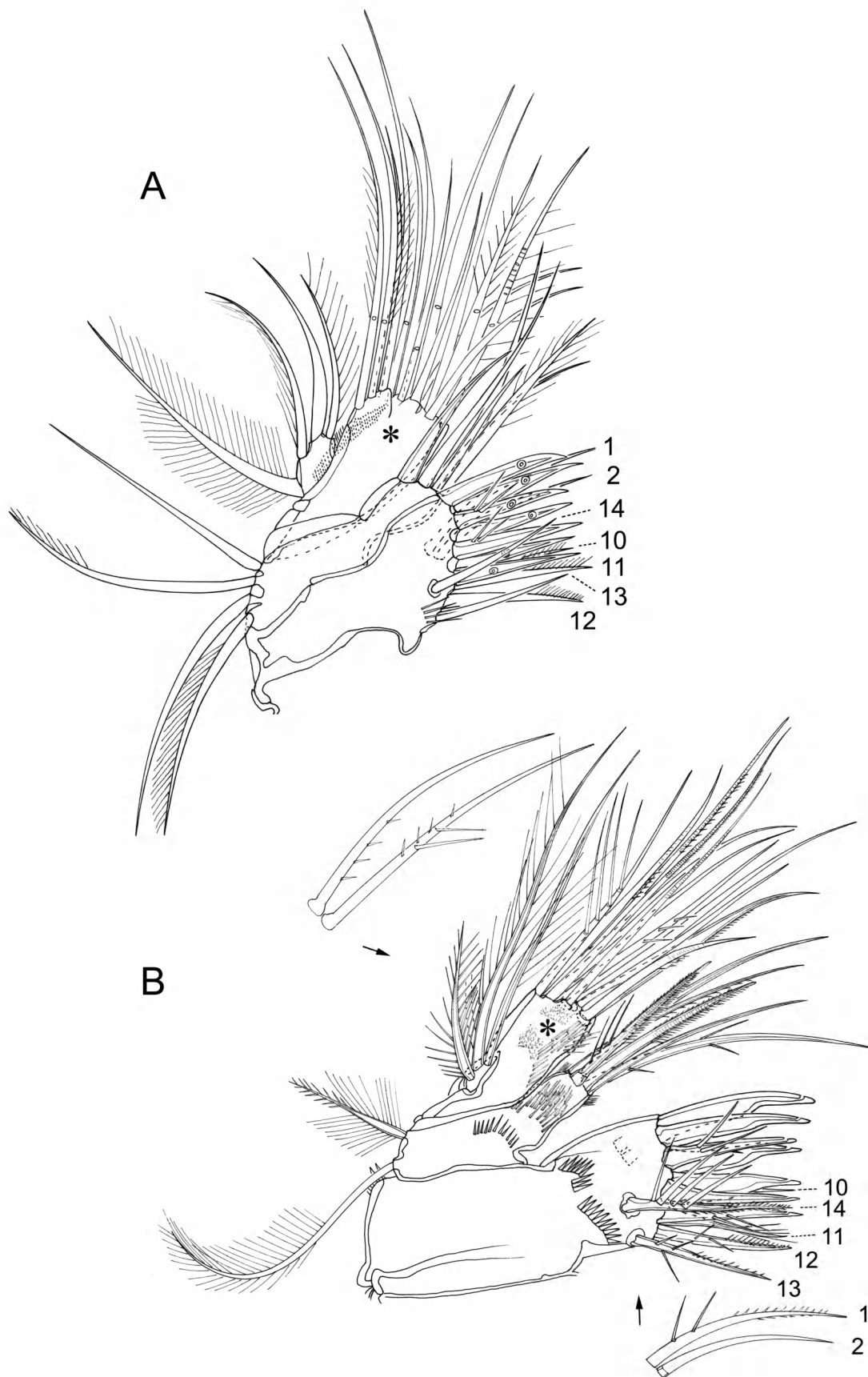


Fig. 9: Maxillula of Aegisthoidea. A. Maxillula of *Romete bulbiseta*. B. Maxillula of *Aegisthidae* gen. spec. 1. -- Asterisks indicate the basis fused to the endopod.

Groundpattern of Aegisthoidea (Fig. 8)

*Female*. **Body** without clear difference in width between prosome and urosome (Fig. 1 C). **Nauplius eye** not confirmed. **Rostrum** fused at base with cephalothorax. **Prosome** consisting of cephalothorax and 4 free pedigerous somites; first pedigerous somite completely separated from dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore, 2 seminal receptacles, 2 gonopores. **Anal somite** not elongated. **Anal operculum** developed. **Caudal rami** twice as long as wide, with 7 setae. **Antennule** 8-segmented; armature formula: 1, 12, 14 + aes, 2, 3, 2, 2, 6 + acrothek; fusion of Oligoarthra segments 3 and 4. **Antenna** 4-segmented comprising coxa, basis and 2 endopod segments; basis and proximal endopod segment with 1 seta each; distal endopod segment with 4 lateral and 7 distal setae; exopod 4-segmented, with 2, 1, 1, 3 setae. **Labrum** not prominent. **Paragnaths** separate. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 1 spine and 2 setae laterally and 7 distal setae; exopod 4-segmented with 2, 1, 1, 2 setae. **Maxillule** (Fig. 9) comprising praecoxa, coxa, exopod, and basis fused with endopod; praecoxal arthrite: anterior surface in the outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III - IX, 2 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: 2, VII, 1, 2, 2; coxa with 6 setae, epipodite represented by 4 setae; basis and endopod fused, fused segment of characteristic rectangular shape, all 14 setae at distal edge; exopod with 4 setae. **Maxilla** 5-segmented comprising syncoxa, allobasis, and 3-segmented endopod; syncoxa with 4 endites with 5, 3, 3, 3 setae; allobasis with well-developed basal endite fused with strong claw (I); accessory armature of fused basis consisting of 1 curved spine (II), 1 seta (3) and 1 tube pore on anterior surface and 1 seta (4) on posterior surface; endopodal armature of maxillar allobasis consisting of displaced seta 10 between anterior and posterior surface, an additional seta closely set to seta 10, displaced seta (9) inserting near seta 10 but on anterior surface, and seta (11) on posterior surface; endopod 3-segmented with armature formula: 2, 2, 4; proximal segment with anterior geniculated seta (7), the middle segment with two geniculated setae (5, 6), and the last segment with only 1 geniculated seta (2). **Maxilliped** 4-segmented, comprising syncoxa, basis and 2-segmented endopod; coxa with incorporated endites represented from proximal to distal by I+1, I+2, I+1 long spines and setae; basis with 1 spine and 1 seta; endopod with 3, II+2 setae and spines. **P1-P4** with 3-segmented rami; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-1; I-1; III-I+1-1	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** praecoxa absent; baseoendopod with 1 outer basal seta, endopodal lobe with 5 setae (2 - 6): 3 inner setae, 1 terminal and 1 outer seta; exopod more than twice as long as wide with 7 setae (7 - 13): 1 inner seta, 3 outer spines, and 1 seta and 2 spines around

apex. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, comprising somite bearing P5 and 4 abdominal somites; posterior border of genital somite with strong spiniform projection, 2 spermatophores. **Antennule** 13-segmented; armature formula: 1, 11 + aes, 7 + aes, 2, 5 + aes, 2, 2, 3 / 3, 1, 2, 2, 6 + acrothek, fusion of Oligoarthra segments 2 and 3. **P5** basis not separated from coxa and endopod, endopodal lobe with 1 seta and 3-segmented exopod with 1-0, 1-1, 1-3-1 setae. **P6** symmetrical with 3 setae.

#### Remarks on systematics and morphology of Aegisthoidea

##### *Systematics.*

Seifried & Schminke (2003) described *Romete bulbiseta* (Rometidae) and synonymized Cerviniidae Sars, 1903 with its senior synonym Aegisthidae Giesbrecht, 1892. In consequence, Aegisthoidea Giesbrecht, 1892 is the senior synonym of Cervinioidea Sars, 1903. Aegisthidae enclose Aegisthinae Giesbrecht, 1892, Cerviniinae Sars, 1903 and "Cerviniopsinae" Brodskaya, 1963 now (Seifried & Schminke, 2003). Aegisthidae and Rometidae are sister taxa (chapter 5). For further details of morphology and systematics within Aegisthoidea see Seifried & Schminke (2003).

##### *Morphology.*

The monophyletic taxon Aegisthoidea is mainly characterised by the lateral spine of mandible endopod (char. 19: 0→1), the fused basis and endopod of maxillule with the characteristic shape (Fig. 9; char. 30: 0→1), and the displaced setae 9 and 10 of the maxillar allobasis (chars 40 and 41: 0→1).

Species of Aegisthidae have no **nauplius eye** and one **egg-sac** (chapter 4.6). However, for species of Rometidae we do not know if they have a nauplius eye or how many egg-sacs they have.

In Rometidae and Aegisthidae basis and endopod of **maxillule** are fused (Fig. 9). The fused segment has a characteristic rectangular shape and all setae arise from the distal edge. There is no other harpacticoid with a maxillule fused in this way.

The accessory armature of the fused endopod segment of the **maxilla** of Aegisthoidea consisting of displaced seta 10 between anterior and posterior surface, displaced seta (9) near seta 10, an additional seta closely set to seta 10, and seta (11) on posterior surface. This exceptional setae pattern is discussed in Seifried & Schminke (2003).

On the anterior side of the basal part of the maxilla *Romete bulbiseta* has a long tube pore, which is inserted more distally than seta 3. Some Aegisthidae like *Stratiopontotes* spec. also have a tube pore at this position. In some species this tube pore is very broad and connected with a mucus gland.

Only the **P5 female** of *Andromastax muricatus* Conroy-Dalton & Huys, 1999 has an exopod with 7 setae. All other Aegisthoidea have fewer setae. The P5 of *Romete* spec. females has a baseoendopod with 5 setae. It is very probable, that the P5 in the groundpattern of Aegisthoidea has an exopod that is more than twice as long as wide (char. 60: 1→2) as *Romete* spec. has an exopod of P5 of this shape. Most species of Aegisthidae have as *Romete* spec. an elongated P5, some species of Aegisthidae have an extremely elongate exopod, some a square one. A complete phylogenetic analysis of Aegisthidae will reconsider the question of whether the ancestors of Aegisthoidea



and Aegisthidae had really an elongate P5. For further discussion of char. 60 see chapter 5.2.3.

Only the **antennule of male** of *Romete bulbiseta* is 13-segmented. The antennule of the other Aegisthoidea is at most 10-segmented due to the fusion of Oligoarthra segments 2 and 3, 10 and 11, 12 to 14.

The **exopod P5 male** of *Romete* spec. has 1-0, 0-1, 1-3-1 setae. Compared with all other Oligoarthra there is one additional terminal seta on the distal segment of the exopod, like in *Longipedia coronata* Claus, 1863 (Polyarthra).

#### 4.5 Rometidae Seifried & Schminke, 2003

##### Taxa belonging to Rometidae

*Romete bulbiseta* Seifried & Schminke, 2003

Undescribed species (8.1 Appendix I.): *Romete* spec.

##### Diagnosis: Autapomorphies of Rometidae (Fig. 4: ■ 5; Fig. 10)

**Deep depressions** with reticular ornamentations lateral in the anterior half of cephalic shield. First pedigerous somite **completely fused to dorsal cephalic shield** (char. 1: 0→1). Enp-2 of antenna with 1 spine (I) and 3 setae (2 - 4) laterally: **element 1 forming a seta** (char. 12: 1→0). Distal segment of mandibular exopod **extremely minute**. Maxilliped 3-segmented, with syncoxa, basis and **1-segmented endopod, enp-1 and enp-2 fused** (char. 48: 0→1). Two outer spines of exp-3 P1 **elongate**. Distal outer corner of enp-2 of P2-P4 **produced into spinous process**; enp-3 of P2-P4 **becomes slender in the distal half, the step strengthened by cuticular thickenings**.

*Male*. Exopod P5 3-segmented, with 1-0, 0-1, 1-3-1 setae.

##### Groundpattern of Rometidae (Fig. 10)

*Male*. **Body** without difference in width between prosome and urosome (Fig. 1 B). **Nauplius eye** not confirmed. **Rostrum** fused at base with cephalothorax. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield; deep lateral depressions in the anterior half of cephalic shield, with reticular ornamentations. **Urosome** 6-segmented, comprising somites bearing P5 and P6 and 4 free abdominal somites; 2 spermatophores. **Anal somite** not elongated. **Anal operculum** developed. **Caudal rami** twice as long as wide, with 7 setae. **Antennule** 13-segmented; armature formula: 1, 9 + aes, 7 + aes, 2, 5 + aes, 2, 2, 1 / 3, 1, 2, 2, 6 + acrothek, fusion of Oligoarthra segments 2 and 3. **Antenna** 4-segmented comprising coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 1 spine (I) and 3 setae (2 - 4) laterally and 7 distal setae; exopod with 2, 1, 1, 3 setae. **Labrum** not prominent. **Paragnaths** separated. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 1 spine and 2 setae laterally and 7 distal setae; exopod 4-segmented with 2, 1, 1, 2 setae, distal segment extremely minute. **Maxillule** (Fig. 9 A) comprising praecoxa, coxa, exopod, and basis fused with endopod; praecoxal arthrite: anterior surface in the outer half with 2 neighbouring

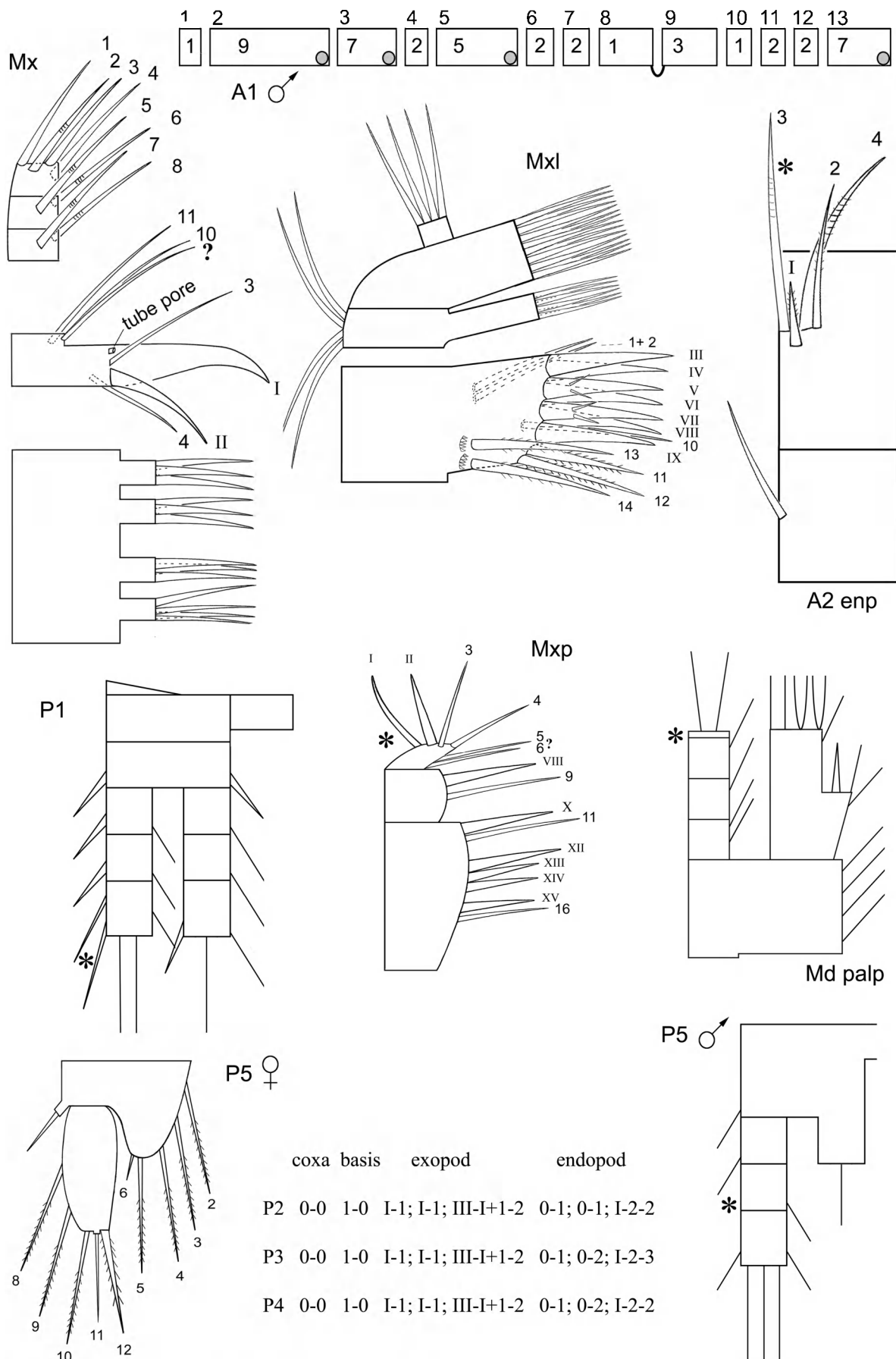


Fig. 10: Groundpattern of Rometidae. Asterisks mark autapomorphies of Rometidae.

setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III - IX, 2 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: 2, VII, 1, 2, 2; coxa with 6 setae, epipodite represented by 4 setae; fused basis and endopod with 14 setae; exopod with 4 setae. **Maxilla** 5-segmented comprising syncoxa, allobasis, and 3-segmented endopod; syncoxa with 4 endites with 4, 3, 3, 3 setae; allobasis with well developed basal endite fused with strong claw (I); accessory armature of fused basis consisting of 1 curved spine (II), 1 seta (3) and 1 tube pore on anterior surface and a seta (4) on posterior surface; accessory armature of fused endopod segment consisting of a seta (10) on inner corner, 1 seta closely set to seta 10 (?) and seta (11) on posterior surface; endopod with armature formula: 2, 2, 4; two proximal segments with two geniculated setae (5 - 8), last segment with 1 geniculated seta (2). **Maxilliped** 3-segmented, comprising syncoxa, basis and 1-segmented endopod; syncoxa with incorporated endites represented from proximal to distal by I+1, III, I+1 long spines and setae; basis with 1 spine and 1 seta; endopod directed inwardly with 4 setae and 2 spines (I - 6?). **P1-P4** with 3-segmented rami; two outer spines of exp-3 P1 elongate; distal outer corner of exp-2 of P2-P4 produced into spinous process; exp-3 of P2-P4 becomes slender in the distal half, the step strengthened by cuticular thickenings; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-1; I-1; II-2-1	0-1; 0-1; I-1-1
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-1; 1-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; 1-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; 1-2-2

**P5** fused medially; basis not separated from coxa and endopod, endopodal lobe with 1 seta; 3-segmented exopod with 1-0, 0-1, 1-3-1 setae. **P6** symmetrical with 3 setae.

*Female*. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 copulatory pore, 2 seminal receptacles, 2 gonopores. **P5** with intercoxal sclerite joining the coxae; praecoxa absent; baseoendopod with 1 outer basal seta, endopodal lobe with 5 setae (2 - 6): 3 inner setae, 1 terminal and 1 outer seta; exopod more than twice as long as wide with 5 setae (8 - 12): 2 outer setae and 2 setae and 1 spines around apex. **P6** with 3 setae.

#### Remarks on the morphology of Rometidae

The monophyletic taxon Rometidae is characterised mainly by the lateral depressions of the cephalothorax, the minute segment of mandibular exopod, the characteristic maxilliped, and the form of the swimming legs (Seifried & Schminke, 2003).

Rometidae have only few own autapomorphies, the autapomorphies of Aegisthoidea and reductions of few setae of the swimming legs and mouthparts, but otherwise they match the groundpattern of Oligoarthra. Some setae of the groundpattern of Oligoarthra can be only found in Rometidae (chapter 4.3).

*Romete* spec. 1 has a **maxillule** with 4 setae representing the epipodite of the coxa (Fig. 9A). *Neobradya pectinifera* and *Antarcticobradya tenuis* have 3 setae. All other described Oligoarthra have no more than 2 setae.

Basis and endopod of the maxillule are fused in *Romete bulbiseta* like in all species of

Aegisthidae (Fig. 9). In *Romete bulbiseta* there are 4 setae on the distal outer side on a projection of the fused segment, representing either the whole endopod or only the distal segment of it. In the former case there would be 10 setae on the basis, 2 more than in all other Oligoarthra. It is more likely that this projection with 4 setae represents only the distal segment of the endopod. The species of Polyarthra, the sister taxon of Oligoarthra, still have a 2-segmented endopod.

*Romete bulbiseta* has lost more setae on **P3** and **P4** than *Romete spec.*

The male of *Romete bulbiseta* has an endopodal lobe of **P5** with 1 seta and the female of *Romete spec.* one with 5 setae. Males and females of Aegisthidae have no endopodal setae of P5 at all and the endopodal section of the baseoendopod is reduced. For the discussion of the exopod of the female P5 see chapters 4.4 and 5.2.3.

## 4.6 Aegisthidae Giesbrecht, 1892

Taxa belonging to Aegisthidae (77 species in 16 genera)

Aegisthinae Giesbrecht, 1892: *Aegisthus* Giesbrecht, 1891, *Andromastax* Conroy-Dalton & Huys, 1999, *Jamstecia* Lee & Huys, 2000, *Nudivorax* Lee & Huys, 2000, *Scabrantenna* Lee & Huys, 2000.

Cerviniinae Sars, 1903: *Cervinia* Norman, 1878, *Cerviniella* Smirnov, 1946, *Eucanuella* T. Scott, 1901, *Expansicervinia* Montagna, 1981, *Paracerviniella* Brodskaya, 1963.

“Cerviniopsinae” Brodskaya, 1963: *Cerviniopsis* Sars, 1909, *Hemicervinia* Lang, 1935, *Herdmaniopsis* Brodskaya, 1963, *Pontostratiotes* Brady, 1883, *Stratiopontotes* Soyer, 1970, *Tonpostratiotes* Itô, 1982.

Undescribed species (8.1 Appendix I): Aegisthidae gen. spec. 1, Aegisthidae gen. spec. 2, Aegisthidae gen. spec. 3, Aegisthidae gen. spec. 4, Aegisthidae gen. spec. 5, *Aegisthus spec.*, *Andromastax spec.*, *Cervinia spec.* 1, *Cervinia spec.* 2, *Cervinia spec.* 3, *Cervinia spec.* 4, *Cervinia spec.* 5, *Cerviniella spec.* 1, *Cerviniella spec.* 2, *Cerviniella spec.* 3, *Eucanuella cf. langi*, *Expansicervinia cf. tenuiseta*, *Expansicervinia spec.* 1, *Expansicervinia spec.* 2, *Stratiopontotes spec.*

Changes in systematics (reasons given below)

*Brotskayaia* Huys, Møbjerg and Kristensen, 1997 is synonymized with *Expansicervinia* Montagna, 1981.

*Neocervinia* Huys, Møbjerg and Kristensen, 1997 and *Pseudocervinia* Brodskaya, 1963, are synonymized with *Cervinia* Norman, 1878.

Diagnosis: Autapomorphies of Aegisthidae (Fig. 4: ■ 6; Figs. 11 + 1 C)

*Female*. Anal somite **elongate, tapering posteriorly** (Fig. 1 C). Caudal rami **more than twice as long as wide**. Antennule of female **8-segmented; fusion of Oligoarthra segments 3 and 4**. Antenna with **allobasis or incomplete basis** (char. 7: 0→1); enp-2 laterally with 1 spine (III) and 2 setae (2 + 4), **spine I lacking**. Endopod of mandible of **one large segment and at least 2 times longer than wide**; proximal segment of exopod **elongate, considerably longer than remaining segments and at least 3 times longer than wide**. Epipodite of maxillular represented by **2 setae**.

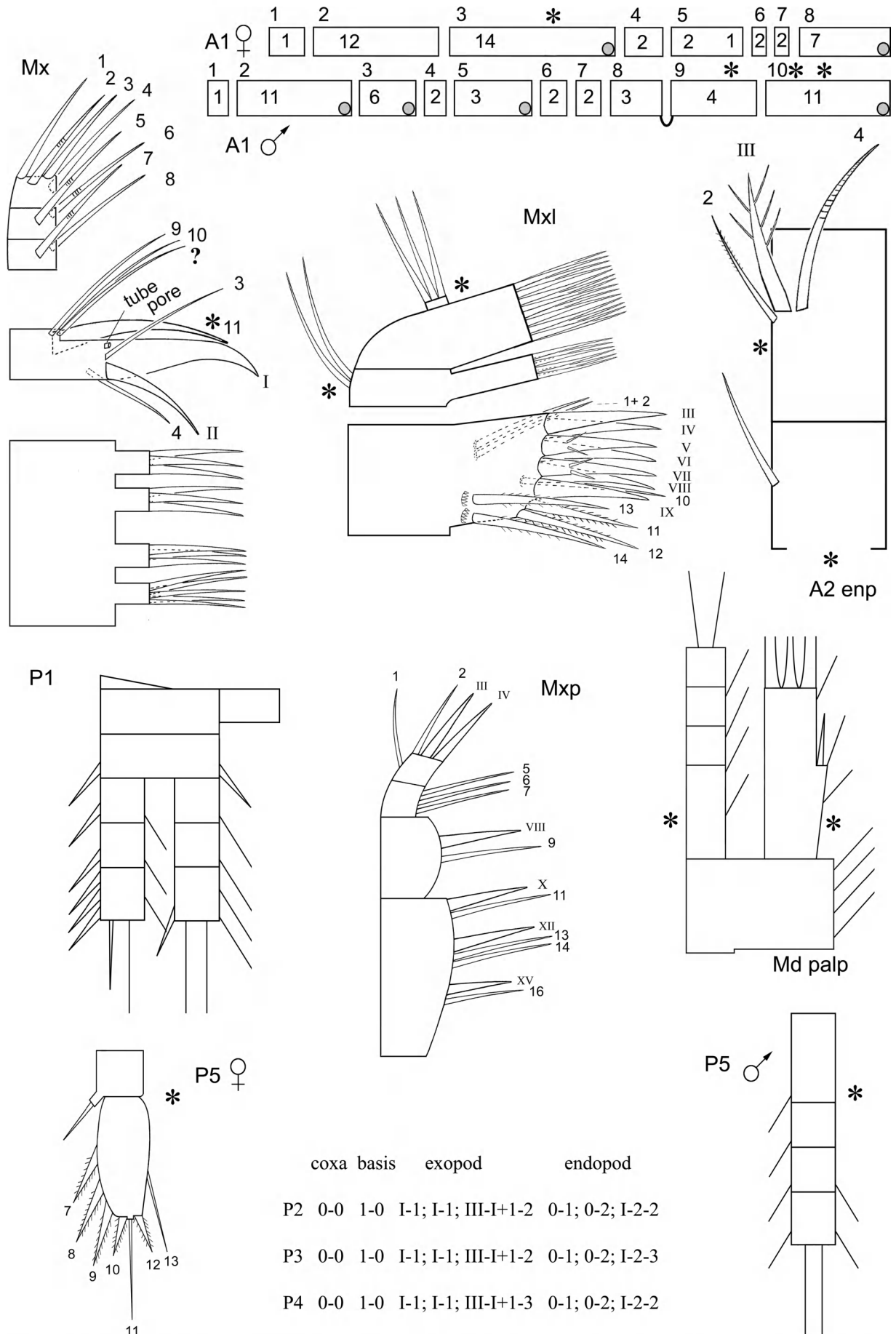


Fig. 11: Groundpattern of Aegisthidae. Asterisks mark autapomorphies of Aegisthidae.

Exopod of maxillule **reduced in size with 3 setae**. Endopodal element 11 of allobasis of maxilla **developed as large, strong spine** inserted on posterior surface. P5 **without endopodal lobe**.

*Male*. Antennule 10-segmented, fusion of Oligoarthra segments 2 and 3, **10 and 11** (char. 63: 0→1), **12 to 14** (char. 64: 0→2). P5 **without endopodal lobe**.

#### Groundpattern of Aegisthidae (Fig. 11)

*Female*. **Body** with difference in width between prosome and urosome (Fig. 1 C). **Nauplius eye** absent. **Rostrum** fused at base with cephalothorax. **Prosome** consisting of cephalosome and 4 free pedigerous somites; first pedigerous somite completely separated from dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; median lateral border of genital double-somite produced into strong spiniform projection, 1 egg-sac, 1 copulatory pore, 2 seminal receptacles, 2 gonopores. **Anal somite** elongate, tapering posteriorly. **Anal operculum** developed. **Caudal rami** more than twice as long as wide, with 7 setae. **Antennule** 8-segmented; armature formula: 1, 12, 14 + aes, 2, 3, 2, 2, 6 + acrothek; fusion of Oligoarthra segments 3 and 4. **Antenna** comprising coxa, incomplete basis and 1-segmented endopod; basis and fused enp-1 with 1 seta each; enp-2 with 1 spine (III) and 2 setae (2 + 4) laterally and 7 distal setae, lateral spine I lacking; exopod 4-segmented, with 2, 1, 1, 3 setae. **Labrum** not prominent. **Paragnaths** separated. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner; palp comprising basis, endopod and exopod; basis with 4 setae; endopod one large segment that is at least 2 times longer than wide, with 1 spine and 2 setae laterally and 7 distal setae; exopod 4-segmented with 2, 1, 1, 2 setae, proximal segment elongate, considerably longer than remaining segments and at least 3 times longer than wide. **Maxillule** (Fig. 9 B) comprising praecoxa, coxa, exopod, and basis fused with endopod; praecoxal arthrite: anterior surface in the outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III - IX, 2 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: 2, VII, 1, 2, 2; coxa with 6 setae, epipodite represented by 2 setae; fused basis and endopod with 14 setae; exopod reduced in size with 3 setae. **Maxilla** 4-segmented comprising syncoxa, allobasis, and 3-segmented endopod; syncoxa with 4 endites with 5, 3, 3, 3 setae; allobasis with well-developed basal endite fused with strong claw (I); accessory armature of fused basis consisting of 1 curved spine (II), 1 seta (3) and 1 tube pore on anterior surface and 1 seta (4) on posterior surface; endopodal armature of maxillar allobasis consisting of displaced seta 10 between anterior and posterior surface, an additional seta closely set to seta 10, displaced seta (9) inserting near seta 10 but on anterior surface, and a spine (11) on posterior surface; endopod with armature formula: 2, 2, 4; proximal segment with 1 geniculated seta anteriorly (7), middle segment with 2 geniculated setae (5, 6), and last segment with 1 geniculated seta (2). **Maxilliped** 4-segmented, comprising syncoxa, basis and 2-segmented endopod; coxa with incorporated endites represented from proximal to distal by I+1, I+2, I+1 long spines and setae; basis with 1 spine and 1 seta; endopod with 3, II+2 setae and spines. **P1-P4** with 3-segmented rami; formula of

armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-1; I-1; III-I+1-1	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** without endopodal lobe; exopod more than twice as long as wide with 7 setae (7 - 13): 1 inner seta, 3 outer spines, and 1 seta and 2 spines around apex. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6.

**Urosome** 6-segmented, comprising somite bearing P5 and 4 abdominal somites; posterior border of genital somite with strong spiniform projection, 2 spermatophores.

**Antennule** 10-segmented; armature formula: 1, 11 + aes, 6 + aes, 2, 3 + aes, 2, 2, 3 / 4, 10 + acrothek, fusion of Oligoarthra segments 2 and 3, 10 and 11, 12 to 14. **P5** with no endopodal lobe, basis separated from coxa, and 3-segmented exopod with 1-0, 1-1, 1-2-1 setae. **P6** symmetrical, with 3 setae.

#### Remarks on the systematics and morphology of Aegisthidae

##### *Morphology.*

The monophyletic taxon Aegisthidae is characterised mainly by the form of the anal somite, the elongated endopod and exopod of mandible, the small exopod of maxillula, the big spine on posterior surface of maxillar allobasis and the P5 without endopodal lobe in both sexes (Seifried & Schminke, 2003).

Species of Aegisthidae have no **nauplius eye** (Lang, 1944, 1948: 117-118). Species of Aegisthidae have 1 egg-sac as be seen in *Eucanuella spinifera* (Fig. 1 C).

At least 3 species (*Cervinia brevipes*, *C. langi*, *Expansicervinia glaceria*) have 2 aesthetascs on Oligoarthra segment 3 of the **female antennule**. The second aesthetasc is secondary. In *Cerviniopsis muranoi* there are 2 more secondary aesthetascs: one on segment 4 and one on the last segment.

Some species of Aegisthidae have an incomplete basis of the **antenna** like *Stratiopontotes mediterraneus* Soyer, 1970 or *Pontostratiotes scotti* Brodskaya, 1959, but most species have an allobasis.

All more plesiomorphic species of Aegisthidae have a typical **mandible**: the endopod is one large segment that is at least twice as long as wide. The form of the endopod is typically oval-rectangular. The proximal segment of exopod is elongated, considerably longer than the remaining segments, and at least 3 times longer than wide. The shapes of the exopod and especially of the endopod are unique for aegisthid species. With the exception of the distal exopod segment, the more plesiomorphic character state within Harpacticoida is visible in *Romete bulbiseta* (Fig. 10). The 1-segmented endopod and the proximal exopod segment are not or only slightly longer than wide. However, the distal segment of the mandibular exopod in *Romete bulbiseta* is extremely minute. It is so small that the segment is only visible by careful examination. This is an advanced character state. The groundpattern within Oligoarthra is a proximal segment of a 4-segmented mandibular exopod that is not shorter than the other exopod segments. Species of Aegisthidae have a proximal exopodal segment that is mostly, but not always, shorter than the other exopod segments (e.g. *Pontostratiotes sixtorum* Por, 1969 *mindanaoensis* Itô, 1982). However, it is not as small as that of rometid species

and (if not fused to another exopod segment) always clearly visible. Sometimes it is even as big as the other exopodal segments as e.g. in *Eucanuella spinifera*, *Cerviniopsis muranoi* and *Expansicervinia glaceria*.

The coxal epipodite of the **maxillule** is only represented by 1 or 2 setae in Aegisthidae (Fig. 9 B), and not by 4 setae as in Rometidae or some Neobryidae (chapter 4.8). The reduction of 2 epipodal setae is convergently evolved in the ancestral line to Aegisthidae and N.N. 1 (chapter 3.1). The exopod of maxillule in Aegisthidae is usually a minute segment with 2 or 3 setae or it is only represented by setae.

The striking spine on posterior surface of **maxillar** allobasis constitutes a very good autapomorphy and a perfect diagnostic character for Aegisthidae, as it can be found in all species of Aegisthidae but not in species of Rometidae, Polyarthra or Syngnathartha.

The **maxillipedal** coxa of some aegisthid species is incompletely fused to the praecoxa. Species of Rometidae and some species of Aegisthidae with a more plesiomorphic morphology have an entire syncoxa. The incompletely fused coxa is interpreted as secondary within Aegisthidae.

The **P1 segment** is fused to the cephalosome in males and females of *Cerviniella*.

For the discussion of the **P5** of females see chapters 4.4 and 5.2.3.

**Caudal rami** that are longer than in *Romete* are plesiomorphic within Aegisthidae. This condition is found in *Cerviniella* and *Eucanuella* in which the caudal rami are slightly longer than twice as long as wide. *Paracerviniella denticulata* Brodskaya, 1963 has caudal rami that are as long as wide. These square caudal rami are interpreted as secondarily shortened. The caudal rami in Aegisthidae are otherwise elongated, sometimes extremely so, and either slightly to markedly divergent or juxtaposed and fused along the entire length. If the caudal rami are compared with other characters such as the morphology of P2 and P3, it is obvious that the extreme elongation of the caudal rami must have evolved within Aegisthidae. The extremely elongated caudal rami are therefore not characteristic for all Aegisthidae.

**Sexual dimorphism** is sometimes developed in general body shape, body ornamentation, rostrum, antenna, labrum, mandible, maxillule, maxilla, maxilliped, P1 exopod segmentation, P1 inner basal spine, P2-P4, and anal somite. Males either display only a small number of the dimorphisms or most of them. The dimorphism is pronounced especially in the nonfeeding males like those of *Andromastax muricatus* or *Aegisthus mucronatus* Giesbrecht, 1891 (Conroy-Dalton & Huys, 1999; Huys, 1988b, Lee & Huys, 2000). Different forms of dimorphisms exist in different evolutionary lines within Aegisthidae.

*Systematics.*

*Aegisthus*, *Andromastax*, *Jamstecia*, *Nudivorax* and *Scabrantenna* (former Aegisthidae) represent a monophyletic group, but clearly belonging to Aegisthidae, as the five taxa share the autapomorphies of Aegisthidae (Seifried & Schminke, 2003).



### Remarks on the systematics within Aegisthidae

The analysis of the morphological characters of the taxa of *Cervinia* (synonym: *Brotskayaia* and *Neocervinia*) and *Expansicervinia* in Huys et al. (1997) is accurate (see their table 2). The transcription of the morphology into the character matrix is debatable (their table 3). This is also true for their computer analysis with PAUP. Huys et al. (1997) have analysed *Cervinia* and *Expansicervinia* mostly based on descriptions. The material used by Huys et al. (1997) was:

*Cervinia* sp. in Huys et al. (1997) female.

*Cervinia synarthra* Sars, 1910 female, det. Por (1967), Gulf of Aqaba (Elat), NHM reg. no. 1970.5.15.4, species near *Cervinia plumosa* Itô, 1983 according to Huys et al. (1997).

*Cervinia* sp., males and females, La Réunion, French MD32 expedition in 1982 (Stn DS139; 20°46'5 S, 55°38'3E, 1600m).

The following analysis is based on the species descriptions of all known *Cervinia* and *Expansicervinia* species and the examination of the 30 described and undescribed species of Rometidae and Aegisthidae (Appendix 1).

### Data matrix

In the following the morphological characters used in the cladistic analysis of *Cervinia* by Huys et al. (1997) (their tables 2 and 3) will be discussed step by step. Changes of the characters and their coding in the data matrix (Table 3) are explained in the following. The consequences of these corrections are indicated in **bold type** in the final character list and the data matrix of the characters (Table 3).

*Cervinia mediocauda* Burgess, 1995 and *C. itoi* (Lee & Yoo, 1998) (synonym: *Neocervinia itoi* Lee & Yoo, 1998) are added to the species previously analysed by Huys et al. (1997).

### Character list

Choice of characters is in accordance with Huys et al. (1997, p. 194), except for changes in characters 4, 5 and 16 (**bold type**). Apomorphic states are in *italic type*.

- 1 Body not sexually dimorphic (tergite P1-bearing somite individualized in both sexes); *sexually dimorphic – cyclopfiform in females, fusiform in males (tergite P1-bearing somite in male completely absorbed in cephalothorax)*
- 2 Rostrum female pointed, anteriorly directed; *not developed*
- 3 Rostrum not sexually dimorphic, *strongly developed in male*
- 4 Antennule female 8-segmented; **7-segmented due to fusion of *Oligoarthra* segments 5 and 6, or 6-segmented**
- 5 Antennular segment 1 without expanded posterior margin; **segment 1 of female *A1 with expanded posterior margin***
- 6 P1 inner basal spine not sexually dimorphic; *elongated in male*
- 7 P1 exp-3 with normal setae; *setae distinctly curly*
- 8 P1 enp-3 with 2 inner setae; *with 1 inner seta*
- 9 P1 exp-3 with 3 outer spines/setae; *with 2 outer spines/setae*
- 10 P2-P4 without spinous process on inner margin of basis; *spinous process present*
- 11 P2-P4 endopods 3-segmented in female; **2-segmented due to a fusion of enp-2 and enp-3**

- 12 P2-P3 enp-1 inner element setiform, not modified; *transformed into curved pinnate spine in both sexes*
- 13 P2 enp-2 female (as part of compound distal endopod segment) with 2 inner setae; *with 1 inner seta.*
- 14 P3 enp-2 female (as part of compound distal endopod segment) with 2 inner setae; *with 1 inner seta.*
- 15 P4 enp-2 female (as part of compound distal endopod segment) with 2 inner setae; *with 1 inner seta.*
- 16 P2 enp-1 female inner distal corner blunt or forming minute process; *with average-sized or very large spinous process*
- 17 P2 enp-2 female inner setae (or proximal setae of compound distal segment) normal; *strongly reduced*
- 18 P2 enp-3 female (or enp-2 if endopod 2-segmented) without spinous process between inner terminal and distal inner spine/seta; *spinous process present*
- 19 P2-P4 male exopodal and endopodal spines not rod-shaped; *rod-shaped*
- 20 P5 female with distinct protopod and exopodal segment; *P5 1-segmented*
- 21 P5 female exopod with 3 setae; *with 2 setae*

**Characters 1, 3, 6, 19:** First and momentous point is the circularity of the arguments of the cladistic analysis of Huys et al. (1997). Among the 13 valid species of *Cervinia* and *Expansicervinia* there are only 3 of which the males are known. Two of them belong to species of which both sexes are known (*C. bradyi* Norman, 1878 and *C. mediocauda*), while the third male is the only specimen known of *C. plumosa*. Huys et al. (1997) investigated males of one further undescribed species. Huys et al. (1997) advanced some weak arguments to the effect that many of the unknown males of *Cervinia* have the same strong sexual dimorphism as the males of *C. plumosa*. "On the basis of this evidence, it is postulated that the unknown males of the *synarthra*-group probably resemble *C. plumosa* very closely and all display strong sexual dimorphism in the swimming legs (endopod segmentation, rod-shaped spines, inner basal spine of P1), the rostrum and the mouthparts" (Huys et al., 1997, p. 193). It remains to be seen, whether this assumption can be confirmed. Huys et al. (1997) then continue with coding the same characters in the data matrix for the unknown males of the *synarthra*-group (*C. langi*, *C. philippinensis* Huys et al., 1997, *C. pilosa* Lang, 1948, *C. synarthra*, *C. synarthra* sensu Por (1967), *C. sp.* in Huys et al., 1997) as the ones for the described male of *C. bradyi* (character state '1' for characters 1, 3, 6, 19). The male of *Expansicervinia glaceria* was also coded as though it had been described, although no male has ever been described to date. However, Huys et al. (1997) assumed without comments that *E. glaceria* does not share the apomorphic state of the 6 fictitious males of *Cervinia* and coded characters 1, 3, 6, and 19 as '0'. The following males were coded as unknown without comments: *C. magna* Smirnov, 1946, *C. unisetosa* Montagna, 1981, *C. tenuicauda* Brodskaya, 1963, *E. tenuiseta* Brodskaya, 1963 and *E. tenuiseta* sensu Por (1969).

The data matrix resulting from this process served as basis for the cladistic analysis with PAUP 3.1.1. This analysis suggests among other things that the following species are related because of characters 1, 3, 6, 19: the species with known males with

Table 3: Data matrix of characters of *Cervinia* and *Expansicervinia*; 0 = plesiomorph, 1 = apomorph; ? missing data. Same characters as in character list. Changes from Huys et al. (1997) are indicated in **bold type**.

taxa / character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
<b>Polyarthra</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
<i>C. bradyi</i>	1	0	1	1	0	<b>0</b>	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	0
<i>C. langi</i>	<b>?</b>	0	<b>?</b>	1	0	<b>?</b>	0	0	0	0	1	1	0	0	0	1	1	1	<b>?</b>	0	0	0
<i>C. magna</i>	0	0	0	1	0	0	0	0	0	0	1	1	0	<b>1</b>	<b>1</b>	1	0	1	0	0	0	0
<i>C. mediocauda</i>	<b>1</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>
<i>C. philippinensis</i>	<b>?</b>	0	<b>?</b>	1	0	<b>?</b>	0	0	0	0	1	1	0	0	0	1	1	0	<b>?</b>	0	0	0
<i>C. pilosa</i>	<b>?</b>	0	<b>?</b>	1	<b>?</b>	<b>?</b>	0	0	0	0	1	1	1	1	1	1	<b>?</b>	<b>?</b>	<b>?</b>	<b>?</b>	0	0
<i>C. plumosa</i>	1	<b>?</b>	1	<b>?</b>	<b>?</b>	1	<b>?</b>	0	1	0	<b>?</b>	1	<b>?</b>	<b>?</b>	<b>?</b>	<b>?</b>	<b>?</b>	<b>?</b>	<b>?</b>	1	<b>?</b>	<b>?</b>
<i>C. synarthra</i>	<b>?</b>	0	<b>?</b>	1	0	<b>?</b>	0	0	0	0	1	1	1	1	1	1	0	1	<b>?</b>	0	0	0
<i>C. synarthra</i> sensu Por	<b>?</b>	0	<b>?</b>	1	0	<b>?</b>	0	0	1	0	1	1	0	0	0	1	0	1	<b>?</b>	1	0	0
<i>C. sp.</i>	<b>?</b>	0	<b>?</b>	1	0	<b>?</b>	0	0	0	0	1	1	0	<b>?</b>	0	1	1	1	<b>?</b>	1	1	1
<i>C. itoi</i>	<b>?</b>	<b>0</b>	<b>?</b>	<b>1</b>	<b>0</b>	<b>?</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>?</b>	<b>1</b>	<b>1</b>	<b>1</b>
<i>C. unisetosa</i>	<b>?</b>	0	<b>?</b>	1	0	<b>?</b>	0	0	0	0	0	<b>1</b>	0	0	0	<b>1</b>	0	0	<b>?</b>	1	<b>1</b>	<b>1</b>
<i>C. tenuicauda</i>	<b>?</b>	0	<b>?</b>	1	0	<b>?</b>	0	0	0	0	0	0	0	0	0	0	0	0	<b>?</b>	1	<b>1</b>	<b>1</b>
<i>E. glaceria</i>	<b>?</b>	1	<b>?</b>	0	1	<b>?</b>	1	1	0	1	0	0	0	0	1	0	0	0	<b>?</b>	0	<b>1</b>	<b>1</b>
<i>E. tenuiseta</i>	<b>?</b>	1	<b>?</b>	1	1	<b>?</b>	1	0	0	1	0	0	0	0	0	0	0	0	<b>?</b>	0	<b>1</b>	<b>1</b>
<i>E. tenuiseta</i> sensu Por	<b>?</b>	1	<b>?</b>	0	1	<b>?</b>	<b>0</b>	1	0	1	0	<b>1</b>	0	0	0	<b>1</b>	0	0	<b>?</b>	0	<b>1</b>	<b>1</b>

apomorphic states ‘1’ in characters 1, 3, 6, 19 and the 6 species of the *synarthra*-group with the **assumed** apomorphic states ‘1’ in those characters. All those taxa are reported by Huys et al. (1997) to belong to *Cervinia* on the basis of the male characters only (1, 3, 6, 19). As a consequence, *E. glaceria* with the assumed plesiomorphic states ‘0’ in characters 1, 3, 6, and 19 and the remaining 4 species with unknown males are not directly related with *Cervinia* and have been removed from *Cervinia* by Huys et al. (1997) (see their figure 6. and p. 196). The circularity of this procedure is obvious. In contrast the characters 1, 3, 6, and 19 are coded here as ‘?’ for the taxa with no male descriptions.

#### Character 5

The segment 1 of female A1 of *E. tenuiseta* and *E. tenuiseta* sensu Por (1969) shows an expanded posterior margin as *E. glaceria*, but no knob-like process. *E. glaceria*, *E. tenuiseta*, and *E. tenuiseta* sensu Por (1969) have the apomorphic state of character 5

when "with knob-like process on posterior margin" (Huys et al., 1997) is changed to "segment 1 of female A1 with expanded posterior margin". *E. glaceria* further has a knob-like process.

The female A1 of *C. pilosa* and *C. plumosa* is not described to date. The character state has to be ‘?’.

#### **Character 6**

The inner basal spine P1 is not elongated in *C. bradyi* males (see Giesbrecht, 1900 and Huys et al., 1996) (0).

#### **Character 7**

The description of the female P1 of *E. tenuiseta* sensu Por (1969) shows no curly setae (0).

#### **Character 12**

The inner element of P2 enp-1 in *E. tenuiseta* sensu Por (1969) and *C. unisetosa* is developed as a curved pinnate spine (1).

#### **Characters 13, 14 and 17**

The P2 and P3 of the female of *C. plumosa* are not described to date. The character state for all 3 characters has to be ‘?’.

#### **Characters 14 and 15**

*C. magna* has 1-2-4 setae on the compound distal endopod segment P3 and P4 female. The character state of characters 14 and 15 has to be ‘1’.

#### **Character 14**

Enp P3 of the *C. sp* female is not described to date (?).

#### **Character 16**

The plesiomorphic state for character 16 in Huys et al. (1997, p. 194) is “P2 enp-1 female inner distal corner blunt or forming minute process”. The apomorphic state is “with very large spinous process”. It is very difficult to decide between minute and large in some taxa, the process of which is of intermediate size. The process of *Cervinia unisetosa* is not minute and not very large, it is average-sized. Most outgroup taxa like Polyarthra have no process on the inner distal corner of P2 enp-1 female. The P2 enp-1 male of Rometidae, the sister taxon of Aegisthidae, forms a minute process on the inner distal corner. It is possible to distinguish between the minute process of Rometidae, *Expansicervinia glaceria*, *E. tenuiseta*, and *C. tenuicauda* (0), and the average-sized process of *Cervinia unisetosa* (1). The character states have to be: blunt distal corner or minute process (0) and average-sized or very large process (1).

The process of *C. tenuiseta* sensu Por (1969) is as big as that of *C. bradyi* (1).

#### **Characters 17 and 18**

The P1-P4 of *C. pilosa* are not described. Lang’s (1948, p. 182) remark: “Enp. P.2-P.4 2-gliedrig und von gleichem Aussehen wie bei *C. synarthra*...” does not allow a clear decision. The character state of characters 17 and 18 has to be ‘?’.

#### **Character 21**

The available descriptions show that *E. tenuiseta*, *E. tenuiseta* sensu Por (1969), *E. glaceria* and *C. unisetosa* have 2 setae on female exp P5 (1).

### Cladistic analysis with PAUP

The analysis of Huys et al. (1997) with PAUP 3.1. (Swofford, 1993).

The first problem in the analysis of Huys et al. (1997) is that they code all characters but one as irreversible (their p. 194). They offer no explanation for this unusual coding, neither for the irreversibility of 20 characters nor for the reversibility of character 18. In 10 characters of Huys et al. (1997) the apomorphic character state is an acquisition. Irreversibility of these characters would mean, that once evolved these characters could never be reduced. There are no laws of character evolution suggesting that losses of evolved characters are impossible (see chapter 5.2.6).

In the other 10 characters the reduction of a feature represents the apomorphic state. To code these characters as irreversible would mean, that once a character is reduced, it can never reappear. We do not have enough knowledge of gene expression and epigenetics to substantiate this assumption (see chapter 5.2.6). Huys et al. (1997) did not explain why it is unlikely that these 10 characters could never return to the plesiomorphic state.

The second problem in the analysis is the choice of *Cerviniopsis* as outgroup to determine character polarity of the irreversible characters (Huys et al., 1997, p. 195). In *Cerviniopsis* species characters 3, 4, 6, 8, 12, and 16 are present in the same two states as in *Cervinia* species. The decision on which is the apomorphic and which is the plesiomorphic state cannot be made on the basis of *Cerviniopsis* as outgroup. The fact that *Cerviniopsis* shares both states with *Cervinia* in many characters, calls the monophyly of the ingroup into question. The polymorphy of *Cervinia*, *Cerviniopsis* and other cerviniid genera indicates that a phylogenetic analysis should consider all taxa of Aegisthidae.

### Analysis of the revised data matrix

#### *Character matrix:*

The taxa used are the same as those studied by Huys et al. (1997). When *C. mediocauda* and *C. itoi* are added, the length but not the topology of the cladogram is changed. The same 21 characters (Table 3) as in Huys et al. (1997) are used. The latter authors chose all informative characters available for the described species to date. Corrections of characters and states are **set in bold type** in the present study (Table 3). Polyarthra and Misophrioida were used as outgroups to root the cladograms. Because of the taxonomic and systematic disorder within Aegisthidae no taxon of this group was used as outgroup. For Rometidae only males have been described so far. Other members of Oligoarthra are out of question, because Aegisthoidea (Rometidae - Aegisthidae) is the sister taxon of all other Oligoarthra.

#### *Methods and analysis:*

The data matrix was analysed and cladograms were generated on a Macintosh G4 (400 Mhz) with PAUP\* 4.0 beta 10 AltiVec (Swofford, 2003). Characters were examined with PAUP\* and MacClade, version 3.05 (Maddison & Maddison, 1992).

All characters in this analysis are of type unordered and have equal weight. Character 6 is parsimony-uninformative and was mostly excluded.

‘Branch-and-bound’ search under maximum parsimony was used to explore the data. Further ‘branch-and-bound’ settings: addition sequence furthest, zero-length branches

not collapsed, 'MulTrees' option in effect. As a result of this search (with *Polyarthra*, *C. mediocauda*, and *C. itoi*) 1386 equally parsimonious cladograms of length 33 were obtained when character 6 was excluded and of length 34 when character 6 was considered. The cladograms were condensed by 'collapsing branches if maximum length is zero' and 'eliminate duplicate trees'. Number of distinct cladograms after condensing was 84 (indices without character 6: CI = 0.606; RI = 0,759; RC = 0.460). Then the cladograms were filtered to remove polytomous topologies for which more highly resolved and compatible topologies were present; 34 cladograms were obtained. The cladograms were rooted using *Polyarthra* as outgroup. The strict consensus tree (Fig. 12) of the 84 cladograms was computed with PAUP\*. This tree should not be interpreted as a phylogeny (Swofford, 1991, p. 311), as it only summarises the information common to all 84 cladograms.

#### *Results and discussion:*

The strict consensus tree computed with the corrected data matrix (Fig. 12) has less clades that are supported than the "two most parsimonious trees" of Huys et al. (1997) (one is the 'Phylogenetic tree' in Fig. 13). Optimising the characters in the strict consensus of the revised matrix reveals that only one clade is well supported. Characters 2, 5, and 10 support a monophyletic group with *Expansicervinia glaceria*, *E. tenuiseta* and *E. tenuiseta* sensu Por (1969). The characters change from character state (0) to character state (1) and have no homoplasy. This is the only clear result of the revised data matrix. In all three taxa the rostrum of the female is not developed (character 2), the segment 1 of female A1 shows an expanded posterior margin (character 5) and the basis P2-P4 has a spinous process at the inner margin (character 10). A knob-like process at the posterior margin of female A1 is a character Montagna (1981) used to characterise *Expansicervinia*. Only *E. glaceria* has an expanded margin and the knob, *E. tenuiseta* and *E. tenuiseta* sensu Por (1969) have only an expanded margin. As Huys et al. (1997) mentioned before, there are several other characters that support a close relationship between *E. glaceria* and *E. tenuiseta*. This is also true for *E. tenuiseta* sensu Por (1996). According to Montagna (1981), the ventral expansion of the P2-bearing somite is unique for species of *Expansicervinia*. *E. glaceria*, *E. tenuiseta* and *E. tenuiseta* sensu Por (1969) have this ventral expansion. Huys et al. (1997) discussed in detail, why *E. glaceria* and *E. tenuiseta* are sister species and that *E. tenuiseta* has all characters of *Expansicervinia* (their page 195). Without any comment Huys et al. (1997) then proposed the genus *Brotskayaia* for *E. tenuiseta* (their pages 195-196). However, the only characters in which they differ from each other are those, which also vary within the whole Aegisthidae. There is no reason to split the group of 2 valid sister species into 2 monotypic genera, as was done by Huys et al. (1997). *E. tenuiseta* is therefore transferred back to *Expansicervinia* here. *Brotskayaia* is synonymized with *Expansicervinia*. *E. tenuiseta* sensu Por (1969) is considered as species inquirenda as suggested by Huys et al. (1997). The copepodid described by Itô (1983) as *Cervinia* sp. aff. *tenuiseta* is a copepodid of *Expansicervinia tenuiseta* as mentioned by Huys et al. (1997).

A new genus *Neocervinia* was erected for *C. tenuicauda* and *C. unisetosa* by Huys et al. (1997) because of the "reduced female fifth legs" and "the present phylogenetic analysis" (Huys et al., 1997; p. 196). The 'phylogenetic trees' in their fig. 6 show no

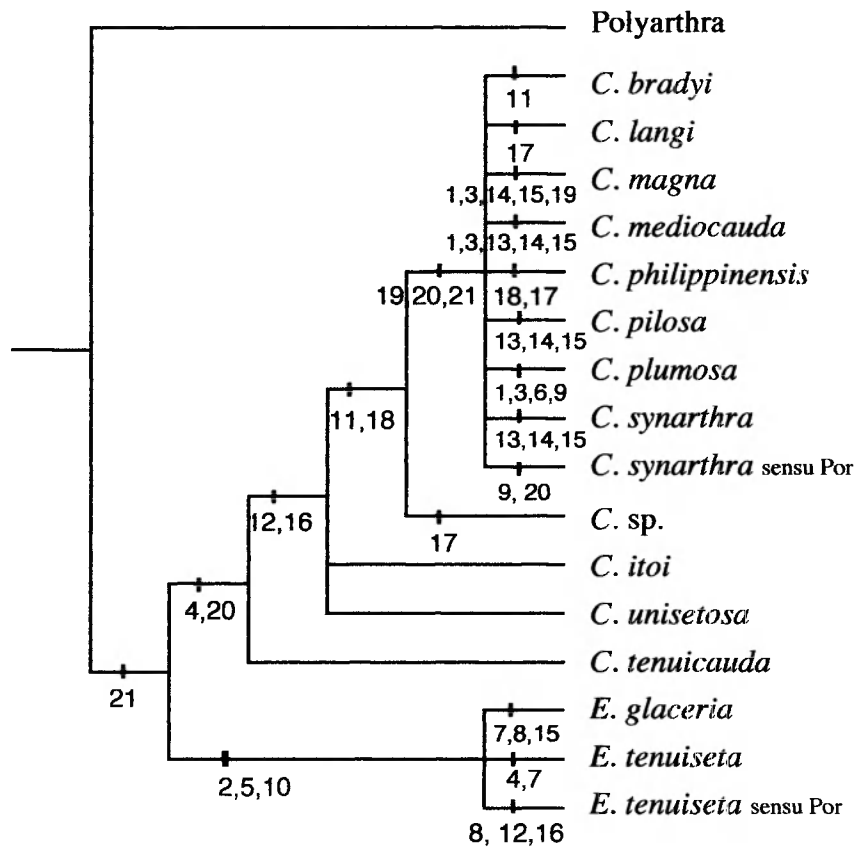


Fig. 12: Strict consensus tree of 84 cladograms for the taxa and characters of table 3; possible state assignment for all 21 characters.

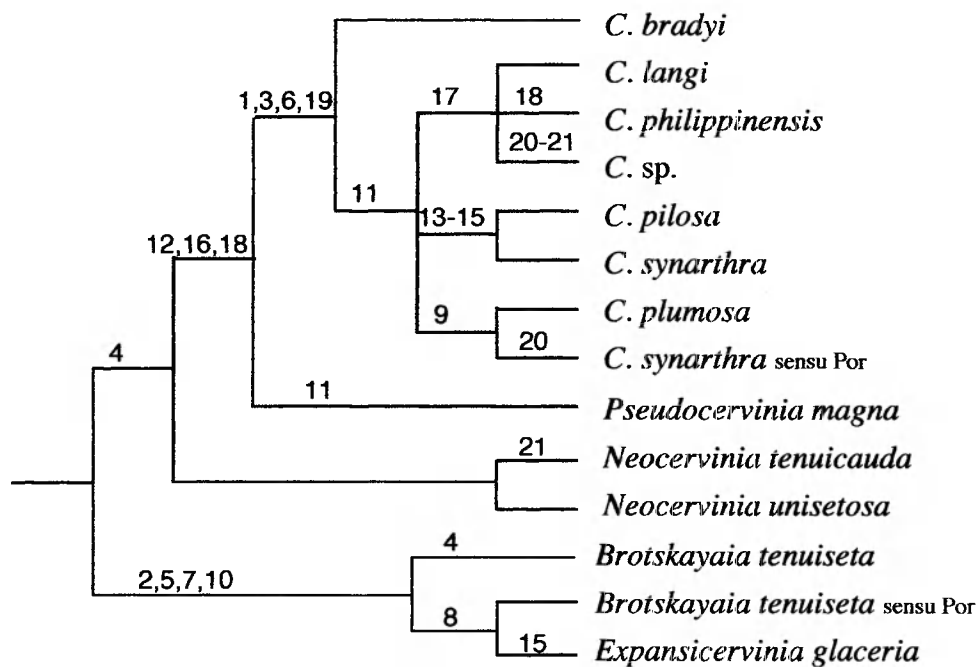


Fig. 13: 'Phylogenetic tree' after Huys et al. (1997; fig. 6 A, p. 192).

support for a clade *C. tenuicauda* - *C. unisetosa* (Fig. 13). I repeated their analysis and found that only character 20 supports this clade, which means that both species have a 1-segmented P5 in the female. However, this apomorphic character is also shared with *C. sp.* of Huys et al. (1997) and *C. synarthra* sensu Por (1969). The strict consensus of the corrected data matrix shows no clade in supports of a monophyly of *C. tenuicauda* and *C. unisetosa*. The strict consensus indicates that *Neocervinia* would be a paraphyletic taxon. Thus *Neocervinia* is synonymized with *Cervinia*. Lee & Yoo (1998) described *C. itoi* and placed it into *Neocervinia* on the basis of the 1-segmented P5 and plesiomorphic characters. Including *C. itoi* into the analysis does not change the results obtained and the decisions made here.

The reinstatement of *Pseudocervinia* of Huys et al. (1997) for *Cervinia magna* is based on the morphology of the males. The sister taxon relationship of *C. magna* with the remaining *Cervinia* species in the analysis of Huys et al. (1997, fig. 6) is based on the circularity of the argument used for characters 1, 3, 6 and 19 as discussed above. *C. magna* has the plesiomorphic state of the characters 1, 3, and 6. The state of character 19 is as yet unknown. It is not clear whether all other species of *Cervinia* have the apomorphic state in these characters. On the other hand, *C. magna* has a “profound sexual dimorphism of the swimming leg and mouthparts, including the peculiar ‘bottle-opener’ modification of the maxillary allobasis and the transformed P4 endopod” (Huys et al., 1997; p. 196). However, until it is not known what all other males of *Cervinia* look like, it is not justified to exclude this single species from *Cervinia* on the basis of this dimorphism. The morphology of *C. magna* males could be an apomorphic state within *Cervinia*. The 2-segmented endopods of P2-P4 in the females are also found in other species of *Cervinia*. The 2-segmented endopod of P-1 is unique for *C. magna* but on its own no justification for the recognition of a monotypic genus. *Pseudocervinia* is therefore synonymized here with *Cervinia*.

No autapomorphy could be found for *Cervinia*, even when conducting a phylogenetic analysis without computer programs. Species of *Cerviniopsis*, *Pontostratiotes* and probably other genera of Aegisthidae share apomorphic characters with species of *Cervinia*. *Cervinia* is a paraphyletic, more likely a polyphyletic taxon. A phylogenetic analysis of all 77 species of Aegisthidae is the only possibility to solve the systematic problems within Aegisthidae and to avoid the erection of monotypic or paraphyletic genera. Every phylogenetic analysis should start with the examination of the monophyly of the ingroup.

#### Characterisation of *Cervinia* and *Expansicervinia*

##### ***Expansicervinia* Montagna, 1981 (Aegisthidae)**

**Synonym:** *Brotskayaia* Huys, Møbjerg & Kristensen, 1997

**Diagnosis** (autapomorphies in bold type)

*Female.* P2-bearing somite **largest, ventrally expanded**. Rostrum **not developed**. First antennular segment **expanded along posterior margin**, sometimes forming a knob-like projection. Setae of P1 exp-3 **curly (?)**. P2 endopod **enlarged, robust, with spines on enp-3**. P2-P4 with **distinct spinous process on inner margin of basis**.

*Male.* Unknown



Type species: *Expansicervinia glaceria* Montagna, 1981.

Other species: *E. tenuiseta* (Brodskaia, 1963).

Species inquirendae: *E. tenuiseta* (Brodskaia, 1963) sensu Por (1969); *E. sp. aff. tenuiseta* (Brodskaia, 1963) sensu Itô, 1983.

### ***Cervinia* Norman (in Brady (1878))**

**Synonym:** *Neocervinia* Huys, Møbjerg & Kristensen, 1997, *Pseudocervinia* Brodskaia, 1963.

### **Diagnosis**

Aegisthidae. *Female*. Tergite of P1-bearing somite free. Rostrum pointed. Antennule 6 or 7-segmented, with 1 or 2 aesthetascs on segment 3, or 2, respectively. P2-P4 endopods 2- or 3-segmented. P2-P3 enp-1 inner seta mostly modified into curved pinnate spine. P2 enp-1 with inner distal corner mostly produced into very large or average-sized spinous process. P2 enp-3 (or enp-2 if endopod 2-segmented) sometimes with spinous process between inner terminal and distal inner seta/spine. Female P1-P4 armature formulae:

	exopod	endopod
P1	I-1; I-1; III-2-1	0-1; 0-1; I-2-2
	or I-1; I-1; II-2-1	or 0-1; [1-2-3]
P2	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
		or 0-1; [1-II-I+3]
		or 0-1; [1-II-I+2]
P3	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-3
		or 0-1; [1-II-I+4]
		or 0-1; [1-II-I+3]
P4	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
		or 0-1; [1-II-I+3]
		or 0-1; [1-II-I+2]
		or 0-1; [1-2-2]

P5 defined at base, 2-segmented, comprising protopod and exopod, or 1-segmented, with a total of 3-4 setae.

Type species: *Cervinia bradyi* Norman, 1878 (in Brady, 1878).

Other species: *C. synarthra* Sars, 1910; *C. pilosa* Lang, 1948; *C. tenuicauda* Brodskaia, 1963; *C. langi* Montagna, 1979; *C. magna*, Smirnov, 1946; *C. unisetosa* Montagna, 1981; *C. plumosa* Itô, 1983; *C. mediocauda* Burgess, 1995; *C. philippinensis* Huys et al., 1997, *C. itoi* (Lee & Yoo, 1998).

Species inquirendae: *C. synarthra* sensu Por (1967), *C. sp.* in Huys et al., 1997.

Species incertae sedis: *C. brevipes* Brodskaia, 1963.

## 4.7 Syngnatharthra Seifried & Schminke, 2003

### Taxa belonging to Syngnatharthra

Adenopleurellidae Huys 1990, Ameiridae Monard, 1927, Ancorabolidae Sars, 1909, Argestidae Por, 1986, Balaenophilidae Sars, 1910, Cancrincolidae Fiers, 1990, Canthocamptidae Sars, 1906, Chappuisiidae Chappuis, 1940, Cletodidae T. Scott, 1905, Cletopsyllidae Huys & Willems, 1989, Cristacoxidae Huys, 1990, Dactylopusiidae Lang, 1936, Darcythompsoniidae Lang, 1936, Ectinosomatidae Sars, 1903, Harpacticidae Sars, 1904, Huntemanniidae Por, 1986, Idyanthidae, Lang, 1944, Laophontidae T. Scott, 1905, Laophontopsidae Huys & Willems, 1989, Latiremidae Bozic, 1969, Leptastacidae Lang, 1948, Leptopontiidae Lang, 1948, Louriniidae Monard, 1927, Metidae Sars, 1910, Miraciidae Dana, 1846, Neobradyidae Olofsson, 1917, Normanellidae Lang, 1944, Novocriniidae Huys & Iliffe, 1998, Orthopsyllidae Huys, 1990, Paramesochridae Lang, 1944, Parastenheliidae Lang, 1944, Parastenocarididae Chappuis, 1933, Peltidiidae Sars, 1904, Phyllognathopodidae Gurney, 1932, Porcellidiidae Sars, 1904, Pseudotachidiidae Lang, 1936, Rhizothricidae Por, 1986, Rhynchothalestridae Lang, 1948, Rotundiclipeidae Huys, 1988, Superornatiremidae Huys, 1996, Tachidiidae Sars, 1909, Tegastidae Sars, 1904, Tetragonicipitidae Lang, 1944, Thalestridae Sars, 1905, Thompsonulidae Lang, 1944, Tisbidae Stebbing, 1910 *sensu strictu*, Zosimidae fam. nov.; taxa incerta et incertae sedis: Ismardiidae Leigh-Sharpe, 1936, *Dactylopina* Brady, 1910, *Flavia* Brady, 1899, *Goffinella* Wilson, 1932, *Ismardis* Leigh-Sharpe, 1936, *Mawsonella* Brady, 1918, *Pyroclctodes* Coull, 1973, *Tisemus* Monard, 1928.

### Diagnosis: Autapomorphies of Syngnatharthra (Fig. 4: ■ 7; Figs. 14 + 15)

*Female*. Prosome consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield (char. 1: 0→1). Syncoxa maxilla with (5 + 3), 3, 3 setae, the two proximal endites fused (char. 34: 0→1; Fig. 15). Coxa of maxilliped with incorporated endites represented from proximal to distal by I, I+2, I+1 spines and setae, seta 16 of proximal endite lost (char. 43: 0→1); maxilliped with joint with high degree of inward flexibility between basis and endopod (char. 47: 0→1); enp-1 with 2 setae (6 + 7) and 1 thin claw (V); the claw displaced to the posterior side of the distal end of enp-1 (char. 49: 0→1); enp-2 reduced in size (char. 48: 0→1) with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4) (char. 50: 0→1). Proximal segment of exopod P1 without inner seta (char. 55: 0→1).

*Male* with 1 spermatophore (char. 5: 0→1).

### Groundpattern of Syngnatharthra (Fig. 14)

*Female*. **Body** without difference in width between prosome and urosome. **Nauplius eye** present. **Rostrum** delimited at base. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to cephalothorax. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore, 2 seminal receptacles, 2 gonopores. **Anal somite** not divided longitudinally; anus located dorsally, covered by

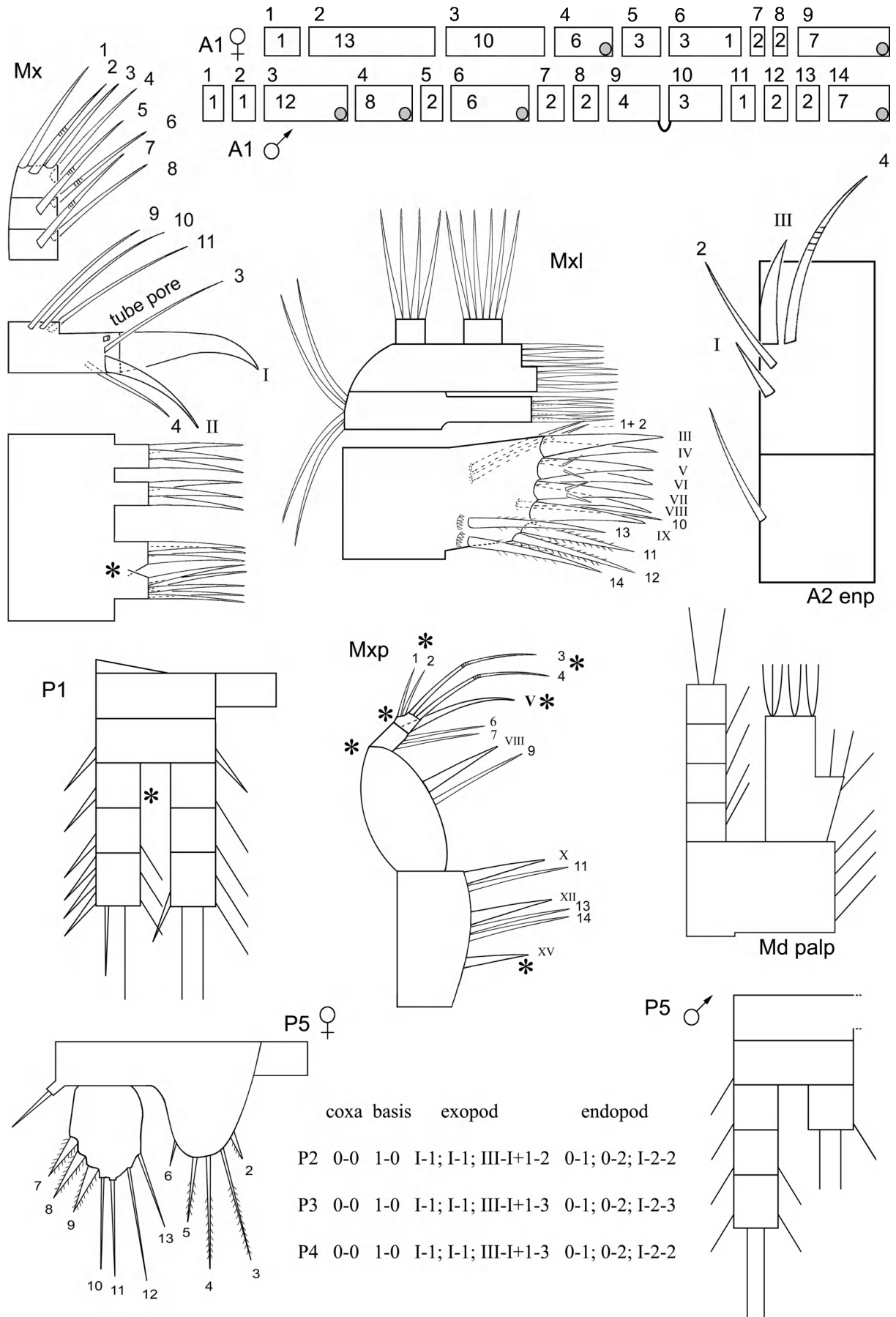


Fig. 14: Groundpattern of Syngnathartha. Asterisks mark autapomorphies of Syngnathartha.

anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 13, 10, 6 + aes, 3, 4, 2, 2, 6 + acrothek. **Antenna** composed of coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 4 subterminal and 7 distal setae; subterminal setation of enp-2 of 1 short proximal spine (I), 1 longer distal spine (III), 1 distal geniculate seta (4) and 1 bare slender seta (2); seta 2 inserts between spine I and spine III; exopod with 2, 1, 1, 3 setae. **Labrum** not prominent. **Paragnaths** separated. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 3 lateral setae and 3 + 2 + 2 apical setae, each group of apical setae basally fused; exopod 4-segmented with 2, 1, 1, 2 setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III – IX; at least 2 posterior spines with 2 long spinules) as well as 1 smaller,

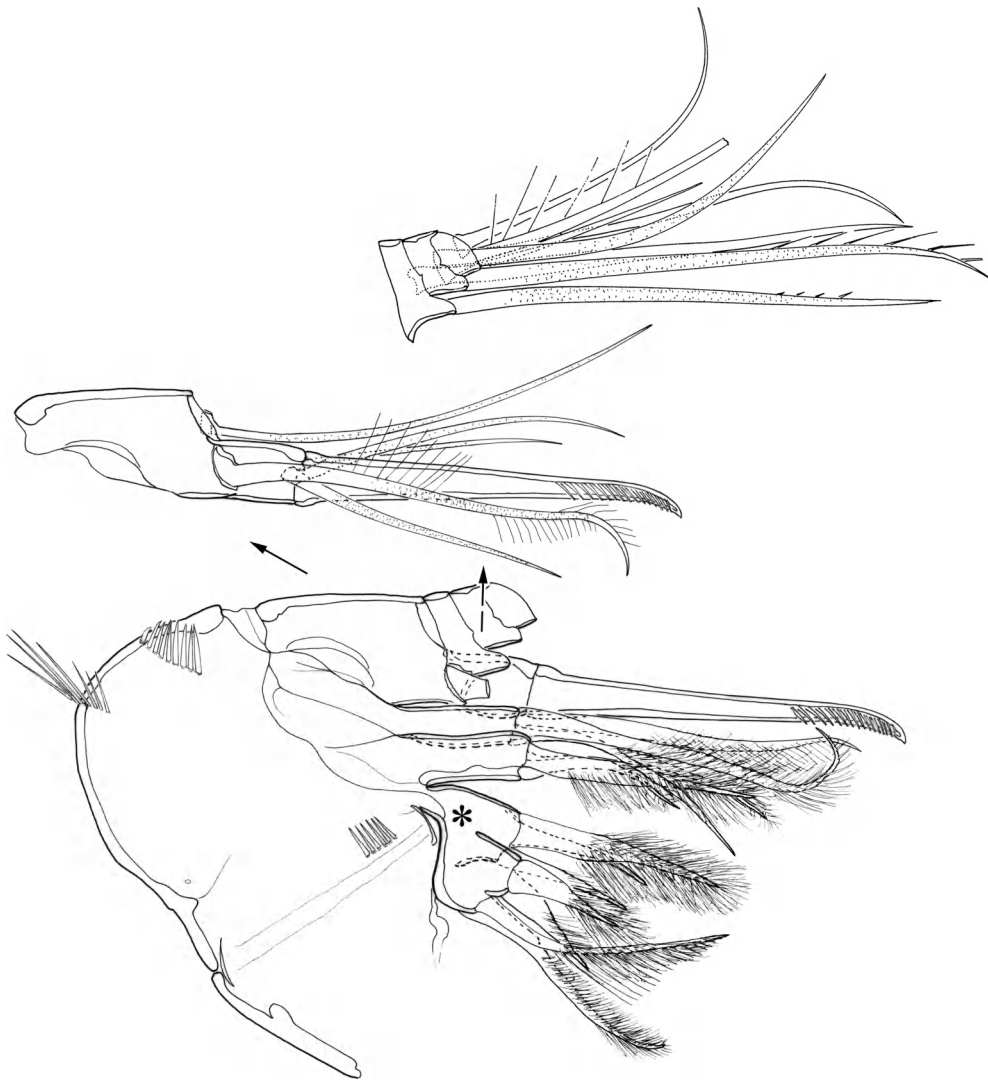


Fig. 15: Maxilla of *Neobradyyidae* gen. spec. 1. Asterisk indicates the fused proximal endites of the syncoxa.

flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: 2, VII, 1, 2, 2; coxa with 6 setae, epipodite represented by 4 setae; basis with 4 + 4 setae; endopod 1-segmented with 6 setae; exopod 1-segmented with 4 setae. **Maxilla** 5-segmented consisting of syncoxa, allobasis, and 3-segmented endopod; syncoxa with (5 + 3), 3, 3 setae, the two proximal endites fused; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II), 1 seta (3) and 1 tube pore on anterior surface and 1 seta (4) on posterior surface; accessory armature of fused endopod segment of 2 setae on anterior surface (9 + 10) and 1 seta on posterior surface (11); endopod with armature formula: 2, 2, 4; proximal segment with geniculated seta anteriorly (7), middle segment with 2 geniculated setae (5 + 6), last segment with 1 geniculated seta (2). **Maxilliped** 4-segmented, comprising syncoxa, basis and 2-segmented endopod; praecoxa without seta; coxa with incorporated endites represented from proximal to distal by I, I+2, I+1 spines and setae, seta 16 of proximal endite lost; basis with 1 spine and 1 seta on inner edge (VII + 9); high degree of inward flexure at the basis-endopod joint; enp-1 with 2 setae (6 + 7) and 1 thin claw (V); the claw displaced to the posterior side of the distal end of enp-1; enp-2 reduced in size with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4). **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-2	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** with intercoxal sclerite joining the coxae; praecoxa absent; baseoendopod with 1 outer basal seta, endopodal lobe with 5 setae (2 - 6): 2 inner setae, 2 terminal setae, 1 outer seta; exopod with 7 setae (7-13): 2 inner setae, 2 terminal setae, 3 outer spines. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** haplocer with 14 segments; armature formula: 1, 1, 12 + aes, 8 + aes, 2, 6 + aes, 2, 2, 4 / 3, 1, 2, 2, 6 + acrothek, characteristic arrangement and shape of setae, aesthetasc on oligoarthran segment 6 fused at base with a seta. **P5** composed of intercoxal sclerite, coxa, basis, endopod with 3 setae and 3-segmented exopod with 1-0, 1-1, 1-2-1 setae. **P6** symmetrical, with 3 setae.

#### Remarks on the morphology of Syngnatharthra

The monophyletic group Syngnatharthra is mainly characterized by the first pedigerous somite that is completely fused to the cephalothorax, the fused proximal endites of the syncoxa of the maxilla, the absence of the inner seta of exp-1 P1 and a characteristic maxilliped: coxa with less than 7 setae and spines, a joint between basis and endopod, a 2-segmented endopod with 1 thin claw (V) and 2 geniculated distal setae (3 + 4).

The fusion of the first pedigerous somite and the cephalothorax is an autapomorphy of Syngnatharthra (char. 1: 0→1). However, some species of Syngnatharthra have a

first pedigerous somite that was secondarily separated from the cephalosome (chapter 5.2.3; char. 1).

Within Syngnatharthra, only *Marsteinia* spec. 5 and *Marsteinia* spec. 8 have a **maxillule** with 4 setae representing the epipodite of the coxa (see chapter 4.8).

In most Syngnatharthra a depression still marks the fusion zone of the **maxillar endites** (Fig. 15). In some taxa the proximal endite is reduced to one small endite with no depression and less than 6 setae. According to the phylogenetic hypothesis, this small endite is the result of the fusion of the two proximal endites (char. 34: 0→1) and subsequent reduction in number of setae and size, and not due to the loss of one of the endites of the oligoarthran groundpattern (chapter 5.2.3; char. 34).

For the discussion of the morphology of the **maxilliped** see chapters 4.8, 5.1.6, 5.2.3 and 5.2.4 (char. 43: 0→1; char. 47: 0→1; char. 48: 0→1; char. 49: 0→1; char. 50: 0→1; Fig. 17 A).

The inner seta of exp-1 **P1** is the only seta that is lost only once in the evolution of all oligoarthran taxa (char. 55: 0→1). All other setae are lost several times. Every single species of Polyarthra and Aegisthoidea has this seta and no species of Syngnatharthra has it. The inner seta of exp-1 P1 is an additional autapomorphy that supports the monophyly of Syngnatharthra.

The existence of only one **spermatophore** at a time is also characteristic for Syngnatharthra (char. 5: 0→1; chapter 5.2.3).

#### 4.8 Neobradyyidae Olofsson, 1917

##### Taxa belonging to Neobradyyidae (10 species in 4 genera)

*Antarcticobradyya* Huys, 1987, *Neobradyya* T. Scott, 1892, *Marsteinia* Drzycimski, 1968, *Tachidiopsis* Sars, 1911.

Undescribed species (8.1 Appendix I.): Neobradyyidae gen. spec. 1, Neobradyyidae gen. spec. 2, Neobradyyidae gen. spec. 3, *Antarcticobradyya* spec., *Marsteinia* spec. 1, *Marsteinia* spec. 2, *Marsteinia* spec. 3, *Marsteinia* spec. 4, *Marsteinia* spec. 5, *Marsteinia* spec. 6, *Marsteinia* spec. 7, *Marsteinia* spec. 8, *Tachidiopsis* spec.

##### Changes in systematics (reasons given below)

*Tachidiopsis* Sars, 1911 (former Tisbidae) is integrated in Neobradyyidae.

*Tachidiopsis bozici* Bodin, 1968, *T. ibericus* Becker, 1974, *T. laubieri* Dinét, 1974, *T. parasimilis* Dinét, 1974, and *T. sarsi* Bodin, 1968 are moved to *Marsteinia*.

“Neobradyyoidea” Olofsson, 1917 (Chappuisiidae, Darcythompsoniidae, Neobradyyidae, Phyllognathopodidae) are not maintained here as they are polyphyletic. Chappuisiidae is part of N.N. 1 (chapter 3.1). Darcythompsoniidae and Phyllognathopodidae are transferred to Podogennonta Lang, 1944.

##### Diagnosis: Autapomorphies of Neobradyyidae (Fig. 4: ■ 8; Figs. 16 - 18)

*Female*. Distal segment of antennule with 1 subterminal seta and 6 terminal setae (char. 6: 0→1). Endopod of mandible with 2 lateral setae. Syncoxa of maxilliped with incorporated coxal endites represented from proximal to distal by **I, II+1, II spines**

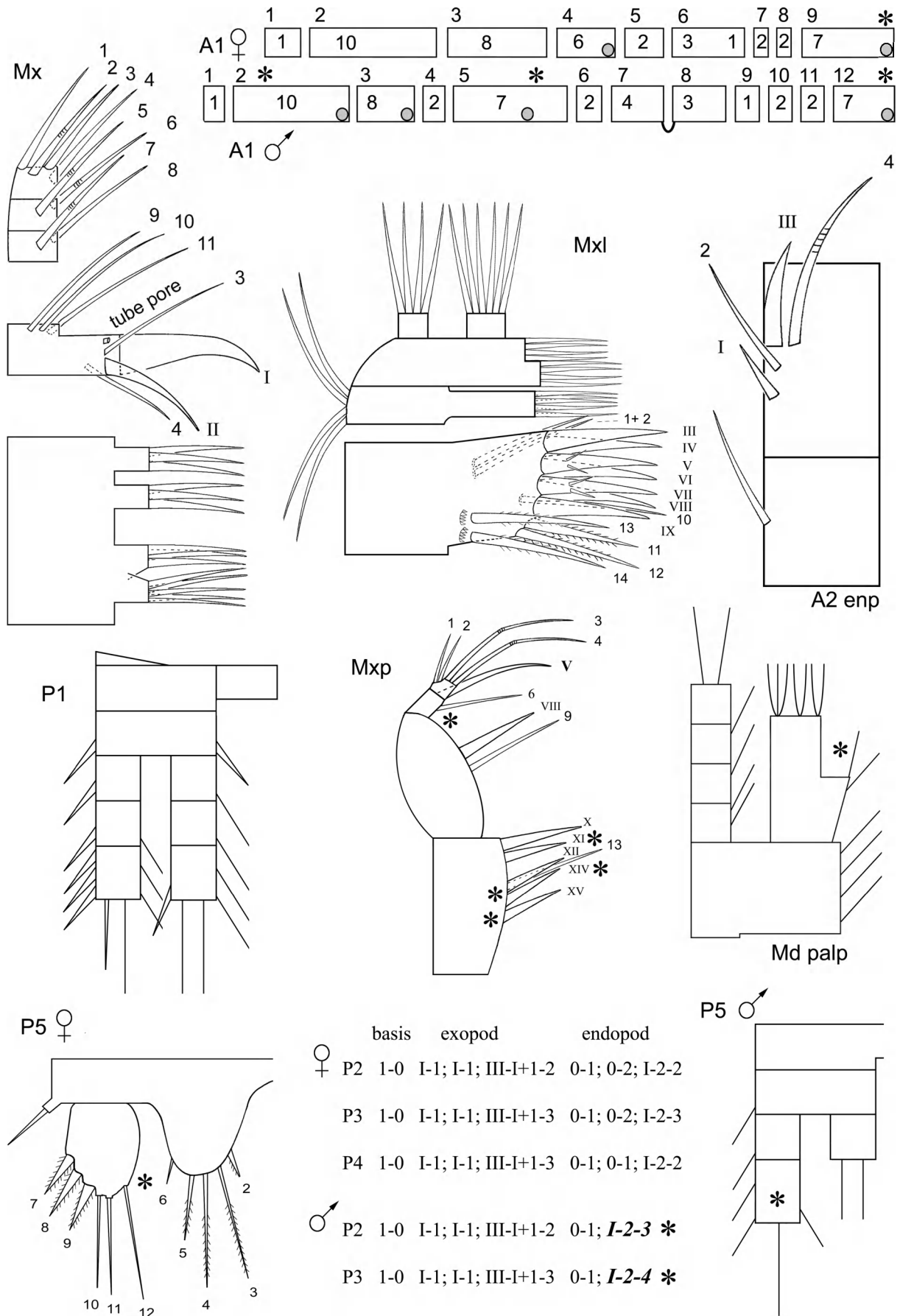


Fig. 16: Groundpattern of Neobradyidae. Asterisks mark autapomorphies of Neobradyidae.

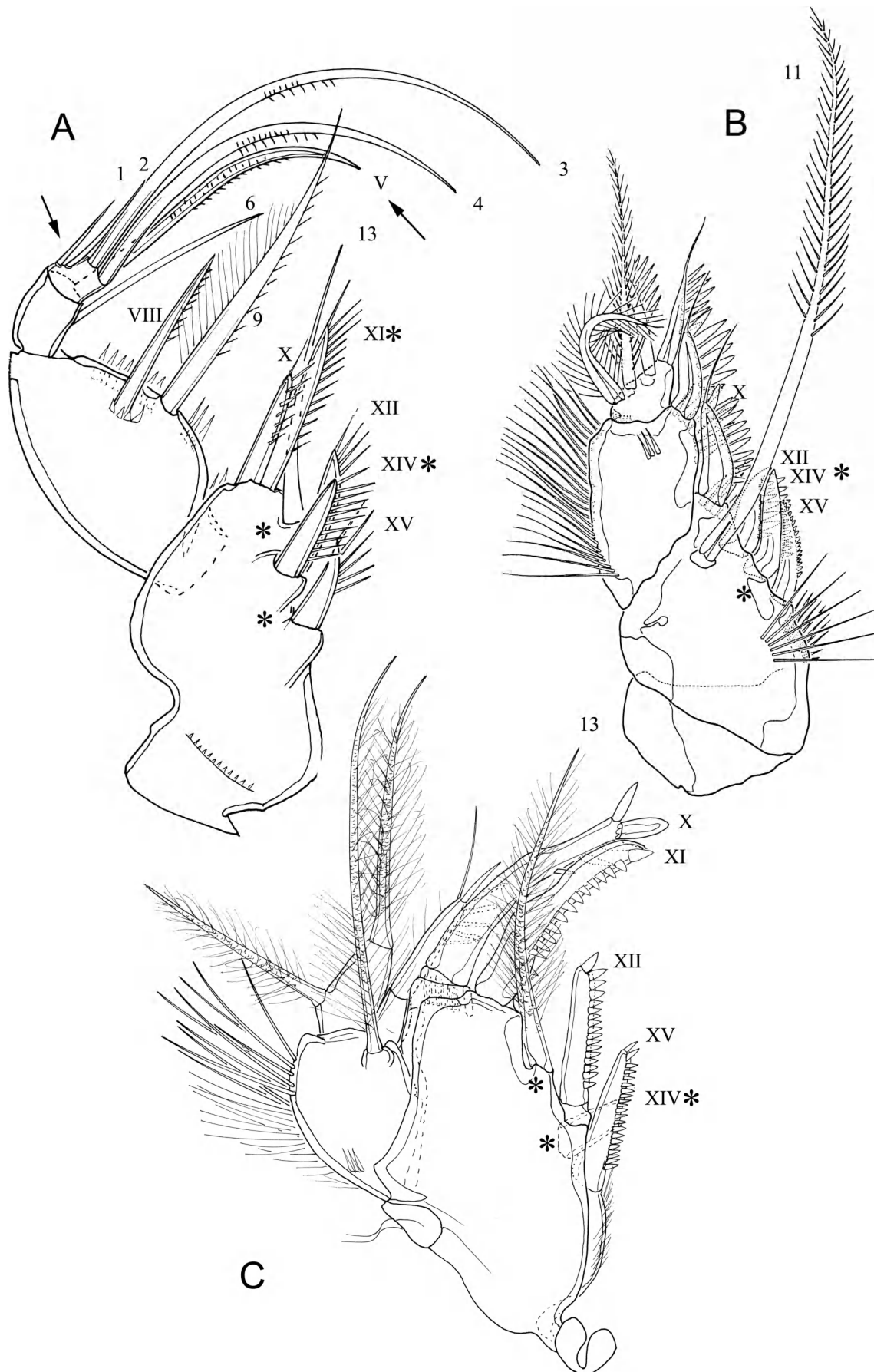


Fig. 17: Maxillipeds of Neobradyidae. A. *Tachidiopsis* spec. B. *Neobradya pectinifera* (after Huys, 1987). C. Neobradyidae gen. spec. 1. -- Arrows indicate the small enp-2 segment with the 4 transformed setae and the thin claw of enp-1. -- Asterisks indicate the characteristic shape and arrangement of the syncoxal setae.



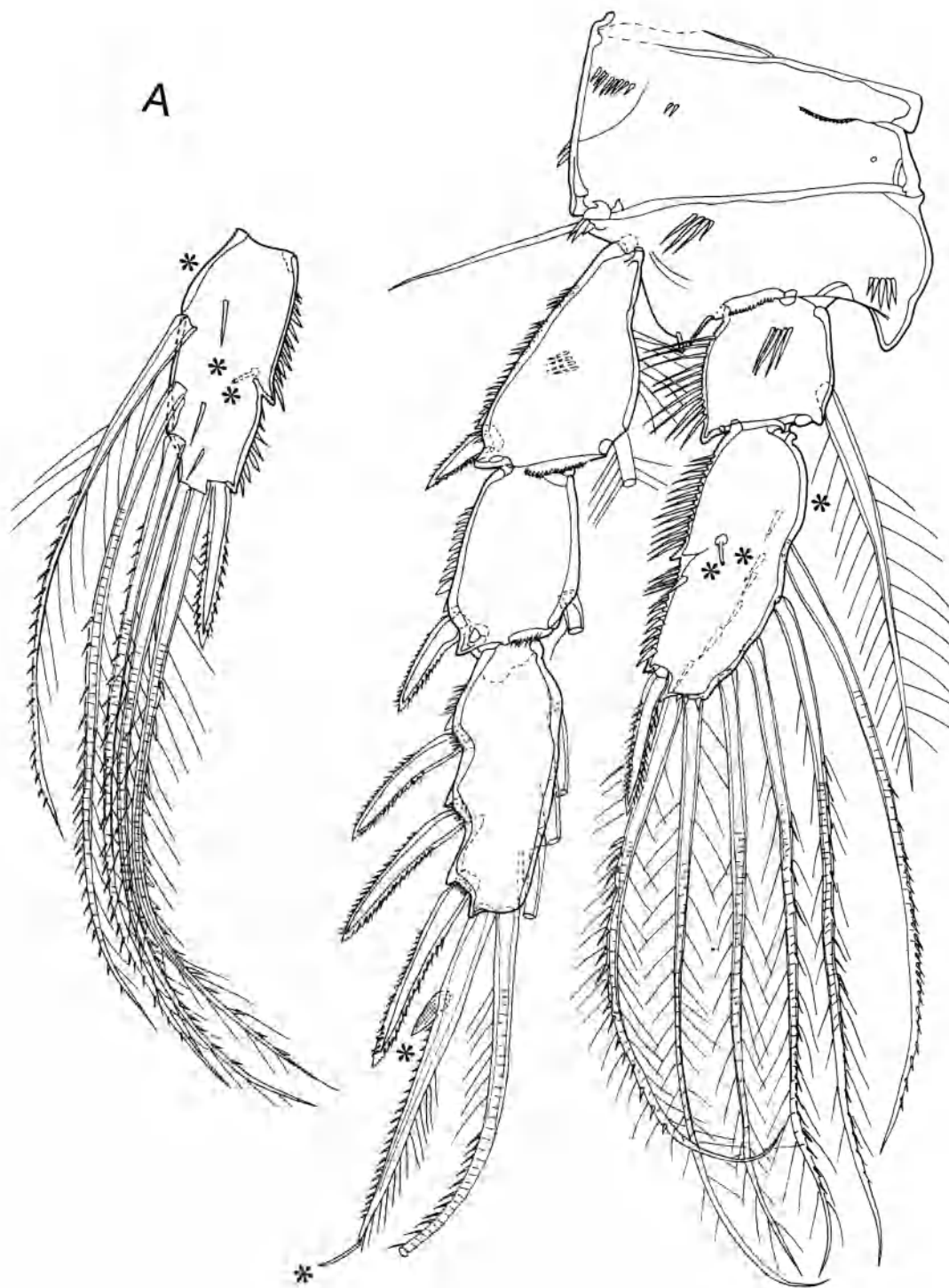


Fig. 18: Sexual dimorphism in male swimming legs of Neobradyidae gen. spec. 1.  
A. Distal endopod segment of P2. B. P3. — Asterisks indicate the sexual dimorphism in the male.

and setae, characteristic shape and arrangement of syncoxal setae: setae 11 and 14 of oligoarthran groundpattern transformed into strong spines; spines XII, XIV and XV in close proximity to each other, seta 13 displaced and inserted at the same level as spine XII; enp-1 with 1 seta (6?) and 1 thin claw (V), 1 seta (7?) missing; claw displaced to posterior side of the distal end of enp-1. P5 exopod with 6 setae (7 - 12): 1 inner seta, 2 terminal setae, 3 outer spines, seta 13 lacking.

*Male*. Antennule haplocer with 12 segments; armature formula: 1, 10 + aes, 8 + aes, 2, 7 + aes, 2, 4 / 3, 1, 2, 2, 6 + acrothek, fusion of *Oligoarthra* segments 2 to 3 and 6 to 7; distal segment of antennule with 1 subterminal seta and 6 terminal setae (char. 68: 0→1). **Sexual dimorphism in P2 and P3: fusion of middle and distal endopod segments of P2 and P3, provided with a tube pore at the anterior surface; fused middle segment of P2 and P3 with 1 inner seta less than female; outer distal spine of P3 exp-3 flagellate with very big spinule located at a slight bend in the proximal part of the spine; armature formula:**

	coxa	basis	exopod	endopod
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; I-2-3
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; I-2-4

P5 with 2-segmented exopod with 1-0, 2-1-1 setae, 2 distal segments of oligoarthran groundpattern fused.

#### Groundpattern of Neobradyyidae (Fig. 16)

*Female*. **Body** without clear difference in width between prosome and urosome (Fig. 1 D). **Nauplius eye** present. **Rostrum** delimited at base. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 10, 8, 6 + aes, 2, 4, 2, 2, 6 + acrothek; 6 setae of distal segment inserting at distal end. **Antenna** composed of coxa, basis and 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 4 subterminal and 7 distal setae; subterminal setation of enp-2 composed of 1 short proximal spine (I) and 1 longer distal spine (III), 1 distal geniculated seta (4) and 1 bare slender seta (2); seta 2 inserts between seta I and seta III; exopod with 2, 1, 1, 3 setae. **Labrum** not prominent. **Paragnaths** separated. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 2 lateral and 3 + 2 + 2 apical setae, each group of apical setae basally fused; exopod 4-segmented with 2, 1, 1, 2 setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III – IX; at least 2 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: 2, VII, 1, 2, 2; coxa with 5 setae, epipodite represented by 4 setae; basis with 4 + 4 setae; endopod 1-segmented with 6 setae; exopod 1-segmented with 4 setae. **Maxilla** 5-segmented consisting of syncoxa,

allobasis, and 3-segmented endopod; syncoxa with (5 + 3), 3, 3 setae, the two proximal endites fused; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II), 1 seta (3) and 1 tube pore on anterior surface and 1 seta (4) on posterior surface; accessory armature of fused endopod segment of 2 setae on anterior surface (9 + 10) and 1 seta on posterior surface (11); endopod 3-segmented with armature formula: 2, 2, 4; proximal segment with geniculated seta anteriorly (7), middle segment with 2 geniculated setae (5 + 6), last segment with 1 geniculated seta (2). **Maxilliped** (Fig. 17) 4-segmented, comprising syncoxa, basis and 2-segmented endopod; syncoxa with incorporated coxal endites represented from proximal to distal by I, II+1, II spines and setae, characteristic shape and arrangement of syncoxal setae: setae 11 and 14 of oligoarthran groundpattern transformed into strong spines; spines XII, XIV and XV in close proximity to each other, seta 13 displaced and inserted at the same level as spine XII; basis with 1 spine and 1 seta on inner edge (VII + 9); high degree of inward flexure at the basis-endopod joint; enp-1 with 1 seta (6?) and 1 thin claw (V?), 1 seta (7?) missing; claw displaced to posterior side of distal end of enp-1; enp-2 reduced in size with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4). **P1-P4** biramous with 3-segmented rami; praecoxa present; members of leg pairs joined by intercoxal sclerite; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-1; I-0; III-I+1-2	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-1; I-2-2

**P5** fused medially; praecoxa absent; baseoendopod with 1 outer basal seta, endopodal lobe with 5 setae (2 - 6): 2 inner setae, 2 terminal setae, 1 outer seta; exopod with 6 setae (7 - 12): 1 inner seta, 2 terminal setae, 3 outer spines, seta 13 lacking. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P2, P3, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** haplocer with 12 segments; armature formula: 1, 10 + aes, 8 + aes, 2, 7 + aes, 2, 4 / 3, 1, 2, 2, 6 + acrothek, fusion of Oligoarthra segments 2 to 3 and 6 to 7; aesthetasc on oligoarthran segment 6 fused at base with a seta; 6 setae of distal segment inserting at distal end. Sexual dimorphism in **P2 and P3** (Fig. 18): fusion of middle and distal endopod segments of P2 and P3, provided with a tube pore at the anterior surface; fused middle segment of P2 and P3 with 1 inner seta less than female; outer distal spine of P3 exp-3 flagellate with very big spinule located at a slight bend in the proximal part of the spine; armature formula:

	coxa	basis	exopod	endopod
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; I-2-3
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; I-2-4

**P5** fused medially; composed of coxa, basis, 1-segmented endopod with 2 setae and 2-segmented exopod with 1-0, 2-1-1 setae. **P6** symmetrical, with 3 setae.

### Remarks on the systematics and morphology of Neobradidae

#### *Morphology.*

Species of Neobradidae are characterised mainly by the particular shape and arrangement of syncoxal setae of maxilliped with incorporated coxal endites represented from proximal to distal by I, II+1, II spines and setae (Fig. 17), the fusion of Oligoarthra segments 2 to 3 and 6 to 7 of male antennule, and the sexual dimorphism in P2 and P3 (Fig. 18).

Neobradidae gen. spec. 1 is very plesiomorphic as compared with all other Neobradidae. This species comes close to the hypothetical morphology of the members of the last common population of Oligoarthra and is described in detail elsewhere.

The **rostrum** of Neobradidae gen. spec. 1 is delimited at base.

The **anal somite** is not divided longitudinally in Neobradidae gen. spec. 1 and the anus is located dorsally, covered by an anal operculum. The lack of the anal operculum, sometimes replaced by a weakly developed pseudoperculum, and the divided anal somite of some species has evolved within Neobradidae.

For the discussion of the 6 terminal setae on the distal segment of male and female **antennule** see chapters 5.2.3 and 5.2.4 (char. 6: 0→1; char. 68: 0→1).

Only Neobradidae gen. spec. 1, *Tachidiopsis* spec. and *T. cyclopoides* have preserved the ancestral seta of the proximal endopod segment of the **antenna** and 3 setae on the proximal exopod segment. All other Neobradidae have no seta on the proximal endopod segment and only 2 setae on the proximal exopod segment.

The cutting edge of the **mandible** of *Neobradia pectinifera* and *Antarcticobradia tenuis* has 2 setae at the proximal corner. This is a secondary phenomenon. The more plesiomorphic Neobradidae like Neobradidae gen. spec. 1 and the species of *Tachidiopsis* and *Marsteinia* have 1 seta at the proximal corner (see chapter 4.1). *Marsteinia* spec. 5 has 7 distal setae on the mandible endopod.

Within Oligoarthra, only the two species of Rometidae, *Marsteinia* spec. 5 and *Marsteinia* spec. 8 have a **maxillule** with 4 setae representing the epipodite of the coxa. *Neobradia pectinifera* and *Antarcticobradia tenuis* have 3 setae. All other described Oligoarthra have no more than 2 setae representing the epipodite of coxa. Seifried & Schminke (2003) assume 3 setae for the groundpattern of Syngnatharthra as *Marsteinia* spec. 5 and *Marsteinia* spec. 8 were not known. The convergent reduction of 2 epipodal setae of the coxa of maxillule happened convergently in the ancestral line to Aegisthidae and N.N. 1 (chapter 3.1) and not to Syngnatharthra as stated by Seifried & Schminke (2003).

The spine (II) of the allobasis of **maxilla** is not very distinct in Neobradidae. In species of *Tachidiopsis* and *Marsteinia* the spine is visible but thin. All other Neobradidae possess a seta (2) and no spine.

Becker's (1974) description of *Marsteinia ibericus* (Becker, 1974) reports a 4-segmented endopod of maxilla. The drawings of it are not sufficiently clear, so that the aberrant morphology of *Marsteinia ibericus* should be confirmed before further conclusions are drawn.

The **maxillipedal** coxa of *Neobradia pectinifera* is incompletely fused to the praecoxa (Fig. 17 B). All species with a more plesiomorphic morphology than *Neobradia pectinifera* such as *Tachidiopsis* spec. and Neobradidae gen. spec. 1 have an entire

syncoxa (Figs. 17 A + C). The incompletely fused coxa of *Neobradya pectinifera* is interpreted as secondary.

*Marsteinia* spec. 2 and *Marsteinia* spec. 4 show the ancestral state of Neobradyidae in the syncoxal setae X-XV (Fig. 16): The spines XII, XIV and XV are in close proximity to each other, seta 13 is displaced to a more distal position and inserts at the same level as spine XII. In some Neobradyidae like *Tachidiopsis* spec. and Neobradyidae gen. spec. 1 seta 13 is displaced to a position between spine XI and XII (Figs. 17 A + C). All species of *Neobradya* and *Antarcticobradya* and some of *Marsteinia* have a transformed and displaced spine XI. In all species this spine is elongated and located on the posterior surface near spine 12. In some species like *Neobradya pectinifera* the spine is retransformed to a long seta (11) and sometimes seta 13 is lacking (Fig. 17 B).

The proximal small lateral seta (1) of the maxillipedal endopod of *Tachidiopsis* species (Fig. 17 A; arrow) belongs to the distal and not to the proximal endopod segment, as drawn by Huys & Boxshall (1991) and Willen (2000, fig. 46, seta "3"). This seta is difficult to see, but inserts on the distal endopod segment without doubt.

The 2 geniculated distal setae (3 + 4) of the small distal endopod segment of the *Tachidiopsis* maxilliped are accompanied by 2 small outer setae (1 + 2) and can be found in many species of Oligoarthra. They are an element of the groundpattern of Syngnathartha. For example, the two geniculated setae occur in Tisbidae, Idyanthidae, Paramesochridae, and Superornatiremidae. The hypothesis is that all species of Syngnathartha without geniculated setae on the maxilliped have lost them. It is very unlikely that this characteristic morphology with the geniculated setae at the distal end of the small endopod accompanied by the two small lateral setae has developed more than once within Oligoarthra (see chapters 5.1.5 and 5.2.3).

It is not easy to establish a homology between the claw of enp-1 of the two *Tachidiopsis* species and the setae of the oligoarthran groundpattern. Species that have the geniculated setae often have one big claw, one smaller second claw and one additional seta on enp-1 (Willen, 2000, p. 125 - 126, fig. 46, type 2). *Tachidiopsis* species have only 1 thin claw and one seta on this segment. The thin claw is a small version of claw V, because it inserts on the posterior side of the distal end of enp-1 as the big claw V in other Oligoarthra. This homology is supported by the cladistic analysis and the phylogenetic relationships of taxa within Harpacticoida (chapter 5.).

The maxilliped of *Tachidiopsis cyclopoides* and *T.* spec. has retained a 2-segmented endopod. In all other Neobradyidae the endopod is reduced to one segment with 2 to 4 setae. It is very likely that the 1-segmented endopod without geniculated setae is the result after reduction of the 2-segmented endopod with the 2 geniculated setae (see chapter 5.).

As indicated in the figure and the text, Bodin (1968) counts 2 inner setae on the distal exopod segment of **P1** of the only existing specimen of *Marsteinia sarsi*. However, it is likely, that Bodin (1968) described the **P2** instead of the **P1** (chapter 4.3). A redescription of *Marsteinia sarsi* is necessary.

Only Neobradyidae gen. spec. 1 has preserved all ancestral setae on **P2-P3** and **P6**, all other Neobradyidae have fewer setae.

The **sexual dimorphism of P2 and P3 male** can be seen in Neobradyidae gen. spec. 1 in its primal state (Fig. 18), all other Neobradyidae show alterations. The fusion of

enp-2 and enp-3 in P2 and P3 male is obvious in species of Neobradyidae with 3-segmented endopods in the female like in Neobradyidae gen. spec. 1 and *Marsteinia*, but not in species with 2-segmented endopods in the female like in *Antarcticobradya* and *Neobradya*. One step in the evolution towards *Antarcticobradya* and *Neobradya* was the (for males characteristic) fusion of the distal segments of P2-P3 in the female. For *Tachidiopsis cyclooides* no males are known, but the female has the (for males typical) fusion of enp-2 and enp-3 of P2 and P3 but not of P4. The female of *Tachidiopsis* spec. has the typical fusion of enp-2 and enp-3 only of P2 and not of P3 and P4. However, the undescribed male of *Tachidiopsis* spec. has, as all males of Neobradyidae, the fusion in P2 and P3!

On the P2 a male tube pore can be found in all taxa of Neobradyidae, but in different places. Males of *Tachidiopsis* spec. also have this typical tube pore. On the P3 a tube pore could only be found in Neobradyidae gen. spec. 1 (Fig. 18 B) and is maybe not an element of the groundpattern of Neobradyidae.

The female of Neobradyidae gen. spec. 1 has 2 inner setae at the middle segment (enp-2) of P2 and P3. The male has retained only one seta at the fused middle segment, one inner seta less than the female. All other females of Neobradyidae have only one inner seta at the middle segment of endopod P2 and P3 like the males.

The outer distal spine of the distal exopod segment is flagellate and has a very big spinule at a slight bend in the proximal part of the spine in Neobradyidae gen. spec. 1 and in males of some *Marsteinia* species (Fig. 18). There are no indications that these species represent a monophyletic group within Neobradyidae, they probably belong to a paraphyletic group with a plesiomorphic morphology. As a consequence the absence of the characteristic shape of this outer distal spine is interpreted as secondary within Neobradyidae.

#### *Systematics.*

Without comment Huys et al. (1996) classified *Marsteinia* as member of Neobradyidae and listed *M. typica* Drzycimski, 1968 and *M. similis* as Northwest European species. Earlier, these two species were members of *Tachidiopsis*, a genus that belonged to Tisbidae. Bodin (1997; p. 41) wrote: "This genus (*Marsteinia*) was reinstated by Huys et al. (1996) and includes two species described by Drzycimski (1968) which were previously attributed to the genus *Tachidiopsis* by Bodin (1971)". According to Bodin (1997) the other six species of *Tachidiopsis* still belong to Tisbidae. Huys et al. (1996) mentioned seven species of *Marsteinia*, without listing them. The only reference is: "Genus *Marsteinia* Drzycimski, 1968 *Synonym: Tachidiopsis* Sars (part.): Bodin (1968), Becker (1974), Dinét (1974). *Diagnosis:* Neobradyidae. ... Seven species known world-wide." (Huys et al., 1996). One could assume that the five species of *Tachidiopsis* described by Bodin (1968), Becker (1974), Dinét (1974) were meant, and that *Tachidiopsis cyclooides* described by Sars (1911) was still as a member of Tisbidae. Bodin (1997) did not take notice of this remark by Huys et al. (1996).

Nevertheless, there are good morphological indications that *T. cyclooides*, *M. bozici*, *M. ibericus*, *M. laubieri* (Dinét, 1974), *M. parasimilis* (Dinét, 1974), *M. sarsi*, *M. similis*, and *M. typica* belong to Neobradyidae. These species share the autapomorphies of Neobradyidae, mainly the very characteristic shape and arrangement of the syncoxal setae of maxilliped and the unique sexual dimorphism of

the male P2 and P3. No other Harpacticoida show this peculiar morphology. *T. cycloptides* is conspicuous because of the morphology of its maxillipedal endopod. As discussed above, this endopod is interpreted as plesiomorphic within Neobradyidae. The endopod of all other Neobradyidae can be derived from it.

Lang (1944) established the taxon Neobradyidomorpha Lang, 1944 to unite Chappuisiidae, Darcythompsoniidae, Neobradyidae, and Phyllognathopodidae. Bowman & Abele (1982) changed Lang's "superfamily"-endings "-idomorpha" in superfamily-endings "-oidea" and introduced "Neobradoidea" Olofsson, 1917 (International Code of Zoological Nomenclature, fourth edition, Art. 29.2). "Neobradoidea" Olofsson, 1917 (Chappuisiidae, Darcythompsoniidae, Neobradyidae, Phyllognathopodidae) are not maintained here, as they are polyphyletic. Lang (1944) used symplesiomorphies to characterize them. One example: After Lang (1948) all "Neobradoidea" have a 4-segmented exopod of mandible and antenna. These characters are present in the groundpattern of Oligoarthra, as most characters mentioned by Lang (1948), which unite the four taxa. Chappuisiidae, Phyllognathopodidae and Darcythompsoniidae are part of N.N.1 (see chapter 5.1.5 and 5.2.3).

#### 4.9 Podogennonta Lang, 1944

##### Taxa belonging to Podogennonta

Adenopleurellidae Huys, 1990, Ameiridae Monard, 1927, Ancorabolidae Sars, 1909, Argestidae Por, 1986, Balaenophilidae Sars, 1910, Cancrincolidae Fiers, 1990, Canthocamptidae Sars, 1906, Cletodidae T. Scott, 1905, Cletopsyllidae Huys & Willems, 1989, Cristacoxidae Huys, 1990, Dactylopusiidae Lang, 1936, Darcythompsoniidae Lang, 1936, Harpacticidae Sars, 1904, Huntemaniidae Por, 1986, Laophontidae T. Scott, 1905, Laophontopsidae Huys & Willems, 1989, Latiremidae Bozic, 1969, Leptastacidae Lang, 1948, Leptopontiidae Lang, 1948, Louriniidae Monard, 1927, Metidae Sars, 1910, Miraciidae Dana, 1846, Normanellidae Lang, 1944, Orthopsyllidae Huys, 1990, Parastenheliidae Lang, 1944, Parastenocarididae Chappuis, 1933, Phyllognathopodidae Gurney, 1932, Pseudotachidiidae Lang, 1936, Rhizothricidae Por, 1986, Rhynchothalestridae Lang, 1948, Tetragonicipitidae Lang, 1944, Thalestridae Sars, 1905, Thompsonulidae Lang, 1944, taxa incerta et incertae sedis: Ismardiidae Leigh-Sharpe, 1936, *Dactylopina* Brady, 1910, *Flavia* Brady, 1899, *Goffinella* Wilson, 1932, *Ismardis* Leigh-Sharpe, 1936, *Mawsonella* Brady, 1918, *Pyroclctodes* Coull, 1973, *Tisemus* Monard, 1928.

##### Changes in systematics (reasons given below)

Darcythompsoniidae Lang, 1936 and Phyllognathopodidae Gurney, 1932 (former "Maxillipedasphalea") are moved to Podogennonta Lang, 1944.

Thompsonulidae Lang, 1944 is excluded from Exanechentera Lang, 1944 and is transferred to Podogennonta Lang, 1944.

Diagnosis: Autapomorphies of Podogenonta (Fig. 4: ■ 10; Fig. 19)

*Female.* Endopod of mandible with 3 proximal lateral setae (from enp-1), **3 more distal lateral setae** (char. 20: 1→0) and 3 + 2 + 2 apical setae. Endopod of maxillule with 4 setae. Syncoxa of maxilla with (3 + 3), 3, 3 setae, the two proximal endites fused, **distal praecoxal endite with 2 flagellate setae; both coxal endites with setae of characteristic shape: anteriorly 1 claw-like seta, posteriorly 2 strong, mostly unilaterally spinulose setae with subterminal flagellum;** accessory armature of fused endopod segment: 1 seta on posterior surface (11), **seta 9 displaced to proximal segment of endopod (?), seta 10 lacking (?);** endopod 3-segmented with armature formula: 2, 1, 3; **setae 4 and 6 lost.** Maxilliped 4-segmented with praecoxa and coxa separated (?), basis, and 1-segmented endopod; endopodal setae 1 to 4 only represented by a group of 4 small setae on anterior surface of endopod, **no setae geniculated.** P1 of characteristic shape: **enp-1 elongate, enp-2 and enp-3 short** (char. 53: 0→1); enp-3 with 1 inner seta, terminally with anterior claw (originated from displaced outer spine), **1 middle geniculate seta and 1 posterior miniaturised seta; 1 inner seta lacking;** exp-3 terminally with **2 geniculated setae, 2 inner setae lacking.** Formula of armature of P1:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; <b>III-2-0</b>	0-1; 0-1; <b>I-2-1</b>

P5 endopodal lobe with 6 setae (1 - 6): **3 inner setae, 2 terminal setae, 1 outer seta;** exopod **foliated with 8 setae (7 - 14): 3 inner, 2 terminal, 3 outer setae.**

Groundpattern of Podogenonta (Fig. 19)

*Female.* **Body** without clear difference in width between prosome and urosome (Fig. 1 F). **Nauplius eye present. Rostrum** delimited at base. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 12, 10, 6 + aes, 3, 4, 2, 2, 6 + acrothek, paedomorphic female antennule. **Antenna** composed of coxa, basis, 2-segmented endopod and 3-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 4 subterminal and 7 distal setae; subterminal setation of enp-2 composed of 1 short proximal spine (I), 1 longer distal spine (III), 1 distal geniculate seta (4) and 1 naked slender seta (2); seta 2 inserts beneath seta 4; exopod with 2, 1, 4 setae; oligoarthran segments 3 and 4 fused. **Labrum** not prominent. **Paragnaths** separated. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented due to fusion of enp-1 and enp-2; endopod with 3 proximal lateral setae (from enp-1), 3 more distal lateral setae and 3 + 2 + 2 apical setae, each group of apical setae basally fused; exopod 4-segmented with 2, 1, 1, 2 setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III – IX; 3 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior



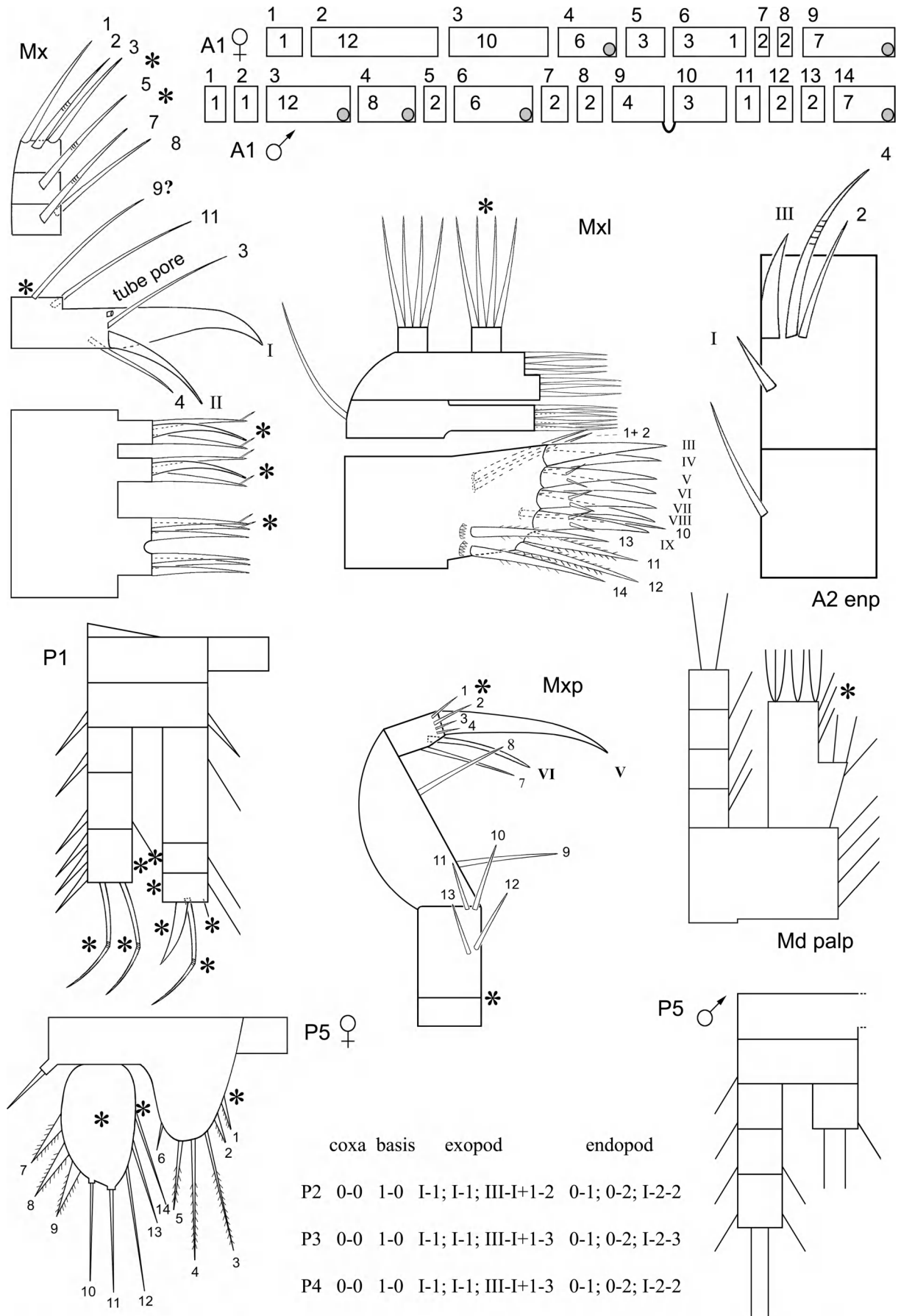


Fig. 19: Groundpattern of Podogenonta. Asterisks mark autapomorphies of Podogenonta.

surface with 2 proximal setae (13 + 14); formula of armature: 2, VII, 1, 2, 2; coxa with 6 setae, epipodite represented by 1 seta; basis with 3 + 4 setae; endopod 1-segmented with 4 setae; exopod 1-segmented with 4 setae. **Maxilla** 5-segmented consisting of syncoxa, allobasis, and 3-segmented endopod; syncoxa with (3 + 3), 3, 3 setae, the two proximal endites fused, distal praecoxal endite with 2 flagellate setae; both coxal endites with setae of characteristic shape: anteriorly 1 claw-like seta, posteriorly 2 strong, mostly unilaterally spinulose setae with subterminal flagellum; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) fused with endite, 1 curved spine (II), 1 seta (3) and 1 tube pore on anterior surface and 1 seta (4) on posterior surface; accessory armature of fused endopod segment: 1 seta on posterior surface (11), seta 9 displaced to proximal segment of endopod (?), seta 10 lacking (?); endopod 3-segmented with armature formula: 2, 1, 3; setae 4 and 6 lost; proximal and middle segment with geniculated seta anteriorly (5 + 7), last segment with 1 geniculated seta (2). **Maxilliped** 4-segmented and subchelate, comprising praecoxa, coxa, basis, and 1-segmented endopod; 4 coxal setae (10 - 13), arranged in 2 pairs from proximal to distal at inner border; 2 spines (X + XII) transformed into setae; 3 setae and spines (14 - 16) of oligoarthran groundpattern lacking; basis elongated with 2 setae on inner edge located medially and distally; enp-1 and enp-2 fused to one small segment with a large distal claw (V, from enp-1); second claw (VI, from enp-1, reduced in thickness and solidity) and seta 7 inserting on the inner lateral border of the fused segment, endopodal setae 1 to 4 only represented by a group of 4 small setae on anterior surface of endopod, no setae geniculated; high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite. P1 of characteristic shape: enp-1 elongate, enp-2 and enp-3 short; enp-3 with 1 inner seta, terminally with anterior claw (derived from displaced outer spine), 1 middle geniculate seta and 1 posterior miniaturised seta; 1 inner seta lacking; exp-3 with 3 outer spines, terminally with 2 geniculated setae, 2 inner setae lacking. Formula of armature of P1-P4

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-2-0	0-1; 0-1; I-2-1
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** with intercoxal sclerite joining the coxae; praecoxa absent; baseoendopod with 1 outer basal seta, endopodal lobe with 6 setae (1 - 6): 3 inner setae, 2 terminal setae, 1 outer seta; exopod foliated with 8 setae (7 - 14): 3 inner, 2 terminal, 3 outer setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6.

**Urosome** 6-segmented, consists of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** haplocer with 14 segments; armature formula: 1, 1, 12 + aes, 8 + aes, 2, 6 + aes, 2, 2, 4 / 3, 1, 2, 2, 6 + acrothek, characteristic arrangement and shape of setae, aesthetasc on segment 6 fused at base with a seta. **P5** composed of intercoxal sclerite, coxa, basis, endopod with 3 setae and 3-segmented exopod with 1-0, 1-1, 1-2-1 setae. **P6** symmetrical, with 3 setae.

### Remarks on the systematics and morphology of Podogennonta

#### *Morphology.*

Willen (2000) reconstructed the groundpattern and autapomorphies of Podogennonta. The reconstruction is quoted here. However, this groundpattern seem to be consisted of to many plesiomorphic character states (see chapter 5.2.5). A revision of the whole Podogennonta is necessary, to check the groundpattern of Podogennonta. Therefore, only small changes are discussed below and some schematic illustrations are added.

The monophyletic group Podogennonta is characterized mainly by the particular arrangement and shape of the setae of the syncoxal endites of the maxilla, the small endopodal setae 1 to 4 on the anterior surface of maxillipedal endopod, the very characteristic P1 and the unique P5 with the foliated exopod and setae 1 and 14.

Willen (2000) reconstructed as groundpattern of Oligoarthra and Podogennonta a 5-segmented exopod of **mandible** and 10 setae inserting on the (fused) distal endopod segment of mandible. As discussed in chapter 4.3, a 4-segmented exopod is assumed here for the groundpattern of Oligoarthra and Podogennonta. For Oligoarthra, 7 setae inserting on the (fused) distal endopod segment of mandible are apomorphic and the 3 additional lateral setae are apomorphic for Podogennonta (chapter 5.2.3; char. **20**).

The number of 4 apical posterior spines with a pair of “double-spinules” in the **maxillular** praecoxa appears to be apomorphic for Miraciidae and not for Podogennonta (see chapter 4.1).

The number of setae of allobasis of **maxilla** is not completely solved in Willen (2000). It is clear that “The number of basal setae corresponds with that of the ancestral copepod” (Willen, 2000, p. 111). Claw I, spine II, 3, 4 and the tube pore are present in the groundpattern of Podogennonta (claw A to spine D in Willen, 2000, see chapter 4.1). Seta 11 (seta 8 in Willen, 2000) is also present. Seta 1 in Willen (2000) inserts in some Podogennonta at the border between basis and enp-1 and the homology of this seta is not clear. It could be seta 9 or an additional seta of enp-1. Seta 10 is possibly lacking in Podogennonta. Willen (2000) mentioned a seta, inserting at the same position on the basal endite as the tube pore in *Rhynchothalestris helgolandica* (Claus, 1863) (according to the description of Huys, 1990), and concludes that it is the displaced endopodal seta 10 (her seta 9). This has to be confirmed. No other Podogennonta has this unique seta and it could be an apomorphy of *Rhynchothalestris helgolandica*.

The fact that in species of Podogennonta the enp-2 of **maxilliped** is represented only by a group of 4 small setae on anterior surface of endopod is secondary. The enp-2 is fused with enp-1 and the geniculated setae (3 + 4) are transformed (see chapter 5).

The short enp-3 of **P1** evolved in 4 taxa convergently (chapter 5; char. **53**: 0→1).

Setae 1 and 14 of female **P5** are secondarily evolved within Podogennonta (see chapter 4.1).

#### *Systematics.*

Harpacticidae belong to Podogennonta as discussed by Willen (2000). Diosaccidae Sars, 1906 is a synonym of Miraciidae Dana, 1846 (Willen, 2002).

There is no doubt that Thompsonulidae (4 species in 2 genera) also belongs to Podogennonta. They have features which make it difficult to recognize this: The setae of the syncoxal endites of maxilla do not have the typical shape and the setae of P1 do not have the podogennontan differentiation. However, the structure of maxilla and P1

allows a derivation from the groundpattern of Podogennonta, so that there is no conflict. All other autapomorphies of Podogennonta can be found in Thompsonulidae like the characteristic endopod of maxilliped.

Lang (1944, 1948) includes Darcythompsoniidae (30 species in 4 genera) and Phyllognathopodidae (21 species in 3 genera) in the “Maxillipedasphalea” on the basis of plesiomorphies or convergences like a maxilliped without a claw. However, some species of *Kristensenia* Por, 1983 (Darcythompsoniidae) contrary to Lang's (1944, 1948) assumption have a claw on the endopod of the maxilliped. Otherwise the morphology of Darcythompsoniidae and Phyllognathopodidae is very reduced, so that it is difficult to recognize whether they have the autapomorphies of Podogennonta, especially in the case of P1. Both taxa do not share any synapomorphies with a taxon outside Podogennonta. On the contrary, all conserved characters of Darcythompsoniidae and Phyllognathopodidae indicate that they belong to Podogennonta. Especially the species of *Leptocaris* T. Scott, 1899 resemble species of Louriniidae (G. Moura, pers. comm.). The maxilliped of Phyllognathopodidae is difficult to derive from that of the podogennontan groundpattern, but it is also difficult to derive it from the maxilliped of any other Oligoarthra. It is hypothesised here that Darcythompsoniidae and Phyllognathopodidae belong to Podogennonta. An examination of the monophyly of Podogennonta and an analysis of the phylogenetic relationships within Podogennonta are necessary to reveal the exact position of Thompsonulidae, Phyllognathopodidae, and Darcythompsoniidae.

*Psammoleptomesochra australis* Mielke, 1994 (Ameiridae) is mentioned twice in Bodin (1997). This species was also listed as *Paramesochra australis* Mielke, 1994, but it is without doubt not a member of Paramesochridae. As long as its systematic position is not solved, this species remains in Ameiridae.

#### 4.10 Chappuisiidae Chappuis, 1940

Taxa belonging to Chappuisiidae (2 species in 1 genus)

*Chappuisius inopinus* Kiefer, 1938, *Chappuisius singeri* Chappuis, 1940

Diagnosis: Autapomorphies of Chappuisiidae (Fig. 4: ■ 12; Figs. 20 + 1 E)

*Female*. Body **cylindrical** (Fig. 1 E). Prosome consisting of cephalothorax and **4 free pedigerous somites; first pedigerous somite completely separated from dorsal cephalic shield** (char. 1: 1→0). Nauplius eye **lacking**. No egg-sac (char. 4: 2→0). Caudal rami with **6 setae; seta I lacking**. Antennule 7-segmented; armature formula: 1, 7, 7, 2 + aes, 1, 4, 8 + acrothek, segments **7 to 9 of oligoarthran groundpattern fused**. Coxa of maxillule **not separated from basis** (char. 28: 0→1); praecoxal arthrite: anterior surface in outer half with **1 seta** (?), apically 2 rows of spines with **2 anterior** and 4 posterior spines (III – VII, IX), **without 2 long spinules on posterior spines** (char. 25: 1→0), **spine VIII and seta 10 lacking** (char. 23: 0→1); subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: **1, VI, 0, 2, 2**; coxa with **3 inner setae**; basis with **6 setae**. Syncoxa of maxilla with (2 + 3), **2, 2 setae; accessory armature of fused basis consisting of 2 spines at the end of the endite (I + II?)**; **no accessory armature of**

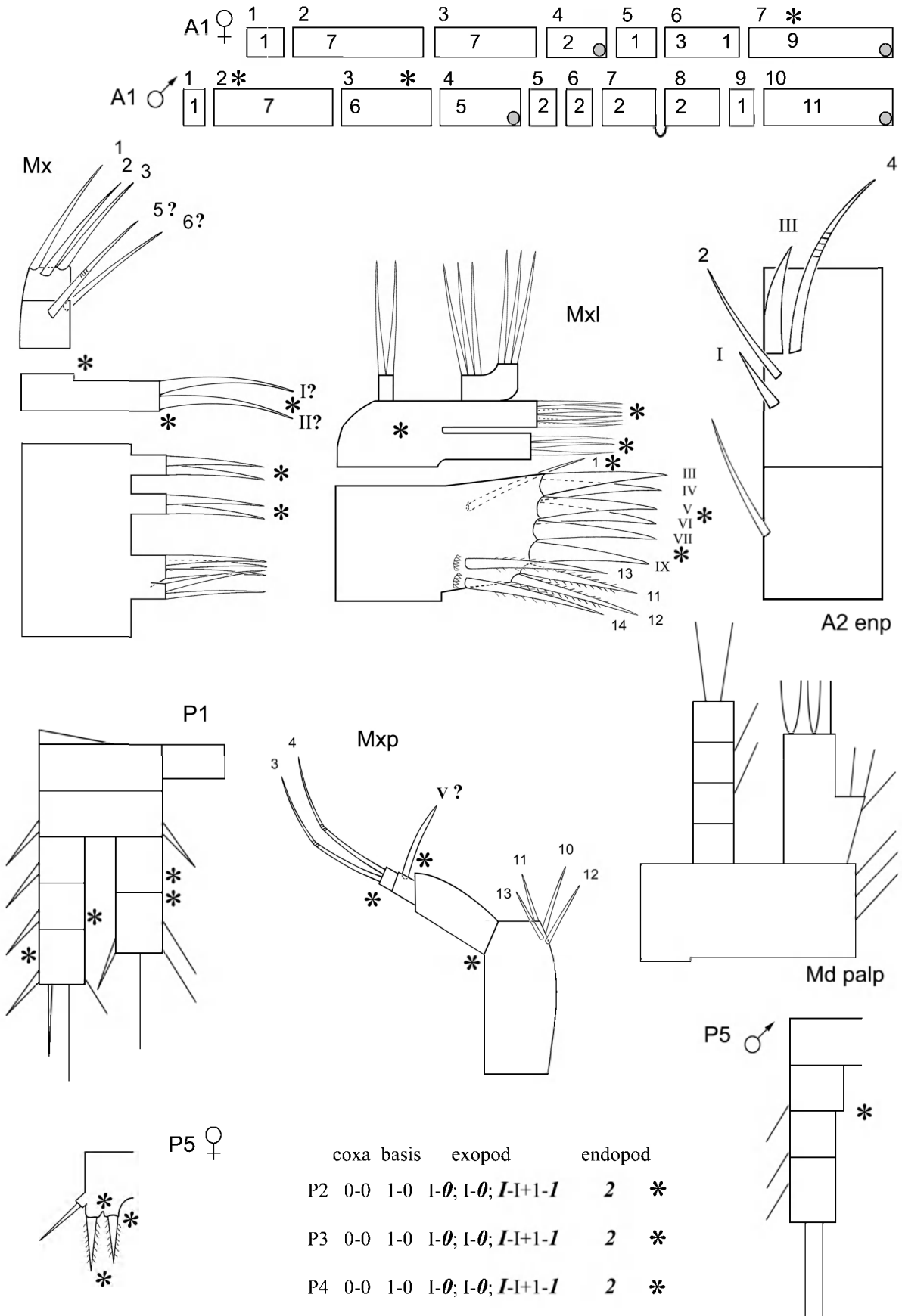


Fig. 20: Groundpattern of Chappuisiidae. Asterisks mark autapomorphies of Chappuisiidae.

**fused endopod segment** (char. 39: 0→1). Maxilliped enp-1 with 1 thin claw (V?), setae 6 and 7 lacking (char. 49: 3→1); setae 1 and 2 of enp-2 lacking; high degree of outward flexibility at the syncoxa-basis joint. P1 2-segmented endopod; P2-P4 1-segmented endopod; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-0; I-I+1-1	0-0; I-1-2
P2	0-0	1-0	I-0; I-0; I-I+1-1	2
P3	0-0	1-0	I-0; I-0; I-I+1-1	2
P4	0-0	1-0	I-0; I-0; I-I+1-1	2

**P5** a small single plate, exopod fused with endopod; with 1 outer basal seta and 2 distal setae.

*Male*. Antennule haplocer with 10 segments; fusion of *Oligoarthra* segments 2 - 3, 4 - 5, and 12 - 14. P5 without endopod.

#### Groundpattern of Chappuisiidae (Fig. 20)

*Female*. **Body** cylindrical without difference in width between prosome and urosome (Fig. 1 E). **Nauplius eye** lacking. **Prosome** consisting of cephalosome and 4 free pedigerous somites; first pedigerous somite completely separated from dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; no egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 6 setae; seta I lacking. **Antennule** 7-segmented; armature formula: 1, 7, 7, 2 + aes, 1, 4, 8 + acrothek, segments 7 to 9 of oligoarthran groundpattern fused. **Antenna** composed of coxa, basis, 2-segmented endopod and 2-segmented exopod; basis without seta; enp-1 with 1 seta; enp-2 with 4 subterminal and 7 distal setae; subterminal setation composed of enp-2 of 1 short proximal spine (I), 1 longer distal spine (III), 1 distal geniculate seta (4) and 1 bare slender seta (2); seta 2 inserts between spine I and spine III; exopod with 1, 2 setae. **Labrum** not prominent. **Paragnaths** separated. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner; palp comprising basis, endopod and exopod; basis with 3 setae; endopod 1-segmented with 3 lateral and 2 + 2 + 1 apical setae, 4 apical setae basally fused to pairs; exopod 4-segmented with 0, 1, 1, 2 setae. **Maxillule** comprised of praecoxa, coxa not separated from basis, exopod, and endopod; praecoxal arthritis: anterior surface in outer half with 1 seta (?), apically 2 rows of spines with 2 anterior and 4 posterior spines (III - VII, IX), spine VIII and seta 10 lacking; subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: 1, VI, 0, 2, 2; coxa with 3 setae, epipodite without setae; basis with 6 setae; endopod 1-segmented with 6 setae; exopod 1-segmented with 2 setae. **Maxilla** 4-segmented consisting of syncoxa, allobasis, and 2-segmented endopod; syncoxa with (2 + 3), 2, 2 setae, the two proximal endites fused; basis with well-developed endite; accessory armature of fused basis consisting of 2 spines at the end of the endite (I + II?); no accessory armature of fused endopod segment on allobasis; endopod 2-segmented with armature formula: 2, 3; proximal segment with geniculated seta anteriorly (5?). **Maxilliped** 4-segmented, comprising syncoxa, basis and 2-segmented endopod; 4 coxal setae (10 - 13), arranged at inner border in 2 pairs from proximal to distal; basis without ornamentation, spine VIII and seta 9 lacking; enp-1

with 1 thin claw (V?), setae 6 and 7 lacking; enp-2 with 2 geniculated setae distally (3 + 4), setae 1 and 2 lacking; high degree of outward flexibility at the syncoxa-basis joint. **P1** biramous with 3-segmented exopod and 2-segmented endopod; praecoxa present; leg pairs joined by intercoxal sclerite; **P2-P4** biramous with 3-segmented exopod and 1-segmented endopod; praecoxa present; members of leg pairs joined by intercoxal sclerite; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-0; I-I+1-1	0-0; I-1-2
P2	0-0	1-0	I-0; I-0; I-I+1-1	2
P3	0-0	1-0	I-0; I-0; I-I+1-1	2
P4	0-0	1-0	I-0; I-0; I-I+1-1	2

**P5** a single plate, fused medially; with 1 outer basal seta and 2 distal setae. **P6** with 1 seta.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites, 1 spermatophore. **Antennule** haplocer with 10 segments; armature formula: 1, 7, 6, 5 + aes, 2, 2, 2 / 2, 1, 10 + acrothek, fusion of Oligoarthra segments 2 - 3, 4 - 5, and 12 - 14; aesthetascs of Oligoarthra segments 3 and 4 lacking; aesthetasc on oligoarthran segment 6 fused at base with a seta. **P5** fused medially, composed of coxa, basis, and 2-segmented exopod with 1-0, 1-2-0 setae; no endopod. **P6** symmetrical, with 1 seta.

#### Remarks on the morphology of Chappuisiidae

The monophyletic group Chappuisiidae is mainly characterized by the size reduction of the big claw of the maxillar basis, the unique maxilliped with a high degree of outward flexibility at the syncoxa-basis joint, the 2-segmented endopod of P1, the 1-segmented endopod of P2 to P4 and the characteristic shape of the P5 in both sexes.

The fusion of the **first pedigerous** somite and the cephalothorax is an autapomorphy of Syngnathartha (char. 1: 0→1). However, some species of Syngnathartha, as species of Chappuisiidae have a first pedigerous somite that was secondarily separated from the cephalosome (chapter 5.2.3; char. 1: 1→0).

For the discussion of the morphology of the **egg-sac** see chapter 5.2.3 (char. 4: 2→0).

The posterior spines of the **maxillular** praecoxa are without 2 long spinules (char. 25: 1→0). This reduction has convergently evolved in the ancestral line to N.N. 4 (chapters 4.1 and 5.2.3; char. 25).

The two species of Chappuisiidae have generally few segments and setae. The reduction of so many segments and setae is probably an effect of their life in the groundwater. As one consequence, the species of Chappuisiidae share many reductions with other taxa (see chapter 5; char. 23: 0→1, char. 28: 0→1, char. 39: 0→1, char. 49: 2→1).

### 4.11 Ectinosomatidae Sars, 1903

#### Taxa belonging to Ectinosomatidae (233 species in 20 genera)

*Arenosetella* Wilson, 1932, *Bradya* Boeck, 1872, *Bradyellopsis* Brian, 1924, *Ectinosoma* Boeck, 1865, *Ectinosomella* Sars, 1910, *Ectinosomoides* Nicholls, 1945, *Halectinosoma* Lang, 1944, *Halophytophilus* Brian, 1917, *Hastigerella* Nicholls, 1935, *Klieosoma* Hicks & Schriever, 1985, *Lineosoma* Wells, 1965, *Microsetella* Brady & Robertson, 1873, *Noodtiella* Wells, 1965, *Oikopus* Wells, 1967, *Peltobradya* Médioni & Soyer, 1967, *Pseudobradya* Sars, 1904, *Pseudectinosoma* Kunz, 1935, *Rangabradya* Karanovic & Pesce, 2001 *Sigmatidium* Giesbrecht, 1881, *Tetanopsis* Brady, 1910.

Undescribed species (8.1 Appendix I.): *Bradya* (*Bradya*) spec. 1, *Bradya* (*Bradya*) spec. 2, *Bradya* (*Parabradya*) spec. 3, innumerable species of *Arenosetella*, *Bradya*, *Bradyellopsis*, *Ectinosoma*, *Microsetella*, *Halectinosoma*, *Halophytophilus*, *Hastigerella*, *Klieosoma*, *Pseudobradya* and undescribed higher taxa of Ectinosomatidae.

#### Changes in systematics

Ectinosomatoidea Sars, 1903 is synonymized with Ectinosomatidae Sars, 1903, as both taxa enclose the same species.

#### Diagnosis: Autapomorphies of Ectinosomatidae (Fig. 4: ■ 14; Figs. 21 + 22)

*Female*. Nauplius eye **absent**. Anal somite **divided longitudinally**. **Anus covered by pseudoperculum**. Antennule indistinctly 7-segmented; armature formula: 1, 10, (6 + 4+aes), 3, 3, 4, 6 + acrothek; **segments 3 and 4 of Oligoarthra groundpattern incompletely fused**, fusion of Oligoarthra segments 7 and 8. Enp-1 of antenna with 1 seta **displaced to the proximal part of the endopod**; enp-2 with **3 subterminal setae**; subterminal setation composed of enp-2 of 1 long proximal spine-like seta (1 or 2?), 1 distal spine (III) and 1 distal slightly geniculate seta; **spine I or seta 2 lacking**. Paragnaths **fused**. Cutting edge of mandible with 1 seta at proximal and **1 seta at distal corner** (Figs. 22 A + D). Praecoxal arthrite of maxillule: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically **with 3 spines and 1 seta, 4 spines and 4 setae lacking (also seta 10 lacking: char. 23: 0→1); formula of armature: 2, III, 1, 0, 0; coxa with short coxal endite with 2 setae**. Syncoxa maxilla (Figs. 22 B + E) with (2 + 2), 2, 3 setae (char. 36: 0→1); **allobasis very large with reduced endite**; accessory armature of allobasis **consisting of a small spine (I?) and 4 setae; claw (I) reduced to spine (?), 2 setae lacking**; endopod 3-segmented with armature formula: **I + 1, I + 1, 4; proximal and middle segment with large spine anteriorly (V + VII)**. Maxilliped (Fig. 22 G): 1-segmented endopod **with 1 small claw (V) on posterior side, 1 small claw (VI) and 1 seta (7) from enp-1 lacking (char. 49: 3→1)**. P5 exopod with **1 surface seta (10)**.

*Male*. Antennule subchirocer with 7 segments; armature formula (?): 1, 1, 11, 9, 10 + aes/ 1, 5 + acrothek, fusion of Oligoarthra segments 4 - 5, 6 - 9, 10 - 11 and 12 - 14; **one characteristically formed cuticular cone on the fused oligoarthran segments 6 - 9**. P5 exopod with **1 surface seta**.



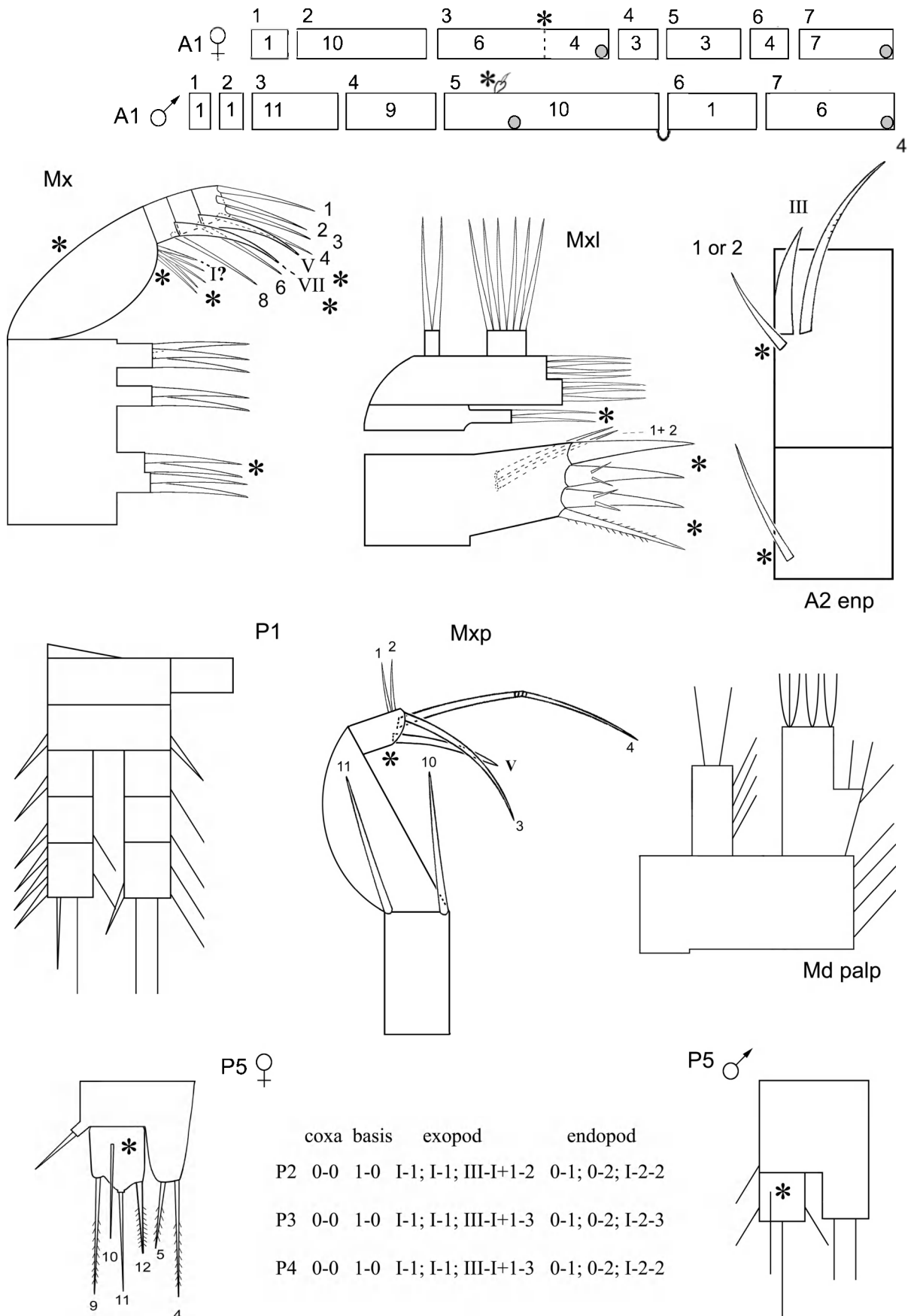


Fig. 21: Groundpattern of Ectinosomatidae. Asterisks mark autapomorphies of Ectinosomatidae.

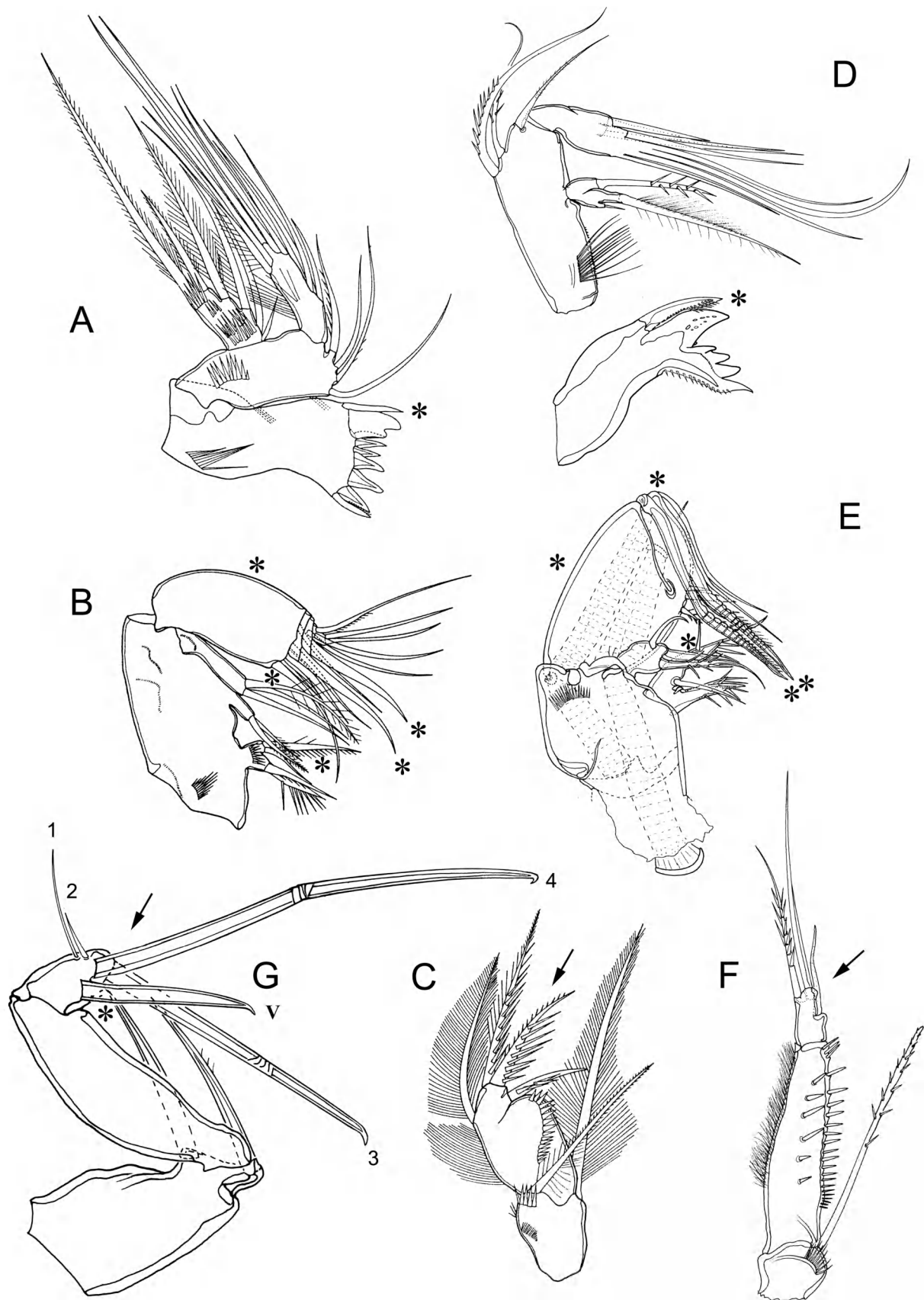


Fig. 22: Mouthparts of Ectinosomatidae. -- *Bradya (B.) typica* (after Huys, et. al., 1996): A. Mandible. B. Maxilla. C. Maxilliped. -- *Ectinosoma carnivora* Seifried & Dürbaum, 2000: D. Mandible. E. Maxilla. F. Maxilliped. G. -- *Bradya (B.) spec. 1*, maxilliped. -- Asterisks mark autapomorphies of Ectinosomatidae. -- Arrows indicate characters discussed in the text.

Groundpattern of Ectinosomatidae (Fig. 21)

*Female*. **Body** without difference in width between prosome and urosome (Fig. 2 A). **Nauplius eye** absent. **Rostrum** incompletely fused at base with cephalothorax. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** divided longitudinally; anus covered by pseudoperculum. **Caudal rami** with 7 setae. **Antennule** indistinctly 7-segmented; armature formula: 1, 10, (6 + 4+aes), 3, 3, 4, 6 + acrothek; segments 3 and 4 of Oligoarthra groundpattern incompletely fused, fusion of Oligoarthra segments 7 and 8. **Antenna** composed of coxa, basis, 2-segmented endopod and 3-segmented exopod; basis without seta, enp-1 with 1 seta displaced to the proximal part of the endopod; enp-2 with 3 subterminal and 7 distal setae; subterminal setation of enp-2 composed of 1 long proximal spine-like seta (1 or 2?), 1 distal spine (III) and 1 distal slightly geniculate seta; spine I or seta 2 lacking; exopod with 2, 1, 2 setae, middle segment shortest. **Labrum** not prominent. **Paragnaths** fused. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal and 1 seta at distal corner (Figs. 22 A + D); palp comprising basis, endopod and exopod; basis wider than high with 4 setae; endopod 1-segmented with 3 setae laterally and 3 + 2 + 2 apical setae, each group of apical setae basally fused; exopod 1-segmented with 4 lateral and 2 distal setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically with 3 spines and 1 seta, 4 spines and 4 setae lacking; formula of armature: 2, III, 1, 0, 0 (?); coxa with short coxal endite with 2 setae, epipodite without setae; basis with 3 + 4 setae; endopod 1-segmented with 6 setae; exopod 1-segmented with 2 setae. **Maxilla** 5-segmented consisting of syncoxa, allobasis, and 3-segmented endopod; syncoxa with (2 + 2), 2, 3 setae, the two proximal endites fused; allobasis very large with reduced endite; accessory armature of allobasis consisting of a small spine (I?) and 4 setae; claw (I) reduced to spine (?), 2 setae lacking; endopod 3-segmented with armature formula: I + 1, I + 1, 4; proximal and middle segment with large spine anteriorly (V + VII). **Maxilliped** 3-segmented, comprising syncoxa, basis and 1-segmented endopod; syncoxa with 2 coxal setae at inner and outer distal corner (10 + 11), 4 setae and spines lacking (12 - 16); basis very large, without setae, 1 spine (VIII) and 1 seta (9) lacking; enp-1 and enp-2 not separated; endopod with 1 thin claw (V) on the posterior side; 1 small claw (VI) and 1 seta (7) of enp-1 missing; high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-1; I-0; III-I+1-1	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** baseoendopod with 1 outer basal seta, endopodal lobe with 2 setae (4 + 5), 3 setae lacking (2 + 3, 6); exopod with 4 setae: 1 inner, 1 terminal, 1 outer and 1 surface seta (9 - 12), 3 setae lacking (7 - 8, 13). **P6** with 1 seta.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** subchirocer with 7 segments; armature formula (?): 1, 1, 11, 9, 10 + aes/ 1, 5 + acrothek, fusion of Oligoarthra segments 4 - 5, 6 - 9, 10 - 11 and 12 - 14; one characteristically formed cuticular cone on the fused oligoarthran segments 6 - 9; aesthetascs of Oligoarthra segments 3 and 4 lacking; aesthetasc on Oligoarthra segment 6 fused at base with a seta. **P5** basis not separated from coxa and endopod; baseoendopod with 1 outer basal seta; endopodal lobe with 2 setae; exopod with 4 setae: 1 inner, 1 terminal, 1 outer and 1 surface seta, 4 setae lacking. **P6** symmetrical, with 3 setae.

#### Remarks on the systematics and morphology of Ectinosomatidae

##### *Systematics.*

Lang (1944) established the taxon Ectinosomidimorpha Lang, 1944 for Ectinosomatidae Sars, 1903. Bowman & Abele (1982) changed Lang's "superfamily"-endings "-idimorpha" in "superfamily"-endings "-oidea" and introduced Ectinosomatoidea Sars, 1903 (International Code of Zoological Nomenclature, fourth edition, Art. 29.2). Ectinosomatoidea Sars, 1903 is synonymized with Ectinosomatidae Sars, 1903 here, as both taxa enclose the same species.

##### *Morphology.*

The monophyletic group Ectinosomatidae is characterized mainly by one seta at the distal corner of the cutting edge of mandible (Figs. 22 A + D), the praecoxal arthrite of the maxillule, with the 6 characteristically grouped spines and setae, the very large allobasis of the maxilla with 1 spine and 4 setae and the reduced endite, the 2 large spines on the endopod of maxilla (Figs. 22 B + E), the surface setae of P5 of females and males, and the characteristically formed cuticular cone on the fused oligoarthran segments 6 - 9 of antennule of male. All species of Ectinosomatidae display all these characters; only all species of *Ectinosoma* and some single species from other genera have no surface setae on the exopod of P5. The seta at the distal corner of the cutting edge of mandible is additional to the oligoarthran groundpattern. To my knowledge no described species of Copepoda has this extraordinary seta. Ectinosomatidae are without doubt monophyletic and belong to Oligoarthra.

The morphology of the 233 described and innumerable undescribed species of Ectinosomatidae is very diverse. Only species of *Bradya* come close to the hypothetical morphology of the members of the last common population of Ectinosomatidae. *Bradya (Bradya)* spec. 1 is very plesiomorphic compared with all other Ectinosomatidae. This species will be described elsewhere. Originating from the groundpattern, many variations evolved within Ectinosomatidae. It would exceed the scope of this discussion to merely report the strong alterations.

The setae and spines of **maxillule, maxilla and antennule of females and males** are very difficult to observe and their homology is uncertain. The groundpattern should therefore be regarded with care.

The **rostrum** of *Bradya (B.)* spec. 1 is only incompletely fused with the cephalothorax. No species of Ectinosomatidae has a seta on the basis of **antenna**. The descriptions of *B. (B.) cladiofera* Lang, 1965, *B. (Parabradya) dilatata* Sars, 1904 and the description by Sars (1904) of *B. (B.) typica* Boeck, 1872 show such seta, but it is the seta of enp-1,

which inserts at the proximal part of the endopod (for museum material see chapter 8.2).

The cutting edge of the **mandible** of some *Halectinosoma* species has 2 setae at the proximal corner. This is a secondary phenomenon. The more plesiomorphic Ectinosomatidae such as *Bradya* and *Pseudobradya* species have 1 seta at the proximal corner (see chapter 4.1).

*Bradya* species have discrete teeth on the cutting edge. This appears to be a secondary phenomenon as well, because all outgroup taxa have teeth that are not delimited.

The most likely formula of armature of the praecoxal arthrite of **maxillule** is: 2, III, 1, 0, 0. It is also possible that the groundpattern is 2, III, 1, 2, 0; the latter armature formula is achieved, when a different homologisation of setae and spines within different genera is used; the morphology of the spines and setae differs a little bit within different genera. However, the latter formula is less probable, because no single species has more than 6 spines and setae on the praecoxa.

For the discussion of reduction of setae in the maxillular praecoxa and **maxillar** syncoxa see chapter 5.2.3 (char. **23**: 0→1; char. **36**: 0→1).

*Bradya* (*B.*) spec. 1 is the only species of Ectinosomatidae with the typical **maxillipedal** endopod of Syngnathartha (Fig. 22 G). This species shows that the ancestors of all Ectinosomatidae had a thin claw (V), 2 distal geniculated setae and 2 outer small setae on the endopod. One claw (VI) and 1 seta (7) of the fused proximal endopod segment are lost (see chapters 5.1.5, 5.2.3 and 5.2.4; chars **48** - **50**). Consequently, the homology of the claw is not absolutely clear. However, the thin claw is displaced to the posterior side of the endopod like the claw V of other Syngnathartha. The claw of Ectinosomatidae is a small realization of large claw V of Syngnathartha. All other species of Ectinosomatidae have reduced the characteristic features of the endopod of Syngnathartha and evolved an endopod with 4 setae: 1 inner seta, 2 distal setae and 1 outer seta (Figs. 22 C + F). Within the different taxa of Ectinosomatidae the forms of these setae are very variable.

*Hastigerella scheibeli* has a surface seta on the enp-3 of **P2**, **P3** and **P4** (Mielke, 1975). Assuming that this seta is the plesiomorphic seta of Oligoarthra, all three swimming legs would have I-2-3 setae on the distal segment in the groundpattern of Oligoarthra. This would mean one lateral seta on P2 and P4 more than in all other species of Oligoarthra. It is more likely that these additional setae of *H. scheibeli* are duplicates of the distal lateral seta, displaced to the surface of the endopod. Examination of the holotype shows that the surface setae and the distal lateral setae insert directly next to each other.

The **antennule of the male** is usually not described in detail and the characteristically formed cuticular cone on the fused oligoarthran segments 6 -9 mostly can be observed only, when the males are dissected. However, it appears that all males of Ectinosomatidae have this typical cone, e.g. *Bradya* (*B.*) spec. 1, *Bradya* (*B.*) spec. 2, *Ectinosoma* species (Seifried, 1997, Seifried & Dürbaum, 2000) and all other analysed species of Ectinosomatidae.

Some of the undescribed males of Ectinosomatidae have an asymmetrical **P6**, but not all of them. It seems that an asymmetrical P6 has evolved within Ectinosomatidae.

## 4.12 Exanechentera Lang, 1944

### Taxa belonging to Exanechentera (485 species in 74 genera)

Idyanthidae Lang, 1944, Novocriniidae Huys & Iliffe, 1998, Paramesochridae Lang, 1944, Peltidiidae Sars, 1904, Porcellidiidae Boeck, 1865, Rotundiclipeidae Huys, 1988, Superornatiremidae Huys, 1996, Tachidiidae Sars, 1909, Tegastidae Sars, 1904, Tisbidae Stebbing, 1910 *sensu strictu*, Zosimidae fam. nov.

### Changes in systematics (reasons given below)

Novocriniidae Huys & Iliffe, 1998, Paramesochridae Lang, 1944, Rotundiclipeidae Huys, 1988, and Superornatiremidae Huys, 1996 are integrated in Exanechentera Lang, 1944.

Thompsonulidae Lang, 1944 is excluded from Exanechentera Lang, 1944 and is transferred to Podogennonta Lang, 1944 (see chapter 4.9).

### Diagnosis: Autapomorphies of Exanechentera (Fig. 4: ■ 15; Figs. 23 -25)

*Female.* Distal border of antennal endopod **bevelled with an angle towards the exopod** (Figs. 24 A - E; char. 13: 0→1). Gnathobase of mandible **with bulge at proximal border** (Figs. 24 G - F; 37 C, E, F; char. 16: 0→1).

*Male.* Antennule **with a claw with a pointed end formed by oligoarthran segments 10 to 14** (Fig. 25; char. 67: 0→1).

### Groundpattern of Exanechentera (Fig. 23)

*Female.* **Body** with difference in width between prosome and urosome. **Nauplius eye** present. **Rostrum** delimited at base. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 13, 10, 6 + aes, 3, 4, 2, 2, 6 + acrothek. **Antenna** composed of coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 4 subterminal and 7 distal setae; subterminal setation of enp-2 composed of 1 short proximal spine (I), 1 longer distal spine (III), 1 distal geniculate seta (4) and 1 bare slender seta (2); seta 2 inserts between spine I and seta 4; distal border of endopod is slightly bevelled with an angle towards the exopod (Figs. 24 A - E); exopod with 2, 1, 1, 3 setae. **Labrum** not prominent. **Paragnaths** separated. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner and bulge at proximal border (Figs. 24 F - J); palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 3 lateral setae and 3 + 2 + 2 apical setae, each group of apical setae basally fused; exopod 2-segmented with proximal segment with 4 lateral setae and distal segment with 2 distal setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III - IX; at least 2 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose

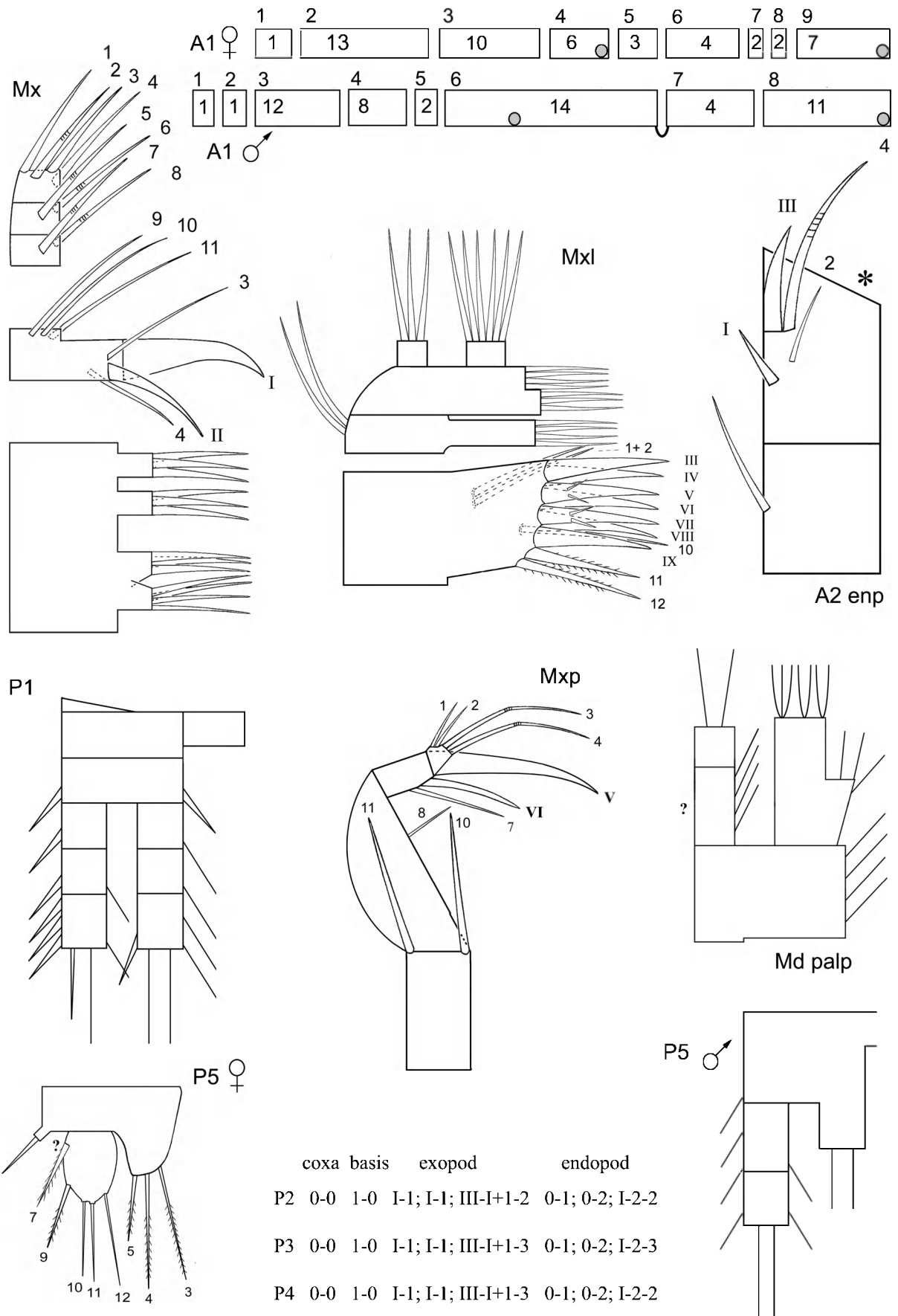


Fig. 23: Groundpattern of Exanechentera. Asterisks mark autapomorphies of Exanechentera.

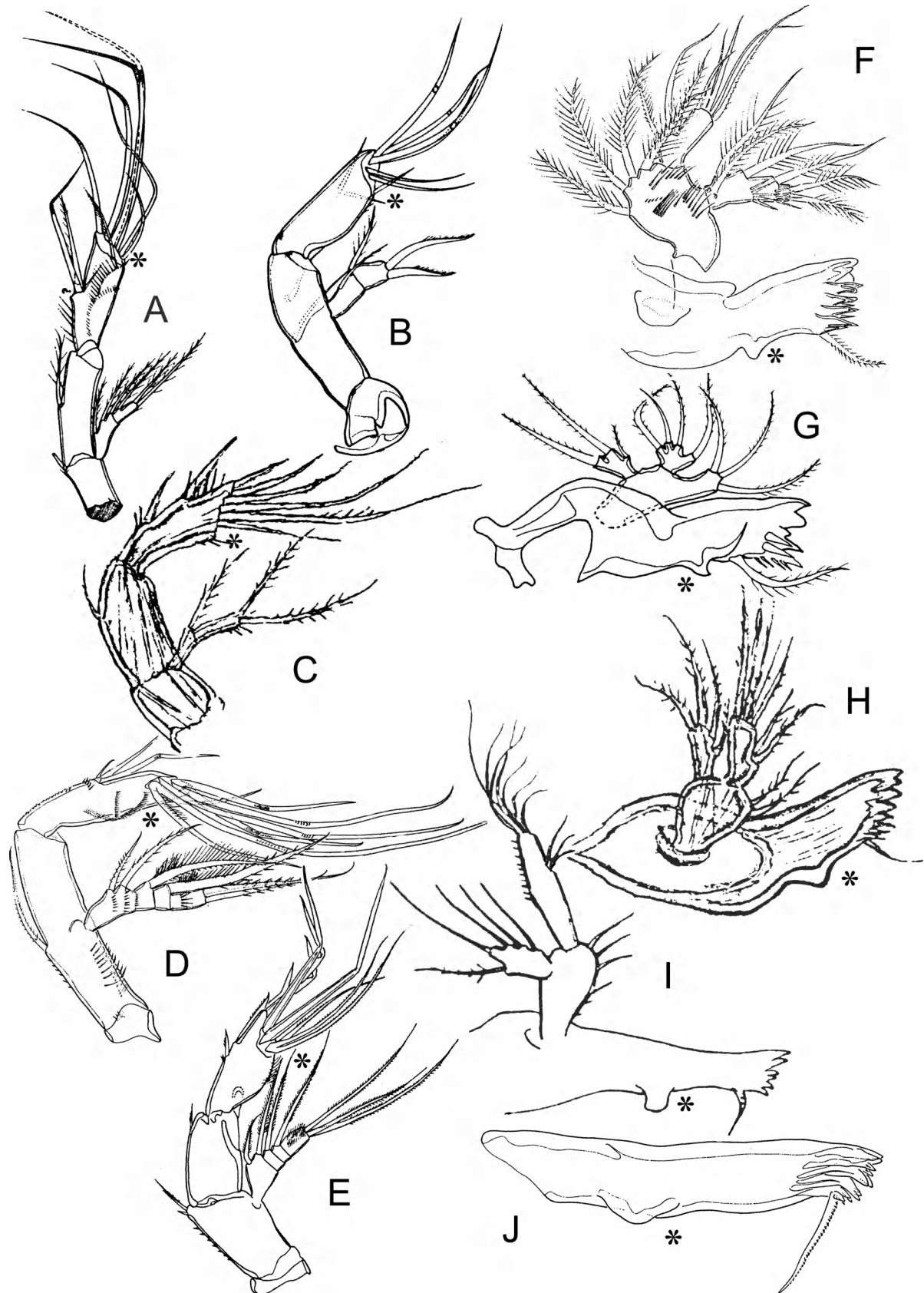


Fig. 24: A2 and Md of Exanechentera. --- A2: A. *Idyella kunzi* Bodin, 1968 (after Bodin, 1968). B. *Diarthrodella neotropica* Mielke, 1984 (after Mielke, 1984). C. *Tachidius* (*T.*) *discipes* (after Sars, 1910). D. *Neoechinophora fosshageni* (after Huys, 1996). E. *Scutellidium boreale* Itô, 1976 (after Itô, 1976). --- Md: F. *Tachidiella kimi* (after Lee & Huys, 1999). G. *Zosimi pacifica* Fiers, 1991 (after Fiers, 1991). H. *Tachidius* (*T.*) *discipes* (after Sars, 1910). I. *Tisbisoma spiniseptum* Bozic, 1964 (after Bozic, 1964). J. *Novicrinia trifida* (after Huys & Iliffe, 1998). -- Asterisks mark autapomorphies of Exanechentera.



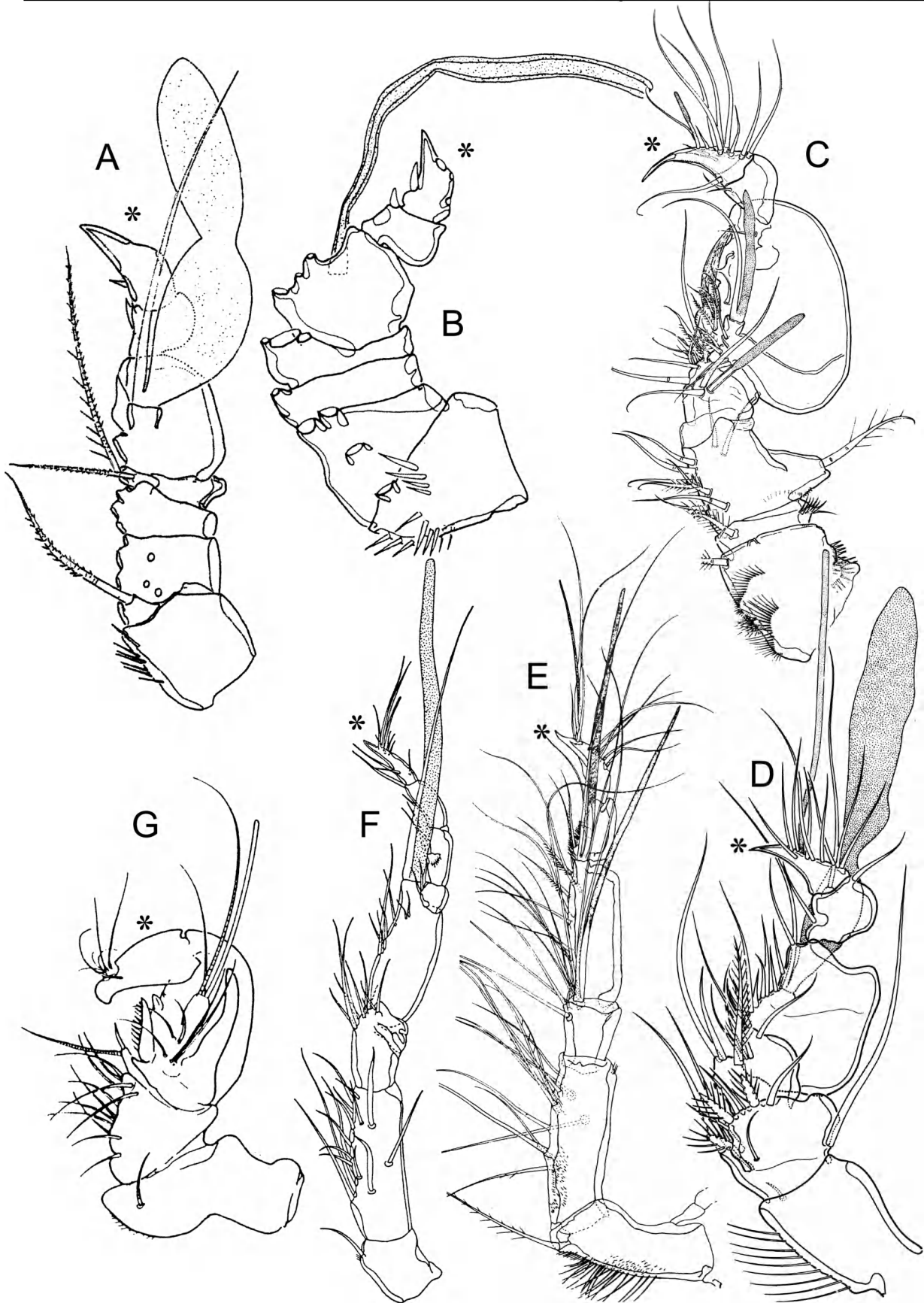


Fig. 25: Male antennules of Exanechentera. A. *Tachidiella kimi* (after Lee & Huys, 1999). B. *Zosime pacifica* (after Fiers, 1991). C. *Geeopsis incisipes* (after Huys & Boxshall, 1991). D. *Paramesochra mielkei* (after Huys & Boxshall, 1991). E. *Eupelte villosa* (after Dahms, 1992). F. *Paraidya occulta* (after Humes & Ho, 1969). G. *Porcellidium pulchrum* Harris & Robertson, 1994 (after Harris & Robertson, 1994). -- Asterisks mark the claw of the male antennules.

setae (11 + 12), 2 proximal setae (13 + 14) of posterior surface lacking; formula of armature: 2, VII, 1, 2, 0; coxa with 4 setae, epipodite represented by 2 seta; basis with 3 + 4 setae; endopod 1-segmented with 6 setae; exopod 1-segmented with 3 setae. **Maxilla** 5-segmented consisting of syncoxa, allobasis, and 3-segmented endopod; syncoxa with (4 + 3), 3, 3 setae, the two proximal endites fused; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II) and 1 seta (3) on anterior surface and 1 seta (4) on posterior surface; tube pore on anterior surface lacking; accessory armature of fused endopod segment of 2 setae on anterior surface (9 + 10) and 1 seta on posterior surface (11); endopod with armature formula: 2, 2, 4; proximal and middle segment with 2 geniculated setae (5 - 8), last segment with 1 geniculated seta (2). **Maxilliped** subchelate and 4-segmented, comprising syncoxa, basis and 2-segmented endopod; syncoxa with 2 coxal setae (10 + 11), inserting on inner and outer border; basis with 1 seta on inner edge (8); enp-1 with 1 seta (7) and 1 thin claw (VI) and 1 large claw (V) displaced to the posterior side of the distal end of enp-1; enp-2 reduced in size with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4); high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** baseoendopod with 1 outer basal seta, endopodal lobe with 3 setae (3 - 5): 1 inner setae and 2 terminal setae; exopod with 5 setae (7, 9 - 12): 1 inner seta, 2 terminal seta, 2 outer spines. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** subchirocer with 8 segments; armature formula: 1, 1, 12, 8, 2, 14 + aes/ 4, 10 + acrothek, fusion of Oligoarthra segments 6 - 9, 10 - 11 and 12 - 14; aesthetascs of Oligoarthra segments 3 and 4 lacking; aesthetasc on Oligoarthra segment 6 fused at base with a seta; segments 7 and 8 (oligoarthran segments 10 - 14) forming claw with a pointed end (Fig. 25) forming a functional unit with segment 6 (oligoarthran segments 6 - 9). **P5** basis not separated from coxa and endopod, endopod with 2 setae and 2-segmented exopod with 2-1, 1-2-1 setae. **P6** symmetrical, with 3 setae.

#### Remarks on the systematics and morphology of Exanechentera

##### *Systematics.*

Lang (1944) established Exanechentera for Harpacticidae, Tachidiidae, Clytemnestridae, Peltidiidae, Tegastidae, Porcellidiidae, and Tisbidae *sensu* Lang. Harpacticidae belong to Podogennonta as discussed by Willen (2000). Thompsonulidae -formerly a subfamily of Tachidiidae- is excluded from Exanechentera and is transferred to Podogennonta (see chapter 4.9). Clytemnestridae is synonym to Peltidiidae (see chapter 4.24). Martínez Arbizu & Moura (1998) and

Willen (2000) excluded Paramesochridae from Podogenmonta, because this taxon does not share the autapomorphies. Paramesochridae is integrated in Exanechentera (see chapter 4.16). The newly described taxa Novocriniidae, Rotundiclipeidae, and Superornatiremidae are integrated in Exanechentera (see chapters 4.18 - 4.22 and 5.2.3). The monophyly of Exanechentera is confirmed (see chapter 5.2.4).

#### *Morphology.*

Species of Idyanthidae resemble the groundpattern of Exanechentera, apart from the autapomorphies of Idyanthidimorpha and Idyanthidae (chapters 4.13 and 4.14).

For the discussion of the bevelled **antennal endopod** (char. 13: 0→1; Figs. 24 A - E), the bulge at the **gnathobase of mandible** (char. 16: 0→1; Figs. 24 F - J) and the claw of the **male antennule** (char. 67: 0→1; Fig. 25) see chapters 5.2.3 and 5.2.4.

### 4.13 Idyanthidimorpha tax. nov.

#### Etymology

The taxon name is derived from Greek morph- = form, shape, appearance, beauty. The name of the taxon is selected in honour of Karl Lang for his contribution to the systematics of Harpacticoida, which includes the revision of all species of Harpacticoida described at that time (Lang, 1944, 1948). Karl Lang (1944, 1948) named many of his new taxa after a typical or common species group and introduced therefore the ending "-idimorpha". Idyanthidimorpha tax. nov. is no "superfamily".

#### Taxa belonging to Idyanthidimorpha (35 species in 9 genera)

Idyanthidae Lang, 1944, Zosimidae fam. nov.

#### Diagnosis: Autapomorphies of Idyanthidimorpha (Fig. 4: ■ 16; Figs. 26 + 27)

*Female.* Coxal setae 10 and 11 of maxilliped **inserting subapical at inner and outer border** (char. 44: 1→2; Figs. 29 B + C). The outer spine of the P1 enp-3 is **displaced terminally**; all exopodal spines of P1 **elongated and with very long spinules on one side**, but exp-3 not small and rounded (char. 56: 0→1; Fig. 30).

*Male.* Enp-3 of P2 terminally **with modified bare spine (I) fused at base (originated from displaced outer spine), 1 middle hyaline seta (2) and 1 inner terminal seta** (Fig. 27 A; char. 69: 0→1).

#### Groundpattern of Idyanthidimorpha (Fig. 26)

*Female.* **Body** width differs between prosome and urosome (Fig. 2 B). **Nauplius eye** present. **Rostrum** delimited at base. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 11, 10, 4 + aes, 3, 4, 2, 2, 6 + acrothek. **Antenna** composed of coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 4 subterminal and 7 distal setae;

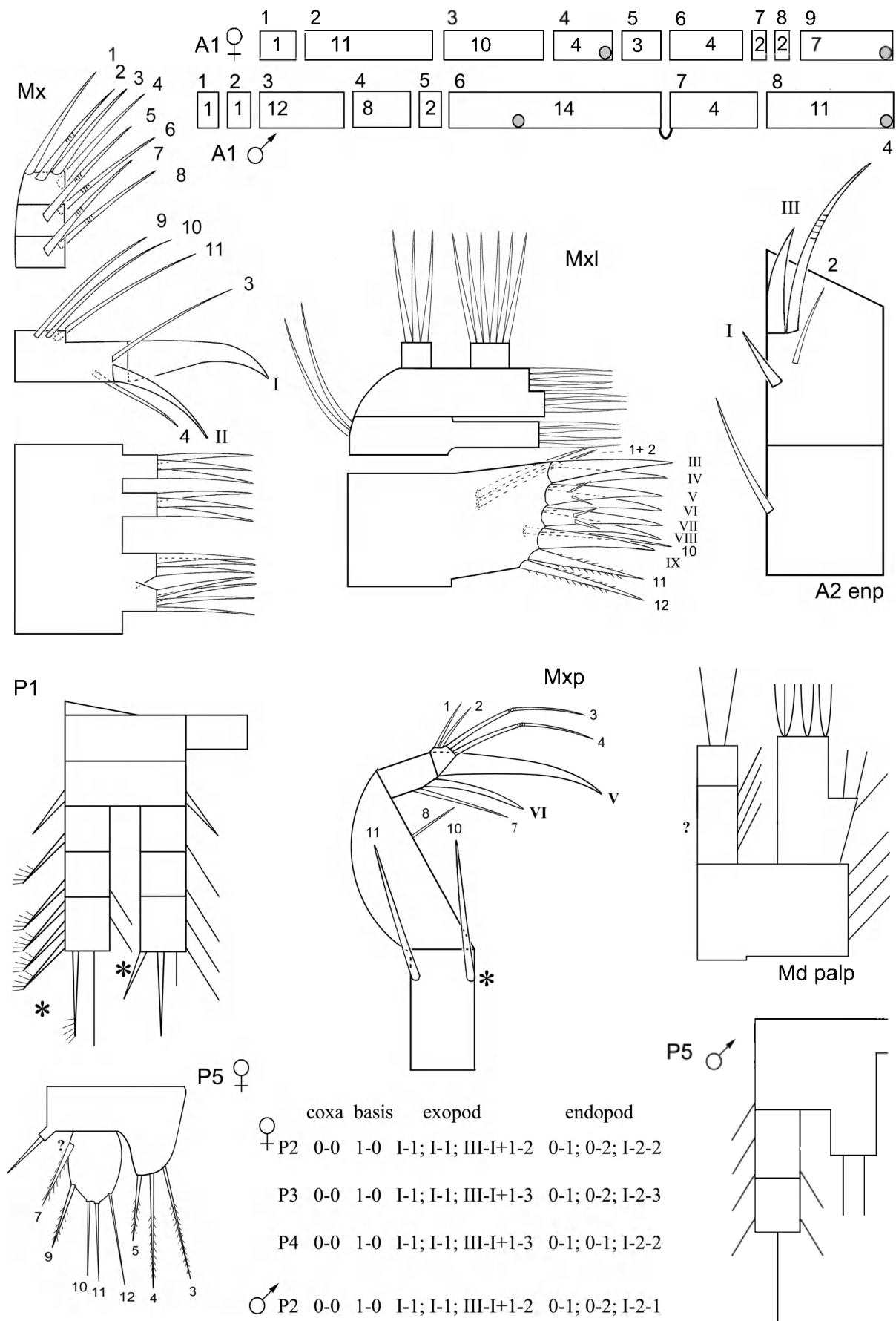


Fig. 26: Groundpattern of Idyanthidimorpha. Asterisks mark autapomorphies of Idyanthidimorpha.

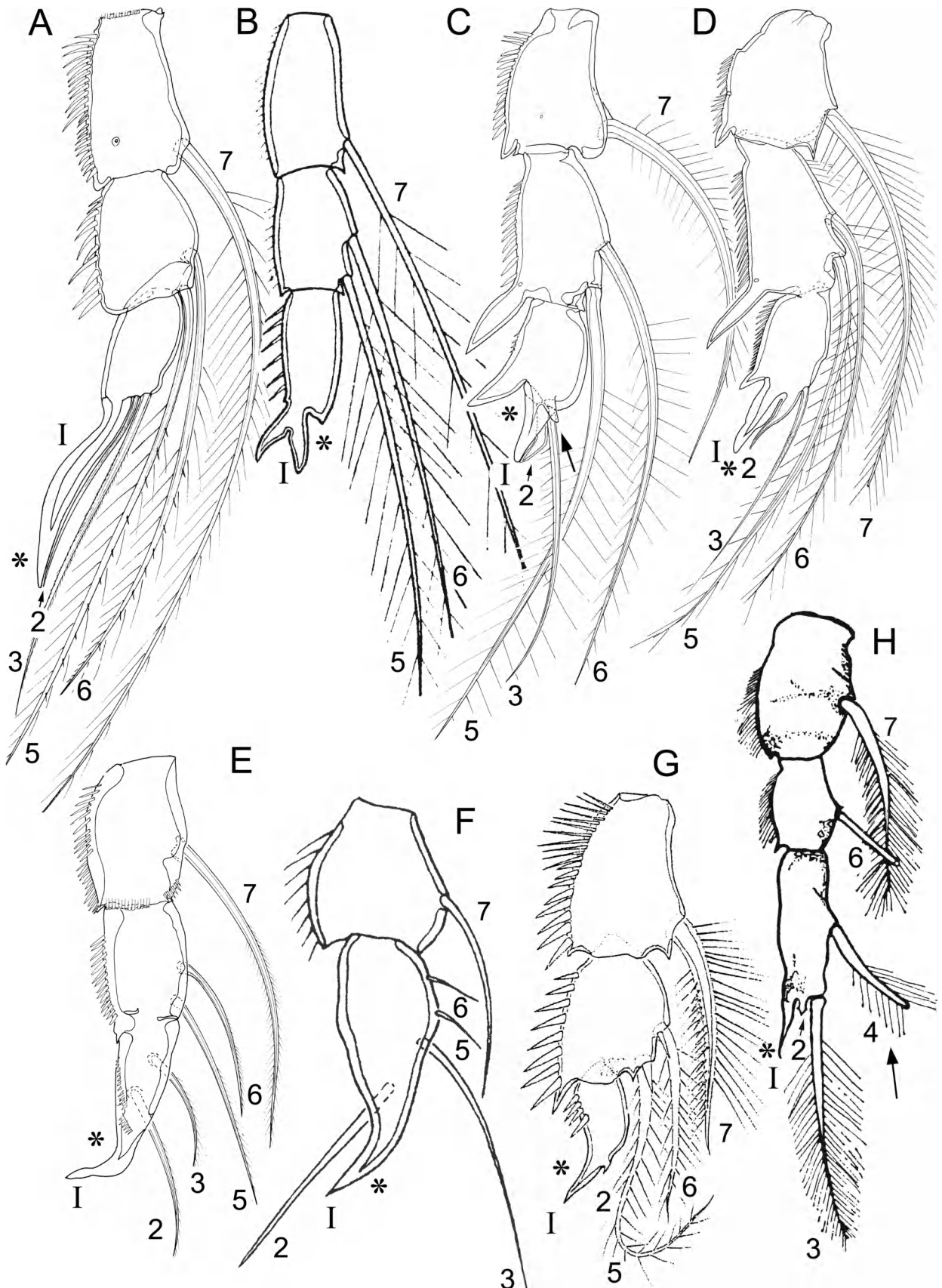


Fig. 27: Male endopod P2 of Idyanthidae and Zosimidae. A. *Idyanthe* spec. 2. B. *Idyanthe dilatata* Sars, 1905 (after Mielke, 1974). C. *Idyella* spec. 1. D. *Idyella* spec. 2. E. *Idyellopsis* spec. 2. F. *Dactylophia peruana* Becker, 1974 (after Becker, 1974). G. *Tachidiella kimi* (after Lee & Huys, 1999). H. *Zosime incrassata* Sars, 1910 (after Coull, 1973). -- Asterisks mark the sexual dimorphism of the males. -- Arrows indicate characters discussed in the text.

subterminal setation of enp-2 composed of 1 short proximal spine (I), 1 longer distal spine (III), 1 distal geniculate seta (4) and 1 bare slender seta (2); seta 2 inserts between spine I and seta 4; distal border of endopod is slightly bevelled with an angle towards the exopod; exopod with 2, 1, 1, 3 setae. **Labrum** not prominent. **Paragnaths** separated. **Mandible** with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner and bulge at proximal border; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 3 lateral setae and 3 + 2 + 2 apical setae, each group of apical setae basally fused; exopod 2-segmented with proximal segment with 4 lateral setae and distal segment with 2 distal setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III – IX; at least 2 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), 2 proximal setae (13 + 14) of posterior surface lacking; formula of armature: 2, VII, 1, 2, 0; coxa with 4 setae, epipodite represented by 2 seta; basis with 3 + 4 setae; endopod 1-segmented with 6 setae; exopod 1-segmented with 3 setae. **Maxilla** 5-segmented consisting of syncoxa, allobasis, and 3-segmented endopod; syncoxa with (4 + 3), 3, 3 setae, the two proximal endites fused; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II) and 1 seta (3) on anterior surface and 1 seta (4) on posterior surface; tube pore on anterior surface lacking; accessory armature of fused endopod segment of 2 setae on anterior surface (9 + 10) and 1 seta on posterior surface (11); endopod with armature formula: 2, 2, 4; proximal and middle segment with 2 geniculated setae (5 - 8), last segment with 1 geniculated seta (2). **Maxilliped** subchelate and 4-segmented, comprising syncoxa, basis and 2-segmented endopod; syncoxa with 2 coxal setae (10 + 11), inserting subterminally on inner and outer border; basis with 1 seta on inner edge (8); enp-1 with 1 seta (7) and 1 thin claw (VI) and 1 large claw (V) displaced to the posterior side of the distal end of enp-1; enp-2 reduced in size with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4); high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; P1 of characteristic shape: enp-3 terminally with 2 spines (1 spine derived from displaced outer spine) and 1 seta; outer and distal spines of exopod elongated and ornamented terminally with very long spinules on one side; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; I-I+1-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** baseoendopod with 1 outer basal seta, endopodal lobe with 3 setae (3 - 5): 1 inner seta and 2 terminal setae; exopod with 5 setae (7, 9 - 12): 1 inner seta, 2 terminal setae, 2 outer spines. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P2, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** subchirocer with 8 segments; armature formula: 1, 1, 12,

8, 2, 14 + aes/ 4, 10 + acrothek, fusion of Oligoarthra segments 6 - 9, 10 - 11 and 12 - 14; aesthetascs of Oligoarthra segments 3 and 4 lacking; aesthetasc on Oligoarthra segment 6 fused at base with a seta; segments 7 and 8 (oligoarthran segments 10 - 14) forming claw with a pointed end (Figs. 25 A + B) forming a functional unit with segment 6 (oligoarthran segments 6 - 9). **P2** enp-3 with 1 inner seta; terminally with big modified bare spine (1) fused at base with segment (derived from displaced outer spine), 1 middle hyaline seta (2) and 1 inner terminal seta (3) (Figs. 27 A + D); armature formula:

	coxa	basis	exopod	endopod
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-1

**P5** fused medially; basis not separated from coxa and endopod; endopod with 2 setae and 2-segmented exopod with 2-1, 1-1-1 setae. **P6** symmetrical, with 3 setae.

#### Remarks on the morphology of Idyanthidimorpha

There is no question that Zosimidae and Idyanthidae are sister taxa (see chapters 5.1.5 and 5.2.4). These two taxa are characterized by strong autapomorphies. For the discussion of the subapically inserting coxal setae of **maxilliped** (char. 44: 1→2; Fig. 29), the modified exopodal spines of **P1** (char. 56: 0→1; Fig. 30), and the **sexual dimorphism** (char. 69: 0→1; Fig. 27) see chapters 5.2.3 and 5.2.4.

Although the species of Idyanthidae have retained more plesiomorphic characters, this taxon evolved specific autapomorphies (see chapter 4.14). The species of Zosimidae are very characteristic (see chapter 4.15). Many derived characters evolved in the ancestor line of this unique monophylum.

Due to the more derived morphology of Zosimidae, it is not clear whether some apomorphies are autapomorphies of Idyanthidae or synapomorphies of Idyanthidae and Zosimidae (see chapter 4.14).

## 4. 14 Idyanthidae Lang, 1944

### Type genus

*Idyanthe* Sars, 1909

This name was proposed by Sars (1909) to replace *Idyopsis* Sars, 1905, because the latter name was already used.

### Type species

*Idyopsis dilatata* Sars, 1905 is fixed here as type species of *Idyanthe* Sars, 1909 (International Code of Zoological Nomenclature, fourth edition, Art. 67.1.2). *Idyanthe dilatata* (Sars, 1905) is the junior homonym of *Idyopsis dilatata* Sars, 1905 (*Idyanthe dilatata* in 8.2 Appendix II. Museum material).

### Taxa belonging to Idyanthidae (18 species in 6 genera)

*Dactylophia* Becker, 1974, *Idyanthe* Sars, 1909, *Idyella* Sars, 1906, *Idyellopsis* Lang, 1944, *Styracothorax* Huys, 1993, *Tachidiella* Sars, 1909.

Undescribed species (8.1 Appendix I): Idyanthidae gen. spec. 1, Idyanthidae gen. spec. 2, Idyanthidae gen. spec. 3, Idyanthidae gen. spec. 4, Idyanthidae gen. spec. 5,

Idyanthidae gen. spec. 6, Idyanthidae gen. spec. 7, Idyanthidae gen. spec. 8, Idyanthidae gen. spec. 9, Idyanthidae gen. spec. 10, Idyanthidae gen. spec. 11, *Idyanthe* spec. 1, *Idyanthe* spec. 2, *Idyella* spec. 1, *Idyella* spec. 2, *Idyella* spec. 3, *Idyella* spec. 4, *Idyella* spec. 5, *Idyella* spec. 6, *Idyella* spec. 7, *Idyellopsis* spec. 1, *Idyellopsis* spec. 2, *Idyellopsis* spec. 3, *Tachidiella* spec.

#### Changes in systematics (reasons given below)

Lang (1944) established Idyanthinae Lang, 1944. Idyanthinae is excluded from Tisbidae Stebbing, 1910 *sensu strictu* and is raised to family rank here (see chapter 4.26).

*Tachidiopsis* Sars, 1911 is excluded from Idyanthidae and is transferred to Neobradylidae Olofsson, 1917 (see chapter 4.8).

*Neoscutellidium* Zwerner, 1967 is excluded from Idyanthidae and is transferred to Cholidiinae Boxshall, 1979 (see chapter 4.26).

*Zosime* Boeck, 1872, *Peresime* Dinet, 1974, and *Pseudozosime* Scott, 1912 are excluded from Idyanthidae and are combined in Zosimidae fam. nov. (see chapter 4.15).

*Dactylophia* Becker, 1974 is integrated in Idyanthidae.

Styracothoracidae Huys, 1993 is synonymized with Idyanthidae (Martínez Arbizu & Moura, in prep.)

*Dactylophia* Becker, 1974 together with *Idyanthe* Sars, 1909, *Idyella* Sars, 1906, *Idyellopsis* Lang, 1944, *Styracothorax* Huys, 1993, *Tachidiella* Sars, 1909 represent the taxon Idyanthidae Lang, 1944.

#### Diagnosis: Autapomorphies of Idyanthidae (Fig. 4: ■ 17; Figs. 28 + 30 A)

**Female.** Exopod of mandible 2-segmented with long proximal segment with 4 lateral setae and short distal segment with 2 distal setae. Exopod of maxillule elongated. P1 of characteristic shape (Fig. 30 A): **enp-1 elongated and broadened on the level of the inner seta, enp-2 and enp-3 short** (char. 53: 0→1); terminally with claw (derived from displaced outer spine), 1 middle spine and 1 seta; outer and distal spines of exopod elongated, ornamented terminally with very long spinules on one side (autapomorphy of Idyanthidimorpha). The 2 outer spines of exopod P5 **inserting near the basis** and near the distal outer edge respectively (7 + 9).

**Male.** P2 enp-3 **without inner setae, the 2 inner setae of female lacking**; terminally with big modified bare spine (1) fused at base with segment (derived from displaced outer spine), 1 middle hyaline seta (2) and 1 inner terminal seta (3) (autapomorphy of Idyanthidimorpha; Figs. 27 A - G);

	coxa	basis	exopod	endopod
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; <b>I-2-0</b>

#### Groundpattern of Idyanthidae (Fig. 28)

**Female.** **Body** width differs between prosome and urosome (Fig. 2 B). **Nauplius eye** present. **Rostrum** delimited at base. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided



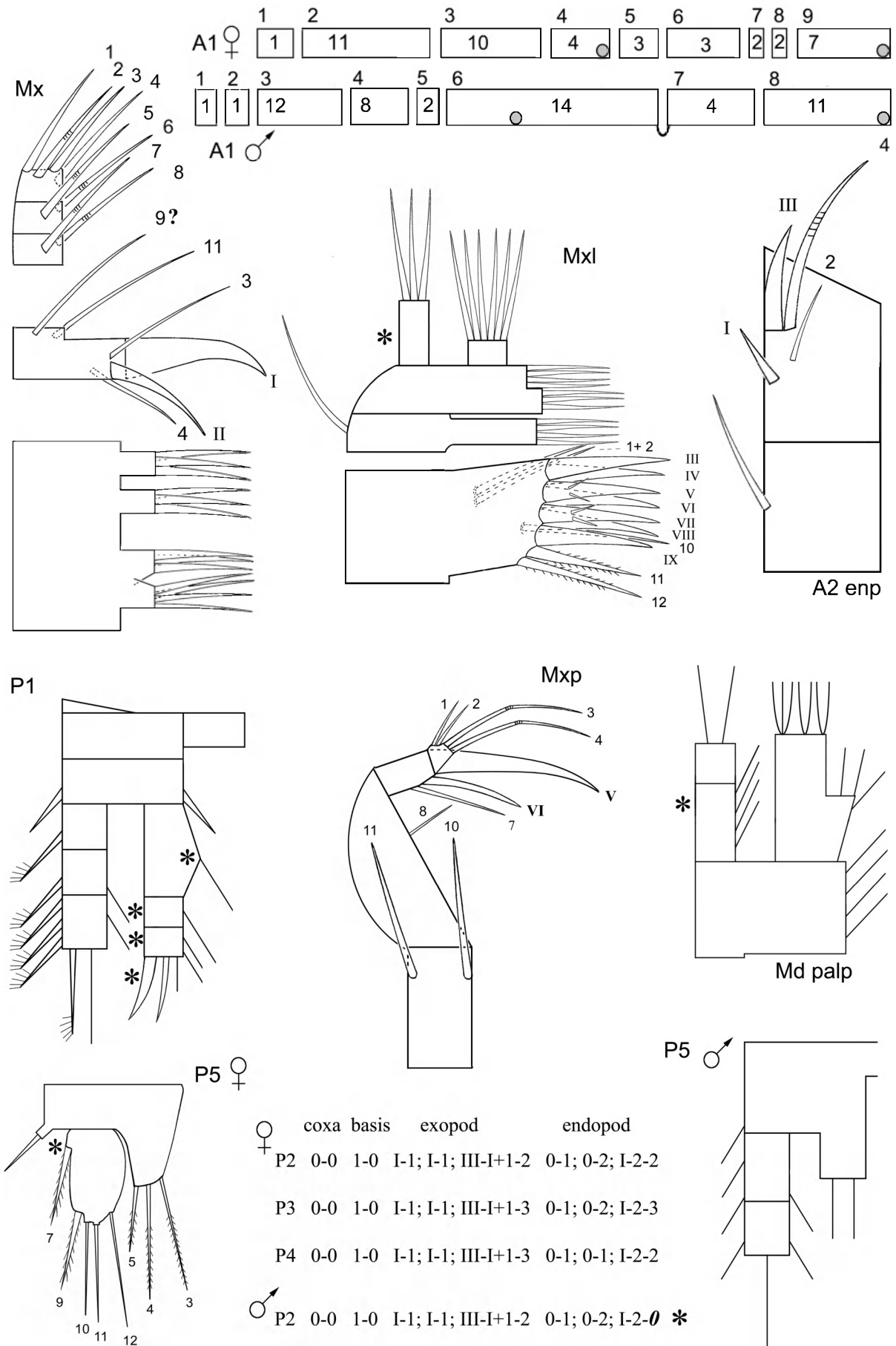


Fig. 28: Groundpattern of Idyanthidae. Asterisks mark autapomorphies of Idyanthidae.

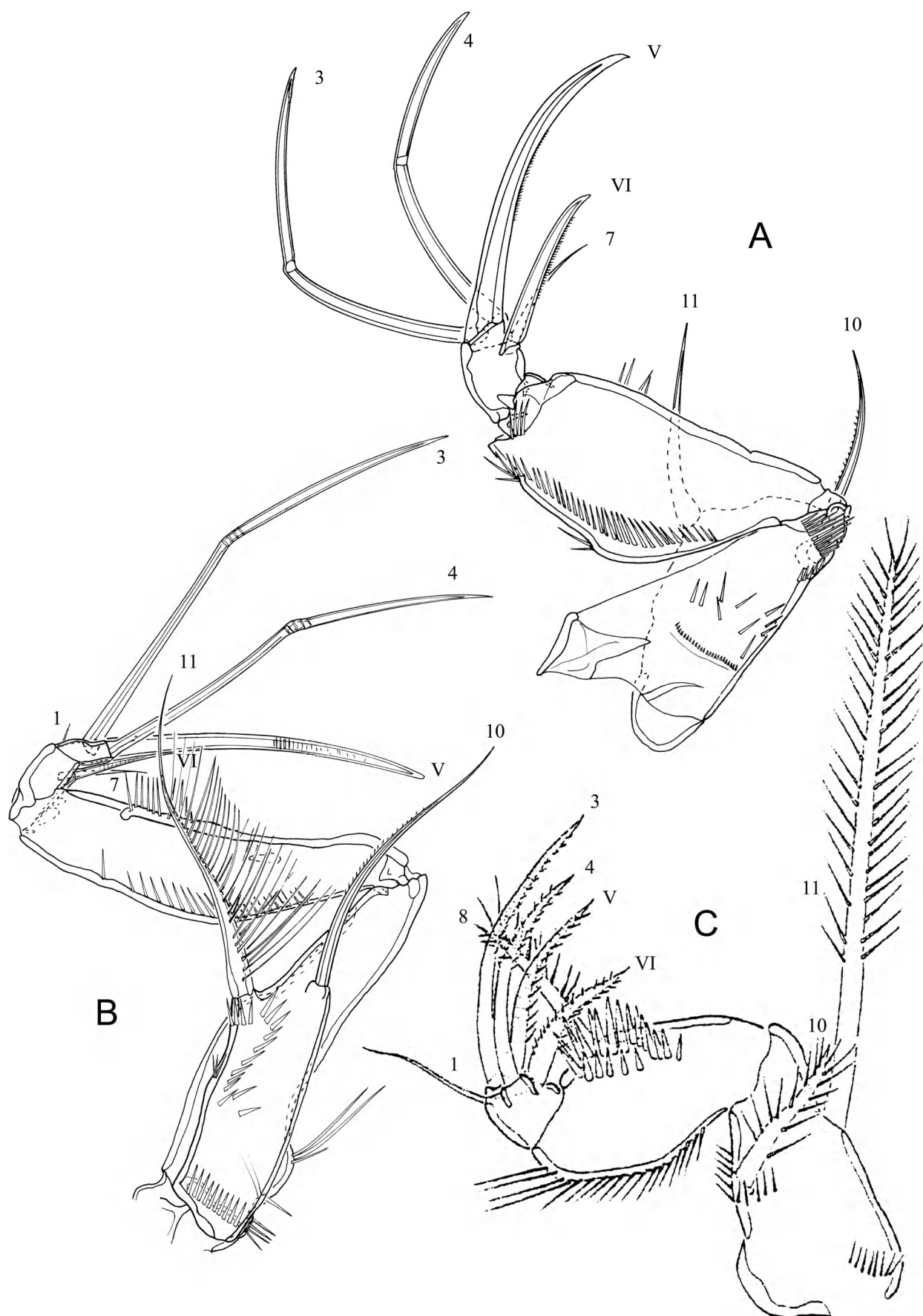


Fig. 29: Maxillipeds of Idyanthidae: A. *Idyanthe* spec 2. B. *Idyella* spec 2. C. *Tachidiella kimi* (after Lee & Huys, 1999).

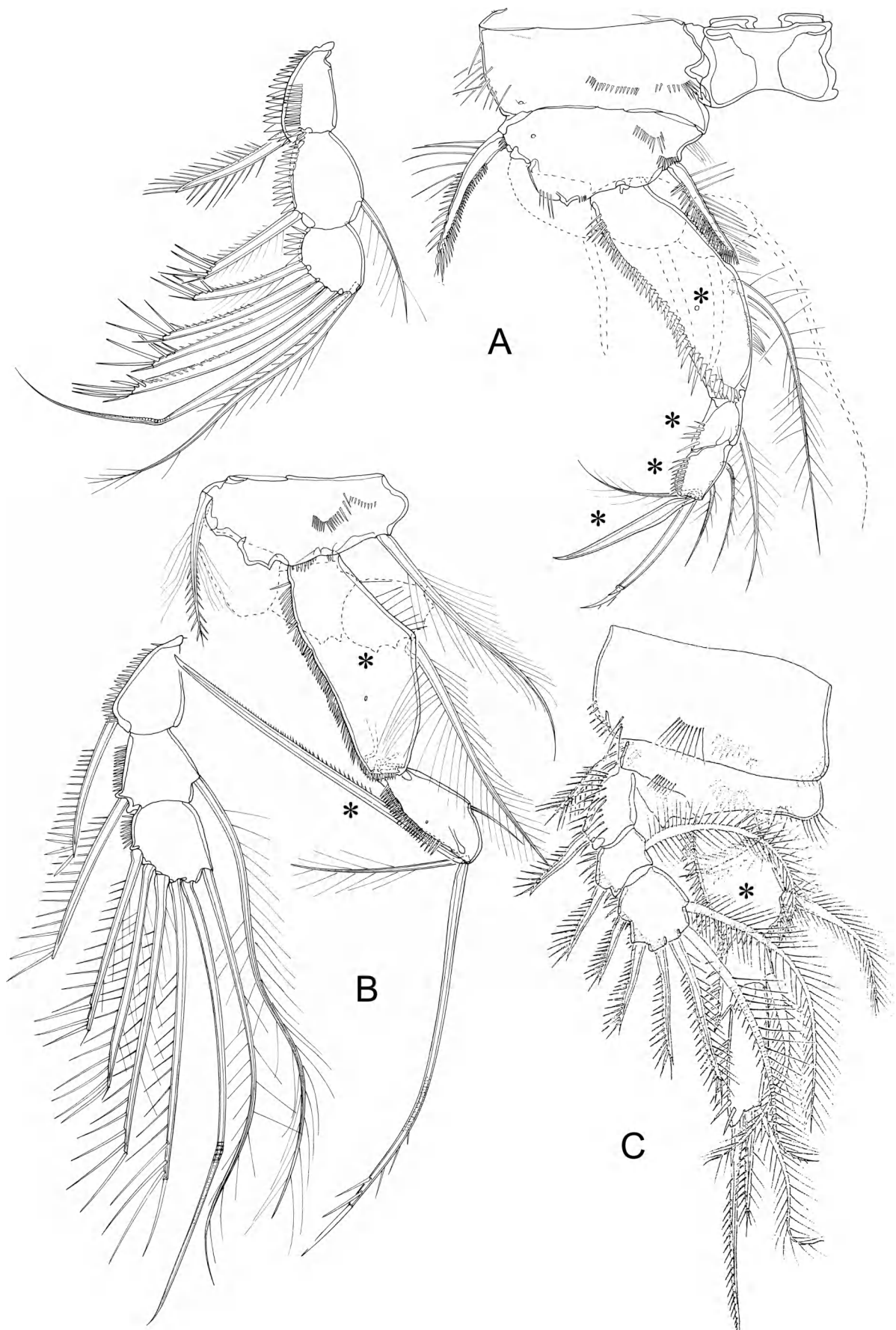


Fig. 30: P1 of Idyanthidae. A. *Idyanthe* spec. 2. B. *Idyella* spec. 2. C. *Tachidiella kimi* (after Lee & Huys, 1999). -- Asterisks mark some autapomorphies of Idyanthidae.

longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 11, 10, 4 + aes, 3, 3, 2, 2, 6 + acrothek. **Antenna** (Fig. 24 A) composed of coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 4 subterminal and 7 distal setae; subterminal setation of enp-2 composed of 1 short proximal spine (I), 1 longer distal spine (III), 1 distal geniculate seta (4) and 1 bare slender seta (2); seta 2 inserts between spine I and seta 4; distal border of endopod is slightly bevelled with an angle towards the exopod; exopod with 2, 1, 1, 3 setae. **Labrum** not prominent. **Paragnaths** separated. **Mandible** (Fig. 24 F) with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner and bulge at proximal border; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 3 lateral setae and 3 + 2 + 2 apical setae, each group of apical setae basally fused; exopod 2-segmented with long proximal segment with 4 lateral setae and short distal segment with 2 distal setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III – IX; at least 2 posterior spines with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), 2 proximal setae (13 + 14) of posterior surface lacking; formula of armature: 2, VII, 1, 2, 0; coxa with 4 setae, epipodite represented by 1 seta; basis with 3 + 4 setae; endopod 1-segmented with 6 setae; exopod 1-segmented and elongated with 3 setae. **Maxilla** 5-segmented consisting of syncoxa, allobasis, and 3-segmented endopod; syncoxa with (4 + 3), 3, 3 setae, the two proximal endites fused; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II) and 1 seta (3) on anterior surface and 1 seta (4) on posterior surface; tube pore on anterior surface lacking; accessory armature of fused endopod segment of 1 seta on anterior surface (9?) and 1 seta on posterior surface (11), 1 anterior seta (10?) missing; endopod with armature formula: 2, 2, 4; proximal and middle segment with 2 geniculated setae (5 - 8), last segment with 1 geniculated seta (2). **Maxilliped** (Figs. 29 A - C) subchelate and 4-segmented, comprising syncoxa, basis and 2-segmented endopod; syncoxa with 2 coxal setae (10 + 11), inserting subterminally on inner and outer border; basis with 1 seta on inner edge (8); enp-1 with 1 seta (7) and 1 thin claw (VI) and 1 large claw (V) displaced to the posterior side of the distal end of enp-1; enp-2 reduced in size with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4); high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; **P1** of characteristic shape (Fig. 30 A): enp-1 elongated and broadened on the level of inner seta, enp-2 and enp-3 short; terminally with claw (derived from displaced outer spine), 1 middle spine and 1 seta; outer and distal spines of exopod elongated and ornamented terminally with very long spinules on one side; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; I-I+1-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** baseoendopod with 1 outer basal seta, endopodal lobe with 3 setae (3 - 5): 1 inner seta and 2 terminal setae; exopod with 5 setae (7, 9 - 12): 1 inner seta, 2 terminal setae, 2 outer spines; the 2 outer spines of exopod inserting near the basis and near the distal outer edge respectively (7 + 9). **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P2, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** subchirocer with 8 segments; armature formula: 1, 1, 12, 8, 2, 14 + aes/ 4, 10 + acrothek, fusion of Oligoarthra segments 6 - 9, 10 - 11 and 12 - 14; aesthetascs of Oligoarthra segments 3 and 4 lacking; aesthetasc on Oligoarthra segment 6 fused at base with a seta; segments 7 and 8 (oligoarthran segments 10 - 14) forming claw with a pointed end (Fig. 25 A) forming a functional unit with segment 6 (oligoarthran segments 6 - 9). **P2** enp-3 (Figs. 27 A - G) without inner setae, the 2 inner setae of female lacking; terminally with big modified bare spine (I) fused at base with segment (derived from displaced outer spine), 1 middle hyaline seta (2) and 1 inner terminal seta (3); armature formula:

	coxa	basis	exopod	endopod
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-0

**P5** fused medially; basis not separated from coxa and endopod; endopod with 2 setae and 2-segmented exopod with 2-1, 1-1-1 setae. **P6** symmetrical, with 3 setae.

### Remarks on the systematics and morphology of Idyanthidae

#### *Systematics.*

Willen (2000, p. 214) excluded “*Dactylopusia peruana* Becker, 1974” from Thalestridimorpha and Podogenmonta and suggested a closer relationship to Idyanthidae. This was a printing error, and she meant *Dactylophia peruana* Becker, 1974. This species belongs indeed to Idyanthidae, as it shares the autapomorphies, i.e. in P1, P5 and male P2 (Fig. 27 F). Only the morphology of the male antennule does not match the groundpattern of Idyanthidae, as Becker (1974) drew 4 segments behind the geniculation. It is difficult to recognize the segments of the male antennule. Therefore a discussion has to be postponed until the antennule of *D. peruana* has been examined.

The female of *Styracothorax gladiator* Huys, 1993 described by Huys (1993) shares some autapomorphies of Idyanthidae, i.e. the characteristic 2-segmented mandible exopod, and the displaced proximal outer setae of exopod P5 (see below). The maxillule and the P1 are reduced, so that it is not possible to confirm the derived morphology of Idyanthidae. Additionally, the female of *Styracothorax gladiator* has the displaced setae of the maxillipedal syncoxa of Idyanthidimorpha. The morphology of the single female shows many reductions compared with the other species of Idyanthidae. For example, the P1 of *Styracothorax gladiator* is much more derived. The endopod is 2-segmented and modified, consequently the apomorphies of Idyanthidae could not be observed. In the DIVA 1 material (chapter 8.1), one female and one male of *Styracothorax gladiator* were identified. The male clearly has the sexual dimorphism of Idyanthidae, precisely a modified form of the dimorphism of *Idyella* with the short and broad hyaline seta 2 (see below). The monotypic taxon Styracothoracidae described on the basis of a single female is therefore synonymized with Idyanthidae. Martínez & Moura (in prep.) were the first to mention the

membership of *Styracothorax* to Idyanthidae. Furthermore, it is probable that *Styracothorax gladiator* is an advanced species of *Idyella*.

Idyanthidae gen. spec. 11 is a species that shares some apomorphies with *Styracothorax gladiator*, such as a long processes of the cephalothorax, the characteristic 2-segmented exopod of P1, and the transversely elongated bases of the swimming legs. The 2-segmented endopod of P-1 is similar to that of *Idyella* species. Idyanthidae gen. spec. 11 has a transitional morphology connecting *Styracothorax gladiator* and Idyanthidae gen. spec. 12. The latter species has no hornlike projections on the cephalothorax nor on the rest of the body. However, the body form, the 2-segmented P1 exopod, the P5 of the female, and the sexual dimorphism of P2 resembles that of Idyanthidae gen. spec. 11 and *Styracothorax gladiator*. Idyanthidae gen. spec. 13 is also a species that shares many apomorphies with *Styracothorax gladiator*, also a modified form of the dimorphism of *Idyella* with the short and broad hyaline seta 2.

#### *Morphology.*

The autapomorphies of Idyanthidae, which are not shared by Zosimidae are mainly the elongated exopod of maxillula, the very characteristic P1 with the broad enp-1, 2 short distal endopod segments and 2 claw-like distal setae, and the sexual dimorphism of the enp-3 P2 with no inner setae in the male. In addition, Idyanthidae are possibly characterized by further apomorphies. However, due to the more derived morphology of Zosimidae, it is not clear whether these further apomorphies are autapomorphies of Idyanthidae or synapomorphies of Idyanthidae and Zosimidae. Species of Idyanthidae have a characteristic 2-segmented exopod of the mandible (with a long proximal segment that has 4 lateral setae and a short distal segment with 2 apical setae) and species of Zosimidae a 1-segmented endopod of mandible with at most 4 setae. Furthermore, species of Idyanthidae have the outer spine 7 of exopod P5 displaced almost to the basis, however species of Zosimidae have spine 7 reduced (chapter 4.15). The short enp-3 of **P1** evolved in four taxa convergently (chapter 5; char. **53**: 0→1).

Some species of Idyanthidae (e.g. Idyanthidae gen. spec. 8 - 12, *Styracothorax gladiator*) have an enp-1 of P1 that is not elongated and only slightly or not broadened. This appears to be a secondary phenomenon.

*Tachidiella* species have an elongated enp-3 of P1 (Fig. 30 C). This is a derived state within Idyanthidae.

The sexual dimorphism of **P2 endopod** in Idyanthidae varies among the genera (Figs. 27 A - G). The plesiomorphic condition of P2 enp-3 within Idyanthidae is as follows: No inner setae present in the male, the transformed and fused outer spine I is displaced to the inner terminal edge, and the middle seta 2 is hyaline. Starting from the groundpattern, there are two different lines of evolution within Idyanthidae. The spine becomes bifurcated in some species of *Idyanthe* (Fig. 27 B) and *Idyella* (Fig. 27 C). Some species of *Idyanthe* lose also seta 2 and 3. Within *Idyella* hyaline seta 2 becomes short and broad (Figs. 27 C - D). The second line of evolution is found in *Idyellopsis* and *Dactylopi*a (Figs. 27 E - F). The endopod becomes 2-segmented due to the fusion of enp-2 and enp-3. Spine I is integrated in that segment as the bent end. The dimorphism of *Tachidiella* appears to be a transition between the groundpattern of Idyanthidae and *Idyellopsis* - *Dactylopi*a as the endopod is still 3-segmented (Fig. 27 G).

#### 4.15 Zosimidae fam. nov.

##### Type genus

*Zosime* Boeck, 1872.

##### Taxa belonging to Zosimidae (17 species in 3 genera)

*Peresime* Dinet, 1974, *Pseudozosime* Scott, 1912, *Zosime* Boeck, 1872.

Undescribed species (8.1 Appendix I.): *Zosime* spec. 1, *Zosime* spec. 2, *Zosime* spec. 3, *Zosime* spec. 4, *Zosime* spec. 5, *Zosime* spec. 6, *Zosime* spec. 7, *Zosime* spec. 8; and dozens of undescribed species of *Zosime*.

##### Changes in systematics (reasons given below)

*Zosime* Boeck, 1872, *Peresime* Dinet, 1974, *Pseudozosime* Scott, 1912 are excluded here from Idyanthidae Lang, 1944 and are combined in Zosimidae fam. nov.

##### Diagnosis: Autapomorphies of Zosimidae (Fig. 4: ■ 18; Fig. 31)

*Female*. Enp-2 of antenna with **3 subterminal and 6 distal setae**; subterminal setation of enp-2 composed of 1 short proximal spine (I), 1 longer distal spine (III), and 1 tiny seta (4), **seta 2 lacking** (char. 10: 0→1); distal border of endopod antenna **not bevelled** (char. 13: 1→0). Mandible (Fig. 24 F): setae of basis **inserting on a bulge of inner border**; endopod with **1 lateral seta** (char. 18: 0→1) and **3 apical setae** (char. 20: 1→2); exopod 1-segmented with **3 lateral setae and 1 distal seta**. Maxillule praecoxal arthrite: **2 spines (VII + VIII) and 2 proximal setae of posterior surface (13 + 14) lacking**; formula of armature: 2, V, 1, 2, 0; exopod **very short**. All syncoxal endites of maxilla **inserting on the distal half of the syncoxa**; basis with **weakly-developed endite**; endopod 1-segmented with **5 setae (1 - 5?)**. Syncoxa of maxilliped **at most 1,5 times longer than wide** (char. 42: 0→1); **without joint between syncoxa and basis** (char. 45: 1→0) and **between basis and endopod** (char. 47: 1→0); 1-segmented endopod **reduced in size and directed outwardly, armature elements of enp-1 lacking, therefore no claw present**. P1 of characteristic shape: **enp-1 almost square, enp-2 and enp-3 fused, forming a long and slender segment with 2 inner setae and 2 terminal spines, 1 spine originated from displaced outer spine**; outer and distal spines of exopod elongated ornamented terminally with very long spinules; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; <b>I-I-2</b>

P5 baseoendopod with 1 outer basal seta **inserting on a long cylindrical extension; incision in baseoendopod between exopod and endopodal lobe**.

*Male*. P5 baseoendopod with **1 outer basal seta** inserting on a long cylindrical extension, **baseoendopod very constricted; endopod very small**.

##### Groundpattern of Zosimidae (Fig. 31)

*Female*. **Body width differs between prosome and urosome (Fig. 2 C). Nauplius eye absent. Rostrum fused at base with cephalothorax. Prosome consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused**

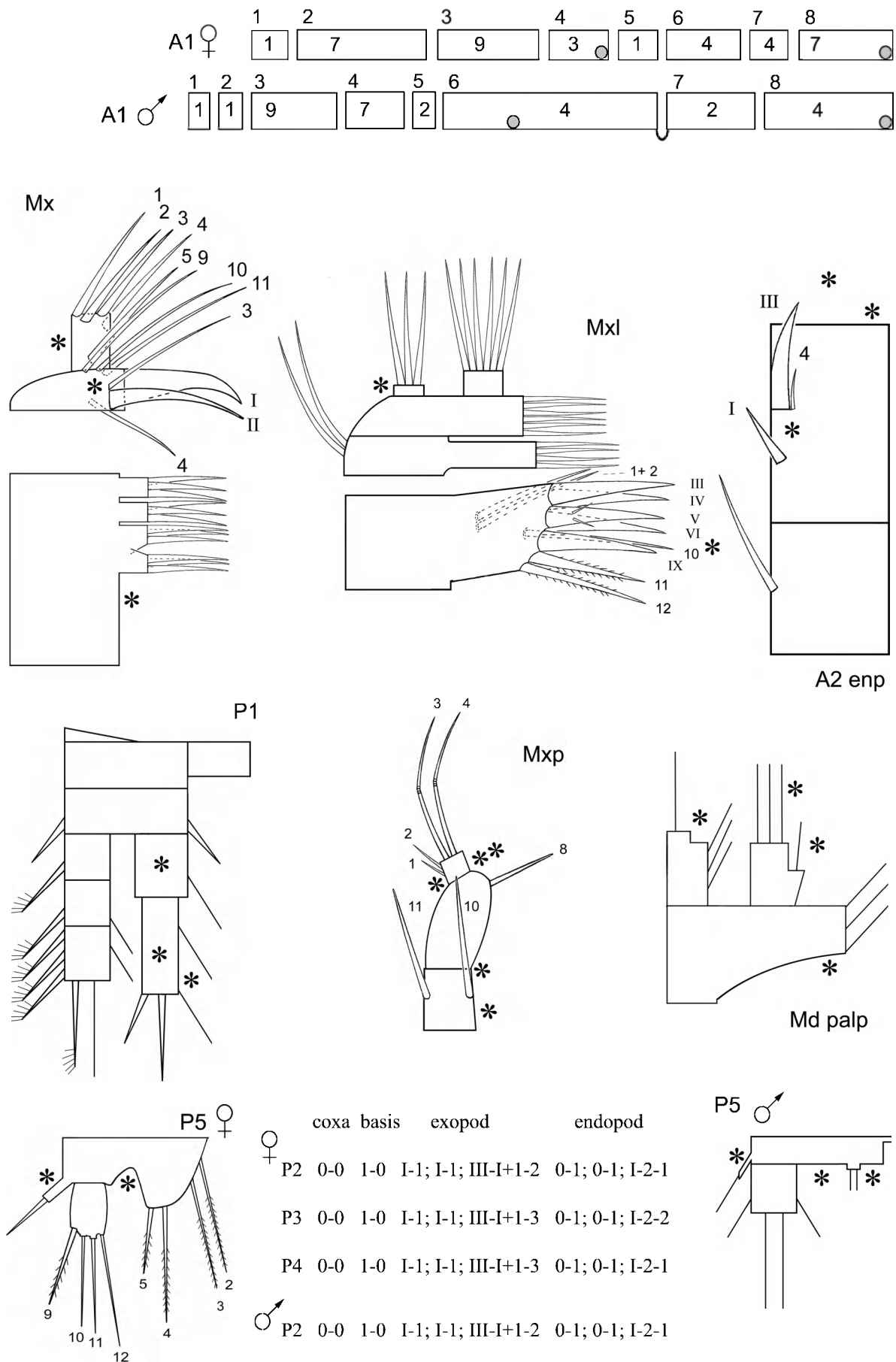


Fig. 31: Groundpattern of Zosimidae. Asterisks mark autapomorphies of Zosimidae.



to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 8-segmented, short and stout; armature formula: 1, 7, 9, 3 + aes, 1, 4, 4, 6 + acrothek. **Antenna** composed of coxa, basis, 2-segmented endopod and 3-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 3 subterminal and 6 distal setae; subterminal setation of enp-2 composed of 1 short proximal spine (I), 1 longer distal spine (III), and 1 tiny seta (4), seta 2 lacking; two distal segments of exopod fused, with 1, 1, 4 setae. **Labrum** not prominent. **Paragnaths** separated. **Mandible** (Fig. 24 F) with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner and bulge at proximal border; palp comprising basis, endopod and exopod; 3 setae of basis inserting on a bulge of inner border; endopod 1-segmented with 1 lateral seta and 3 apical setae; exopod 1-segmented with 3 lateral setae and 1 distal seta. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 2 anterior and 3 posterior spines (III – VI + IX; at least 1 posterior spine with 2 long spinules) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), 2 spines (VII + VIII) and 2 proximal setae of posterior surface missing (13 + 14); formula of armature: 2, V, 1, 2, 0; coxa with 4 setae, epipodite represented by 2 setae; basis with 3 + 3 setae; endopod 1-segmented with 6 setae; exopod 1-segmented and short with 3 setae. **Maxilla** 3-segmented consisting of syncoxa, allobasis, and 1-segmented endopod; syncoxa with (3 + 3), 3, 3 setae, the two proximal endites fused, all syncoxal endites inserting on the distal half of the syncoxa; basis with weakly-developed endite; accessory armature of fused basis consisting of claw (I) at the end of the endite, 1 big curved spine (II) and 1 seta (3) on anterior surface and 1 seta (4) on posterior surface; tube pore on anterior surface lacking; accessory armature of fused endopod segment of 2 setae on anterior surface (9 + 10) and 1 seta on posterior surface (11); endopod with 5 setae (1 - 5?). **Maxilliped** 3-segmented, comprising syncoxa, basis and 1-segmented endopod; syncoxa at most 1,5 times longer than wide with 2 coxal setae (10 + 11), inserting subterminally on inner and outer border; without joint between syncoxa and basis and between basis and endopod; basis with 1 seta on inner edge (8); 1-segmented endopod reduced in size and directed outwardly, with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4), armature elements of enp-1 lacking, therefore no claw present. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; P1 of characteristic shape: enp-1 almost square, enp-2 and enp-3 fused, forming a long and slender segment with 2 inner setae and 2 terminal spines, 1 spine originated from displaced outer spine; outer and distal spines of exopod elongated and ornamented terminally with very long spinules; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; I-I-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-1
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-1; I-2-2
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-1; I-2-1

**P5** baseoendopod with 1 outer basal seta inserting on a long cylindrical extension,

endopodal lobe with 4 setae (2 - 5): 2 inner and 2 terminal setae; exopod with 4 setae (9 - 12): 1 inner seta, 2 terminal setae, 1 outer spine; incision in baseoendopod between exopod and endopodal lobe. **P6** with 2 setae.

*Male.* Sexual dimorphism in body size, genital segmentation, antennule, P2, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** subchirocer with 8 segments; armature formula: 1, 1, 9, 7, 2, 4 + aes/ 2, 4 + acrothek, fusion of Oligoarthra segments 6 - 9, 10 - 11 and 12 - 14; aesthetascs of Oligoarthra segments 3 and 4 lacking; aesthetasc of Oligoarthra segment 6 fused at base with a seta; segments 7 and 8 (oligoarthran segments 10 - 14) forming claw with a pointed end (Fig. 25 B) forming a functional unit with segment 6 (oligoarthran segments 6 - 9). **P2** enp-3 (Fig. 27 H) with 1 inner seta (4), all inner setae of female present; enp-3 terminally with modified bare spine (I) fused at base with segment (derived from displaced outer spine), 1 middle hyaline seta (2) and 1 inner terminal seta (3); armature formula:

	coxa	basis	exopod	endopod
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-1

**P5** fused medially; basis not separated from coxa and endopod, baseoendopod with 1 outer basal seta inserting on a long cylindrical extension, baseoendopod very constricted; endopod very small with 2 setae; 1-segmented exopod with 1-2-1 setae. **P6** symmetrical, with 3 setae.

#### Remarks on the morphology and systematics of Zosimidae

##### *Morphology.*

The main apomorphies of Zosimidae are the unique palp of the mandible, the short maxillular exopod, the striking maxilla, the conspicuous maxilliped, the characteristic 2-segmented P1 endopod, and the unique male and female P5.

The species of Zosimidae are very characteristic. Many derived characters evolved in the ancestor line of this unique monophylum. Few alterations have evolved within Zosimidae. Especially the morphology of the habitus, maxilliped, P2 to P4 and the P5 is variable. Some species of Zosimidae have seta 2 of the baseoendopod of P5 and some species don't have this seta. Because no species of Paramesochridae, Idyanthidae, Ectinosomatidae, and Chappuisiidae have this seta it is the most parsimonious hypothesis to assume that this seta was not present in the groundpattern of Idyanthidimorpha. Otherwise the species of Zosimidae resemble each other, as only details differ.

The species of Zosimidae have generally few segments and setae. As a consequence, the species of Zosimidae share some reductions with other taxa (see chapter 5; char. 10: 0→1, char. 18: 0→1, char. 20: 1→2). For the discussion of the morphology of the antennal endopod and the maxilliped see chapters 5.2.3 and 5.2.4 (char. 13, char. 42, char. 45, char. 47).

##### *Systematics.*

Only 17 species of Zosimidae are described to date, but hundreds of undescribed species, mainly from the deep sea and the continental slope, are awaiting description.

Huys et al. (1992; p. 37) mentioned the taxa “Zosimidae (*Zosime*, *Tachidiella*)” and “Idyanthidae (*Idyella*, *Idyanthe*, *Tachidiopsis*)” without author or comments. They give no diagnosis and no autapomorphies for these taxa. In the classification of Huys

et al. (1996; p. 42) Zosimidae and Idyanthidae are not mentioned and *Zosime*, *Idyella*, *Idyanthe*, *Tachidiella* and *Tachidiopsis* are assigned to Idyanthinae (Tisbidae). As characterised here, *Tachidiella* (and *Dactylophia*, *Idyanthe*, *Idyella*, *Idyellopsis*, *Styracothorax*) belongs to Idyanthidae Lang, 1944 and not to Zosimidae fam. nov. *Tachidiopsis cyclopoidea* has the autapomorphies of Neobradyidae (chapter 4.8) and *Zosime*, *Peresime*, and *Pseudozosime* are combined here in the monophyletic Zosimidae fam. nov.

#### 4.16 Paramesochridae Lang, 1944

Taxa belonging to Paramesochridae (115 species in 13 genera)

Diarthrodeellinae Huys, 1987: *Diarthrodeella* Klie, 1949, *Rossopsyllus* Soyer, 1975, *Tisbisoma* Bozic, 1964.

Paramesochrinae Huys, 1987: *Apodopsyllus* Kunz, 1962, *Biuncus* Huys, 1996, *Caligopsyllus* Kunz, 1975, *Leptopsyllus* T. Scott, 1894, *Kliopsyllus* Kunz, 1962, *Kunzia* Wells, 1967, *Meiopsyllus* Cottarelli & Forniz, 1994, *Paramesochra* T. Scott, 1892, *Remanea* Klie, 1929, *Scottopsyllus* Kunz, 1962.

Undescribed species (8.1 Appendix I): *Apodopsyllus* spec., *Kliopsyllus* spec. 1, *Kliopsyllus* spec. 2, *Kliopsyllus* spec. 3, *Paramesochra* spec.

Diagnosis: Autapomorphies of Paramesochridae (Fig. 4: ■ 20; Figs. 32 + 2 D)

*Female.* Body with difference in width between prosome and urosome; **fourth pedigerous somite forming a narrow waist** (Fig. 2 D). Antenna: subterminal setation of enp-2 composed of 1 short proximal spine (I), **2 distal spines (III + IV)** and 1 slender seta (2); **element 4 forming a spine**. Seta 13 of praecoxal arthrite of maxillula present and **displaced almost to the outer border**; seta 14 absent; **formula of armature: 2, VII, 1, 2, 1**. Distal endite of maxillar praecoxa (fused to proximal one) **with 2 setae** (char. 36: 0→1). Syncoxa of maxilliped with 1 seta **displaced to the posterior side of inner distal corner** (10). Endopod of P1 of **characteristic shape: enp-1 elongate, enp-2 and enp-3 short** (char. 53: 0→1); **enp-3 with 2 claw-like distal setae**. P1-P4 **formula of armature:**

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; 0-2-0
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-1
P3	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-1
P4	0-0	1-0	I-1; I-1; III-I+1-1	0-1; 0-1; I-2-0

*Male.* P5 with an endopod al lobe without setae.

Groundpattern of Paramesochridae (Fig. 32)

*Female.* **Body** with difference in width between prosome and urosome; fourth pedigerous somite forming a narrow waist (Fig. 2 D). **Nauplius eye** not confirmed. **Rostrum** delimited at base. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided

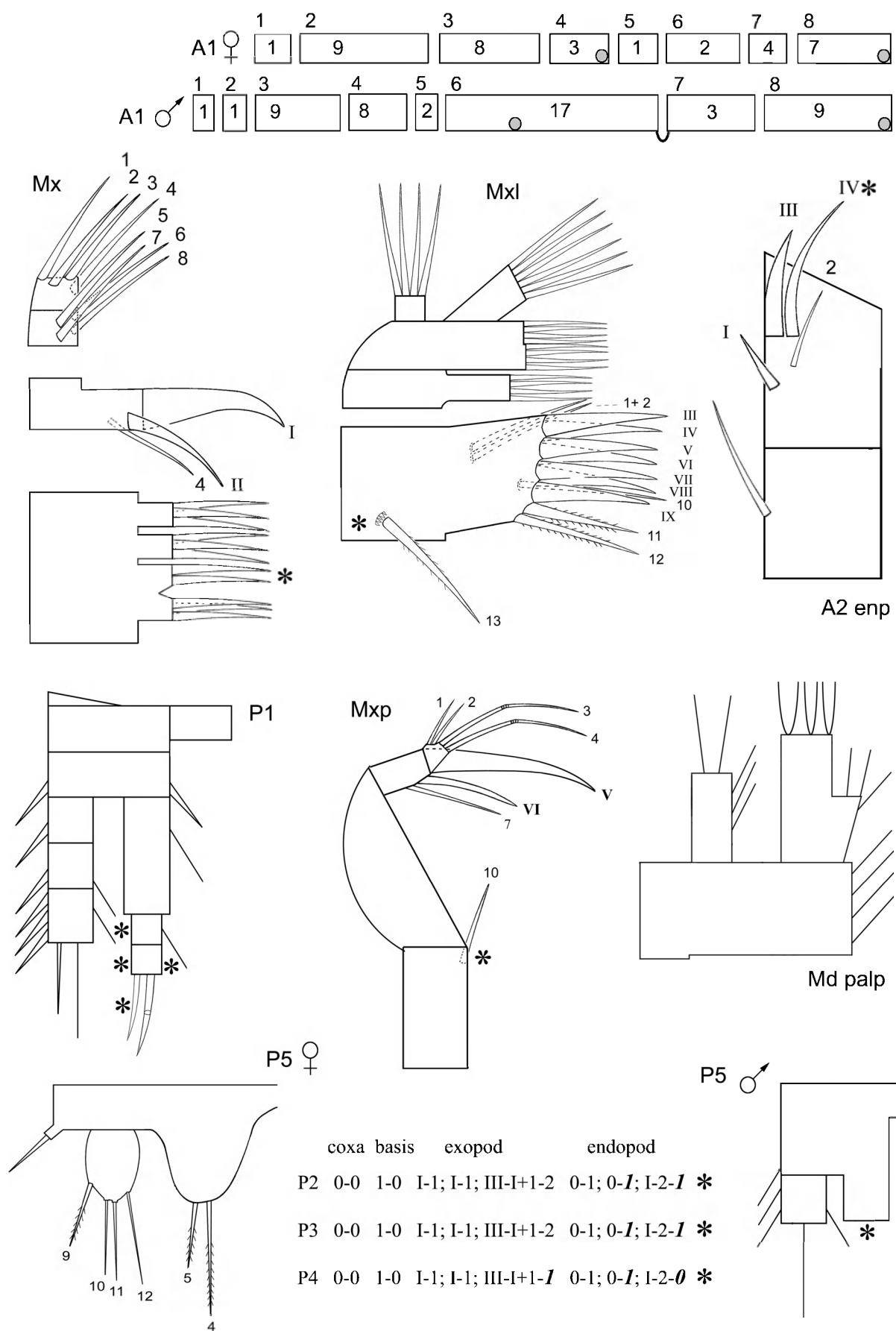


Fig. 32: Groundpattern of Paramesochridae. Asterisks mark autapomorphies of Paramesochridae.

longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 8-segmented; armature formula: 1, 9, 8, 3 + aes, 1, 2, 4, 6 + acrothek; fusion of Oligoarthra segments 7 and 8. **Antenna** (Fig. 24 B) composed of coxa, basis, 2-segmented endopod and 2-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 4 subterminal and 7 distal setae; subterminal setation composed of enp-2 of 1 short proximal spine (I), 2 distal spines (III + IV) and 1 slender seta (2); seta 2 inserts between spine I and spine IV; distal border of endopod is slightly bevelled with an angle towards the exopod; exopod with 2, 4 setae. **Labrum** not prominent. **Paragnaths** separate. **Mandible** (Fig. 24 I) with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner and big bulge at proximal border; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 3 lateral and 2 + 2 + 2 apical setae, apical setae basally fused to pairs; exopod 1-segmented with 5 setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III – IX) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 1 proximal seta displaced almost to the outer border (13); seta 14 absent; formula of armature: 2, VII, 1, 2, 1; coxa with 4 setae, no epipodal setae; basis with 4 + 4 setae; endopod 1-segmented, prolonged, and directed inwards with 6 setae; exopod 1-segmented with 4 setae. **Maxilla** 4-segmented consisting of syncoxa, allobasis, and 2-segmented endopod; syncoxa with (3 + 2), 3, 3 setae, the two proximal endites fused; basis with well-developed endite; accessory armature of fused basis consists of strong claw (I) at the end of the endite, and 1 curved spine (II) on anterior surface and 1 seta (4) on posterior surface, 1 anterior seta lacking (3); accessory armature of fused endopod segment absent; endopod with armature formula 4, 4. **Maxilliped** subchelate and 4-segmented, comprising syncoxa, basis and 2-segmented endopod; syncoxa with 1 seta displaced to the posterior side of inner distal corner (10); basis without ornamentation; enp-1 with 1 lateral seta (7), 1 thin lateral claw (VI), and 1 large distal claw (V); enp-2 reduced in size with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4); high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; endopod of P1 of characteristic shape: enp-1 elongate, enp-2 and enp-3 short; enp-3 with 2 claw-like distal setae; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; 0-2-0
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-1
P3	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-1
P4	0-0	1-0	I-1; I-1; III-I+1-1	0-1; 0-1; I-2-0

**P5** fused medially; baseoendopod with 1 outer basal seta, endopodal lobe with 2 terminal setae (4 + 5); exopod with 4 setae (9 - 12): 1 inner seta, 2 terminal setae, 1 outer spines. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** subchirocer with 8 segments; armature formula: 1, 1, 9, 8, 2, 17 + aes/ 3, 8 + acrothek; fusion of Oligoarthra segments 6 - 9, 10 - 11 and 12 - 14;

aesthetascs of Oligoarthra segments 3 and 4 lacking; aesthetasc on Oligoarthra segment 6 fused at base with a seta; 2 additional setae on oligoarthran segments 6 to 9 compared to the groundpattern of Oligoarthra; segments 7 and 8 (oligoarthran segments 10 - 14) forming strong claw with a pointed end (Fig. 25 D) forming a functional unit with segment 6 (oligoarthran segments 6 - 9). **P5** fused medially; basis not separated from coxa and endopod; 1-segmented exopod with 2-1-1 setae and endopodal lobe without setae. **P6** symmetrical, with 3 setae.

#### Remarks on the systematics and morphology of Paramesochridae

##### *Systematics.*

Martínez Arbizu & Moura (1998) and Willen (2000) excluded Paramesochridae from Podogennonta because this taxon does not share the autapomorphies. Martínez Arbizu & Moura (1998) indicated that Paramesochridae are allied with Tisboidea (Exanechentera). Paramesochridae is indeed a member of Exanechentera. However, as sister group of Tachidiidae - Palinarthra (N.N. 5) not directly allied with Tisboidea (see chapters 5.1.3, 5.1.5, 5.2.3 and 5.2.4).

*Psammoleptomesochra australis* Mielke, 1994 (Ameiridae) is mentioned twice in Bodin (1997). This species was also listed as *Paramesochra australis* Mielke, 1994, but it is without doubt not a member of Paramesochridae. It has evolved some convergences with Paramesochridae in maxillula and P1, but analysis of the details shows that they differ. As long as its systematic position is not solved, this species remains in Ameiridae.

*Diarthrodella psammophila* (Bocquet & Bozic, 1955) (Paramesochridae) is also mentioned twice in Bodin (1997). This species was also listed as *Idyanthopsis psammophila* Bocquet & Bozic, 1955 as *genus incertum et species incerta sedis* in Tisbidae. There is no doubt that this species belongs to *Diarthrodella* and Paramesochridae, because it shares the autapomorphies of both taxa. As a consequence *Idyanthopsis* Bocquet & Bozic, 1955 is a junior synonym to *Diarthrodella* as mentioned by Kunz (1962) and Bodin (1997).

##### *Morphology.*

The monophyletic group Paramesochridae is characterized above all by the fourth pedigerous somite forming a narrow waist, the characteristic maxillule with the proximal seta 13 that is displaced almost to the outer border of the posterior praecoxal surface, the endopod of P1 with the short distal segments and the 2 distal claw-like setae. Many variations evolved within this group. It would exceed the scope of this discussion to merely report the strong alterations.

For the discussion of the morphology of the **mandible endopod** see chapter 4.3 and of reduction of setae in the **maxillar** syncoxa see chapter 5.2.3 (char. 36: 0→1).

The complete plesiomorphic setation of the endopod of the **maxilliped** is not realized in a single species of Paramesochridae. Many species have a 2-segmented endopod with 5 setae (1 - 4, 7) and the big claw V, but the thin claw VI is lacking. *Biuncus ingens* Huys, 1995 has a 1-segmented endopod with 1 big claw (V), 1 thin claw (VI), and 1 seta (7) from enp-1 and 2 setae from enp-2.

The endopod **P-1** of Paramesochridae resembles that of Podogennonta. This is the main reason why Lang (1944, 1948) placed Paramesochridae within Podogennonta. However, the endopods of both taxa have evolved convergently and the morphology

differs. The elongation of the proximal endopod segment and the shortening of one or two distal segments have developed several times within Oligoarthra. The short enp-3 of P1 evolved in four taxa convergently (chapter 5; char. 53: 0→1). Sometimes the enp-1 of P1 is elongated within the taxa (e.g. Ectinosomatidae). The characteristic podogennontan setation of the endopod (and exopod) is lacking in Paramesochridae. The distal endopodal segment of Podogennonta has 1 inner, 1 distal geniculated, 1 distal miniaturised seta, and 1 distal claw. The claw is derived from the displaced outer spine. Species of Paramesochridae have transformed 1 or 2 of the distal setae to a claw-like seta, but not the outer spine. The outer spine of enp-3 P1 is missing in Paramesochridae. Furthermore, species of Paramesochridae have preserved more setae on the maxillular basis and the exopod of P1 than Podogennonta and they have a 2-segmented maxillipedal endopod.

The **male antennule** of *Caligopsyllus primus* Kunz, 1975 has 17 setae on the 6th segment (oligoarthran segments 6 to 9), while the same segment of *Scottopsyllus* (*Sc.*) *praecipuus* Veit-Köhler, 2000 has 16. It follows that there are 2 or 3 additional setae compared to the groundpattern of Oligoarthra. These 2 (or 3?) setae are homologous to the additional setae of the oligoarthran segment 6 in Tisboidea (see chapter 4.26).

#### 4.17 Tachidiidae Boeck, 1865

##### Taxa belonging to Tachidiidae (13 species in 5 genera)

*Cithadius* Bowman, 1972, *Euterpina* Norman, 1903, *Geeopsis* Huys, 1996, *Microarthridion* Lang, 1944, *Tachidius* Lilljeborg, 1853.

Undescribed species (8.1 Appendix I): *Tachidius* spec.

##### Changes in systematics (reasons given below)

The monotypic Euterpinidae Brian, 1921 is synonymised with Tachidiidae.

“Tachidioidea” Sars, 1909 is polyphyletic and therefore not maintained here as Harpacticidae was transferred to Podogennonta (Willen, 2000).

##### Diagnosis: Autapomorphies of Tachidiidae (Fig. 4: ■ 22; Figs. 33, 2 E, 34)

**Female.** Body slightly dorso-ventrally flattened (Fig. 2 E; char. 2: 0→1). **Dorsal nuchal organ on cephalothorax; paired accessory nuchal organs on cephalothorax and somites bearing P2 and P4.** Enp-2 antenna with subterminal setation composed of enp-2 of 1 short proximal spine (I), 1 longer distal spine (III), and 1 distal geniculate seta (4); **spine I inserts near border to enp-1, seta 2 missing.** Formula of armature of praecoxal arthrite maxillule: **2, V, 1, 2, 2; 1 posterior and 1 anterior spine lacking (VII + VIII); basis with 3 setae; exopod lacking.** Maxilliped endopod 1-segmented with a large distal claw (V); **other endopodal setae represented by a group of 2 small setae on anterior surface of endopod, no setae geniculated.** Exp-3 of P2-P4 with 2 outer spines; P2-P4 formula of armature:

	coxa	basis	exopod	endopod
P2	0-0	1-0	I-1; I-1; II-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; II-I+1-2	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; II-I+1-2	0-1; 0-2; I-2-2

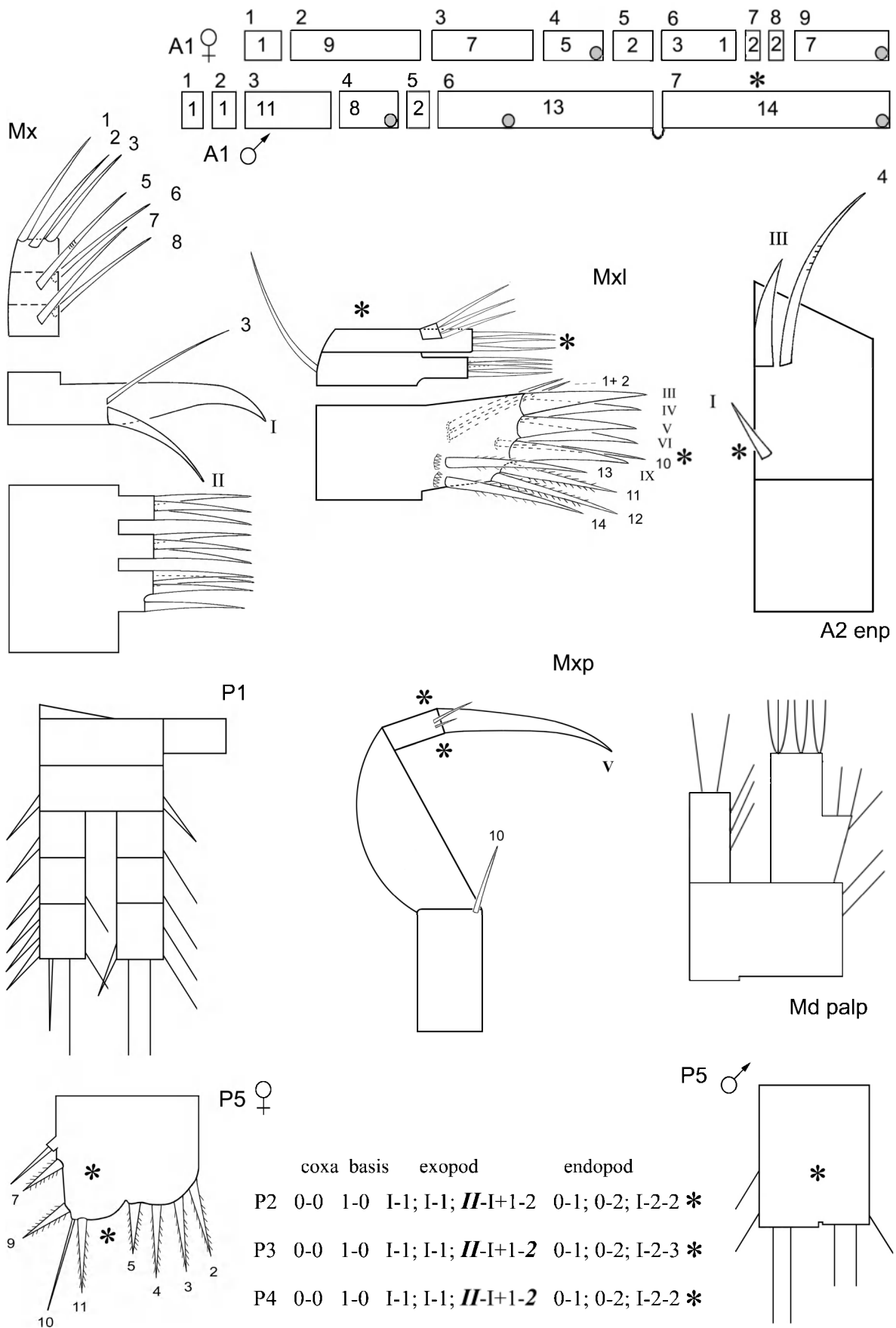


Fig. 33: Groundpattern of Tachidiidae. Asterisks mark autapomorphies of Tachidiidae.



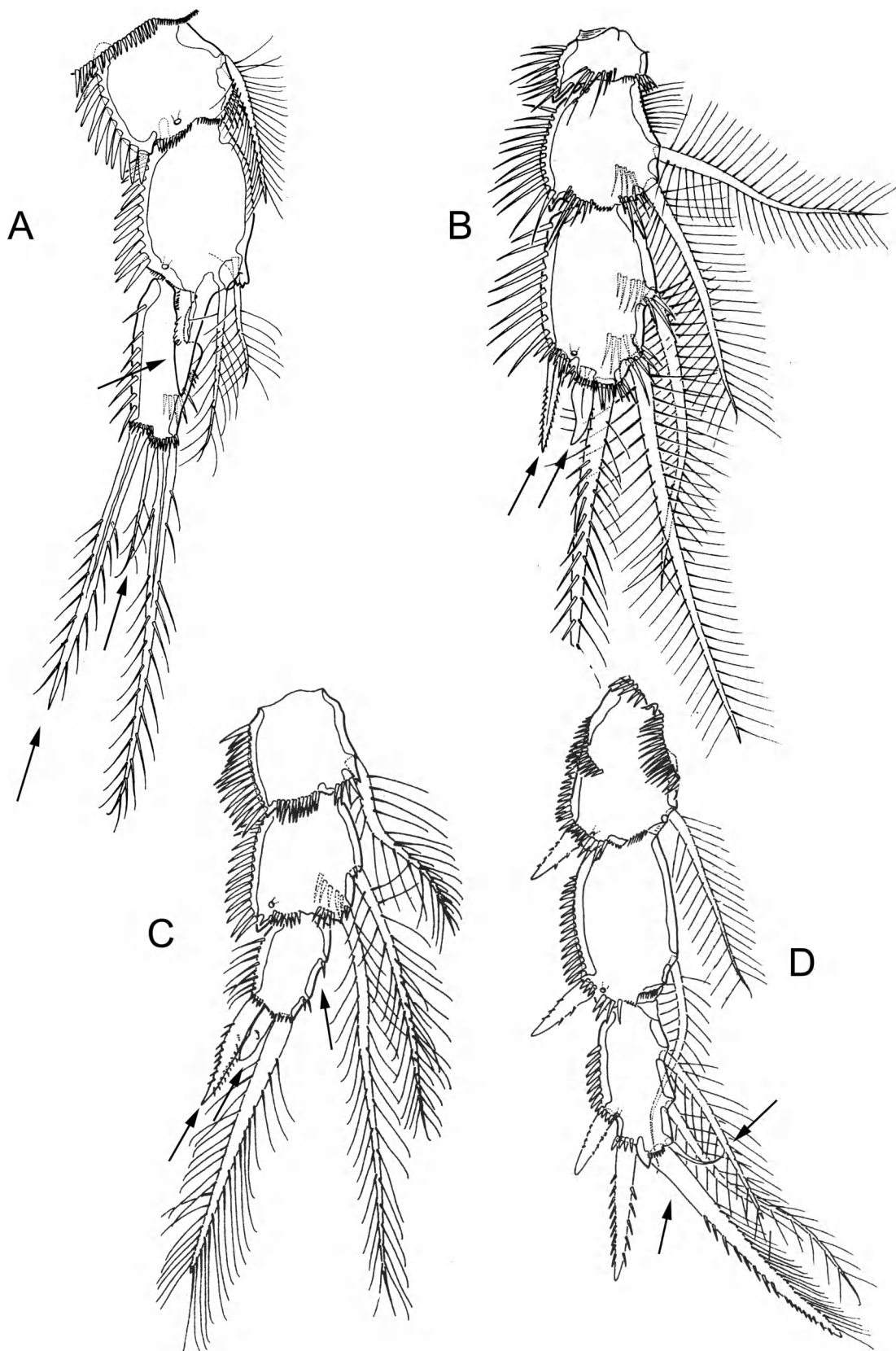


Fig. 34: Sexual dimorphism in swimming legs of Tachidiidae. A. *Tachidius* (*Tachidius*) *discipes*, male P2 enp (after Huys et al., 1996). B. *Microarthridion littorale*, male P2 enp (after Huys et al., 1996). C. *Geeopsis incisipes*, male P2 enp (after Huys et al., 1996). D. *Geeopsis incisipes*, male P3 exp (after Huys et al., 1996). -- Arrows indicate characters discussed in the text.

**P5 a single plate** with 4 endopodal setae (2 - 5), and 4 exopodal setae (7, 9 - 11); **seta 12 absent**.

*Male*. **Sexual dimorphism in P2 and P3** (?; Fig. 34). Antennule **chirocer** because of **fusion of Oligoarthra segments 10 - 14**. **P5 a single plate**.

#### Groundpattern of Tachidiidae (Fig. 33)

*Female*. **Body** slightly dorso-ventrally flattened, prosome and urosome of different width (Fig. 2 E). **Nauplius eye** present. **Rostrum** defined at base. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Dorsal nuchal organ** on cephalothorax; paired accessory nuchal organs present on cephalothorax and somites bearing P2 and P4. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 9, 7, 5 + aes, 2, 4, 2, 2, 6 + acrothek. **Antenna** (Fig. 24 C) composed of coxa, basis, 2-segmented endopod and 2-segmented exopod; basis and enp-1 without seta; enp-2 with 3 subterminal and 7 distal setae; subterminal setation of enp-2 composed of 1 short proximal spine (I), 1 longer distal spine (III), and 1 distal geniculate seta (4); spine I inserts near enp-1, seta 2 missing; exopod with 2, 3 setae. **Labrum** not prominent. **Paragnaths** not fused. **Mandible** (Fig. 24 H) with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner and big bulge at proximal border; palp comprising basis, endopod and exopod; basis with 2 setae; endopod 1-segmented with 3 setae laterally and 3 + 2 + 2 apical setae, each group of apical setae basally fused; exopod 1-segmented with 5 setae. **Maxillule** comprised of praecoxa, coxa, basis, and endopod; exopod lacking; praecoxal arthrite: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 2 anterior and 3 posterior spines (III - VI, IX) as well as 1 smaller, flexible seta (10) inserting on anterior surface, subapical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); formula of armature: 2, V, 1, 2, 2; coxa with 4 setae, epipodite represented by 1 seta; basis with 3 setae; small inwardly directed endopod with 3 setae. **Maxilla** indistinctly 5-segmented consisting of syncoxa, allobasis, and endopod; syncoxa with (1 + 3), 3, 3 setae, the two proximal endites fused, fused segment bilobed; basis with well developed endite; accessory armature of fused basis consisting of strong claw fused with endite (I), 1 curved spine (II) and 1 seta (3) on anterior surface; tube pore, posterior seta 4, and 3 setae of fused endopod segment (9-11) lacking; endopod indistinctly 3-segmented with armature formula: 2, 2, 3; endopodal seta 4 missing; middle segment with geniculated seta anteriorly (5). **Maxilliped** subchelate and 3-segmented, comprising syncoxa, basis and 1-segmented endopod; coxa with 1 seta (10) on inner distal corner; basis without setae, spine VII and seta 8 lacking; enp-1 and enp-2 fused to one small segment with a large distal claw (V, of enp-1); other endopodal setae represented by a group of 2 small setae on anterior surface of endopod, no setae geniculated; high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; exp-3 of P2-P4 with 2 outer spines; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; II-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; II-I+1-2	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; II-I+1-2	0-1; 0-2; I-2-2

**P5** a single plate; with 1 outer basal seta, 4 endopodal setae (2 - 5), and 4 exopodal setae (7, 9 - 11); seta 12 absent. **P6** with 1 seta.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P2 and P3 (?; Fig 34), P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** chirocer with 7 segments; armature formula: 1, 1, 11, 8 + aes, 2, 13 + aes/ 13 + acrothek, fusion of Oligoarthra segments 6 - 9 and 10 - 14; aesthetasc of Oligoarthra segments 3 lacking; aesthetasc on Oligoarthra segment 6 fused at base with a seta; segment 7 (oligoarthran segments 10 - 14) forming strong claw with a pointed end (Fig. 25 C) forming a functional unit with segment 6 (oligoarthran segments 6 - 9). **P5** a single plate; with 1 outer basal seta, 3 endopodal and 3 exopodal setae. **P6** symmetrical, with 3 setae.

#### Remarks on the systematics and morphology of Tachidiidae

##### *Systematics.*

“In Huys et al. (1996), the Tachidiidae *sensu* Lang (1944, 1948) are split up (without argumentation) in Euterpinidae Brian, 1921 (with the genus *Euterpina*) and Tachidiidae Boeck, 1865 ...” (Bodin, 1997, p 45). However, *Euterpina acutifrons* the only species of the former Euterpinidae Brian, 1921 shares the autapomorphies of Tachidiidae. All setae lacking in Tachidiidae are also reduced in *E. acutifrons*; furthermore, *E. acutifrons* fails to display some more setae of the groundpattern of Tachidiidae. It is the only planktonic species in Tachidiidae and therefore has evolved many morphological alterations. However, all mouthparts of *E. acutifrons* have the characteristic form of tachidiid mouthparts and the lateral spine I of the distal antennal endopod segment inserts near the proximal endopod segment, the exopod of the maxillule is lacking, the proximal endite of the syncoxa of the maxilla is bilobed with (1 + 3) setae, the maxilliped has a 1-segmented endopod with a large distal claw, the other endopodal setae of maxilliped are represented by 1 small seta on the anterior endopod surface, the P5 of both female and male is a single plate and the antennule of the male is chirocer.

Lang (1944) united Tachidiidae and Harpacticidae in the taxon Tachidiidimorpha Lang, 1944. Bowman & Abele (1982) changed Lang's “superfamily”-endings “-idimorpha” in “superfamily”-endings “-oidea” and introduced “Tachidioidea” Sars, 1909 (International Code of Zoological Nomenclature, fourth edition, Art. 29.2). As Harpacticidae was transferred to Podogennonta (Willen, 2000) “Tachidioidea” is polyphyletic and therefore not maintained here.

##### *Morphology.*

The monophyletic taxon Tachidiidae is characterized mainly by the nuchal organs, the displaced spine I of antennal enp-2, the maxillula with the reduced exopod and armature elements of basis and praecoxa, the reduced setation of maxilliped and the characteristic P5 of female and male.

For the discussion of the **slightly dorso-ventrally flattened** body see chapter 5.2.3

(char. 2).

In *Tachidius (T.) discipes* the **rostrum** is defined at base. SEM ascertained this.

The **first pedigerous somite** is not completely fused to the dorsal cephalic shield in *T. (T.) discipes* (Hosfeld, pers. com.). This situation is probably more common in Oligoarthra than has been assumed to date (see chapter 4.3).

The **male antennule** is chirocer, because segments 6 to 9 and 10 to 14 of the oligoarthran groundpattern are fused (Willen, 2000). Huys et al. (1996) show a separation of the oligoarthran segments 10 and 11 in *Geeopsis incisipes* (Klie, 1913) (Fig. 25 C). This appears to be a secondary phenomenon.

It is still unclear whether **P2 and P3** are sexually dimorphic in the groundpattern of Tachidiidae and what the groundpattern of the swimming legs looks like in the male. The males of *Geeopsis*, *Microarthridion*, and *Tachidius* have a longer exopod of P3 than the females with an exopod bent inwardly and a vestigial inner distal seta of exp-3 (Fig. 34 D). The outer spine of the enp-3 of P2 is also transformed and displaced in these genera, and sometimes the inner setae are minute or even lacking (Figs. 34 A - C). Male specimens of *Tachidius* have an enp-2 with an inner spinous apophysis overlapping a deep notch of enp-3 (Fig. 34 A). *Euterpina acutifrons* has dimorphic males. All males have a 2-segmented P2 endopod, but some have 1 seta and some have 2 inner setae less than the females. They also differ in the number of antennule setae and the form of the antenna. *Cithadius cyathurae* Bowman, 1972 has no sexual dimorphism in the swimming legs at all.

#### 4.18 Palinarthra tax. nov.

##### Etymology

The taxon name is derived from Greek palin- = back, again and arthr- = limb, joint, alluding to the regained segments and setae in the ancestor line of and within Palinarthra.

##### Taxa belonging to Palinarthra (322 species in 46 genera)

Novocriniidimorpha tax. nov., Tisboidea Stebbing, 1910.

##### Diagnosis: Autapomorphies of Palinarthra (Fig. 4: ■ 23; Figs. 35 - 37)

*Female*. **Strongly developed, triangular labrum and fused lobes of paragnaths forming an oral cone** (char. 3: 0→1). Lateral element 1 of distal endopod segment of antenna **forming a seta** (char. 11: 1→0). Gnathobase of mandible **elongated and narrow** (char. 15: 0→1). Praecoxal arthrite of maxillula **elongated and narrow** (char. 22: 0→1); seta 10 of praecoxa **absent** (char. 23: 0→1). Maxilla: distal endite of praecoxa (fused to proximal one) **with 2 setae** (char. 36: 0→1). Syncoxa of maxilliped **at most twice as long as wide** (char. 42: 0→1). Seta 8 of exopod P5 **present** (char. 61: 1→0).

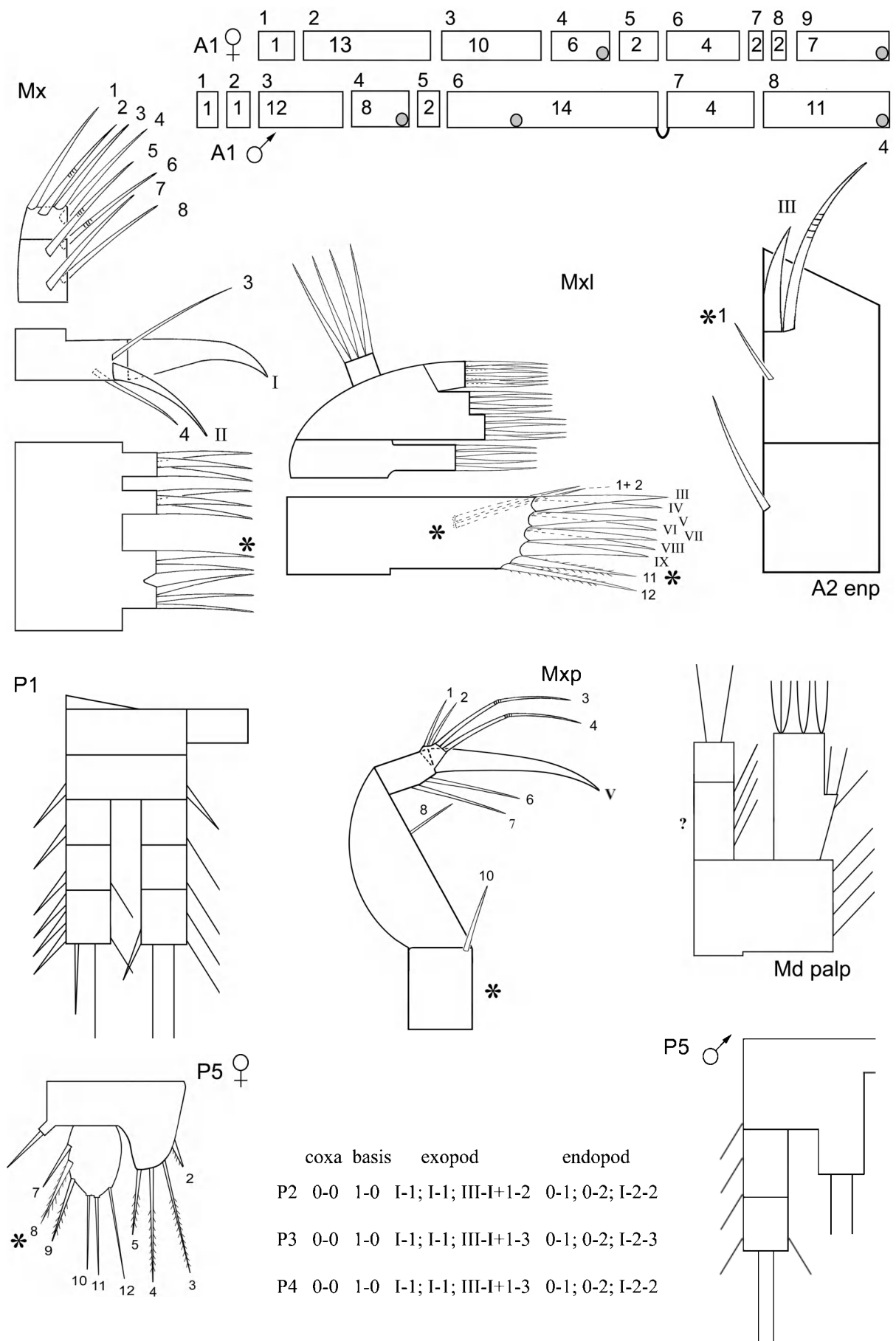


Fig. 35: Groundpattern of Palinarthra. Asterisks mark autapomorphies of Palinarthra.

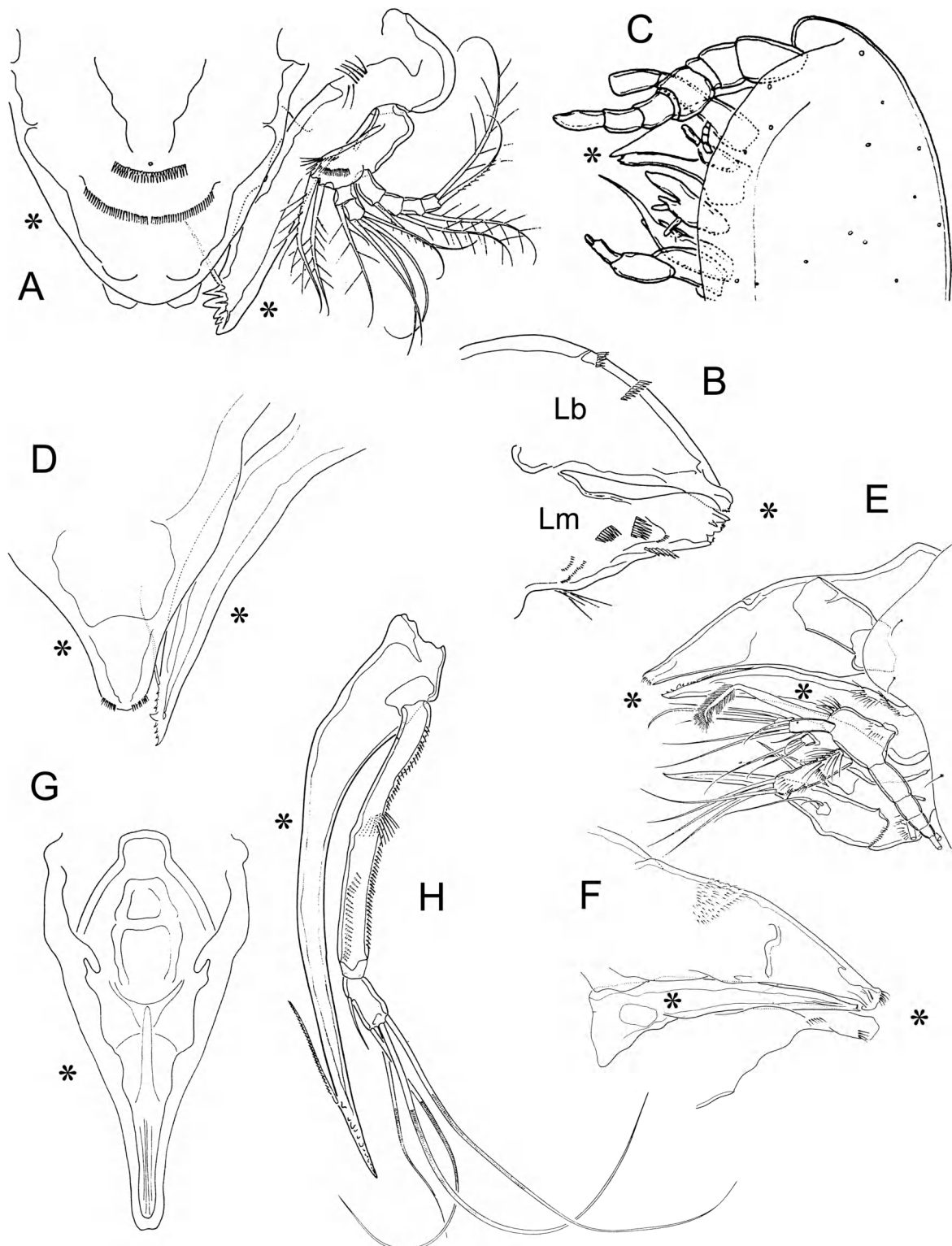


Fig. 36: Oral cone of Novocriniidimorpha: A. Labrum and mandible of *Novocrinia trifida* (after Huys & Iliffe, 1998). B. Labrum (Lb) and labium (Lm) of *N. trifida* (after Huys & Iliffe, 1998). C. *Atergopedia vetusta* (after Martinez Arbizu & Moura, 1998). D. Labrum and mandible of *Neoechinophora daltonae* Huys, 1996 (after Huys, 1996). E. *N. daltonae* (after Huys, 1996). F. Labrum, mandibular gnathobase and labium of *Intercrusia problematica* Huys, 1996 (after Huys, 1996). G. Labrum of *Rotundiclipeus canariensis* (after Huys, 1988a). H. Mandible of *R. canariensis* (after Huys, 1988a). -- Asterisks mark the oral cone or the elongated gnathobase mandible (autapomorphies of Palinarthra).

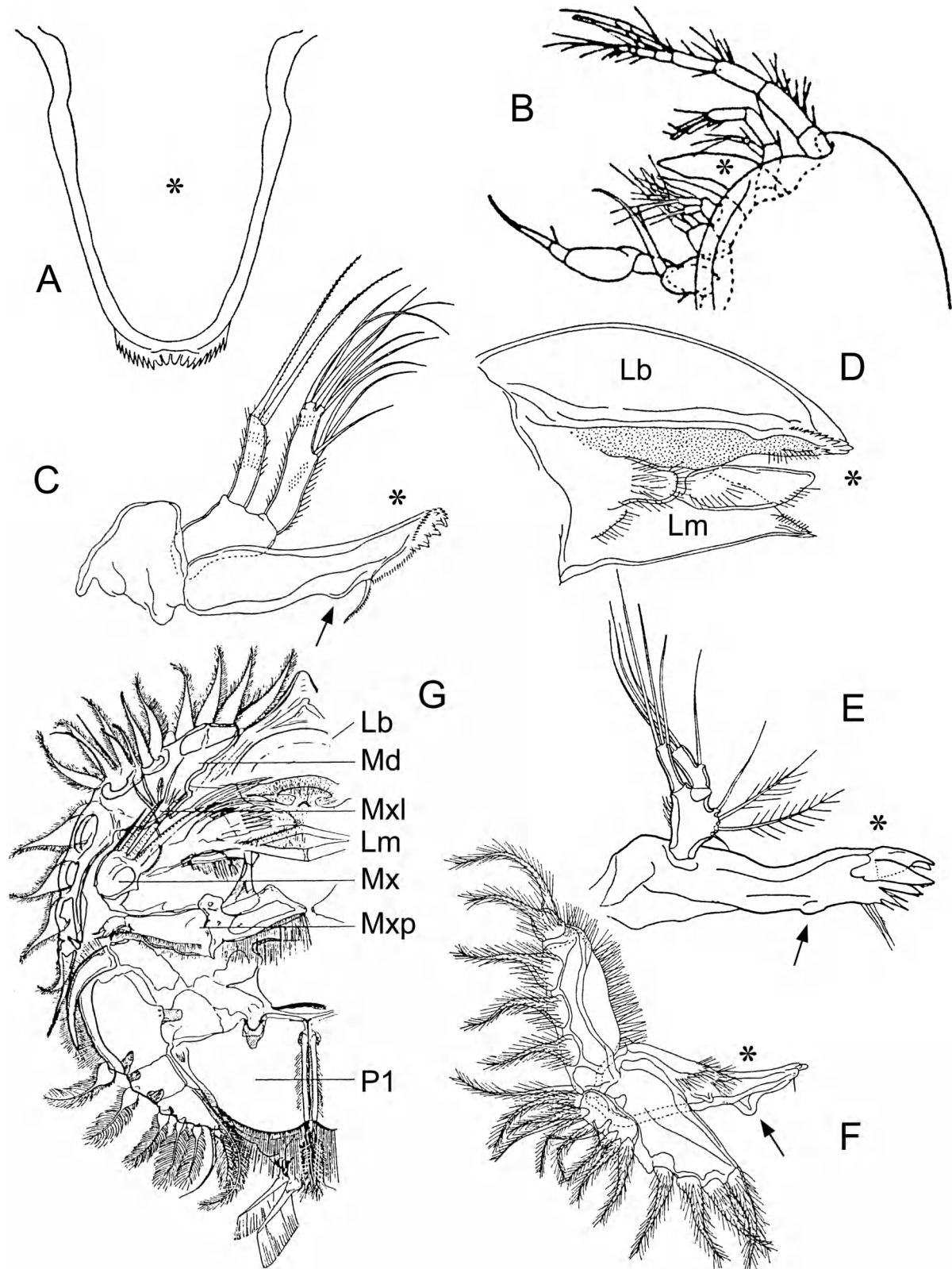


Fig. 37: Mouthparts of Tisboidea. A. Labrum of *Paraidya occulta* (after Humes & Ho, 1969). B. *P. occulta* (after Humes & Ho, 1969). C. Mandible of *P. occulta* (after Humes & Ho, 1969). D. Labrum (Lb) and labium (Lm) of *P. occulta* (after Humes & Ho, 1969). E. Mandible of *Eupelte simile* Monk, 1941 (after Itô, 1974). F. Mandible of *Porcellidium brevicaudatum* (after Humes & Ho, 1969). G. Sucker of *P. tenuicauda* Claus, 1860 (after Bocquet, 1948). -- Asterisks mark the oral cone or the elongated gnathobase of mandible (autapomorphies of Palinarthra). -- Arrows indicate the bulge at the proximal border of gnathobase of mandible.

Groundpattern of Palinarthra (Fig. 35)

*Female*. **Body** with difference in width between prosome and urosome (?). **Nauplius eye** present. **Rostrum** fused at base with cephalothorax. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 13, 10, 6 + aes, 2, 4, 2, 2, 6 + acrothek. **Antenna** composed of coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 3 subterminal and 7 distal setae; subterminal setation of enp-2 composed of 1 proximal seta (1), 1 longer distal spine (III), and 1 distal geniculate seta (4); lateral seta 2 missing; distal border of endopod is bevelled with an angle towards the exopod (Figs. 24 A - E); exopod with 2, 1, 1, 3 setae. Labrum, labium and elongated mandibular gnathobases forming a projected **oral cone** (Figs. 36 + 37): **labrum** strongly developed, triangular; median fusion of paired **paragnaths** forming a labium; labium partly fused to labrum. **Mandible** with coxa bearing elongated and narrow gnathobase (Figs. 36 + 37); cutting edge with 1 seta at proximal corner and bulge at proximal border; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 3 lateral and 7 apical setae, exopod 2-segmented with proximal segment with 4 lateral setae and distal segment with 2 distal setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite elongated and narrow: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III - IX), seta (10) lacking, subapical inner margin with 2 plumose setae (11 + 12) on anterior surface, setae 13 + 14 lacking; formula of armature: 2, VII, 0, 2, 0; coxa with 4 setae, no epipodal setae; basis with 4 + 4 setae; endopod directed inwards with 6 setae; exopod 1-segmented with 4 setae. **Maxilla** consisting of syncoxa, allobasis, and endopod; syncoxa with (3 + 2), 3, 3 setae, the two proximal endites fused; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II) and 1 seta (3) on anterior surface and 1 seta (4) on posterior surface; tube pore on anterior surface lacking; allobasis without setae of fused endopod segment; endopod 2-segmented with armature formula: 4, 4 (?). **Maxilliped** subchelate and indistinctly 4-segmented, comprising syncoxa, basis and indistinctly 2-segmented endopod; syncoxa at most twice as long as wide with 1 coxal seta (10), inserting on inner border; basis with 1 seta on inner edge (8); enp-1 with 2 setae (6 + 7) and 1 big claw (V); the claw displaced to posterior side of distal end of enp-1; enp-2 demarcated by posterior surface suture, reduced in size and with 2 short outer setae (1 + 2) and 2 geniculated distal setae (3 + 4); high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2



**P5** baseoendopod with 1 outer basal seta, endopodal lobe with 4 setae (2 - 5): 2 inner setae and 2 terminal setae; exopod with 6 setae (7 - 12): 1 inner seta, 2 terminal setae, 2 outer spines, and 1 outer seta. **P6** with 3 setae.

*Male.* Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites, 1 spermatophore. **Antennule** subchirocer with 8 segments; armature formula: 1, 1, 12, 8 + aes, 2, 14 + aes/ 4, 10 + acrothek, fusion of Oligoarthra segments 6 - 9, 10 - 11 and 12 - 14; aesthetascs of Oligoarthra segment 3 lacking; aesthetasc on Oligoarthra segment 6 fused at base with a seta; segments 7 and 8 (oligoarthran segments 10 - 14) forming claw with a pointed end (Figs. 25 E - G) forming a functional unit with segment 6 (oligoarthran segments 6 - 9). **P5** basis not separated from coxa and endopod, endopod with 2 setae and 2-segmented exopod with 2-0, 1-2-1 setae. **P6** symmetrical, with 3 setae.

#### Remarks on the morphology of Palinarthra

The monophyletic taxon Palinarthra is characterized mainly by an oral cone, an elongated and narrow gnathobase of the mandible, an elongated and narrow praecoxal arthrite of the maxillula and the short syncoxa of maxilliped.

The hypothesis of the monophyly of Palinarthra is strongly supported (chapter 5.2.4). The morphology of Palinarthra is discussed in chapters 4.20 to 4.26, 5.2.3, and 5.2.4 (char. 3; char. 11; char. 15; char. 22; char. 23; char. 36; char. 42; char. 61).

### 4.19 Novocriniidimorpha tax. nov.

#### Etymology

The taxon name is derived from Greek morph- = form, shape, appearance, beauty. The name of the taxon is selected in honour of Karl Lang for his contribution to the systematics of Harpacticoida, which includes the revision of all species of Harpacticoida described at that time (Lang, 1944, 1948). Karl Lang (1944, 1948) named many of his new taxa after a typical or common species group and introduced therefore the ending "-idimorpha". Novocriniidimorpha tax. nov. is no "superfamily".

#### Taxa belonging to Novocriniidimorpha (12 species in 6 genera)

Novocriniidae Huys & Iliffe, 1998, Superornatiremidae Huys, 1996, Rotundiclipeidae Huys, 1988.

#### Diagnosis: Autapomorphies of Novocriniidimorpha (Fig. 4: ■ 24; Figs. 38 + 39)

*Female.* Antennula: **1 subterminal and 6 terminal setae on oligoarthran segment 9** (char. 6: 0→1). Lateral element 3 of distal endopod segment of antenna **forming a seta** (char. 12: 1→0). Mandible endopod **with 1 lateral seta** (char. 18: 0→1); exopod **with 4 segments** (char. 21: 2→1). Coxa of maxillule **with 6 inner setae** (char. 27: 1→0). Proximal endite of maxillar coxa **with 1 seta** (char. 37: 0→1). Maxilliped (Figs. 39 A + B) **without joint between syncoxa and basis** (char. 45: 1→0); consequently **no flexibility** between syncoxa and basis, **both cylindrical and with the same orientation; elongated** endopod. All pinnate spines of P2-P4 **swollen, flattened and**

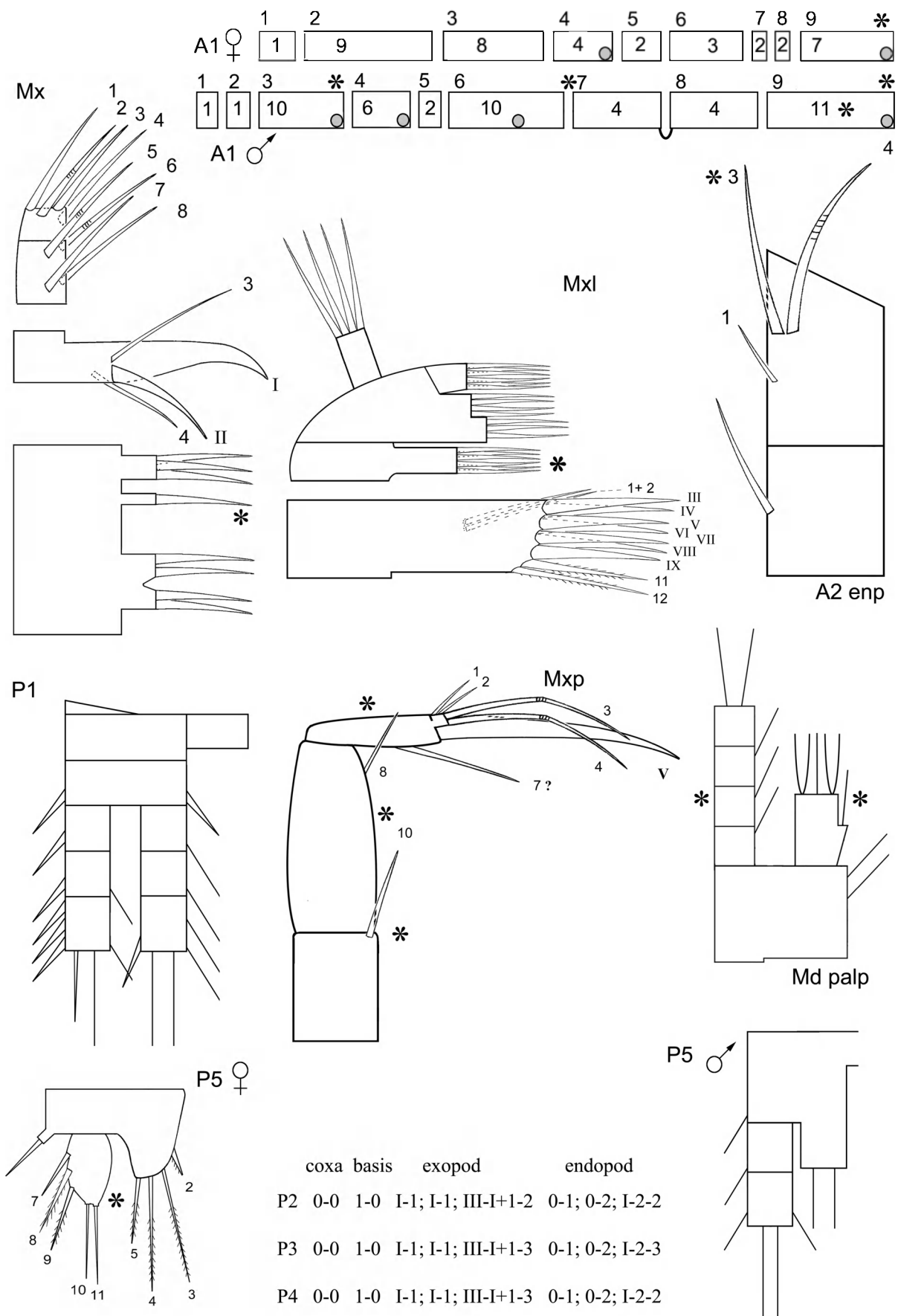


Fig. 38: Groundpattern of Novocriniidomorpha. Asterisks mark autapomorphies of Novocriniidomorpha.

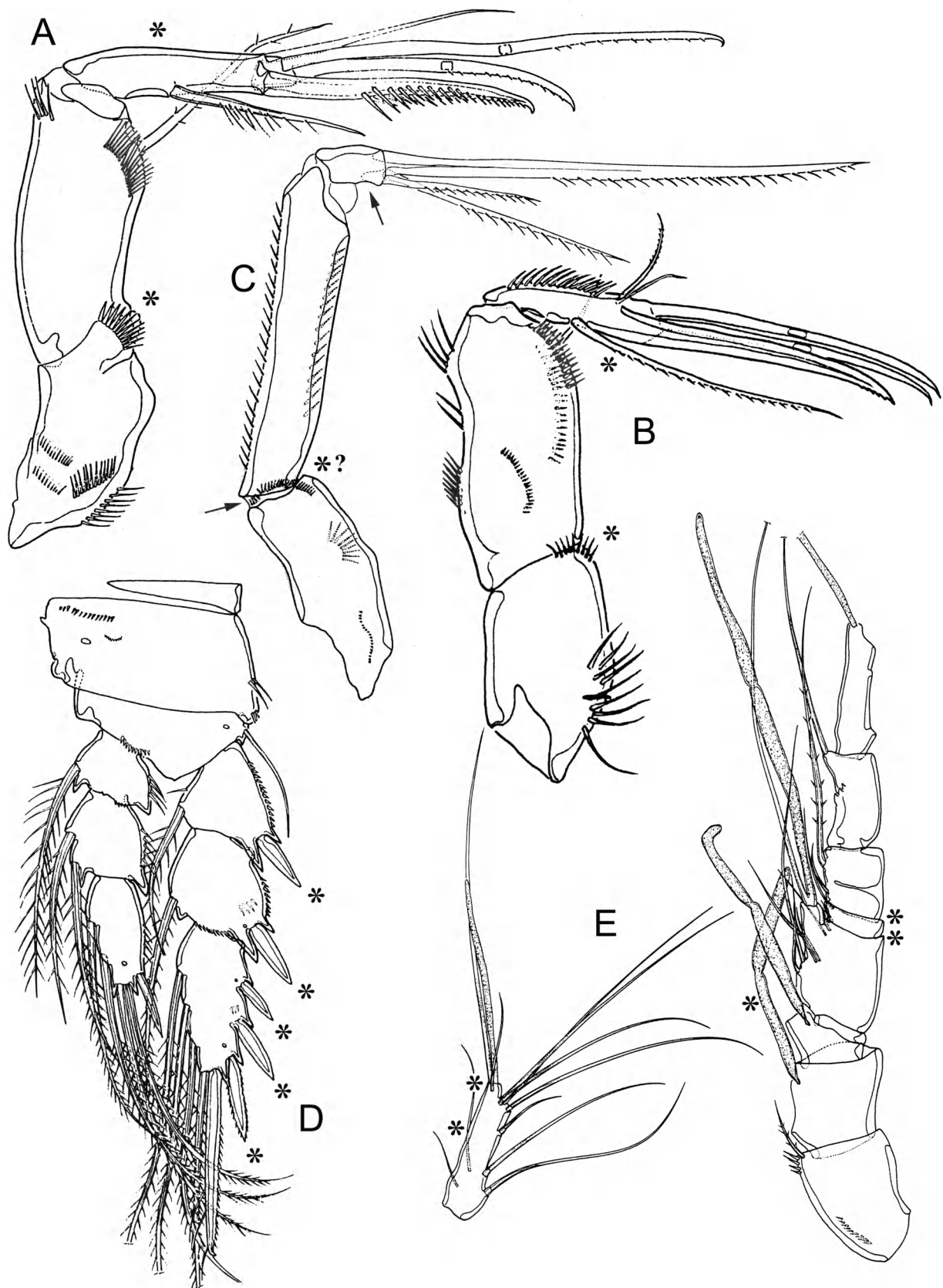


Fig. 39: Morphology of Novocriniidimorpha. A. Mxp of *Novocrinia trifida* (after Huys & Iliffe, 1998). B. Mxp of *Neochinophora xoni* Jaume, 1997 (after Jaume, 1997). C. Mxp of *Rotundiclipeus canariensis* (after Huys, 1988a). D. P4 of *Atergopedia vetusta* (after Martínez Arbizu & Moura, 1998). E. Male antennule of *Atergopedia vetusta* (after Martínez Arbizu & Moura, 1998). -- Asterisks mark some autapomorphies of Novocriniidimorpha. -- Arrows indicate characters discussed in the text.

**spatulate** (Fig. 39 D; char. 58: 0→1). Seta 12 of female exopod **reduced**.

*Male*. Antennule (Fig. 39 E): aesthetasc on oligoarthran segment 3 **present** (char. 65: 1→0); **some of the oligoarthran segments 6 to 9 separated, haplocer** (Copepod segments XIV to XX) (char. 62: 1→0); **without a claw formed by oligoarthran segments 10 to 14** (char. 67: 1→0); **1 subterminal seta and 6 terminal setae on oligoarthran segment 14** (char. 68: 0→1).

#### Groundpattern of Novocriniidimorpha (Fig. 38)

*Female*. **Body** with difference in width between prosome and urosome (?). **Nauplius eye** not confirmed. **Rostrum** fused at base with cephalothorax. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 9, 8, 4 + aes, 2, 3, 2, 2, 6 + acrothek; setae of oligoarthran segment 9: 1 subterminal seta and 6 distal setae. **Antenna** composed of coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 3 subterminal and 7 distal setae; subterminal setation of enp-2 composed of 1 proximal seta (1), 1 longer distal seta (3), and 1 distal geniculate seta (4); lateral seta 2 missing; distal border of endopod is bevelled with an angle towards the exopod (Fig. 24 D); exopod with 2, 1, 1, 3 setae. Labrum, labium and elongated mandibular gnathobases forming a projected **oral cone** (Fig. 36): **labrum** strongly developed, triangular; median fusion of paired **paragnaths** forming a labium; labium partly fused to labrum. **Mandible** with coxa bearing elongated and narrow gnathobase (Fig. 36); cutting edge with 1 seta at proximal corner and bulge at proximal border (Fig. 24 J); palp comprising basis, endopod and exopod; basis with 2 setae; endopod 1-segmented with 1 lateral seta and 5 apical setae, exopod 4-segmented with 1, 1, 1, 2 setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite elongated and narrow: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III – IX), seta (10) lacking, subapical inner margin with 2 plumose setae (11 + 12) on anterior surface, setae 13 + 14 lacking; formula of armature: 2, VII, 0, 2, 0; coxa with 6 setae, no epipodal setae; basis with 4 + 4 setae; endopod directed inwards with 6 setae; exopod 1-segmented with 4 setae. **Maxilla** consisting of syncoxa, allobasis, and endopod; syncoxa with (2 + 2), 1, 3 setae, the two proximal endites fused; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II) and 1 seta (3) on anterior surface and 1 seta (4) on posterior surface; tube pore on anterior surface lacking; allobasis without setae of fused endopod segment; endopod 2-segmented with armature formula: 4, 4 (?). **Maxilliped** (Figs. 39 A + B) indistinctly 4-segmented, comprising syncoxa, basis and indistinctly 2-segmented endopod; no joint, consequently no flexibility between syncoxa and basis, both cylindrical and with the same orientation; syncoxa at most twice as long as wide with 1 coxal seta (10), inserting on inner border; basis with 1 seta on inner edge (8); enp-1 elongated and directed inwards with 1 seta (7?) and 1 big claw (V); the claw displaced to posterior side of distal end of enp-1; enp-2 demarcated by posterior surface suture,

reduced in size and with 1 long outer seta (1) and 2 geniculated distal setae (3 + 4). **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; all pinnate spines of P2-P4 swollen, flattened and spatulate; (Fig. 39 D) formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** baseoendopod with 1 outer basal seta, endopodal lobe with 4 setae (2 - 5); exopod with 5 setae (7 - 11); seta 12 of female exopod reduced. **P6** with 3 setae.

Male. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites, 1 spermatophore. **Antennule** (Fig. 39 E) with 9 segments; armature formula: 1, 1, 10 + aes, 6 + aes, 2, 10 + aes, 6/ 4, 10 + acrothek, 2 additional setae on oligoarthran segment 6; fusion of oligoarthran segments 6 - 7, 8 - 9, 10 - 11 and 12 - 14; aesthetasc on oligoarthran segment 3 present; aesthetasc on oligoarthran segment 6 fused at base with a seta; some of the oligoarthran segments 6 to 9 separated, haplocer (Copepod segments XIV to XX); without a claw formed by oligoarthran segments 10 to 14; setae of oligoarthran segment 9: 1 subterminal seta and 6 distal setae. **P5** basis not separated from coxa and endopod, endopod with 2 setae and 2-segmented exopod with 1-0, 1-2-1 setae. **P6** symmetrical, with 3 setae.

#### Remarks on the morphology of Novocriniidimorpha

The monophyletic taxon Novocriniidimorpha is characterized mainly by the characteristic maxilliped, the spatulate spines of P2-P4, and the male antennule.

The characters of the novocriniidimorph maxilliped are not clearly visible in *Rotundiclipeus canariensis* (Fig. 39 C). The endopod is relatively short and it is doubtful whether the connection between syncoxa and basis is inflexible. The maxilliped of *R. canariensis* is secondarily transformed.

The peculiar morphology of Novocriniidimorpha is discussed further in chapters 4.20 to 4.22, 5.2.3 and 5.2.4 (char. 6; char. 12; char. 18; char. 21; char. 27; char. 37; char. 45; char. 58; char. 62; char. 65; char. 67; char. 68) The hypothesis of the monophyly of Novocriniidimorpha is strongly supported (chapter 5.2.4).

## 4.20 Novocriniidae Huys & Iliffe, 1998

### Taxa belonging to Novocriniidae (2 species in 2 genera)

*Atergopedia* Martínez Arbizu & Moura, 1998, *Novocrinia* Huys & Iliffe, 1998.

### Diagnosis: Autapomorphies of Novocriniidae (Fig. 4: ■ 25; Fig. 40)

*Female*. Subterminal setation of antennal enp-2: **proximally with 1 setoid tuft**, probably the transformed short spine (I), distally with 1 long seta (3) and 1 geniculate seta (4), seta (2) probably lacking. Maxillular praecoxal arthrite: 2 plumose setae of subapical inner margin (11 + 12) **displaced to anterior surface**; coxa with 1 spine

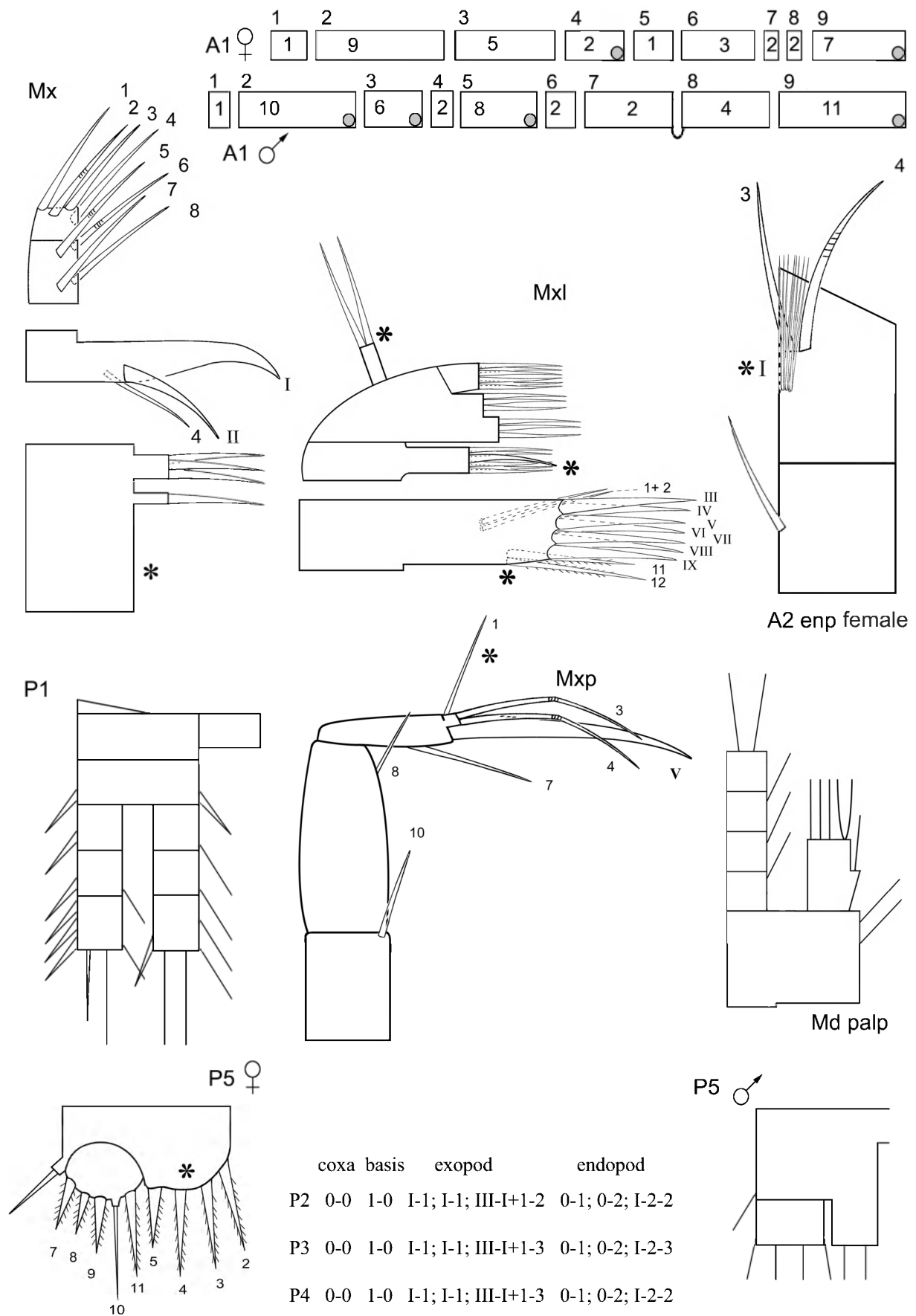


Fig. 40: Groundpattern of Novocriniidae. Asterisks mark autapomorphies of Novocriniidae.

and 5 setae; exopod **elongated, with 2 setae**. Maxillar syncoxa **with 1, 3 setae, praecoxal endites lacking**. Seta 1 of maxillipedal enp-2 **elongated**. Endopodal lobe of P5 **short and broad** with 4 spines (2 - 5).

*Male*. **Sexual dimorphism in antenna: a distal setoid tuft**, probably a transformed distal seta.

#### Groundpattern of Novocriniidae (Fig. 40)

*Female*. **Body** without difference in width between prosome and urosome (Fig. 3 A). **Nauplius eye** unconfirmed. **Rostrum** fused at base with cephalothorax. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; number of egg sacs unconfirmed, 1 copulatory pore, 2 seminal receptacles, gonopores fused forming transverse common genital slit. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 9, 5, 2 + aes, 1, 3, 2, 2, 6 + acrothek; setae of oligoarthran segment 9: 1 subterminal seta and 6 distal setae. **Antenna** composed of coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 7 distal setae; subterminal setation of enp-2: proximally with 1 setoid tuft, probably the transformed short spine (I), distally with 1 long seta (3) and 1 geniculate seta (4), seta (2) probably missing; distal border of endopod slightly bevelled with an angle towards the exopod; exopod with 1, 1, 1, 3 setae. Labrum, labium and elongated mandibular gnathobases forming a projected **oral cone** (Figs. 36 A - C): **labrum** strongly developed, partly fused to labium; median fusion of paired **paragnaths** forming a labium. **Mandible** with coxa bearing elongate and narrow gnathobase (Fig. 36 A); cutting edge with 1 seta at proximal corner and bulge at proximal border (Fig. 24 J); palp comprising basis, endopod and exopod; basis with 2 setae; endopod 1-segmented with 1 lateral seta and 3 + 2 apical setae, 2 apical setae fused basally; exopod 4-segmented with 1, 1, 1, 2 setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite elongated and cylindrical: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III - IX), seta (10) lacking, subapical inner margin with 2 plumose setae (11 + 12) on anterior surface, setae 13 + 14 lacking; formula of armature: 2, VII, 0, 2, 0; coxa with 1 spine and 5 setae, no epipodal setae; basis with 4 + 3 setae; endopod directed inwards with 6 setae; exopod 1-segmented and elongated with 2 setae. **Maxilla** 4-segmented consisting of syncoxa, allobasis, and 2-segmented endopod; syncoxa with 1, 3 setae, praecoxal endites lacking; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) fused to endite, 1 curved spine (II) on anterior surface and 1 seta (4) on posterior surface; seta 3, tube pore and accessory armature of fused endopod segment lacking; endopod with armature formula: 4, 4; proximal segment with 1 geniculated seta anteriorly (5) and 1 posteriorly (6), last segment with 2 geniculated seta (2 + 3). **Maxilliped** (Fig. 39 A) indistinctly 4-segmented, comprising syncoxa, basis and indistinctly 2-segmented endopod; no joint, consequently no flexibility between syncoxa and basis, both cylindrical and with the same orientation; syncoxa at most twice as long as wide with 1 coxal seta (10), inserting on inner border; basis with

1 seta on inner edge (8); enp-1 elongate and directed inwards with 1 seta (7?) and 1 big claw (V); the claw displaced to posterior side of distal end of enp-1; enp-2 demarcated by posterior surface suture, reduced in size and with 1 long outer seta (1) and 2 geniculated distal setae (3 + 4), seta 1 displaced to the end of enp-1. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; all spines of P2-P4 slightly swollen and spatulate (Fig. 39 D); formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5**: baseopod with 1 outer basal seta, endopodal lobe short and broad with 4 spines (2 - 5); exopod with 1 seta (10) and 4 spines (7 - 9, 11). **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, antenna, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** (Fig. 39 E) with 9 segments; armature formula: 1, 10 + aes, 6 + aes, 2, 8 + aes, 2, 2 / 4, 10 + acrothek, 2 additional setae on oligoarthran segment 6; fusion of oligoarthran segments 2 - 3, 8 - 9, 10 - 11 and 12 - 14; aesthetasc on oligoarthran segment 6 fused at base with a seta; setae of oligoarthran segment 9: 1 subterminal seta and 6 distal setae. **Antenna** with a distal setoid tuft, probably a transformed distal seta. **P5** fused medially; basis not separated from coxa and endopod; endopodal lobe broad with 2 setae; exopod 1-segmented with 5 spines. **P6** symmetrical (?), with 3 setae.

#### Remarks on the systematics and morphology of Novocriniidae

##### *Systematics.*

Atergopediidae Martínez Arbizu & Moura, 1998 is a synonym of Novocriniidae.

Martínez Arbizu & Moura (1998) thought about placing Novocriniidae within Exanechentera, "having a basal phylogenetic position". Novocriniidae belong without doubt to Exanechentera, as sister group of Superornatiremidae - Rotundiclipeidae (see chapters 5.1.5, 5.2.4, and 5.2.5).

##### *Morphology.*

The monophyletic group Novocriniidae is characterized mainly by the setoid tuft of the antenna, the spine of the maxillular coxa, the reduction of the proximal endites of the maxillar syncoxa and the spines of the P5 in the female.

*Atergopedia vetusta* has an incompletely fused **P1 segment** that lacks a tergite and conceals beneath a carapace-like extension of the cephalosome. This is a secondary phenomenon. The fusion of the P1 segment to the cephalosome is not always realized in Oligoarthra. The presented results indicate that a partly free P1-segment is not unusual (see chapter 4.3).

For a discussion of the **oral cone, the elongated gnathobase of mandible and the praecoxal arthritis of maxillula** see chapters 4.26, 5.2.3 and 5.2.4.

The **mandibular** endopod of *Novocrinia trifida* is indistinctly 2-segmented. This is a secondary phenomenon as described in chapter 4.3.

The male of *N. trifida* has 4 spines on the endopodal lobe of **P5** as has the female. This has secondarily evolved (see chapter 4.1).



Compared to the oligoarthran groundpattern *A. vetusta* has 2 additional setae on the oligoarthran segment 6 of **male antennule**. This is also true for some species of Tisbidae *sensu strictu*, Paramesochridae and Tegastidae (see chapter 4.26).

#### 4.21 Superornatiremidae Huys, 1996

Taxa belonging to Superornatiremidae (9 species in 3 genera)

*Intercrusia* Huys, 1996, *Neoechinophora* Huys, 1996, *Superornatiremis* Huys, 1996.

Diagnosis: Autapomorphies of Superornatiremidae (Fig. 4: ■ 27; Figs. 41 + 36 E)

*Female*. Urosome with 1 copulatory pore **partly covered by hyaline epicopulatory flap**. Anal somite **elongated**. Basis of mandible (Fig. 36 E) with 2 setae, **the proximal one enlarged and modified**; endopod **small with no lateral setae**. **Spine III of praecoxal arthrite of maxillule fused at base to endite**; coxa with 4 terminal and 2 subterminal setae; basis with 2 + 3 setae; endopod directed inwards with 3 setae. Maxilla endopod **incorporated into allobasis, represented by 3 setae**; syncoxa with (2 + 2), 3 setae, the fused praecoxal endites **trilobate, resulting from additional proximal lobe, proximal coxal endite lacking**. P1 with additional spines and setae on exopod and endopod. P2 enp-1 elongated, enp-2 and enp-3 partly fused; distal inner seta of P2-P3 enp-3 and outer distal seta of P4 enp-3 transformed to a **pinnate spine**; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	III-0; II-1; IV-I-2	0-1; 2-1; II-I+1-3
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; (0-2; I-2-I+1)
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-1; I-2-I+2
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-1; I-I+1-1

P5 **laterally displaced, exopod more than twice as long as wide** (char. 60: 1→2).

*Male*. Antennule **without an aesthetasc on oligoarthran segment 3** (char. 65: 0→1).

P5 **laterally displaced**.

Groundpattern of Superornatiremidae (Fig. 41)

*Female*. **Body** with clear difference in width between prosome and urosome (Fig. 3 B). **Nauplius eye lacking**. **Rostrum** fused at base with cephalothorax. **Prosome** consists of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; number of egg-sacs unconfirmed, 1 copulatory pore, partly covered by hyaline epicopulatory flap, median seminal receptacle, gonopores separate, laterally displaced. **Anal somite** elongate, not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9-segmented; armature formula: 1, 9, 8, 4 + aes, 2, 3, 2, 2, 6 + acrothek; setae of oligoarthran segment 9: 1 subterminal seta and 6 distal setae. **Antenna** (Fig. 24 D) composed of coxa, allobasis, 1-segmented endopod and 4-segmented exopod; fused basis without seta, fused enp-1 with 1 seta; enp-2 with 7 distal setae; subterminal setation of enp-2: proximally with 1 seta (1), distally with 1 long seta (3) and 1 geniculate seta (4), seta (2) lacking; distal border of endopod

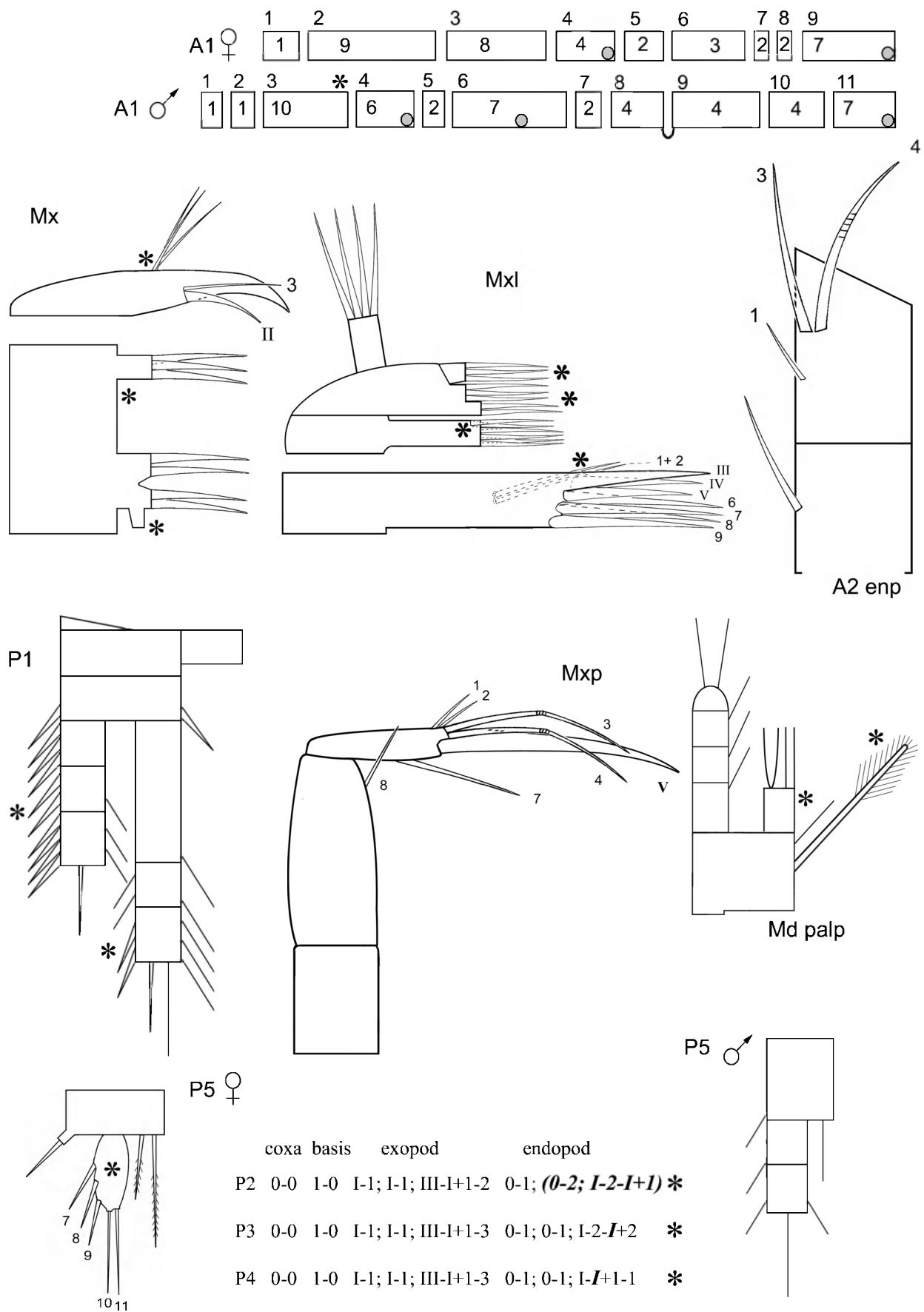


Fig. 41: Groundpattern of Superornatiremidae. Asterisks mark autapomorphies of Superornatiremidae.

slightly bevelled with an angle towards the exopod; exopod with 2, 1, 1, 2 setae. Labrum, labium and elongated mandibular gnathobases forming a projected **oral cone** (Figs. 36 D - F): **labrum** strongly developed, triangular, tapering towards apical process, partly fused to labium; median fusion of paired **paragnaths** forming a labium. **Mandible** with coxa bearing elongated and stylet-like gnathobase (Figs. 36 D - F); cutting edge with 1 seta at proximal corner and no bulge at proximal border; palp comprising basis, endopod and exopod; basis with 2 setae, the proximal one enlarged and modified; endopod 1-segmented and small with no lateral setae and 2 + 2 apical setae, 2 apical setae basally fused; exopod 4-segmented with 1, 1, 1, 2 setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite elongated, narrow and cylindrical: anterior surface in outer half with 2 neighbouring setae (1 + 2), bearing 3 spiniform and 4 setiform elements, all tightly together (III - V + 6 - 9), spine III fused at base to endite; seta 10 to 14 lacking; formula of armature: 2, III + 4, 0, 0, 0; coxa with 4 terminal and 2 subterminal setae, no epipodal setae; basis with 2 + 3 setae; endopod 1-segmented and directed inwards with 3 setae; exopod 1-segmented and elongate with 4 setae. **Maxilla** consisting of syncoxa, allobasis, and endopod incorporated into allobasis; syncoxa with (2 + 2), 3 setae, the fused praecoxal endites trilobate, resulting from additional proximal lobe; proximal coxal endite lacking; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) fused to the endite, 1 curved spine (II) and 1 seta (3) on anterior surface; seta 4, tube pore and accessory armature of fused endopod segment missing; endopod incorporated into allobasis, and represented by 3 setae. **Maxilliped** (Fig. 39 B) 3-segmented, comprising syncoxa, basis and 1-segmented endopod; no joint, consequently no flexibility between syncoxa and basis, both cylindrical and with the same orientation; syncoxa at most twice as long as wide with no setae; basis with 1 seta on inner edge (8); fused enp-1 elongate and directed inwards with 1 seta (7?), and 1 fused big claw (V); fused enp-2 reduced in size and forming apical pedestal with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4). **P1** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; P1 with additional spines and setae on exopod and endopod, enp-1 elongated; **P2-P4** biramous; praecoxa present; leg pairs joined by intercoxal sclerite; P2 enp-1 elongated, enp-2 and enp-3 partly fused; otherwise all rami of P2-P4 3-segmented; distal inner seta of P2-P3 enp-3 and outer distal seta of P4 enp-3 transformed to pinnate spine; all spines of P2-P4 exopod and endopod swollen and spatulate; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	III-0; II-1; IV-I-2	0-1; 2-1; II-I+1-3
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; (0-2; I-2-I+1)
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-1; I-2-I+2
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-1; I-I+1-1

**P5** laterally displaced; baseoendopod with 1 outer basal seta, endopodal lobe represented by 2 setae; exopod with 5 setae (7-11): 1 inner, 1 terminal seta and 3 outer setae. **P6** with 2 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** with 11 segments; armature formula: 1, 1, 10, 6 + aes, 2, 7 + aes, 2, 4 / 4, 4, 6 + acrothek; fusion of oligoarthran segments 6 - 7, 10 - 11 and 12 -

13; aesthetasc on oligoarthran segment 3 lacking; aesthetasc on oligoarthran segment 6 fused at base with a seta; setae of oligoarthran segment 9: 1 subterminal seta and 6 distal setae. **P5** laterally displaced; basis not separated from coxa and endopod; baseoendopod with 1 outer basal seta, endopodal lobe represented by 1 seta; exopod 2-segmented with 1-0, 1-I-1 setae. **P6** asymmetrical, with 3 setae.

#### Remarks on the systematics and morphology of Superornatiremidae

##### *Systematics.*

Huys & Boxshall (1991) were the first to mention Superornatiremidae Huys, 1996, *Neoechinophora* Huys, 1996, *Neoechinophora fosshageni* Huys, 1996, *Superornatiremis* Huys, 1996 (type genus), and *Superornatiremis mysticus* Huys, 1996 and figured the P1 of these species. Huys et al. (1996) also showed the P1 of *S. mysticus*. These taxa were treated as *nomina nuda* until Huys (1996) described them. Huys (1996, p. 541) placed the Superornatiremidae “in the tisburyid complex of families” and assumed “that the Superornatiremidae occupy an intermediate position between the two free-living tisburyid subfamilies Tisbinae and Idyanthinae...”. Indeed, Novocriniidimorpha (Novocriniidae - Superornatiremidae - Rotundiclipeidae) has an intermediate position between Idyanthidimorpha (Idyanthidae - Zosimidae) and Tisbidae *sensu strictu* (see chapter 5).

##### *Morphology.*

The monophyletic group Superornatiremidae is characterized mainly by the elongated anal somite, the enlarged and modified seta of the mandibular basis, the fusion of spine III with the praecoxal arthrite of maxillula, the trilobate praecoxal endite of maxilla, the reduction of the proximal endite of the maxillar coxa, the incorporated endopod of the maxilla, the additional spines of P1, the hyaline epicopulatory flap of the female, and the laterally displaced P5 of both sexes.

For a detailed description and discussion of the **oral cone** and the **P1** of Superornatiremidae see Huys (1996).

For a discussion of the **oral cone**, the elongated gnathobase of **mandible** and the praecoxal arthrite of **maxillula** of Palinarthra see chapters 4.26, 5.2.3, and 5.2.4.

For the discussion of the elongated exopod of **P5** (char. **60**: 1→2) and the reduction of the aesthetasc of oligoarthran segment 3 of the **male antennule** (char. **65**: 0→1) see chapters 5.2.3 and 5.2.4.

## 4.22 Rotundiclipeidae Huys, 1988

### Taxa belonging to Rotundiclipeidae (1 species in 1 genus)

*Rotundiclipeus canariensis* Huys, 1988

#### Diagnosis: Autapomorphies of Rotundiclipeidae (Fig. 4: ■ 28; Figs. 3 C, 36 H, 39 C)

*Female.* Prosome consisting of cephalothorax and **4 free pedigerous somites**; **first pedigerous somite completely separated from dorsal cephalic shield** (char. **1**: 0→1) but reduced in size; **cephalothorax forming a subcircular shield, which is deeply incised anteriorly** and covers the P1 segment almost entirely (Fig. 3 C). Anal operculum **lacking**. Exopod of mandible (Fig. 36 H) **lacking** (char. **21**: 1→2); basis

extraordinarily elongated, with no setae. Maxillule with exopod completely incorporated in basis represented by 2 setae; coxa with 1 spine and 5 setae. Maxillar syncoxa only with bilobed praecoxal endite with (2 + 1) setae, coxal endites lacking; basis with weakly-developed endite; armature of allobasis consisting of a thin, long and geniculated claw fused to the endite (I?), 3 setae and 1 aesthetasc. Endopod of maxilliped not elongated (Fig. 39 C). P1 with 1-segmented rami, exopod and endopod long and slender; P2-P4 with 2-segmented endopod; P2 slender, P3 and P4 robust; some spines of P2 and all spines of P3-P4 extremely swollen and spatulate; formula of armature:

	Coxa basis		exopod	endopod
P1	0-0	I-1	2-1-1	0-1-2
P2	0-0	1-0	I-0; I-0; III-I-1	0-1; 0-2-1
P3	0-0	1-0	I-0; I-0; II-I-1	0-I; 0-I+1-II
P4	0-0	1-0	I-0; I-0; II-I-2	0-I; 0-I+1-II

Both P5 form a smooth common plate, which is incorporated into the ventral integument, represented by 2 strong spines on either side (char. 61: 0→1).

*Male.* P5 as in female, i.e. no sexual dimorphism.

#### Groundpattern of Rotundiclipeidae

*Female.* **Body** without difference in width between prosome and urosome (Fig. 3 C). **Nauplius eye** unconfirmed. **Rostrum** tiny, fused at base with cephalothorax. **Prosome** consisting of cephalothorax and 4 free pedigerous somites; first pedigerous somite completely separated from dorsal cephalic shield, but reduced in size; cephalothorax forming a subcircular shield, which is deeply incised anteriorly and covering almost entirely the P1 segment. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; number of egg-sacs unconfirmed, 1 copulatory pore, gonopores fused forming transverse common genital slit. **Anal somite** not divided longitudinally; anal operculum lacking. **Caudal rami** with 7 setae. **Antennule** 8-segmented; armature formula: 1, 6, 5, 1 + aes, 1, 2, 4, 6 + acrothek; setae of oligoarthran segment 9: 1 subterminal seta and 6 distal setae. **Antenna** composed of coxa, allobasis, 1-segmented endopod and 4-segmented exopod; fused basis and enp-1 with no seta; enp-2 with 7 distal setae; subterminal setation of enp-2: proximally with 1 short seta (1), distally with 2 long setae (3 + 4), seta (2) missing; distal border of endopod barely bevelled with an angle towards the exopod; exopod with 0, 1, 1, 2 setae. Labrum and elongated mandibular gnathobases forming a projected **oral cone** (Fig. 36 G): **labrum** strongly developed, triangular, tapering towards apical process. **Mandible** (Fig. 36 H) with coxa bearing extremely elongate and stylet-like gnathobase; cutting edge with 1 seta at proximal corner and no bulge at proximal border; palp comprising basis and endopod, exopod lacking; basis extraordinarily elongated, without setae; endopod 1-segmented with 1 lateral seta and 4 apical setae. **Maxillule** comprised of praecoxa, coxa, basis, incorporated exopod, and endopod; praecoxal arthrite elongated and cylindrical: anterior surface in outer half with 2 neighbouring setae (1 + 2), bearing 2 spiniform and 4 setiform elements, all tightly together; formula of armature: 2, II + 4, 0, 0, 0; coxa with 1 spine and 5 setae, no epipodal setae; basis with 3 + 4 setae; endopod 1-segmented and directed inwards with 6 setae; exopod completely incorporated into basis represented by 2 setae. **Maxilla** 5-

segmented consisting of syncoxa, allobasis, and 3-segmented endopod; syncoxa with bilobed praecoxal endite with (2 + 1) setae, coxal endites lacking; basis with weakly-developed endite; armature of allobasis consisting of a thin, long and geniculated claw fused to endite (I?), 3 setae and 1 aesthetasc; endopod with armature formula: 2, 2, 2; no geniculated setae. **Maxilliped** (Fig. 39 C) 3-segmented, comprising syncoxa, basis and 1-segmented endopod; no joint (?), consequently no flexibility between syncoxa and basis, both cylindrical and with the same orientation; syncoxa at most twice as long as wide; coxa and basis without setae; enp-1 not elongated and directed inwards with 1 seta (7?) and 1 big claw (V); the claw displaced to posterior side of distal end of enp-1; enp-2 completely incorporated in enp-1, represented by 1 long seta. **P1** with 1-segmented rami, exopod and endopod long and slender; **P2-P4** biramous with 2-segmented endopod and 3-segmented exopod; P2 slender, P3 and P4 robust; praecoxa present; leg pairs joined by intercoxal sclerite; some spines of P2 and all spines of P3-P4 extremely swollen and spatulate; formula of armature:

	Coxa	basis	exopod	endopod
P1	0-0	I-1	2-1-1	0-1-2
P2	0-0	1-0	I-0; I-0; III-I-1	0-1; 0-2-1
P3	0-0	1-0	I-0; I-0; II-I-1	0-I; 0-I+1-II
P4	0-0	1-0	I-0; I-0; II-I-2	0-I; 0-I+1-II

**Both P5** form a smooth common plate, which is incorporated into the ventral integument, represented by 2 strong spines on either side. **P6** with 1 seta.

*Male.* Sexual dimorphism in body size, genital segmentation, antennule, and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** with 10 segments; armature formula: 1, 6 + aes, 3 + aes, 6 + aes, 1, 2, 2 / 4, 4, 6 + acrothek; fusion of oligoarthran segments 2 - 3, 5 - 6, 10 - 11 and 12 - 14; aesthetasc on oligoarthran segment 6 fused at base with a seta; setae of oligoarthran segment 9: 1 subterminal seta and 6 distal setae. **Both P5** form together a smooth common plate, which is incorporated into the ventral integument, represented by 2 spines on either side, as in female. **P6** symmetrical with 1 seta.

#### Remarks on the morphology of Rotundiclipeidae

The monotypic Rotundiclipeidae is characterized mainly by the form of the body, the decreased setation of all mouthparts and legs, the extraordinary palp of mandible, the maxillule exopod completely incorporated into the basis, the unique armature of the maxillar allobasis, the P1 with 1-segmented rami, the 2-segmented endopods of P2-P4 and the P5 of both sexes.

The **first pedigerous somite** of *Rotundiclipeus canariensis* is completely separated from the dorsal cephalic shield; however, it is reduced in size. Size and evolution of the P1 segment in Oligoarthra indicate that the separated P1 segment is a secondary phenomenon (char. 1: 0→1; see chapters 4.3 and 5.2.3).

It remains to be examined whether the **paragnaths** are fused to form a labium or not. For a discussion of the **oral cone** and the elongated gnathobase of **mandible** and the praecoxal arthrite of **maxillula** of Palinarthra see chapters 4.26, 5.2.3, and 5.2.4.

As for the setation of the **maxillular** basis see chapter 4.3, the **maxilliped** see chapter 4.19, and the **mandible** lacking an exopod (char. 21) and the P5 of female (char. 61: 0→1) see chapter 5.2.3.

### 4.23 Tisboidea Stebbing, 1910

Taxa belonging to Tisboidea (310 species in 40 genera)

Peltidiidae Sars, 1904, Porcellidiidae Boeck, 1865, Tegastidae Sars, 1904, Tisbidae Stebbing, 1910 *sensu strictu*.

Autapomorphies and diagnosis of Tisboidea (Fig. 4: ■ 29; Figs. 42 + 43)

*Female*. Body dorso-ventrally flattened (char. 2: 0→1). Setae 11 and 12 of maxillular praecoxa absent (char. 24: 0→1). Coxa and basis of maxillule fused (char. 28: 0→1). Fused praecoxal endites of maxilla displaced to the inner proximal corner of syncoxa (Figs. 43 A - D; char. 35: 0→1). P1 (Figs. 43 E + F): enp-2 elongated (char. 52: 0→1); exp-1 and exp-2 elongated (char. 54: 0→1); exp-3 small and rounded, all spines of exp-3 elongated, with long spinules on one side (char. 56: 0→2). Exopod of P5 more than twice as long as wide (char. 60: 1→2).

Groundpattern of Tisboidea (Fig. 42)

*Female*. **Body** with difference in width between prosome and urosome, dorso-ventrally flattened. **Nauplius eye** present. **Rostrum** fused at base with cephalothorax. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae. **Antennule** 9 -segmented; armature formula: 1, 13, 10, 6 + aes, 2, 4, 2, 2, 6 + acrothek. **Antenna** composed of coxa, basis, 2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 3 subterminal and 7 distal setae; subterminal setation of enp-2 composed of 1 proximal seta (1), 1 longer distal spine (III), and 1 distal geniculate seta (4); lateral seta 2 missing; distal border of endopod is bevelled with an angle towards the exopod (Fig. 24 E); exopod with 2, 1, 1, 3 setae. Labrum, labium and elongated mandibular gnathobases forming a projected **oral cone** (Figs. 37 A, B, D): **labrum** strongly developed, triangular; median fusion of paired **paragnaths** forming a labium; labium partly fused to labrum. **Mandible** (Figs. 37 C, E, F) with coxa bearing elongated and narrow gnathobase; cutting edge with 1 seta at proximal corner and bulge at proximal border; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 3 lateral and 7 apical setae; exopod 1-segmented with 4 lateral and 2 distal setae. **Maxillule** comprised of praecoxa, exopod, endopod, and fused coxa and basis; praecoxal arthrite elongated and cylindrical: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III - IX), setae 10 - 14 lacking; formula of armature: 2, VII, 0, 0, 0; coxa with 4 setae, no epipodal setae; basis with 4 + 4 setae; endopod directed inwards with 6 setae; exopod 1-segmented with 3 setae. **Maxilla** (Figs. 43 A - D) consisting of syncoxa, allobasis, and endopod; syncoxa with (3 + 2), 3, 3 setae, the two proximal endites fused; fused praecoxal endites displaced to inner proximal corner of syncoxa; basis with well-developed endite; accessory armature of fused basis consisting of strong claw (I) at the end of the endite, 1 curved spine (II) and 1 seta (3)

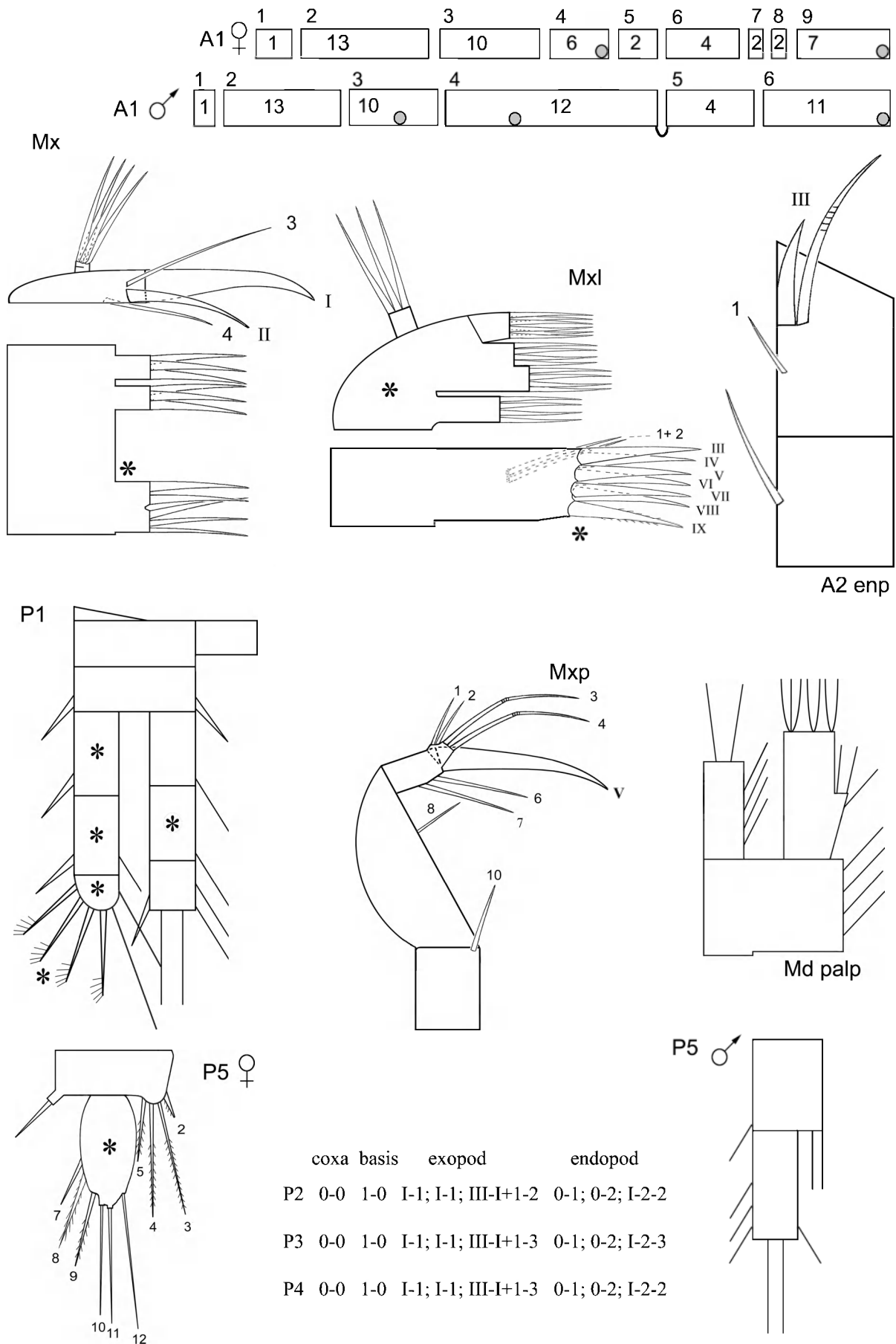


Fig. 42: Groundpattern of Tisboidea. Asterisks mark autapomorphies of Tisboidea.



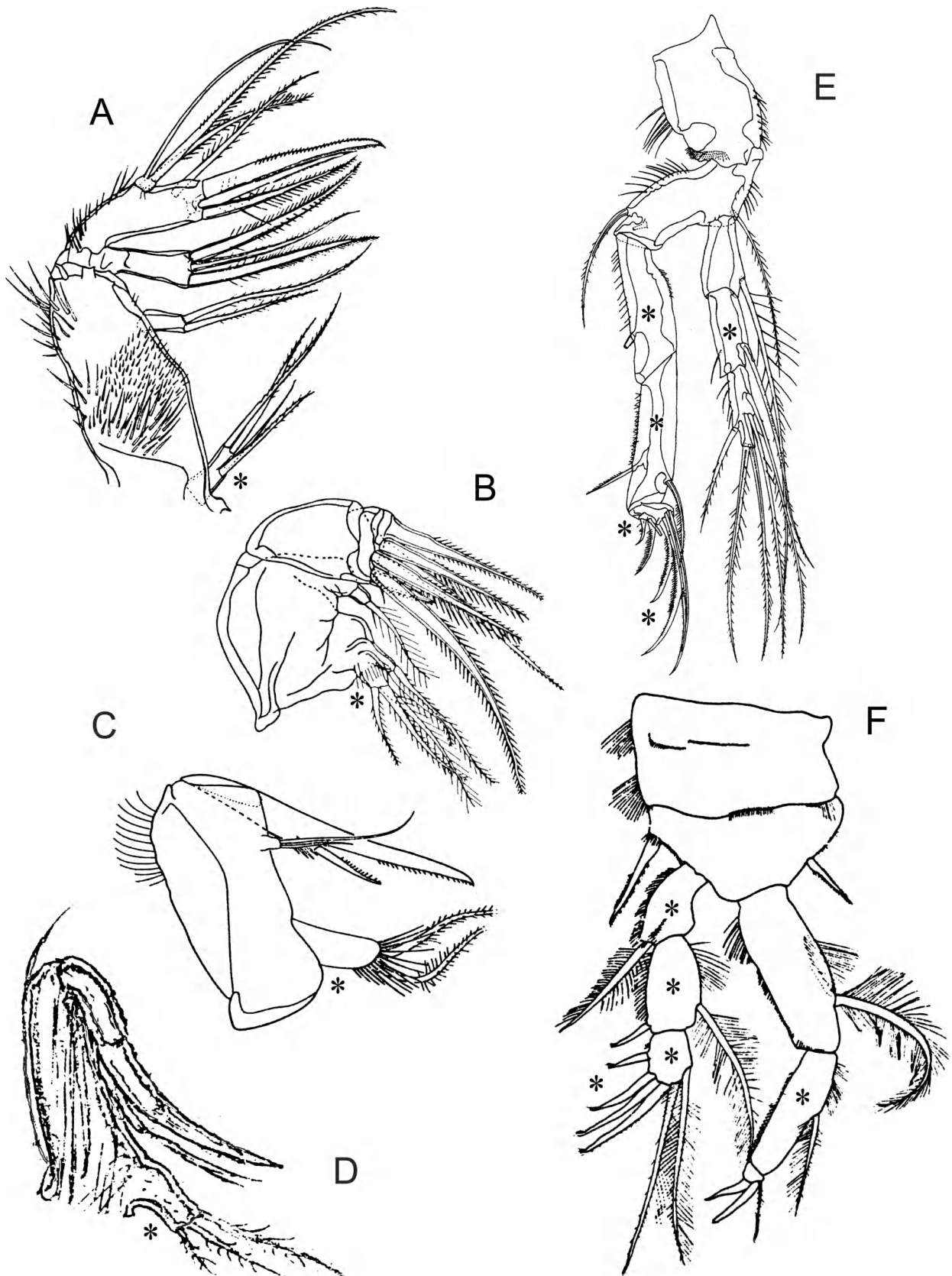


Fig. 43: Maxilla and P1 of Tisboidea. --- **Mx**: A. *Eupelte villosa* (Brady, 1910) (after Dahms, 1992). B. *Porcellidium brevicaudatus* (after Humes & Ho, 1969). C. *Tisbe longipes* Volkman-Rocco, 1979 (after Volkman-Rocco, 1979). D. *Tisbe tenella* (after Sars, 1911). --- **P1**: E. *Alteutha polarsternae* (after Dahms, 1992). F. *Tisbe prolata* Waghorn, 1997 (after Bradford und Wells, 1983). -- Asterisks mark some autapomorphies of Tisboidea.

on anterior surface and 1 seta (4) on posterior surface; tube pore on anterior surface lacking; allobasis without setae of fused endopod segment; endopod indistinctly 2-segmented with armature formula: (0, 4). **Maxilliped** subchelate and indistinctly 4-segmented, comprising syncoxa, basis and indistinctly 2-segmented endopod; syncoxa at most twice as long as wide with 1 coxal seta (10), inserting on inner border; basis with 1 seta on inner edge (8); enp-1 with 2 setae (6 + 7) and 1 big claw (V); the claw displaced to posterior side of distal end of enp-1; enp-2 demarcated by posterior surface suture, reduced in size and with 2 short outer setae (1 + 2) and 2 geniculated distal setae (3 + 4); high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; **P1** (Fig. 37 G; Figs. 43 E + F) of characteristic shape: exp-1 and exp-2 elongated; exp-3 small and rounded, all spines of exp-3 elongated, with long spinules on one side; enp-1 and enp-2 elongated; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; I-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** baseoendopod with 1 outer basal seta, endopodal lobe represented by 4 setae (2 - 5): 2 inner setae and 2 terminal setae; exopod more than twice as long as wide with 6 setae (7 - 12): 1 inner seta, 2 terminal setae, 2 outer spines, and 1 outer seta. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consisting of somite bearing P5 and 4 abdominal somites, 1 spermatophore. **Antennule** subchirocer with 6 segments; armature formula: 1, 13, 10 + aes, 12 + aes/ 4, 10 + acrothek, fusion of Oligoarthra segments 2 - 3, 4 - 5, 6 - 9, 10 - 11 and 12 - 14; aesthetascs of Oligoarthra segment 3 lacking; aesthetasc on Oligoarthra segment 6 fused at base with a seta; segments 5 and 6 (oligoarthran segments 10 - 14) forming claw with a pointed end (Figs. 25 E - G) forming a functional unit with segment 4 (oligoarthran segments 6 - 9). **P5** basis not separated from coxa and endopod, endopodal lobe represented only by 2 setae; exopod 1-segmented with 3 outer, 2 terminal setae and 1 inner seta. **P6** symmetrical, with 3 setae.

#### Remarks on systematics and morphology of Tisboidea

##### *Systematics.*

Lang (1944) established the taxon Tisbidimorpha Lang, 1944 to unite Peltidiidae, Tegastidae, Porcellidiidae, and Tisbidae *sensu* Lang (1944). Bowman & Abele (1982) changed Lang's "superfamily"-endings "-idimorpha" in "superfamily"-endings - "oidea" and introduced Tisboidea Stebbing, 1910 (see ICZN, 1999, Art. 29.2. Tisboidea still enclose the same taxa with exception of Idyanthidae and Zosimidae, which are excluded from Tisbidae *sensu* Lang and Tisboidea.

##### *Morphology.*

The monophyletic group Tisboidea is characterized mainly by the lack of setae 11 and 12 of maxillular praecoxa, the fused coxa and basis of maxillule, the displaced praecoxal endites of maxilla, the elongated exopod P5 of the female and the

characteristic P1.

The monophyly and morphology of Tisboidea is discussed in chapters 4.24 to 4.26, 5.2.3 and 5.2.4 (char. 2; char. 24; char. 28; char. 35; char. 52; char. 54; char. 56; char. 60).

#### 4.24 Peltidiidae Sars, 1904 - Tegastidae Sars, 1904

Taxa belonging to Peltidiidae - Tegastidae (132 species in 15 genera)

Peltidiidae: (68 species in 10 genera): *Alteutha* Baird, 1845, *Alteuthella* A. Scott, 1909, *Alteuthellopsis* Lang, 1944, *Alteuthoides* Hicks, 1986, *Clytemnestra* Dana, 1847, *Eupelte* Claus 1860, *Goniopsyllus* Huys & Conroy-Dalton, 2000, *Neopeltopsis* Hicks, 1976, *Parapeltidium* A. Scott, 1909, *Peltidium* Philippi, 1839.

Undescribed species (8.1 Appendix I.): *Peltidium* spec. 1, *Peltidium* spec. 2.

Tegastidae: (64 species in 5 genera): *Arawella* Cottarelli & Baldari, 1987, *Feregastes* Fiers, 1986, *Parategastes* Sars, 1904, *Syngastes* Monard, 1924, *Tegastes* Norman, 1903.

Undescribed species (8.1 Appendix I.): *Parategastes* spec., *Tegastes* spec. 1., *Tegastes* spec. 2.

Changes in systematics (reasons given below)

Clytemnestridae A. Scott, 1909 is synonymized with Peltidiidae Sars, 1904.

Diagnosis: Autapomorphies of Peltidiidae - Tegastidae (Fig. 4: ■ 30; Fig. 44, 3 D, 37 E, 43 A + E)

*Female*. Body with **strongly developed integument**. Rostrum **broad and fused at base with cephalothorax**. Cephalothorax **large**; epimeral plates of free prosomites **laterally expanded**. Urosome **much shorter than prosome** (Fig. 3 D). Seta IV and V of caudal rami **reduced in size and length**. Antenna: subterminal setation of enp-2 composed of 1 proximal seta (1) and **2 distal spines (III + IV)**, seta (2) missing and **element 4 forming a spine**. **No oral cone**; paragnaths fused, **not prominent**; labrum large, **not prominent** (char. 3: 1→0). Mandible endopod with **1 lateral seta** (Fig. 37 E; char. 18: 0→1). Basis of maxillule **extremely elongated** (mainly proximal endite) with 4 + 3 setae; endopod **small, displaced to the endites** and directed inwards with 3 setae. Maxillar endopod **vestigial, displaced towards the end of endite**, with 3 setae (Fig. 43 A). Maxillipeds of both sides **inserted on a raised area of the ventral body surface, the pedestal**; syncoxa of maxilliped **more than 3 times longer than wide** (char. 42: 1→0) with **2 coxal setae** inserting on inner distal corner (10) and **between inner and outer distal corner (?)** (char. 43: 4→3); basis with 1 short seta and **1 distal pad-like sensory element on inner edge**; enp-1 fused with **1 big claw (V)** and with **1 seta (7)** and **1 short strong spine (VI?)** on posterior side. P1 (Fig. 43 E) coxa and basis **elongated**; exopod **longer than endopod**. Basis of P2-P4 **transversally elongated**; all segments of exopod and endopod of P2-P4 **long and with elongated spines**.

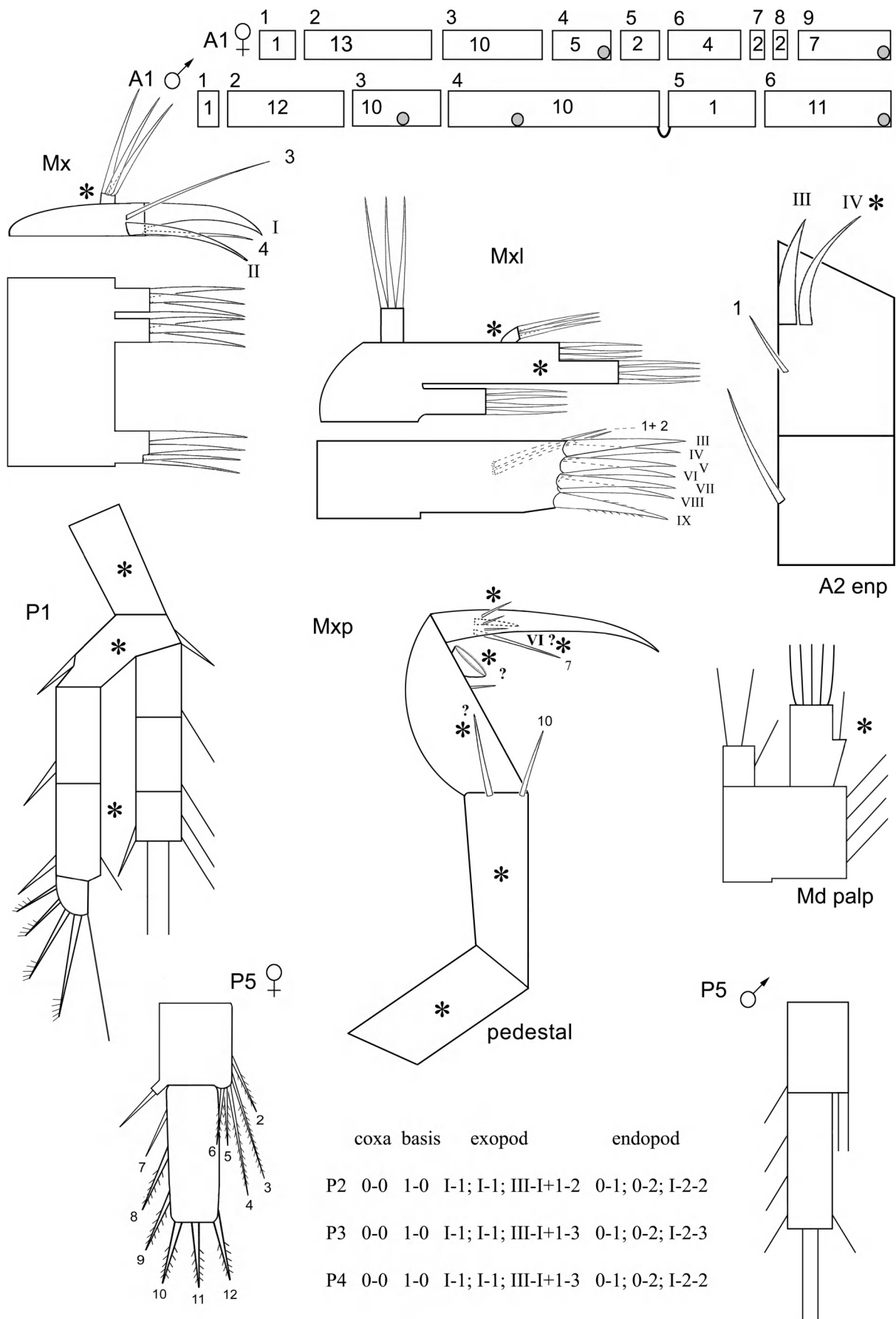


Fig. 44: Groundpattern of Pelitidiidae - Tegastidae. Asterisks mark autapomorphies of Pelitidiidae - Tegastidae

Groundpattern of Peltidiidae - Tegastidae (Fig. 44)

*Female.* **Body** with difference in width between prosome and urosome; dorso-ventrally flattened with strongly developed integument (Fig. 3 D). **Nauplius eye** present. **Rostrum** broad and fused at base with cephalothorax. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield; cephalothorax large; epimeral plates of free prosomites laterally expanded. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; urosome much shorter than prosome; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae; seta IV and V reduced in size and length. **Antennule** 9-segmented; armature formula: 1, 13, 10, 5 + aes, 2, 4, 2, 2, 6 + acrothek. **Antenna** composed of coxa, basis, 2-segmented endopod and 2-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 3 subterminal and 7 distal setae; subterminal setation of enp-2 of 1 proximal seta (1) and 2 distal spines (III + IV), seta (2) missing and element 4 forming a spine; distal border of endopod is slightly bevelled with an angle towards the exopod; exopod with 2, 3 setae. **Paragnaths** fused, not prominent. **Labrum** large, not prominent. **Mandible** (Fig. 37 E) with coxa bearing elongated and narrow gnathobase; cutting edge with 1 seta at proximal corner and bulge at proximal border; palp comprising basis, endopod and exopod; basis with 4 setae; endopod 1-segmented with 1 lateral seta and 5 apical setae; exopod 1-segmented with 1, 2 setae. **Maxillule** comprised of praecoxa, coxa fused with basis, exopod, and endopod; praecoxal arthrite elongated: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (III – IX), setae 10 - 14 missing; formula of armature: 2, VII, 0, 0, 0; fused coxa with 4 setae, without epipodal setae; fused basis extremely elongated (mainly the proximal endite) with 4 + 3 setae; endopod 1-segmented and small, displaced towards the endites and directed inwards with 3 setae; exopod 1-segmented and slightly elongated with 3 setae. **Maxilla** (Fig. 43 A) 3-segmented consisting of syncoxa, allobasis, and 1-segmented endopod; syncoxa with (2 + 2), 3, 3 setae, fused praecoxal endites displaced to inner proximal corner of syncoxa; basis with well-developed endite; accessory armature of fused basis consisting of 1 small claw (I) and 1 seta (4) at end of endite, 1 curved spine (II) and 1 seta (3) on anterior surface; tube pore and accessory armature of fused endopod segment lacking; endopod vestigial, displaced to end of endite with 3 setae. **Maxilliped** subchelate and 3-segmented, comprising syncoxa, basis and 1-segmented endopod; maxillipeds of both sides inserted on a raised area of the ventral body surface, the pedestal; syncoxa with 2 coxal setae (10 + ?) inserting on inner distal corner and between inner and outer distal corner; basis with 1 short seta, and 1 distal pad-like sensory element on inner edge; enp-1 fused with 1 big claw (V) and with 1 seta (7) and 1 short strong spine (VI?) on posterior side; enp-2 represented by 3 short setae on anterior surface of endopod; high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; **P1** of characteristic shape (Fig. 43 E): coxa and basis elongated; exp-1 and exp-2 extremely elongated and exp-3 small and rounded; exp-3 with 4 spines and 1 seta; endopod also elongated but not as much as exopod. Basis of **P2-P4** transversally elongated; all segments of exopod and endopod P1-P4 long and narrow; spines of P2-

P4 elongated; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; IV+1	0-1; 0-1; 1-2-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5**: baseoendopod with 1 outer basal seta, endopodal lobe represented by 5 setae (2 - 6); exopod elongated with 1 seta (7) and 5 spines (8 - 12). **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5 and P6. **Urosome** 6-segmented, consists of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** (Fig. 25 E) subchirocer, with 6 segments; armature formula: 1, 12, 10 + aes, 10 + aes/ 1, 10 + acrothek; fusion of oligoarthran segments 2 - 3, 4 - 5, 6- 9, 10 - 11 and 12 - 14; aesthetasc on oligoarthran segment 3 lacking; aesthetasc on oligoarthran segment 6 fused at base with a seta; 2 additional setae on oligoarthran segment 6; segments 5 and 6 (oligoarthran segments 10 - 14) forming strong claw with a pointed end forming a functional unit with segment 4 (oligoarthran segments 6 - 9). **P5**: basis not separated from coxa and endopod; endopodal lobe represented only by 2 setae; exopod 1-segmented with 3 outer, 2 terminal setae and 1 inner seta. **P6** symmetrical (?), with 3 setae.

#### Remarks on the systematics and morphology of Peltidiidae - Tegastidae

##### *Systematics.*

Lang (1948) recognized the close relationship of Peltidiidae and *Clytemnestra* - *Goniopsyllus*. The eight species of *Clytemnestra* and *Goniopsyllus* (former Clytemnestridae) share the apomorphies with Peltidiidae: the pedestal of the maxilliped is present, the epimeral plates of free prosomites are laterally expanded, the swimming legs are elongated, the P1 endopod looks exactly like that of Peltidiidae, the P2-P4 basis is transversally elongated, the P5 is similar and all setae of the caudal rami are short. No other Harpacticoida share these apomorphies, except the species of Tegastidae. Species of the peltidiid genera besides *Clytemnestra* - *Goniopsyllus* do not share any apomorphies that are not shared by *Clytemnestra* - *Goniopsyllus* species as well. All setae that are lacking in Peltidiidae are also reduced in species of *Clytemnestra* and *Goniopsyllus*; moreover, these species fail to display further setae of the groundpattern of Peltidiidae. The planktonic life-style of *Clytemnestra* and *Goniopsyllus* species led to morphological alterations. However, all mouthparts of *Clytemnestra* and *Goniopsyllus* can be derived from the peltidiid mouthparts. *Clytemnestra* and *Goniopsyllus* are sister taxa and together represent an advanced monophyletic species group characterized by many autapomorphies as implied by Huys & Conroy-Dalton (2000). The taxon *Clytemnestra* - *Goniopsyllus* evolved within Peltidiidae and is not the sister taxon of Peltidiidae as described by Lang (1948).

Tegastidae is characterized by many autapomorphies, which are not shared by species of *Clytemnestra* and *Goniopsyllus* or any other Peltidiidae. Species of Tegastidae mainly are characterized by their unique body form: the whole body is laterally compressed, the cephalothorax is extremely extended ventrolaterally, and the epimeral plates of the free prosomites are rudimentary. The genital and the first abdominal somite are fused in both sexes to form a ventrally extended genital somite. The P5-

bearing somite is often incorporated in the genital somite in both sexes to form a triple-somite. The remaining urosomites are very reduced. Additionally, the mouthparts are advanced. However, with reference to the reductions and great alterations of Tegastidae, this monophyletic group shares all apomorphies with Peltidiidae. Especially the elongated maxillular basis, the maxilla, the maxilliped, the swimming legs, the P5 and the caudal rami have the same characters in both taxa. The habitus and nearly all other derived characters of Tegastidae can be derived from the morphology of Peltidiidae. It is very likely that Tegastidae is an advanced group within Peltidiidae. However, the male antennule and the female P5 of Tegastidae seem to be more plesiomorphic than those of Peltidiidae, because some more setae exists. More knowledge of the evolution within Peltidiidae - Tegastidae is required to decide whether the morphology of the female P5 and the male antennule of Tegastidae is plesiomorphic or advanced within Peltidiidae. A complete phylogenetic system of this group on the species level is needed to clarify whether Tegastidae is a monophyletic taxon within Peltidiidae probably related with *Clytemnestra* and *Goniopsyllus* or the sister taxon of Peltidiidae.

#### *Morphology.*

The monophyletic group Peltidiidae - Tegastidae is characterized mainly by the large cephalothorax, the elongated maxillular basis, the small displaced maxillar endopod, the pedestal of the maxilliped, the P1, the elongated swimming legs, the transversally elongated P2-P4 basis and the short setae of the caudal rami.

Males of *Clytemnestra* have longer setae IV and V of the caudal rami than the females. This is an apomorphy of *Clytemnestra* as shown by Huys & Conroy-Dalton (2000).

For a discussion of the **reduced oral cone** (char. 3: 1→0), the elongated gnathobase of **mandible** and the praecoxal arthrite of **maxillula** see chapters 4.26, 5.2.3, and 5.2.4.

For the discussion of the reduced lateral setation of **mandible** endopod (char. 18: 0→1), the long syncoxa of maxilliped (char. 42: 1→0), and the additional coxal seta of **maxilliped** (char. 43: 4→3) see chapter 5.2.3.

The description of the distal endite of the **maxillular** basis and the **maxillipedal** basis of *Alteuthoides affinis* Kim & Kim, 1998 shows one additional seta on each. The description of the **maxillipedal** endopod shows 4 setae on the posterior side and not 2 posterior and 3 anterior ones as in the other species of Peltidiidae. These additional setae should be confirmed before considering them for the groundpattern of Peltidiidae - Tegastidae.

The pedestal of the **maxilliped** appears to be an element of the groundpattern of Peltidiidae - Tegastidae. Many but not all drawings of species of Peltidiidae show this pedestal. However, all species of Peltidiidae seem to have it. The pedestal of *Clytemnestra* and *Goniopsyllus* is only incompletely separated from the basis. To my knowledge, this raised area of the ventral body surface is not mentioned in any description of a tegastid species. However, many drawings of the maxilliped of tegastid species show a pedestal that is only slightly shorter than that in Peltidiidae (e.g. *Eupelte villosa*; *Syngastes indicus* Sewell, 1940; *Parategastes sphaericus* Pallares, 1970; *Tegastes paulipes* Humes, 1984) and the analysed specimens have it (*Parategastes* spec., *Tegastes* spec. 1., *Tegastes* spec. 2).

In the groundpattern of Peltidiidae - Tegastidae the basis of the maxilliped has 1 short seta and 1 distal pad-like sensory element on the inner edge. The pad-like sensory

element is an autapomorphy of this species group (Huys & Conroy-Dalton, 2000). As long as it is not clear whether this element is a transformed seta, the number of setae on the basis of maxilliped in Peltidiidae - Tegastidae remains uncertain. All species of the sister group and the outgroups of Peltidiidae - Tegastidae have only one or no seta on the basis of maxilliped (Ectinosomatidae, Idyanthidae, Zosimidae, Tachidiidae, Paramesochridae, Novocriniidae, Superornatiremidae and Rotundiclipeidae, N.N. 7).

For a discussion of the setation of **P5** see chapter 4.1.

Some species of Tegastidae have an additional aesthetasc on oligoarthran segment 3 of **female antennules**. This is a secondary character.

Some species of Tegastidae have 2 additional setae on the oligoarthran segment 6 of **male antennule** as compared to the oligoarthran groundpattern. This is also true for some species of Tisbidae *sensu strictu*, Paramesochridae and *Atergopedia vetusta* (see chapter 4.26).

Huys & Conroy-Dalton (2000, p. 45) described “an additional aesthetasc on ancestral segment XI” (oligoarthran segment 4) of the male antennule of former Peltidiidae, *Clytemnestra* - *Goniopsyllus* and Tegastidae. It is possible that this aesthetasc-like element is an autapomorphy of this species group. However, to date I could not observe this element in species of Peltidiidae besides *Clytemnestra* - *Goniopsyllus* and to my knowledge it is not mentioned in any description of a peltidiid species. Accordingly, only some species of Peltidiidae (and not all) can have this aesthetasc. This additional aesthetasc may be an autapomorphy of a species group within Peltidiidae enclosing Tegastidae, *Clytemnestra* - *Goniopsyllus* and some (but not all) remaining species of Peltidiidae.

Males of *Goniopsyllus* - *Clytemnestra* and Tegastidae have no claw at the end of the male antennule. This is a secondary phenomenon also occurring convergently within other taxa of Palinarthra as Novocriniidimorpha and Tisbidae *sensu strictu* (see chapters 5.2.3 and 5.2.4).

Species of *Goniopsyllus* have indistinctly fused oligoarthran segments 4 and 5 and separated oligoarthran segments 8 and 9 of the male antennule. These segments are secondarily separated. Species of Tegastidae also have separated male antennular segments, which are fused in Peltidiidae. A detailed analysis of the male antennule within Peltidiidae - Tegastidae is necessary to trace the evolution of the male antennule in this species group.



## 4.25 Porcellidiidae Boeck, 1865

Taxa belonging to Porcellidiidae (58 species in 6 genera)

*Brevifrons* Harris, 1994, *Clavigofera* Harris & Iwasaki, 1996, *Dilatatiocauda* Harris, 2002, *Kushia* Harris & Iwasaki, 1996, *Porcellidium* Claus, 1860, *Tectacingulum* Harris, 1994.

Undescribed species (8.1 Appendix I.): *Porcellidium* spec. 1, *Porcellidium* spec. 2, *Porcellidium* spec. 3, *Porcellidium* spec. 4.

Diagnosis: Autapomorphies of Porcellidiidae (Fig. 4: ■ 32; Figs. 3 E, 25 G, 37 F + G, 43 B)

*Female*. Body dorso-ventrally flattened, shield-shaped, with very large prosome and small urosome; integument strongly chitinised (Fig. 3 E). Rostrum fused at base with cephalothorax, broad and lamellar. Large, expanded cephalothorax; epimeral plates of first two prosomites well developed, those of third rudimentary. Urosome 3-segmented, short and flattened; somite bearing P5 largely fused to genital double-somite, following 2 abdominal somites fused to genital double-somite. Anal somite deeply cleft medially. Caudal rami lamelliform, with 7 setae, from which originate 5 very short apical setae. Antennule 6-segmented and short, distal segment indistinctly subdivided; armature formula: 1, 13, 10, 6 + aes, 6, 10 + acrothek; majority of setae annulated; oligoarthran segments 5 - 6 and 7 - 9 fused. Antenna with elongated 1-segmented exopod; subterminal setation of enp-2: 1 proximal seta (1), 2 long distal setae (3 + 4) (char. 12: 1→0) and 1 vestigial seta (2) beneath seta 4. No oral cone (char. 3: 1→0); labrum not prominent; median fusion of paired paragnaths forming a small labium (Fig. 37 G). Mandible (Fig. 37 F) basis and endopod fused to form elongated foliaceous segment; anterior lobe derived from basis, with 4 swollen fringed setae; posterior lobe derived from endopod, with 10 slender or swollen setae; exopod with 6 swollen setae. Mandibular palp and P1 forming a ventral sucker (Fig. 37 G). Maxillule without distinct trace of subdivision between praecoxa, coxa, basis, exopod, and endopod; fused endopod long and broad, not directed inwards with 3 lateral and 3 terminal setae. Whole maxilla (Fig. 43 B) broad and robust; basis without endite; accessory armature of fused basis consisting of a very short claw (I), 2 long and 1 short seta (2 - 4?); endopod broad and directed inwards with 4 strong distal setae. Maxilliped not subchelate; no joints, consequently no flexibility between basis and syncoxa (char. 45: 1→0) and basis and endopod (char. 47: 1→0); syncoxa, basis and endopod with the same orientation; basis widened into rounded process with 1 wide, rounded spine on inner edge (8); fused segments of indistinctly 2-segmented endopod broad and foliated. P1 intercoxal sclerite broad; outer basal seta extremely swollen and plumose; endopod 2-segmented, enp-1 a wide trapezoidal plate; exopod with basally expanded soft setae on outer margin, enp-1 long and wide, enp-2 short and enp-3 wide and rounded. P2-P4: intercoxal sclerite extremely broad and plane; basis transversely elongated; all spines elongated; exopod terminally with 2 setae; endopod with some setae transformed into spines and outer spine of enp-3 transformed into seta; P2 endopod elongated; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-1	I-0; I-0; III-I+1-1	0-1; <b>0-2-0</b>
P2	0-0	1-0	I-1; I-1; III-2-2	0-1; 0-2; <b>1-2-I</b>
P3	0-0	1-0	I-1; I-1; III-2-3	0-1; 0-I+1; <b>1-2-I+1</b>
P4	0-0	1-0	I-1; I-1; III-2-3	0-1; 0-I; <b>1-2-I</b>

P5 exopod and baseoendopod **largely fused**; baseoendopod **reduced**, with 2 setae on **weakly developed endopodal lobe**; exopod **a large keeled plate tapering distally and embracing genital double-somite and anal somite**. P6 without setae.

*Male*. Sexual dimorphism also in **epimeral plate of third prosomite, rostrum, P2, and caudal rami**. Rostrum vestigial. Epimeral plate of third prosomite well developed. Urosome 3-segmented, **somite bearing P5 not fused to following somite**. Caudal rami **square and shorter than in female**. Antennule (Fig. 25 G) subchirocer, **short and stout, with 5 segments, segment 1 laterally expanded; armature formula: 1, 13, 22 + aes / 3, 9 + acrothek**; fusion of oligoarthran segments 2 - 3, 4 - 9, 10 - 11 and 12 - 14. The 2 inner setae of P2 enp-3 **variable, differing in details from female**. P5 exopod 1-segmented, **rectangular**, with oblique distal margin bearing **6 short distal spines**. P6 asymmetrical, **large membranous flap on one side, without any armature or ornamentation**.

#### Groundpattern of Porcellidiidae

*Female*. **Body** (Fig. 3 E) dorso-ventrally flattened, shield-shaped, with very large prosome and small urosome; integument strongly chitinised. **Nauplius eye present**. **Rostrum** fused at base with cephalothorax; broad and lamellar. **Prosome** consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite incorporated in large, expanded cephalothorax; epimeral plates of first two prosomites well developed, those of third rudimentary. **Urosome** 3-segmented, short and flattened; somite bearing P5 largely fused to genital double-somite, following 2 abdominal somites fused to genital double-somite; 1 egg-sac, 1 copulatory pore. **Anal somite** deeply cleft medially. **Caudal rami** lamelliform, with 7 setae, from which originate 5 very short apical setae; seta II displaced to dorsal surface. **Antennule** 6-segmented and short, distal segment indistinctly subdivided; armature formula: 1, 13, 10, 6 + aes, 6, 10 + acrothek; majority of setae annulated; oligoarthran segments 5 - 6 and 7 - 9 fused. **Antenna** composed of coxa, basis, 2-segmented endopod and 1-segmented exopod; basis and enp-1 without seta; enp-2 with 7 distal setae and spines; subterminal setation of enp-2: 1 proximal seta (1), 2 long distal setae (3 + 4) and 1 small seta (2) beneath seta 4; distal border of endopod slightly bevelled with an angle towards the exopod; elongated exopod with 3 lateral and 3 distal setae. No **oral cone**; **labrum** not prominent; median fusion of paired **paragnaths** forming a small labium (Fig. 37 G). **Mandible** (Fig. 37 F) with coxa bearing narrow and slightly elongated gnathobase; cutting edge with 1 seta at proximal corner and large bulge at proximal border; basis and endopod fused to form elongated foliaceous segment; anterior lobe derived from basis, with 4 swollen fringed setae; posterior lobe derived from endopod, with 10 slender or swollen setae; exopod with 6 swollen setae. Mandibular palp and P1 forming a **ventral sucker** (Fig. 37 G). **Maxillule** without distinct trace of subdivision between praecoxa, coxa, basis, exopod, and endopod; praecoxal arthrite elongated and narrow: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2

rows of setae with 3 anterior and 4 posterior setae (3 - 9), setae 10 - 14 lacking; formula of armature: 2, 7, 0, 0, 0; fused coxa with 4 setae, without epipodal setae; fused basis with 2 short endites with 4 + 4 setae; fused endopod long and broad, not directed inwards with 3 lateral and 3 terminal setae; fused exopod elongated, with 2 setae. **Maxilla** (Fig. 43 B) indistinctly 4-segmented consisting of syncoxa, allobasis, and indistinctly 2-segmented endopod; whole maxilla broad and robust; syncoxa with (3 + 2), 3 setae, the fused praecoxal endites displaced to inner proximal corner of syncoxa; proximal coxal endite lacking; basis without endite; accessory armature of fused basis consisting of very short claw (I), 2 long setae and 1 short seta (2 - 4?); tube pore and accessory armature of fused endopod segment lacking; endopod broad and directed inwards with 4 strong distal setae. **Maxilliped** indistinctly 4-segmented, comprising syncoxa, basis and indistinctly 2-segmented endopod; not subchelate; no joints, consequently no flexibility between basis and syncoxa and basis and endopod; syncoxa, basis and endopod with the same orientation; syncoxa broad, with 1 seta (10); basis widened into rounded process with 1 wide, rounded spine on inner edge (8); fused segments of indistinctly 2-segmented endopod broad and foliated; endopod not directed inwards with 1 seta (7?) and 1 small claw (V) from enp-1 and 2 geniculated setae (3 + 4) from enp-2. **P1** (Fig. 37 G) of characteristic shape: intercoxal sclerite broad; outer basal seta extremely swollen and plumose; endopod 2-segmented, enp-1 a wide trapezoidal plate, with long plumose seta; enp-2 distal segment small with 2 terminal, densely unipinnate claws; exopod 3-segmented with basally expanded soft setae on outer margin, enp-1 long and wide, enp-2 short and enp-3 wide and rounded. **P2-P4** biramous with 3-segmented rami; praecoxa present; intercoxal sclerite extremely broad and plane; basis transversely elongated; all spines elongated; exopod terminally with 2 setae; endopod with some setae transformed into spines and outer spine of enp-3 transformed into seta; P2 endopod elongated; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-1	I-0; I-0; III-I+1-1	0-1; 0-2-0
P2	0-0	1-0	I-1; I-1; III-2-2	0-1; 0-2; 1-2-I
P3	0-0	1-0	I-1; I-1; III-2-3	0-1; 0-I+1; 1-2-I+1
P4	0-0	1-0	I-1; I-1; III-2-3	0-1; 0-I; 1-2-I

**P5** with 1 outer basal seta; exopod and baseoendopod largely fused; baseoendopod reduced, with 2 setae on weakly-developed endopodal lobe; exopod a large keeled plate tapering distally and embracing genital double-somite and anal somite, with 5 setae (8 - 12). **P6** without setae.

*Male*. Sexual dimorphism in body size, epimeral plate of third prosomite, rostrum, genital segmentation, antennule, P2, P5 P6 and caudal rami. **Rostrum** vestigial and fused at base with cephalothorax. **Epimeral plate** of third prosomite well developed. **Urosome** 3-segmented, short and flattened; somite bearing P5 not fused to following somite, following 4 abdominal somites fused together and anal somite deeply cleft medially; 1 spermatophore. **Caudal rami** square and shorter than in female. **Antennule** (Fig. 25 G) subchirocer, short and stout, with 5 segments, segment 1 laterally expanded; armature formula: 1, 13, 22 + aes / 3, 9 + acrothek; fusion of oligoarthran segments 2 - 3, 4 - 9, 10 - 11 and 12 - 14; aesthetasc on oligoarthran segment 3 and 4 lacking; aesthetasc on oligoarthran segment 6 fused at base with a seta; segments 4 and 5 (oligoarthran segments 10 - 14) forming claw with a pointed

end forming a functional unit with segment 3 (oligoarthran segments 4 - 9). The 2 inner setae of **P2** enp-3 variable, differing in details from female. **P5** basis not separated from coxa and endopod; baseoendopod with 1 outer basal seta, endopodal lobe represented by 1 seta; exopod 1-segmented, rectangular with oblique distal margin bearing 6 short distal spines. **P6** asymmetrical, large membranous flap on one side, without any armature or ornamentation.

#### Remarks on the systematics and morphology of Porcellidiidae

##### *Systematics.*

Harris & Robertson (1994), Harris & Iwasaki (1997), Walker-Smith (2001), and Harris (2002) give details about the systematics within Porcellidiidae.

##### *Morphology.*

The sucker mainly built by the mandible palp and the P1 is unique (Fig. 37 G). The morphological alterations affect all mouthparts, legs and the body, so that practically the whole animal represents a sucker (Fig. 3 E). Consequently, the monophyly of Porcellidiidae is founded on many unique autapomorphies.

The **paragnaths** are fused to form a labium, but the ends of the paragnaths are still visible (e.g. *Porcellidium* spec. 1, *Porcellidium* spec. 2). However, the labium (Fig. 37 G) is not prominent as it is in other Palinarthra (Figs. 36 + 37). For a discussion of the **reduced oral cone** (char. 3: 1→0), the **elongated gnathobase of mandible and the praecoxal arthritis of maxillula** see chapters 4.26, 5.2.3, and 5.2.4.

The **antennule of the male** is short and stout, has only 5 segments, and the proximal segment is laterally expanded (Fig. 25 G). Despite the unique form, the claw with the pointed end is still visible.

For the discussion of the subterminal setation of **antennal** enp-2 (char. 12: 1→0), and the **maxilliped** without any flexibility between basis and syncoxa (char. 45: 1→0) and basis and endopod (char. 47: 1→0) see chapter 5.2.3.

#### **4.26 Tisbidae Stebbing, 1910 *sensu strictu***

##### Taxa belonging to Tisbidae *sensu strictu* (120 species in 19 genera)

“Tisbinae” Lang, 1944 (107 species in 10 genera): *Bathyidia* Farran, 1926, *Drescheriella* Dahms & Dieckmann, 1987, *Neotisbella* Boxshall, 1979, *Paraidya* Sewell, 1940, *Sacodiscus* Wilson, 1924, *Scutellidium* Claus, 1866, “*Tisbe*” Lilljeborg, 1853, *Tisbella* Gurney, 1927, *Tisbentra* Sewell, 1940, *Volkmanina* Boxshall, 1979.

Cholidyinae Boxshall, 1979 (13 species in 9 genera): *Avdeevia* Bresciani & Lützen, 1994, *Brescianiana* Avdeev, 1982, *Cholidyella* Avdeev, 1982, *Cholidya* Farran, 1914, *Genesis* López-González, Bresciani, Huys, González, Guerra & Pascual, 2000, *Neoscutellidium* Zwerner, 1967, *Octopinella* Avdeev, 1986, *Tripartisoma* Avdeev, 1983, *Yunona* Avdeev, 1983.

Undescribed species (8.1 Appendix I.): Tisbidae gen. spec. 1, Tisbidae gen. spec. 2, *Tisbe* spec. 1 *Tisbe* spec. 2, *Tisbe* spec. 3, *Tisbe* spec. 4, *Tisbe* spec. 5, *Tisbe* spec. 6, *Tisbe* spec. 7, *Tisbe* spec. 8, *Tisbella* spec.

Changes in systematics (reasons given below)

*Neoscutellidium* Zwerner, 1967 is transferred from Idyanthidae Lang, 1944 to Cholidiinae Boxshall, 1979.

Idyanthinae Lang, 1944 is excluded from Tisbidae Stebbing, 1910 *sensu strictu* and is raised to family rank (see chapter 4.14).

*Tachidiopsis* Sars, 1911 is excluded from Idyanthidae and is transferred to Neobradylidae Olofsson, 1917 (see chapter 4.8).

*Dactylophia* Becker, 1974 together with *Idyanthe* Sars, 1909, *Idyella* Sars, 1906, *Idyellopsis* Lang, 1944, *Styracothorax* Huys, 1993, *Tachidiella* Sars, 1909 represent Idyanthidae Lang, 1944 (see chapter 4.14).

*Zosime* Boeck, 1872, *Peresime* Dinert, 1974, *Pseudozosime* Scott, 1912 are combined in Zosimidae fam. nov. (see chapter 4.15).

*Idyanthopsis psammophila* Bocquet & Bozic, 1955 belongs as *Diarthrodella psammophila* (Bocquet & Bozic, 1955) to Paramesochridae Lang, 1944 (see chapter 4.16).

Diagnosis: Autapomorphies of Tisbidae *sensu strictu* (Fig. 4: ■ 33; Fig. 45, 3 F, 24 E, 25 F, 43 C, D, F)

*Female*. Prosome oval; somite bearing P5 hexagonal; **widest extension of genital double-somite at the fusion zone of the segments** (Fig. 3 F). Antenna (Fig. 24 E): subterminal setation of enp-2 composed of 1 **short proximal spine (I)** (char. 11: 0→1), 1 longer distal spine (III) and 1 distal geniculate seta (4) and 1 bare slender seta (2) beneath seta 4. Praecoxal arthrite of maxillula: **spine IX** and setae 10, 11, 13 and 14 **lacking**, seta 12 **present and displaced towards the transition zone from arthrite to praecoxa**, formula of armature: **2, VI, 0, 1, 0**; coxa with 3 setae; basis with short endite with 1 subapical seta and 4 apical setae. Maxilla (Figs. 43 C + D) **2-segmented consisting of syncoxa and allobasis; free endopodal segments lacking**; claw (I) fused with allobasis with 1 **short stout spine inserting on its terminal third**. P1 (Fig. 43 F) **endopod much longer than elongated exopod**; enp-2 and enp-3 **directed outwards, forming an angle with enp-1**. All spines of P2-P4 **swollen, flattened and spatulate** (char. 58: 0→1).

*Male*. Antennule haplocer (Fig. 25 F), with 8 segments; armature formula: 1, 13, 10, 8 + aes, 2, 2 / 3, 10 + acrothek; **free oligoarthran segments 6 and 7 secondarily separated from fused segments 8 and 9** (char. 62: 1→0).

Groundpattern of Tisbidae *sensu strictu* (Fig. 45)

*Female*. **Body** with clear difference in width between prosome and urosome (Fig. 3 F); dorso-ventrally flattened. **Nauplius eye present**. **Rostrum** delimited at base. **Prosome** oval, consisting of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield. **Urosome** 5-segmented, comprising somite bearing P5, genital double-somite, and 3 free abdominal somites; somite bearing P5 hexagonal; widest extension of genital double-somite at the fusion zone of the segments; 1 egg-sac, 1 copulatory pore. **Anal somite** not divided longitudinally; anus located dorsally, covered by anal operculum. **Caudal rami** with 7 setae; seta II displaced to dorsal surface. **Antennule** 9-segmented; armature formula: 1, 13, 10, 5 + aes, 2, 4, 2, 2, 6 + acrothek. **Antenna** (Fig. 24 E) composed of coxa, basis,

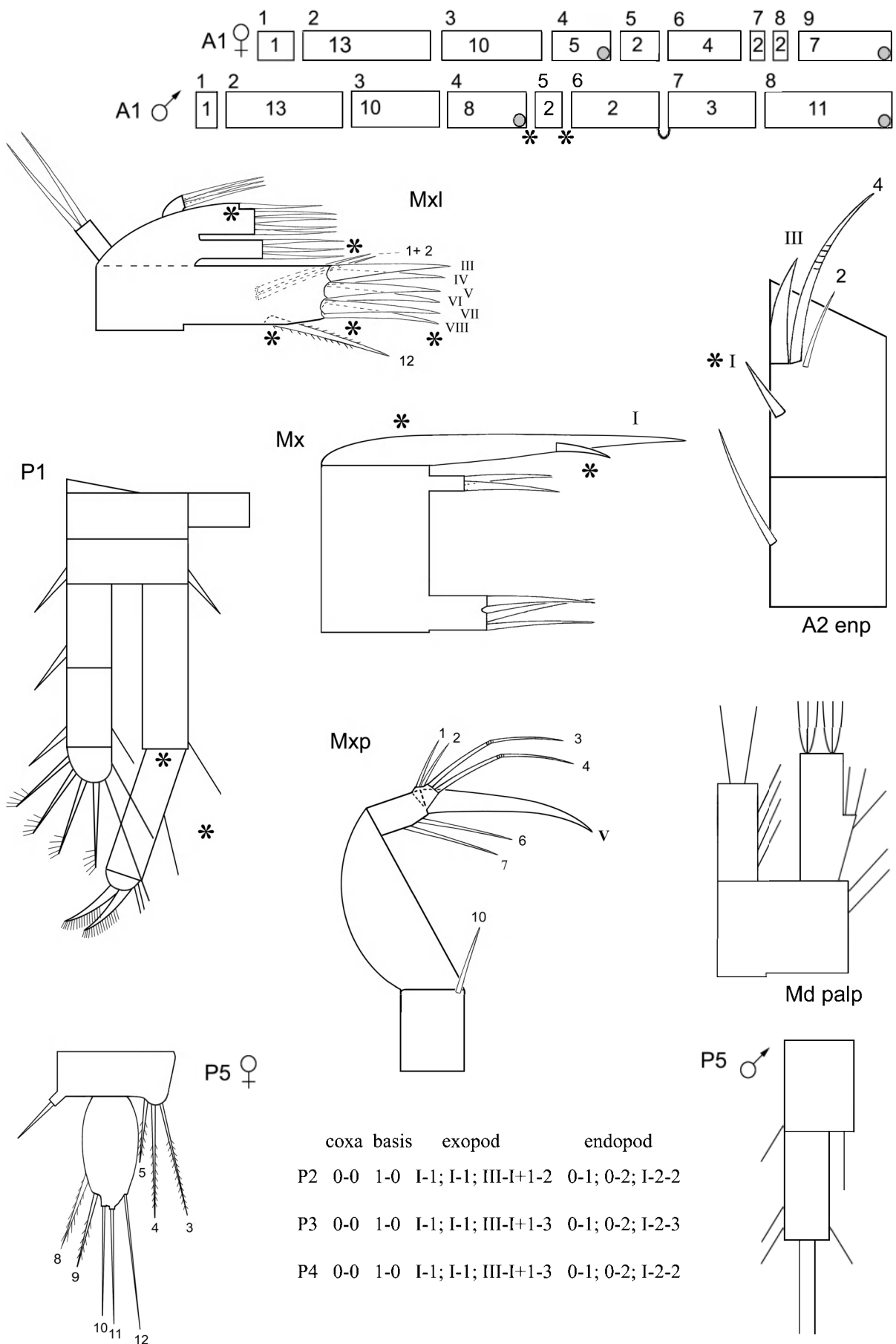


Fig. 45: Groundpattern of Tisbidae. Asterisks mark autapomorphies of Tisbidae.

2-segmented endopod and 4-segmented exopod; basis and enp-1 with 1 seta each; enp-2 with 7 distal setae; subterminal setation of enp-2 composed of 1 short proximal spine (I), 1 longer distal spine (III) and 1 distal geniculated seta (4) and 1 bare slender seta (2) beneath seta 4; distal border of endopod considerably bevelled with an angle towards the exopod; exopod with 2, 1, 1, 3 setae. Labrum, labium and elongated mandibular gnathobases forming a projected **oral cone** (Figs. 37 A, B, D): **labrum** strongly developed, triangular; median fusion of paired **paragnaths** forming a labium; labium partly fused to labrum. **Mandible** (Fig. 37 C) with coxa bearing elongated and narrow gnathobase; cutting edge with 1 seta at proximal corner and bulge at proximal border; palp comprising basis, endopod and exopod; basis with 2 setae; endopod 1-segmented with 3 lateral and 3 + 3 apical setae, each group of apical setae basally fused; exopod 1-segmented with 4 lateral and 2 apical setae. **Maxillule** comprised of praecoxa, coxa, basis, exopod, and endopod; praecoxa, coxa, and basis not separated; praecoxal arthrite elongated and cylindrical: anterior surface in outer half with 2 neighbouring setae (1 + 2), apically 2 rows of spines with 3 anterior and 3 posterior spines (III – VIII), spine IX and setae 10 and 11 lacking, seta 12 on anterior surface present and displaced towards the transition zone from arthrite to praecoxa, setae 13 + 14 lacking; formula of armature: 2, VI, 0, 1, 0; coxa with 3 setae, without epipodal setae; basis with short endite with 1 subapical seta and 4 apical setae; endopod 1-segmented and directed inwards with 3 setae; exopod 1-segmented and elongated with 2 setae. **Maxilla** (Figs. 43 C + D) 2-segmented consisting of syncoxa and allobasis; free endopodal segments lacking; syncoxa with (1 + 2), 2 setae, the fused praecoxal endites displaced to the inner proximal corner of the syncoxa; proximal coxal endite lacking; allobasis fused with strong claw (I); claw with 1 stout short spine inserting on its terminal third. **Maxilliped** subchelate and indistinctly 4-segmented, comprising syncoxa, basis and indistinctly 2-segmented endopod; coxa with 1 seta at inner distal corner (10); basis without setae; enp-1 with 2 setae (6 + 7) and 1 big claw (V); the claw displaced to posterior side of distal end of enp-1; enp-2 demarcated by posterior surface suture, reduced in size and with 2 short outer setae (1 + 2) and 2 geniculated distal setae (3 + 4); high degree of inward flexibility at the syncoxa-basis and basis-endopod joints. **P1-P4** biramous with 3-segmented rami; praecoxa present; leg pairs joined by intercoxal sclerite; **P1** of characteristic shape (Fig. 43 F): exp-1 and exp-2 elongated and exp-3 small and rounded; all spines of exp-3 elongated, ornamented terminally with very long spinules on one side; enp-1 and enp-2 extremely elongated and enp-3 very small with 2 terminal, densely unipinnate claws and 2 small inner setae; endopod much longer than elongated exopod; enp-2 and enp-3 directed outwards, forming an angle with enp-1; all spines of **P2-P4** swollen, flattened and spatulate; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-0; I-1; III-I+1-1	0-1; 0-1; 0-II-2
P2	0-0	1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	1-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

**P5** baseoendopod with 1 outer basal seta, endopodal lobe short with 3 setae (3 - 5); exopod elongated with 5 setae (8 - 12): 1 inner seta, 2 terminal, and 2 outer setae. **P6** with 3 setae.

*Male*. Sexual dimorphism in body size, genital segmentation, antennule, P5, and P6. **Urosome** 6-segmented, consists of somite bearing P5 and 4 abdominal somites; 1 spermatophore. **Antennule** haplocer (Fig. 25 F), with 8 segments; armature formula: 1, 13, 10, 8 + aes, 2, 2 / 3, 10 + acrothek, 2 additional setae on oligoarthran segment 6; fusion of oligoarthran segments 2 - 3, 4 - 5, 8 - 9, 10 - 11 and 12 - 14; free oligoarthran segments 6 and 7 secondarily separated from fused segments 8 and 9; aesthetascs on oligoarthran segments 3 and 4 lacking; aesthetasc on oligoarthran segment 6 fused at base with a seta; segments 7 and 8 (oligoarthran segments 10 - 14) forming claw with a pointed end forming a functional unit with segments 4 - 6 (oligoarthran segments 6 - 9). **P5** basis not separated from coxa and endopod; endopodal lobe represented by 1 seta; exopod 1-segmented with 5 setae, 1 inner seta, 2 terminal, and 2 outer setae. **P6** symmetrical, with 3 setae.

#### Remarks on the systematics and morphology of Tisbidae *sensu strictu*

##### *Systematics.*

Idyanthidae, Zosimidae, and *Tachidiopsis* do not belong to Tisbidae *sensu strictu*, as these four taxa are not united by autapomorphies. Lang (1944, 1948) list mainly plesiomorphic characters for a taxon uniting Tisbidae *sensu strictu* with Idyanthidae, Zosimidae, and *Tachidiopsis*. The statement “P.1 stets verändert” (Lang, 1948) meant, that the P1 is always transformed. As Lang (1948) discussed, the morphology of the P1 is very different in the taxa in question. After careful examination, no homologous apomorphy in the P1 were found for Tisbidae *sensu strictu*, Idyanthidae, Zosimidae, and *Tachidiopsis*. Tisbidae *sensu strictu* is the sister taxon of Porcellidiidae, Idyanthidae - Zosimidae is the sister taxon of N.N. 4 (chapter 3.1) and *Tachidiopsis* belong to Neobradyidae (see chapters 4.8, 5.1.5, 5.2.3 and 5.2.4).

Cholidiinae is a derived monophyletic taxon within the poly- or paraphyletic “Tisbinae”. However, “Tisbinae” is still valid until a complete revision of Tisbidae *sensu strictu* on species level is presented. This is also true for the poly- or paraphyletic “*Tisbe*”.

*Neoscutellidium yeatmani* Zwerner, 1967 was described as a member of “Tisbinae”. Bodin (1997) listed *Neoscutellidium* as Idyanthinae (now Idyanthidae). However, this monotypic genus belongs without doubt to the monophyletic group Cholidiinae (Tisbidae *sensu strictu*), as the fish symbiont *Neoscutellidium yeatmani* shares the autapomorphies of these parasites, e.g. the reduced ornamentation of the characteristic antenna, maxillula, maxilla, and the maxilliped.

*Diarthrodella psammophila* (Bocquet & Bozic, 1955) (Paramesochridae) is mentioned twice in Bodin (1997). This species has also been listed as *Idyanthopsis psammophila* Bocquet & Bozic, 1955 as *genus incertum et species incerta sedis* within Tisbidae. This species belongs without doubt to *Diarthrodella* (Paramesochridae), because it shares the autapomorphies of this family and this genus (see chapter 4.16).

##### *Morphology.*

The monophyletic group Tisbidae *sensu strictu* is characterized mainly by the oval prosome, the hexagonal somite bearing P5 and the genital double-somite with widest extension at the fusion zone of the segments, the maxillula with the regained and displaced praecoxal seta 12 and the short endite of the basis with 1 subapical and 4 apical setae, the characteristic allobasis of the maxilla with the displaced short stout



spine on the strong, bent claw, and the characteristic tisbid P1.

The groundpattern of Tisbidae *sensu strictu* includes the slightly dorso-ventrally flattened **body**. Most species of Tisbidae *sensu strictu* have this habitus. However, two different evolutionary lines evolved within Tisbidae. One line led to extremely dorso-ventrally flattened species of the monophyletic group *Scutellidium* - *Sacodiscus*, named *Scutellidium* group (Boxshall, 1979). The other trend of evolution produced more slender and cylindrical animals, which are practically not flattened dorso-ventrally.

For the discussion of the subterminal setation of the **antennal enp-2** (char. 11), the setation of praecoxal arthrite of **maxillula** (char. 24), the swollen and spatulate spines of **P2-P4** (char. 58), and free oligoarthran segments 6 and 7 secondarily separated from fused segments 8 and 9 of the male antennule (char. 62: 1→0) see chapter 5.2.3.

Some species of Tisbidae *sensu strictu*, e.g. *Drescheriella glacialis* have additional setae on the **antennule** of the female oligoarthran segment 2 and the male oligoarthran segment 3. The more plesiomorphic species of Tisbidae *sensu strictu* and the species of all outgroups do not possess these additional setae. It is very likely that these additional setae of both sexes appeared as evolutionary innovations within Tisbidae.

The **antennal endopod** of all species of Exanechentera (with the exception of Zosimidae species) is bevelled (Figs. 24 A - E), that of Tisbidae *sensu strictu* quite considerably so (Fig. 24 E). Therefore, the outer distal setae of enp-2 in tisbid species insert on the opposite side of the lateral setae.

The **oral cone** of Palinarthra formed by the labrum and the labium is reduced in the extremely dorso-ventrally flattened tisbid *Scutellidium* and *Sacodiscus*. The paragnaths are still fused (but not prominent) and the gnathobase of the mandible and the praecoxal arthrite of maxillula are still elongated in *Scutellidium* - *Sacodiscus*. In other Palinarthra these two elongated mouthparts belong to the functional unit of the oral cone comprising labrum and labium (Figs. 36 E + F). It is very likely that the complex oral cone evolved only once in Palinarthra and that it was reduced in *Scutellidium* - *Sacodiscus*. The species of Tisbidae *sensu strictu* with a more slender habitus have a big prominent oral cone (Figs. 37 A + D) composed of the labrum and the labium, supported by the elongated gnathobase of the mandible and the praecoxal arthrite of maxillula (char. 3; chapter 5.2.3).

The enp-1 of **maxilliped** has 1 strong claw (V) and 2 lateral setae (6 + 7). It is very likely that seta 6 is the transformed small claw (VI) of the groundpattern of Syngnatharthra (see chapter 5).

The characteristic **P1** of Tisbidae *sensu strictu* (Fig. 43 F) is transformed occasionally and therefore not always easy to recognize. Some species such as *Paraidya occulta* Humes & Ho, 1969 have elongated spines and setae so that the special nature of the tisbid spines is lost. Additionally, *P. occulta* has short exopodal segments in P1 and only moderately elongated proximal segments in the endopod. The P1 of *P. occulta* appears to be plesiomorphic within Tisbidae *sensu strictu*. However, phylogenetic considerations within Tisbidae lead to the conclusion that the P1 of *P. occulta* has been secondarily transformed into a shape resembling a more plesiomorphic P1. Others, e.g. species of *Tisbella* have a 2-segmented endopod that is less conspicuously elongated than the endopod of other Tisbidae *sensu strictu*.

The spines of **P1 - P4** are swollen and spatulate in Tisbidae *sensu strictu*, as in

Novocriniidomorpha. This could be a further autapomorphy of Palinarthra. Only the dorso-ventrally flattened taxa with the elongated swimming legs and setae have elongated spines, in which the swelling of the spines is probably grown out (Peltidiidae - Tegastidae, Porcellidiidae, *Scutellidium* - *Sacodiscus*). However, the cladistic computer analysis indicates that the swollen and spatulate spines evolved convergently in Tisbidae *sensu strictu* and Novocriniidomorpha (see chapter 5.1.3 and 5.2.4).

Compared to the oligoarthran groundpattern many species of Tisbidae *sensu strictu* have 2 additional setae on the oligoarthran segment 6 of **male antennule**, as have species of Paramesochridae, Peltidiidae - Tegastidae and *Atergopedia vetusta*. Otherwise these additional setae are not described for the male antennule of Exanechentera, but this is probably due to the mainly incompletely described antennule of the males. It is very likely that these additional setae are widespread within Exanechentera and that they are an autapomorphy of this taxon or of N.N.4 (chapter 3.1).

Most species of Tisbidae *sensu strictu* have no claw on the antennule of the male. However, species of *Bathydia*, *Neotisbella*, *Paraidya*, *Volkmannia*, and maybe others, have a male antennule with a claw, which reminds of the claw of other Exanechentera (Fig. 25). The claw of tisbid species is also derived from the oligoarthran segments 10 to 14, has a pointed end, and forms a functional unit with the oligoarthran segments 6 to 9. All taxa that have this claw, with the exception of *Paraidya*, belong to a derived group of planktonic species. Two possibilities are conceivable: 1. The claw is not homologous with the claw of other Exanechentera and therefore evolved convergently within Tisbidae *sensu strictu*. 2. The claw is homologous with the claw of other Exanechentera and therefore is an element of the groundpattern of Tisbidae *sensu strictu*. The latter possibility is better supported, because the details of the claw of tisbid species agree with those of other Exanechentera, especially with the claw of Peltidiidae (Figs. 25 E + F). It would thus follow that the claw has been reduced at least twice within Tisbidae *sensu strictu* or reduced and regained. More knowledge of the evolution within Tisbidae *sensu strictu* is necessary.

Some males of Tisbidae *sensu strictu* have a **sexual dimorphism** in the maxilliped, the inner basal spine of P1, or the inner seta of P2 enp-1. These sexual dimorphisms evolved within Tisbidae *sensu strictu*, as all species with a more plesiomorphic morphology within Tisbidae *sensu strictu* have none of these dimorphisms.

## 5. PHYLOGENETIC ANALYSIS

Two procedures to infer phylogeny on the basis of morphological characters of adult Oligoarthra were used and compared. First

the methods of **Phylogenetic Systematics** were applied (i.e. Hennig, 1966, 1982; Ax, 1984, 1987; Wägele, 2000; chapter 5.1.4).

A **computer-aided cladistics** was used as a second method to identify the relationships of species of Harpacticoida. An analysis on the basis of reconstructed groundpatterns was made with monophyletic taxa (chapter 5.1.3).

The same taxa and characters were used in both procedures. The **ingroup** was the monophyletic taxon Oligoarthra. The parsimony analysis on the basis of reconstructed groundpatterns was made with **72 characters** (chapter 5.1.1 List of characters) and **16 monophyletic taxa**, which are characterised by strong autapomorphies (Character matrix, chapter 5.1.2, Table 4;). The 16 taxa enclose all species of Oligoarthra. Polyarthra, Misophrioida, and Calanoida were used as **outgroups**.

For a detailed description and discussion of all **methods** see chapters 2, 5.1.3, 5.2.1, 5.2.2, and 5.2.5. The results of the phylogenetic analysis and the cladistic analysis are compared in chapter 5.1.3 to 5.1.5. For description, selection, polarisation, coding and discussion of characters see chapters 5.1.5, 5.2.1 - 5.2.3, and 5.2.5. First steps towards the characterisation of the **evolution** of Harpacticoida are made (chapter 5.1.6).

The methods of Phylogenetic Systematics were applied for the substantiation of the monophyly and the reconstruction of the groundpattern of the **terminal taxa**. The character states, especially the number of segments and setae in the groundpattern of most terminal taxa, were ascertained by additional cladistic analysis within the terminal taxa (these analyses will partially be published elsewhere). When the maximum number of segments and setae is not regarded as the most plesiomorphic state within a taxon, it is discussed in the chapter of the respective taxon (see chapter 4, 5.2.5, and 5.2.6). For the groundpattern of Podogennonta see chapter 4.9 and 5.2.5.

Additionally, an analysis of the phylogeny of Harpacticoida was made with **species** selected from the over 3,000 described species (this analysis will be published elsewhere).

A new taxon name was given only if the monophyly of the respective taxon was well supported. Taxa named with **N.N.** followed by a number (e.g. N.N. 1) are probably monophyletic taxa but the monophyly of these taxa has to be confirmed. N.N. stands for *nomen nominandum* ("name to be given"). The subordinated taxa belonging to these taxa are listed in chapter 3.1.

## 5.1 Results

### 5.1.1 List of characters

The numerous autapomorphies of the terminal taxa that do not appear in another investigated taxa are not considered in this list of characters, because they do not help to infer the phylogenetic relationships of these taxa (uninformative characters). Autapomorphies of the terminal taxa are listed under “Diagnosis: Autapomorphies” of the respective taxa (chapter 4).

This character list contains only an abbreviated version of single character states. More detailed descriptions and their discussion can be found in chapters 4., 5.2.3, and 5.2.4.

Characters and their states according to the character list and the character matrix (chapters 5.1.1 and Table 4) are marked in the text as follows: e.g. char. 1: 0→1 symbolizes the transformation of character 1 from character state 0 to character state 1. The autapomorphies supporting the phylogenetic relationships within Harpacticoida are summarized in character sets symbolized by black squares ■ followed by the branch number leading to the respective taxon (Fig. 4: e.g. ■ 3 represents the autapomorphies of Oligoarthra).

The most plesiomorphic state of a character within Copepoda and Harpacticoida is marked with P (= plesiomorphy). The more derived character states within Copepoda and Harpacticoida are marked with A (= apomorphy). For the discussion of the polarity of characters and the choice of the outgroups see chapters 5.1.3, 5.2.2 and 5.2.3.

#### Body

1. 0: P1-bearing somite not fused to cephalothorax; P.  
1: P1-bearing somite fused to cephalothorax; A.
2. 0: body not dorso-ventrally flattened; P.  
1: body dorso-ventrally flattened; A.
3. 0: no oral cone; P.  
1: strongly developed, triangular labrum and fused lobes of paragnaths forming an oral cone; A.
4. 0: female without egg-sacs; P.  
1: female with 2 egg-sacs; A.  
2: female with 1 egg-sac; A.
5. 0: male with 2 spermatophores; P.  
1: male with 1 spermatophore; A.

#### Female antennule

6. 0: setae of oligoarthran segment 9 without pattern described below; P.  
1: 1 subterminal seta and 6 terminal setae on oligoarthran segment 9; A.

#### Antenna

7. 0: basis and proximal endopod segment separated; P.  
1: allobasis or basis and proximal endopod segment incompletely fused; A.

8. 0: with 4 or 3-segmented endopod; P.  
1: with 2-segmented endopod (some with allobasis); A.
9. 0: 3- or 4-segmented endopod; second segment with more than 4 setae or 2-segmented endopod; distal endopod segment with more than 4 lateral setae; P.  
1: distal endopod segment with 4 or 3 lateral setae and spines of characteristic oligoarthran appearance; A.
10. 0: lateral seta 2 of distal endopod segment (or second segment) present; P.  
1: lateral seta 2 of distal endopod segment missing; A.
11. 0: lateral element 1 of distal endopod segment (or second segment) forming a seta; P.  
1: lateral element I of distal endopod segment forming a spine; A.
12. 0: lateral element 3 of distal endopod segment (or second segment) forming a seta; P.  
1: lateral element III of distal endopod segment forming a spine; A.
13. 0: distal border of endopod not bevelled; P.  
1: distal border of endopod bevelled with an angle towards the exopod; A.
14. 0: with 10 to 8 exopodal segments; P.  
1: with less than 5 exopodal segments; A.

### Mandible

15. 0: gnathobase not elongated and narrow; P.  
1: gnathobase elongated and narrow; A.  
2: gnathobase style-like; A.
16. 0: gnathobase without bulge at proximal border; P.  
1: gnathobase with bulge at proximal border; A.
17. 0: endopod 2-segmented; P.  
1: endopod 1-segmented; A.
18. 0: 2-segmented endopod with 4 or 3 setae on enp-1 or 1-segmented endopod with 4 or 2 lateral setae; P.  
1: endopod with 1 or 0 lateral seta; A.
19. 0: 2-segmented endopod with setae on enp-1 or 1-segmented endopod with setae laterally; P.  
1: 1-segmented endopod with 1 spine and 2 setae laterally; A.
20. 0: endopod with 11 to 8 distal setae; P.  
1: endopod with 7 to 5 distal setae; A.  
2: endopod with 4 to 3 distal setae; A.
21. 0: exopod with 5 or 4 segments, 2 proximal copepod segments separated; P.  
1: exopod with 4 or 3 segments, 2 proximal copepod segments fused; A.  
2: exopod with 2 or 1 segment(s), 3 proximal segments of Oligoarthra fused or exopod missing; A.

### Maxillule

22. 0: praecoxal arthrite not elongated; P.  
1: praecoxal arthrite elongated and narrow; A.  
2: praecoxal arthrite elongated, narrow, and cylindrical; 4 distal spines

- transformed to setae, all terminal elements tightly together; A.
23. 0: seta 10 of praecoxa present; P.  
1: seta 10 of praecoxa absent; A.
24. 0: setae 11 and 12 of praecoxa present; P.  
1: setae 11 of praecoxa absent, mostly also seta 12 absent; A.
25. 0: 2 long spinules of posterior distal spines of praecoxa missing; P.  
1: 2 long spinules of posterior distal spines of praecoxa present; A.
26. 0: praecoxa and coxa separated; P.  
1: praecoxa and coxa fused; A.
27. 0: coxa with 6 or 5 inner setae; P.  
1: coxa with 4 or 3 inner setae; A.
28. 0: coxa and basis separated; P.  
1: coxa and basis fused; A.
29. 0: endopod 3- or 2-segmented; P.  
1: endopod 1-segmented or fused with basis; A.
30. 0: endopod without pattern described below; P.  
1: endopod fused with basis, forming a rectangular segment, and all setae inserting at distal edge; A.
31. 0: endopod not directed inwards and some setae inserting at outer border of endopod, or endopod completely fused to basis; P.  
1: endopod and all setae directed inwards.
32. 0: exopod and endopod with 11 or more setae each; P.  
1: exopod and endopod with fewer than 11 setae each; A.

### Maxilla

33. 0: with praecoxa and coxa; P.  
1: with syncoxa; A.
34. 0: endites of praecoxa not fused; P.  
1: endites of praecoxa fused; A.
35. 0: (fused) praecoxal endites not displaced to the inner proximal corner of syncoxa; P.  
1: fused praecoxal endites displaced to the inner proximal corner of syncoxa; A.
36. 0: distal endite of praecoxa (possibly fused to proximal one) with 3 setae; P.  
1: distal endite of praecoxa (fused to proximal one) with 2, 1, or 0 setae; A.
37. 0: proximal endite of coxa with 3 or 2 setae; P.  
1: proximal endite of coxa with 1 seta, or endite absent; A.
38. 0: tube pore of allobasis absent; P.  
1: tube pore of allobasis present; A.
39. 0: proximal endopod segment of 4-segmented endopod with 4 setae, or allobasis with 2 or 3 setae from fused endopod segment (9 - 11); P.  
1: allobasis without setae of fused endopod segment; A.
40. 0: proximal endopod segment of Copepoda free or proximal endopod segment fused with basis and endopodal seta 10 on anterior surface of allobasis; P.  
1: endopodal seta 10 of allobasis between anterior and posterior surface; A.
41. 0: additional seta very closely set to endopodal seta 10 absent; P.  
1: additional seta very closely set to endopodal seta 10 present; A.

Maxilliped

42. 0: syncoxa or praecoxa and coxa together more than 3 times longer as wide; P.  
1: syncoxa at most twice as long as wide; A.
43. 0: syncoxa or praecoxa and coxa together with 11, 10 or 7 (X - 16) setae and spines on inner border; P.  
1: syncoxa with 6 setae and spines (X - XV); A.  
2: syncoxa with 4 setae (10 - 13), 2 spines (X, XII) transformed to setae; A.  
3: syncoxa with 2 setae (10 + 11); A.  
4: syncoxa with 1 seta (10); A.  
5: syncoxa without setae; A.
44. 0: more than 1 coxal seta inserting at inner distal corner of coxa; P.  
1: setae 10 and 11 inserting at inner and outer distal corner of coxa or only coxal setae 10 present and inserting at inner distal corner of coxa; A.  
2: coxal setae 10 and 11 inserting subapically at inner and outer border of coxa; A.
45. 0: without joint between syncoxa and basis; P.  
1: with highly flexible joint between syncoxa and basis; A.
46. 0: basis with 3 setae or 1 seta and 1 spine inserting side by side (VIII + 9); P.  
1: basis with 2 setae inserting medially and distally on inner edge (8 + 9) or with 1 seta (8) or with 1 wide and rounded spine (VIII) or without setae; A.
47. 0: without joint between basis and endopod; P.  
1: with highly flexible joint between basis and endopod; A.
48. 0: endopod 6-segmented, or 2-segmented and enp-2 not reduced in size; P.  
1: endopod 2-segmented and enp-2 reduced in size, indistinctly 2-segmented or 1-segmented; A.
49. 0: enp-1 (2-segmented) or the 4 to 5 proximal segments (6-segmented) only with setae; P.  
1: enp-1 with 1 small claw (V) and 2, 1 or 0 setae; A.  
2: enp-1 with 1 large claw displaced to posterior side of the distal end (V), and 2, 1 or 0 setae and spines; A.  
3: enp-1 with 1 large claw displaced to posterior side of the distal end (V), 1 thin claw (VI) and 1 or 0 setae; A.
50. 0: enp-2 or the distal endopod segment with 4 spines and setae or more than 4 setae, no geniculated setae; P.  
1: enp-2 with 2 geniculated distal setae (3 + 4) and 2 or 0 small outer setae (1 + 2); A.

P 1

51. 0: coxa with 1 inner seta; P.  
1: coxa without inner seta; A.
52. 0: enp-2 not elongated; P.  
1: enp-2 elongated; A.
53. 0: enp-3 not small; P.  
1: enp-3 small; A.
54. 0: exp-1 and exp-2 not elongated; P.  
1: exp-1 and exp-2 elongated; A.

55. 0: exp-1 with 1 inner seta; P.  
1: exp-1 without inner seta; A.
56. 0: exopod without pattern described below; P.  
1: all spines of exp-1 to exp-3 elongated and with very long spinules on one side; exp-3 not small and rounded; A.  
2: exp-3 small and rounded, spines only of exp-3 elongated or transformed, all spines with long spinules on one side; A.

#### P2-P4 female

57. 0: coxa with inner seta; P.  
1: coxa without inner seta; A.
58. 0: spines not swollen, flattened and spatulate; P.  
1: all pinnate spines swollen, flattened and spatulate; A.

#### P5 female

59. 0: endopod separated from basis; P.  
1: basis and endopod fused to baseoendopod; A.
60. 0: exopod 3-segmented; P.  
1: exopod 1-segmented, less than 1,5 times as long as wide; A.  
2: exopod 1-segmented, more than twice as long as wide; A.
61. 0: spine / seta 8 of exopod present; P.  
1: spine / seta 8 of exopod missing; A

#### Male antennule

62. 0: antennule haplocer; all or some segments of oligoarthran segments 6 to 9 separated, (copepod segments XIV to XX); P.  
1: antennule subchirocer or chirocer; oligoarthran segments 6 to 9 fused to one segment, (copepod segments XIV to XX); A.
63. 0: oligoarthran segments 10 and 11 separated (copepod segments XXI-XXII and XXIII); P.  
1: oligoarthran segments 10 and 11 fused (copepod segments XXI-XXII and XXIII); A.
64. 0: oligoarthran segments 12 to 14 separated (copepod segments XXIV to XXVIII); P.  
1: only oligoarthran segments 12 and 13 fused to one segment (copepod segments XXIV and XXV); A.  
2: oligoarthran segments 12 to 14 fused to one segment (copepod segments XXIV to XXVIII); A.
65. 0: with aesthetasc on oligoarthran segment 3; P.  
1: without aesthetasc on oligoarthran segment 3; A.
66. 0: with aesthetasc on oligoarthran segment 4; P.  
1: without aesthetasc on oligoarthran segment 4; A.
67. 0: without claw formed by oligoarthran segments 10 to 14; P.  
1: with claw with a pointed end formed by oligoarthran segments 10 to 14; A.
68. 0: setae of oligoarthran segment 14 without the pattern described below; P.  
1: 1 subterminal seta and 6 terminal setae on oligoarthran segment 14; A.



P2 male

69. 0: terminal and outer setae without the pattern described below; P.

1: enp-3 terminally with modified bare spine (I) fused at base (originated from displaced outer spine), 1 middle hyaline seta (2) and 1 inner terminal seta; A.

P5 male

70. 0: coxa and basis separate; P.

1: coxa and basis fused; A.

71. 0: endopod separate from basis; P.

1: endopod fused to basis; A.

Caudal rami

72. 0: setae II anterolateral; P.

1: seta II displaced to dorsal surface; A.

**5.1.2 Character matrix**

Table 4: Data matrix of the taxa of Oligoarthra (Harpacticoida). Calanoida (Copepoda), Misophrioida (Copepoda) and Polyarthra (Harpacticoida) are the outgroups of the monophyletic taxon Oligoarthra. The characters used are the same as in the character list.

Taxa /character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
Calanoida	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Misophrioida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyarthra	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rometidae	1	0	0	?	0	0	0	1	1	0	1	0	0	1	0	0	1	0	1	1	1	0	0	0	0
Aegisthidae	0	0	0	2	0	0	1	1	1	?	?	1	0	1	0	0	1	0	1	1	1	0	0	0	0
Neobryadiidae	1	0	0	2	1	1	0	1	1	0	1	1	0	1	0	0	1	0	0	1	1	0	0	0	0
Podogennonta	1	0	0	2	1	0	0	1	1	0	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0
Chappuisiidae	0	0	0	0	1	0	0	1	1	0	1	1	0	1	0	0	1	0	0	1	1	0	1	0	0
Ectinosomatidae	1	0	0	2	1	0	0	1	1	?	?	1	0	1	0	0	1	0	0	1	2	0	1	?	?
Idyanthidae	1	0	0	2	1	0	0	1	1	0	1	1	1	1	0	1	1	0	0	1	2	0	0	0	0
Zosimidae	1	0	0	2	1	0	0	1	1	1	1	1	0	1	0	1	1	1	0	2	2	0	0	0	0
Paramesochridae	1	0	0	2	1	0	0	1	1	0	1	1	1	1	0	1	1	0	0	1	2	0	0	0	0
Tachidiidae	1	1	0	2	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1	2	0	0	0	0
Novocriniidae	1	0	1	?	1	1	0	1	1	1	?	0	1	1	1	1	1	1	0	1	1	1	1	0	0
Superornatiremidae	1	0	1	?	1	1	1	1	1	0	0	1	1	2	0	1	1	0	2	1	2	1	1	1	1
Rotundiclepidae	0	0	1	?	1	1	1	1	1	0	0	1	1	2	0	1	1	0	2	2	2	1	1	1	1
Peltidiidae-Tegastidae	1	1	0	2	1	0	0	1	1	1	0	1	1	1	1	1	1	1	0	1	2	1	1	1	1
Porcellidiidae	1	1	0	2	1	0	0	1	1	0	0	0	1	1	1	1	1	0	0	1	2	1	1	1	1
Tisbidae	1	1	1	2	1	0	0	1	1	0	1	1	1	1	1	1	1	0	0	1	2	1	1	1	1

Taxa /character	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48
Calanoida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	?	0
Misophrioida	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0
Polyarthra	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rometidae	1	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	1
Aegisthidae	1	0	0	0	1	1	0	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0
Neobryadiidae	1	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1
Podogennonta	1	0	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0	0	2	0	1	1	1	1
Chappuisiidae	0	0	1	1	1	0	0	1	1	1	0	0	0	0	1	?	?	?	0	2	0	1	1	1
Ectinosomatidae	1	0	1	0	1	0	0	1	1	1	0	1	0	0	?	?	?	?	0	3	1	1	1	1
Idyanthidae	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0	?	?	?	0	3	2	1	1	1
Zosimidae	1	0	1	0	1	0	0	1	1	1	0	0	0	0	0	?	?	?	1	3	2	0	1	0
Paramesochridae	0	0	1	0	1	0	1	1	1	1	0	1	0	0	1	?	?	?	0	4	1	1	1	1
Tachidiidae	0	0	1	0	1	0	1	1	1	1	0	0	0	0	1	?	?	?	0	4	1	1	1	1
Novocriniidae	0	0	0	0	1	0	1	1	1	?	?	?	1	1	0	1	?	?	?	1	4	1	0	1
Superornatiremidae	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	?	?	?	1	5	?	0	1	
Rotundiclepidae	0	0	0	0	1	0	1	1	1	1	0	1	1	0	1	?	?	?	1	5	?	0	1	
Peltidiidae-Tegastidae	0	0	1	1	1	0	1	1	1	1	1	1	0	0	1	?	?	?	0	3	1	1	1	
Porcellidiidae	0	1	1	1	1	0	1	1	1	1	1	1	1	0	1	?	?	?	1	4	1	0	1	
Tisbidae	0	1	1	1	1	0	1	1	1	1	1	1	1	0	1	?	?	?	1	4	1	1	1	

Taxa /character	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72
Calanoida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Misophrioida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polyarthra	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?	?	?	?	?	0	0	1	0	0
Rometidae	0	0	1	0	0	0	0	0	1	0	1	2	0	0	0	0	0	0	0	0	0	1	1	0
Aegisthidae	0	0	1	0	0	0	0	0	1	0	1	2	0	0	1	2	0	0	0	0	0	1	1	0
Neobryadiidae	1	1	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
Podogennonta	3	0	1	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Chappuisiidae	1	1	1	0	?	0	1	0	1	0	1	1	1	0	0	2	1	1	0	0	0	0	1	0
Ectinosomatidae	1	1	1	0	0	0	1	0	1	0	1	1	1	1	1	2	1	1	0	0	0	1	1	0
Idyanthidae	3	1	1	0	1	0	1	1	1	0	1	1	1	1	1	2	1	1	1	0	1	1	1	0
Zosimidae	?	1	1	?	0	0	1	1	1	0	1	1	1	1	1	2	1	1	1	0	1	1	1	0
Paramesochridae	3	1	1	0	1	0	1	0	1	0	1	1	1	1	1	2	1	1	1	0	0	1	1	0
Tachidiidae	2	?	1	0	0	0	1	0	1	0	1	1	1	1	1	2	1	0	1	0	0	1	1	0
Novocriniidae	2	1	1	0	0	0	1	0	1	1	1	1	0	0	1	2	0	0	0	1	0	1	1	0
Superornatiremidae	2	1	1	0	0	0	1	0	1	1	1	2	0	0	1	1	1	0	0	1	0	1	1	0
Rotundiclepidae	2	?	1	0	?	0	1	0	1	1	1	1	0	1	1	0	0	0	1	0	1	1	0	0
Peltidiidae-Tegastidae	2	?	1	1	0	1	1	2	1	0	1	2	0	1	1	2	1	0	1	0	0	1	1	0
Porcellidiidae	2	1	1	?	1	?	1	2	1	0	1	2	0	1	1	2	1	1	1	0	0	1	1	1
Tisbidae	2	1	1	1	1	1	1	2	1	1	1	2	0	0	1	2	1	1	1	0	0	1	1	1

### 5.1.3 Cladistic analysis

#### Methods and settings

The cladistic analysis was made with 72 characters (chapter 5.1.1), 3 outgroup taxa, and 16 ingroup taxa (Table 4). The data matrix was analysed and cladograms were generated on a Macintosh G4 (400 Mhz) with **PAUP\* 4.0 beta 10 Altimec** (Swofford, 2003). Characters were examined with PAUP\* and **MacClade, version 3.05** (Maddison & Maddison, 1992).

All characters in this analysis were of type **unordered** and had **equal weight**. The character matrix can be ordered from the author as nexus file. I used '**branch-and-bound**' **search under maximum parsimony** to explore the data. Further 'branch-and-bound' settings were: addition sequence furthest, zero-length branches not collapsed, 'MulTrees' option in effect. The cladogram was **rooted** using Polyarthra, Misophrioida and Calanoida as outgroups (chapter 5.2.2).

All characters in this analysis were of type **unordered** and had **equal weight**. This was a conscious decision. For an analysis according to the methods of Phylogenetic Systematics (i.e. Hennig, 1966, 1982; Ax, 1984, 1987; Wägele, 2000), the polarisation of characters has to be determined prior to cladogram construction. To run a computer parsimony analysis no hypotheses about the **polarity of characters** are necessary prior to the cladogram construction. In this case the hypotheses about the polarity of characters are the result of the topology of the unrooted cladogram (or network topology) and the rooting between the ingroup and the outgroups. To test the decisions on the polarisation of characters with the aid of an algorithm (e.g. with PAUP\*) was regarded as one advantage of a cladistic analysis (see also chapters 5.2.2 Polarity of characters and 5.2.6 Oligomerization). The polarity of all 72 characters determined for the analysis according to the methods of Phylogenetic Systematics prior to cladogram construction, was the same as that indicated by the cladistic analysis (chapter 5.2.2). To test the opinion that it is inconsiderate to code all characters as irreversible, an analysis of the data in table 4 with all characters coded as irreversible was made (chapter 5.2.5). The **complexity** of characters was considered in an extreme sense, as some characters were not considered in the parsimony analysis and therefore had the weight zero (chapter 5.2.1, see also chapters 5.2.5 and 5.2.6).

**Bootstrap** and **Bremer support** values were estimated using the same 'branch-and-bound' settings described above using PAUP\*. The Bremer support stands for "the number of extra steps required before a clade is lost from the strict consensus tree of near-minimum length cladograms. Also known as *branch support, clade stability, decay index, length difference*" (Kitching et al., 1998, p. 201, Glossary). Bootstrap is "a statistical procedure for achieving a better estimate of the parametric variance of a distribution than the observed sample variation by averaging *pseudoreplicate* variances. The original data set is sampled with replacement to procedure a pseudoreplicate of the same dimension as the original" (Kitching et al., 1998, p. 200, Glossary). There are several limitations to the use of the bootstrap. In particular, "the confidence intervals obtained through resampling methods are only approximate unless the original sample size, that is, the number of characters in the data matrix, is large. This is 'large' in the statistical sense (more than 1000 and preferably 10 000)" (Kitching et al., 1998, p. 130). The present cladistic analysis was made with 72

characters. However, the bootstrap is given here, as it is often demanded for analyses with a character number below 1000 characters.

“The reconstruction of character state at internal (ancestral) nodes on a given tree is called character-state optimization or character mapping. **Character optimization** does *not* come into play at any time during the search for optimal trees; *only* when character reconstructions are requested” (Swofford & Begle, 1993, p. 21). “In most cases there will only be one optimal assignment at a node, but it is possible that more than one optimum may exist. In that case, a particular reconstruction may be favoured on the basis of additional criteria. The most common ancillary criteria are accelerated transformation (ACCTRAN) and delayed transformation (DELTRAN)” (Swofford & Begle, 1993, p. 22). DELTRAN carries the transformation as far up as possible in the cladogram. ACCTRAN carries the transformation as close to the root as possible. Delayed transformation will lead to a preference for two independent origins of a character state, while accelerated transformation will lead to a preference for a single origin followed by reversal.

The support of the **monophyly hypotheses** of all taxa indicated by the parsimony analyses, thus also the **clade stability** is analysed and discussed in chapters 5.1.4 and 5.2.4.

### Cladogram and character optimisation

The result of the cladistic analysis (72 characters, 3 outgroup taxa, 16 ingroup taxa) with Polyarthra, Misophrioida and Calanoida as outgroups was one minimum length cladogram of a length of 154 (Fig. 46; indices: CI = 0.57; RI = 0.77; RC = 0.44). The cladogram has no branches of maximum length zero. This single minimum length cladogram should not be interpreted as a phylogeny, as it only summarizes the information given in the data matrix. However, the diagram of the phylogenetic relationships within Harpacticoida (Fig. 4) describes the same relationships as obtained from the cladistic computer analysis (Fig. 46). The character polarity of all characters indicated by the cladistic analysis is also the same as the polarity determined with the methods of Phylogenetic Systematics (see chapter 5.1.1 List of characters and chapters 5.2.2 - 5.2.3). For 55 of the 72 used characters in the cladistic analysis only one possibility of character optimisation is the most parsimonious (unambiguous optimisation), which means that only one way of evolution for these 55 characters is more parsimonious than all other possibilities. There exists more than one most parsimonious possibility of optimisation (ambiguous optimisation) for 17 characters.

For 10 of the “ambiguous” characters the DELTRAN optimisation was chosen (characters **1, 2, 18, 23, 24, 36, 37, 39, 48, 70**). Of the 10 characters 9 are characters, where the apomorphic state is a reduced segment or a reduced setae (characters **1, 18, 23, 24, 36, 37, 39, 48, 70**). For these cases a delayed transformation means that the segments and setae were reduced more than once. The alternative to DELTRAN would be that the segments or setae were reduced once and regained once or more times. This seems to be less likely than a multiple loss. A delayed transformation for character **2** means, that the dorso-ventrally flattened body has evolved twice (Tachidiidae and Tisboidea) and not once (Tachidiidae - Palinarthra) and was retransformed into a non-flattened body (Novocriniidimorpha).

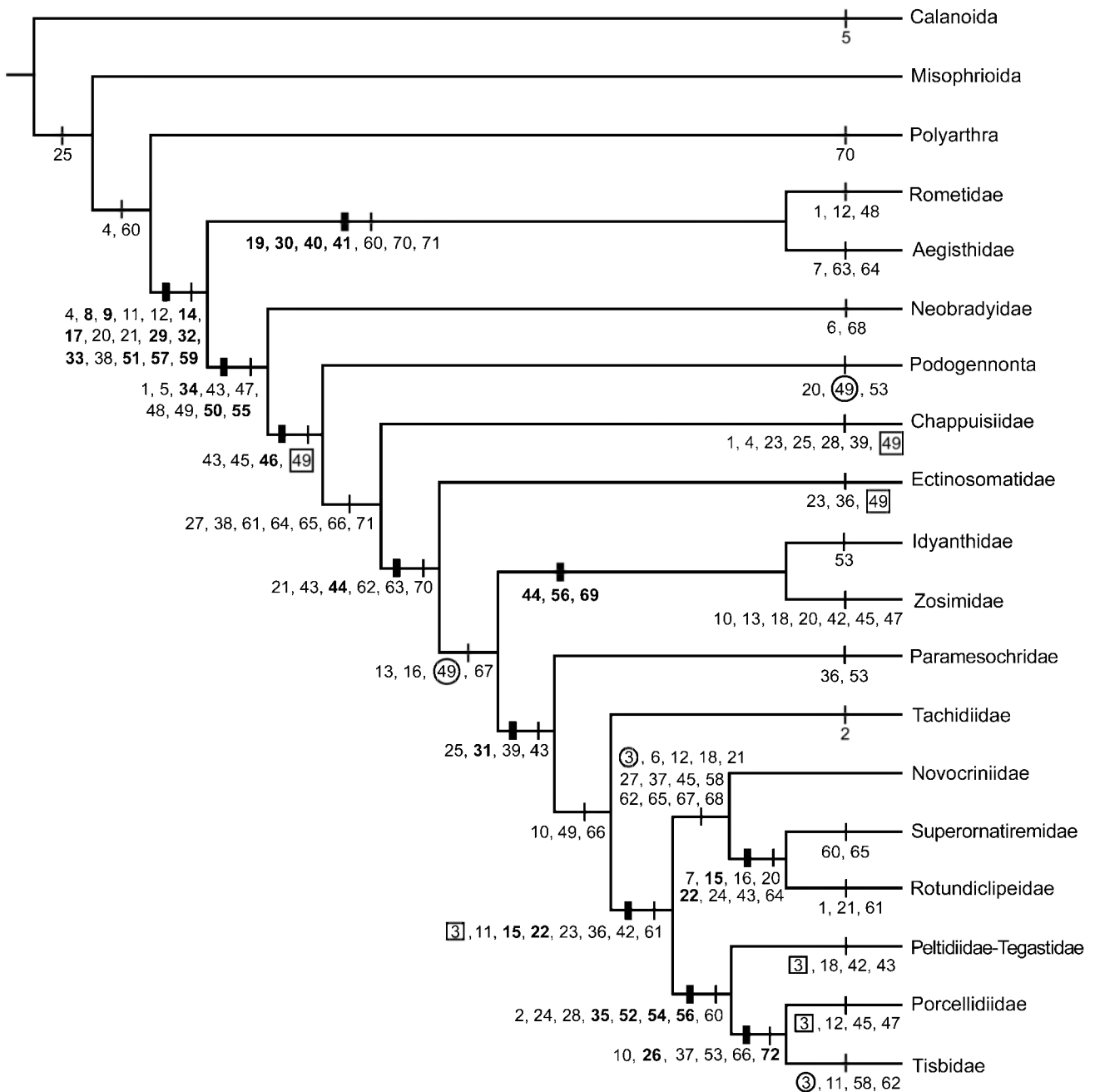


Fig. 46: Single minimum length cladogram for the taxa and characters in the character matrix (Table 4); length = 154; CI = 0.57; RI = 0.77; RC = 0.44. The character optimisation of the cladistic analysis is described in the text (chapter 5.1.3). Open circles indicate the character optimisation of the cladistic analysis; open squares indicate the transformation of characters reconstructed with the methods of Phylogenetic Systematics (chapter 5.1.4). Bold numbers and a thick bar symbolize characters without homoplasy.

For 7 “ambiguous” characters the ACCTRAN optimisation was chosen (characters **4**, **12**, **13**, **21**, **42**, **43**, **65**). As ACCTRAN favours reductions before convergences, an accelerated transformation for characters **12**, **13**, and **42** means that the characteristic novelty evolved once and was reduced afterwards. This seems to be more likely than the characteristic novelties having evolved twice (DELTRAN). The “accelerated” optimisation of character **4** results in the evolution from a female without egg-sacs (character state 0 in Calanoida and Misophrioida), to females with 2 egg-sacs as in Canuellidae and further to females with only 1 egg-sac as in Harpacticoida (char. **4**: 0→1→2). The alternative possibility would be an evolution from ancestral females with no egg-sac to females with one and with two egg-sacs independently (char. **4**: 0→1 and 0→2). The females of Miraciidae (Podogenmonta), that have two egg-sacs again indicate, that the first possibility is more likely. The 2 egg-sacs in Miraciidae seems to be a reversal to the character state in Canuellidae (see chapter 5.2.3). The “accelerated” optimisation of character **21** results in the single transformation of the 1-segmented exopod mandible of N.N. 3 (Ectinosomatidae - Exanechentera; chapter 3.1) into the 4-segmented exopod mandible of Novocriniidomorpha (char. **21**: 2→1). *Rotundiclipeus canariensis* has a 1-segmented exopod again (char. **21**: 1→2). The other possibility would be that a 4-segmented exopod mandible evolved independently from a 1-segmented exopod in Novocriniidae and Superornatiremidae (char. **21**: 2→1). The “accelerated” optimisation of character **43** results in the evolution from a maxillipedal syncoxa with 11 to 7 armature elements (character state 0 in the outgroups and Aegisthoidea), to a syncoxa with 6 armature elements and further to a syncoxa with 4 setae (char. **43**: 0→1→2). The alternative possibility would be an evolution from 11 - 7 armature elements to 6 and to 4 armature elements independently (char. **43**: 0→1 and 0→2). The “accelerated” optimisation of character **65** results in the single transformation of the male antennule without an aesthetasc on the oligoarthran segment 3 (plesiomorphic within Exanechentera) to an antennule with an aesthetasc on this segment as in the groundpattern of Novocriniidomorpha (char. **65**: 1→0). *Rotundiclipeus canariensis* lost the aesthetasc again (char. **65**: 0→1). The other possibility would be that the aesthetasc on the oligoarthran segment 3 was regained independently in Novocriniidae and Superornatiremidae (char. **65**: 1→0). For further discussion of these characters see chapter 5.2.3.

### **Bremer support and bootstrap**

The Bremer support and the bootstrap values of the different clades of and within Oligoarthra are shown in Fig. 47. Some remarks on Bremer support and bootstrap are added above. The Bremer support is also mentioned in chapter 5.2.4. The Bremer support is only a weak indication of the support of the monophyly of a taxon, when the characters are not weighted according to their complexity. Although the Bremer support of e.g. Exanechentera and Idyanthidimorpha is only 2, the monophyly of these two taxa is very probable, because the complexity of the characters supporting their monophyly is relatively high. On the other hand, the monophyly of e.g. N.N. 3 (Ectinosomatidae - Exanechentera; chapter 3.1) is not beyond doubt, although the Bremer support is 5. The characters supporting the monophyly of N.N. 3 are mainly reduction characters that are weakened by homoplasy (see chapters 5.1.5 and 5.2.4).

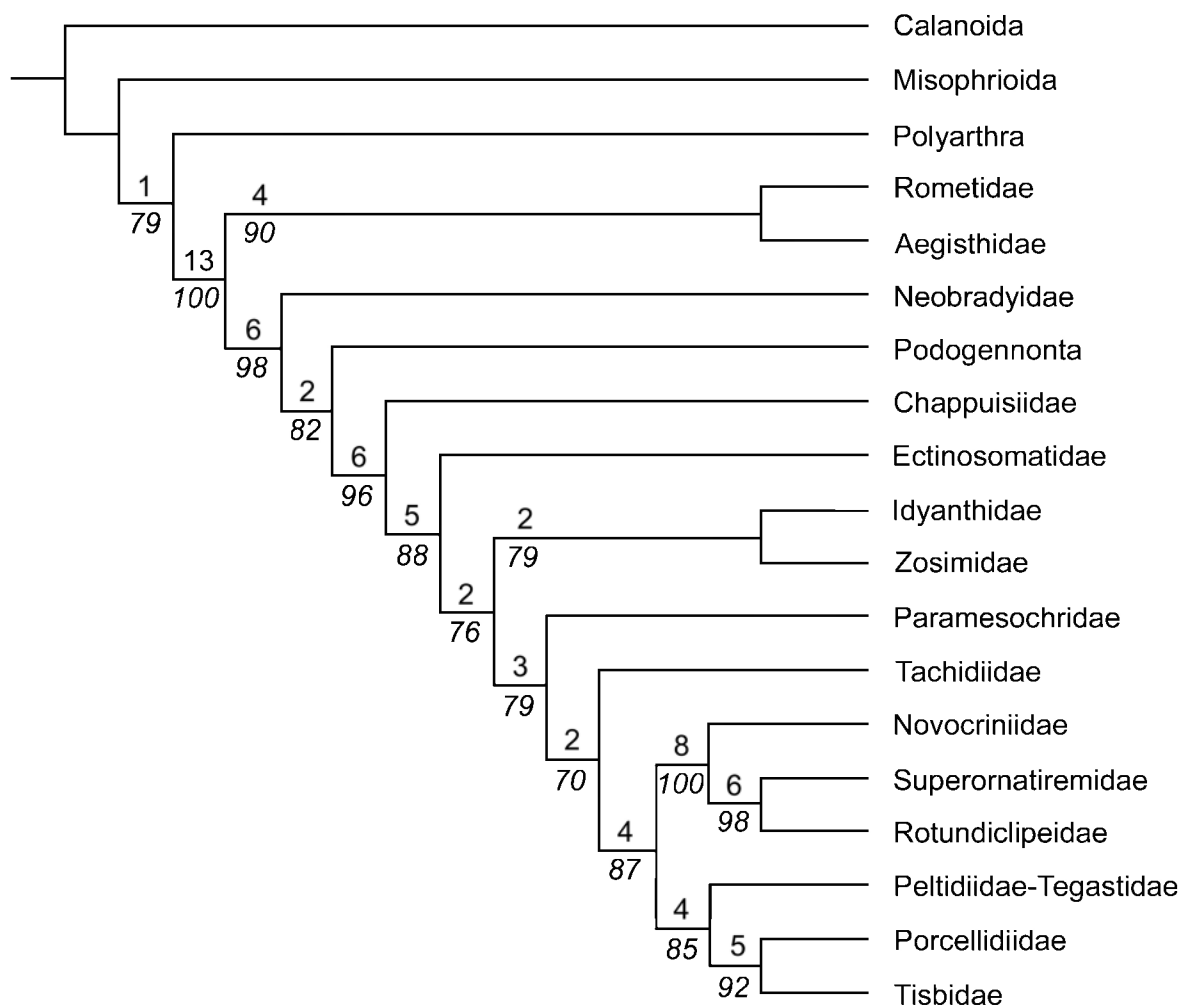


Fig. 47: Bremer support and bootstrap for single minimum length cladogram with length 155 for the taxa and characters in the character matrix (Table 4). Bremer support and bootstrap values (in italics) are given above and below branches, respectively.

### 5.1.4 Phylogenetic Systematics

The methods of Phylogenetic Systematics were applied (i.e. Hennig, 1966, 1982; Ax, 1984, 1987; Wägele, 2000; chapter 2). The analysis was made with 72 characters (chapter 5.1.1), 3 outgroup taxa, and 16 ingroup taxa (Table 4). Calanoida and Misophrioida were used as outgroups to polarise characters (chapter 5.2.2). The resulting cladogram was the same as the minimum length cladogram of the cladistic analysis, but the character distribution was slightly different (Fig. 46; see chapter 5.1.5). In Fig. 46, the open circles indicate the character optimisation of the cladistic analysis and the open squares indicate the transformation of characters reconstructed with the methods of Phylogenetic Systematics.

The presented diagram of the phylogenetic relationships within Harpacticoida (Fig. 4), the autapomorphies of harpacticoid taxa (chapters 4 and 5.1.5), and the evolution of some appendages within Harpacticoida (chapters 5.1.6 and 5.2.3) exactly represent the results of the methods of Phylogenetic Systematics.

### 5.1.5 Phylogenetic relationships within Harpacticoida and autapomorphies of harpacticoid taxa

The new system of Harpacticoida is presented as a result of the application of the methods of Phylogenetic Systematics and cladistic analysis (chapter 3. and Fig. 4). The autapomorphies supporting the phylogenetic relationships within Harpacticoida are summarized in character sets symbolized by black squares ■ followed by the branch number leading to the respective taxon (Fig. 4: e.g. ■ 3 represents the autapomorphies of Oligoarthra). Characters and their states according to the character list and the character matrix (chapters 5.1.1; Table 4) are marked in the text as follows: e.g. char. 1: 0→1 symbolizes the transformation of character 1 from character state 0 to character state 1. A new taxon name was given only if the monophyly of the respective taxon was well supported. Taxa named with N.N. followed by a number (e.g. N.N. 1) are probably monophyletic taxa but the monophyly of these taxa has to be confirmed. N.N. stands for *nomen nominandum* (“name to be given”). The taxa belonging to these taxa are listed in chapter 3.1. Sister taxa or more than two taxa which together represent a monophyletic taxon are connected with a dash (e.g. Tachidiidae - Palinarthra).

#### Phylogenetic relationships within Harpacticoida

The diagram of the phylogenetic relationships within Harpacticoida (Fig. 4) describes the same relationships as obtained from the cladistic computer analysis (Fig. 46). Given attentive studies of morphology and carefully selected and coded characters (chapter 5.2.1), both methods, those of Phylogenetic Systematics and the cladistic computer analysis, achieve similar results.

However, the indicated evolution of characters 3 and 49 differs between the two methods (Fig. 46). The oral cone (char. 3) probably evolved once in Palinarthra (■ 23) and was reduced twice in Peltidiidae - Tegastidae (■ 30) and Porcellidiidae (■ 32), as argued in chapter 5.2.3. This character transformation is one step longer than that indicated by the computer analysis. The same is true for the evolution of the setae of the enp-1 of maxilliped (char. 49). It is much more likely to assume that the large, displaced claw (V) has evolved only once (■ 9; N.N. 1) and was reduced to a smaller size in Chappuisiidae (■ 12) and Ectinosomatidae (■ 14), respectively. There is no satisfactory reason to assume that the large, displaced claw (V) evolved twice in Podogennonta and Exanechentera from a small claw like that of Neobradyidae. Especially an independent evolution of the exceptional innervation of the claw is unlikely (chapter 5.2.3). The reconstructed phylogeny of Harpacticoida with the alternative evolution of characters 3 and 49 is two steps longer ( $l = 156$ ) than the single minimum length cladogram ( $l = 154$ ).

Running the cladistic analysis with an upper boundary of a length of 156 and the taxa and characters of the data matrix (Table 4) results in eight cladograms. The length distribution is: the single minimum length cladogram with a length of 154 (indices: CI = 0.57; RI = 0.77; RC = 0.44), two cladograms with a length of 155 (indices: CI = 0.56; RI = 0.77; RC = 0.43) and five cladograms with a length of 156 (indices: CI = 0.56; RI = 0.77; RC = 0.43). In this case the indices, the Bremer support, and the bootstrap do not help to decide which of the cladograms show the best-supported



hypotheses of phylogenetic relationships. However, looking at the evolution a decision is obvious:

The two cladograms with a length of 155 differ only in the relation of the three outgroups. This is not relevant for the situation within Oligoarthra. Two cladograms with a length of 156 differ only in the position of Podogennonta. In these cladograms Podogennonta is the sister group of all other Syngnatharthra, including Neobradyidae, or Podogennonta and Neobradyidae together are the sister group of all other Syngnatharthra. None of the characters have a shorter length in these two cladograms compared to the minimum length cladogram or evolve in a more plausible way. The evolution of the setae of the enp-1 of maxilliped (char. 49) is the same in the minimum length cladogram and these two cladograms. To assume an alternative evolution of character 49 that is one step longer (see above) is necessary in all three cases. The length of characters 45 and 46 is one step longer in these two cladograms compared to the minimum length cladogram. That the joint between the syncoxa and the basis of the maxilliped has convergently evolved one more time (char. 45) is improbable. Although the length of character 43 is the same in all three cladograms the evolution of character 43 is doubtful in the two cladograms with a length of 156. The “accelerated” optimisation of character 43 in the minimum cladogram results in the evolution from a maxillipedal syncoxa with 11 to 7 armature elements (character state 0 in the outgroups and Aegisthoidea), to a syncoxa with 6 armature elements and further on to a syncoxa with 4 setae (char. 43: 0→1→2). In the two other cladograms the alternative would be an evolution from 11 - 7 armature elements to 4 and then to 6 armature elements (char. 43: 0→2→1). The transformation of characters, mainly the evolution of the maxilliped, is altogether somewhat less probable in the two cladograms with length 156. Both hypotheses, that Podogennonta is the sister group of all other Syngnatharthra including Neobradyidae or that Podogennonta and Neobradyidae together are the sister group of all other Syngnatharthra are untenable.

Of the remaining three cladograms of a length of 156, one cladogram differs in the position of Ectinosomatidae, the second cladogram differs in the position of Idyanthidae and Zosimidae to each other, and in the third cladogram the position of Tachidiidae and Paramesochridae is exchanged. Overall, the transformation of characters in these three cladograms is less more likely than in the single minimum length cladogram:

The hypothesis, that Idyanthidae and Zosimidae are no sister taxa as Idyanthidimorpha is paraphyletic has no support. No strong autapomorphy supports the sister group relationship of Idyanthidae and N.N. 4 (chapter 3.1). The only fact that supports this relationship is that the evolution of the antennal endopod is without homoplasy in this case (char. 13: 0→1). In contrast, the evolution indicated by the minimum length cladogram is one transformation step longer: The bevelled distal border of the antennal endopod is very characteristic for species of Exanechentera (char. 13: 0→1; below and chapter 5.2.1). However, species of Zosimidae have a rectangular antennal endopod (char. 13: 1→0), as the outgroup species. The monophyly of Idyanthidimorpha indicated by the single minimum cladogram is supported by three autapomorphies not weakened by homoplasy. Furthermore, the autapomorphies of Idyanthidimorpha are complex characters (see chapter 5.2.4).

The factor that causes the change in relationships in the next cladogram of length 156

is the morphology of Ectinosomatidae. Species of Ectinosomatidae can have a carnivorous feeding mode (Seifried & Dürbaum, 2000). This is exceptional for species of Harpacticoida (Seifried & Dürbaum, 2000). Therefore, the mouthparts have a unique form and setation. No strong synapomorphy connects Ectinosomatidae to any other oligoarthran taxon. There is a vague possibility indicated by one cladogram of length 156 that Ectinosomatidae is the sister group of N.N. 4 (chapter 3.1) and Idyanthidimorpha is the sister group of Ectinosomatidae - N.N. 4. As a consequence, Exanechentera would be polyphyletic. However, no strong apomorphy supports these relationships. Only character **36** is one step shorter as in the minimum length cladogram. In this case the 3 setae of the distal endite of maxillar praecoxa (fused to proximal one) are not convergently reduced 3 times in Ectinosomatidae, Paramesochridae and Palinarthra (char. **36**: 0→1) but reduced and regained (char. **36**: 0→1→0). This is only a very weak support for a sister group relationship of Ectinosomatidae - N.N. 4. Additionally, the length of characters **49** and **67** is one step longer as in the minimum length cladogram. In contrast, three distinctive characters support the monophyly of Exanechentera without Ectinosomatidae (chapter 5.2.4). The most parsimonious hypothesis to date is: Ectinosomatidae is the sister group of the monophyletic taxon Exanechentera (see chapter 5.2).

The relationship of Paramesochridae and Tachidiidae is uncertain. As indicated by one cladogram of length 156, it is also possible that Paramesochridae and not Tachidiidae is the sister group of Palinarthra. Paramesochridae has all autapomorphies of Exanechentera. However, there is no apomorphy connecting Paramesochridae with Palinarthra that is not present in Tachidiidae, too. Hypothesising the sister group relationship of Paramesochridae and Palinarthra, the evolution of char. **36** is one step shorter, as the 3 setae of the distal endite of maxillar praecoxa (fused to proximal one) are not reduced 3 times convergently, but only two times. On the other hand, the transformation of characters **10**, **49** and **66** is one step longer. Especially the repeated reduction of the small endopodal claw of maxilliped is not reasonable (char. **49**). The most parsimonious hypothesis to date is: Tachidiidae is the sister group of Palinarthra and Paramesochridae is the sister group of Tachidiidae - Palinarthra (N.N. 5). However, the characters supporting a sister group relationship of Tachidiidae - Palinarthra are not very convincing (see chapter 5.2.4).

The phylogenetic relationships indicated by the single minimum length cladogram with the alternative evolution of characters **3** and **49** are chosen here as the best supported hypothesis of the phylogeny of Oligoarthra (Fig. 4 and chapter 5.1.5, autapomorphies of harpacticoid taxa). The autapomorphies, which support the phylogenetic relationships within Harpacticoida, thus also the clade stability, are described and analysed below.

### **Autapomorphies of harpacticoid taxa**

The following list contains all autapomorphies of harpacticoid taxa deduced from the phylogenetic analysis on the basis of reconstructed groundpatterns.

For the phylogenetic analysis only informative characters are chosen, i.e. characters that appear in the groundpattern of more than one terminal taxon. As shown by the phylogenetic analysis, some of these characters are convergences. It was also shown,

that some of the evolved characters are reduced in advanced taxa. The convergently evolved characters and the reductions are additional autapomorphies of the terminal taxa. They are listed here. The numerous autapomorphies of the 17 terminal taxa that do not appear in another investigated taxon are not considered in the list of characters for the phylogenetic analysis (chapter 5.1.1) and in the following list of autapomorphies. The complete list of autapomorphies of the supraspecific taxa inferred from the phylogenetic analysis and of the terminal taxa can be found in chapter 4. The autapomorphies of the respective taxon are marked by **bold type**.

### ■ 1 Harpacticoida

*Female* with **2 egg-sacs** (char. 4: 0→1). Antennule **9-segmented**. Mandible endopod with **3 setae** on enp-1 and **9 setae** on enp-2. Praecoxal arthrite of maxillule bearing **12+2 setae**. **Claw-like appearance of the basal seta II (seta "D")** of maxilla. Endopod of maxilliped **2-segmented**, enp-1 representing segments 1-5 and enp-2 segment 6 of Copepoda; syncoxal formula of maxilliped: **1, I+1, I+3, I+2, three elements transformed to spines**. P1 enp-2 with **only 1 inner seta**; P2 exp-3 with **only 2 inner setae**; P1+P2 formula of armature:

	coxa basis	exopod	endopod
P1	0-1 1-I	I-1; I-1; III-I+2-2	0-1; 0-1; I-2-3
P2	0-1 1-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-3

Exopod P5 **1-segmented, as long as wide** (char. 60: 0→1).

*Male*. Antennule **14-segmented**.

### ■ 2 Polyarthra (for further autapomorphies see also chapter 4.2)

*Male*. Coxa of P5 **not separated from basis** (char. 70: 0→1).

### ■ 3 Oligoarthra (only some autapomorphies of Oligoarthra are listed in the character list).

*Female* with **1 egg-sac** (char. 4: 1→2); genital double-somite with **1 copulatory pore**. Antennule **9-segmented; armature formula: 1, 13, 10, 6 + aes, 3, 4, 2, 2, 6 + acrothek**; segments of Copepoda: 1-I, 2-(II-VIII), 3-(IX-XIV), 4-(XV-XVIII), 5-(XIX-XX), 6-(XXI-XXIII), 7-XXIV, 8-XXV, 9-(XXVI-XXVIII). Antenna with **2-segmented endopod, due to the fusion of 2 distal endopod segments of Polyarthra** (char. 8: 0→1); enp-1 with **1 seta**; enp-2 with **4 subterminal setae** (char. 9: 0→1); subterminal setation of enp-2 antenna consisting of **1 short proximal spine (I)** (char. 11: 0→1), **1 longer distal spine (III)** (char. 12: 0→1), **1 distal geniculate seta (4)** and **1 bare slender seta (2)**, inserted between spine I and spine III; **seta 5 of Polyarthra lacking**; exopod **4-segmented, armature formula: 2, 1, 1, 3** (char. 14: 0→1). Mandible endopod **1-segmented, due to fusion of enp-1 and enp-2** (char. 17: 0→1); endopod with **3 proximal lateral setae** (from enp-1), and **3 + 2 + 2 apical setae** (char. 20: 0→1), **each group of apical setae basally fused**; exopod **4-segmented, due to the fusion of two proximal segments of Polyarthra** (char. 21: 0→1), with **2, 1, 1, 2 setae**. Epipodite of maxillular coxa represented by **4 setae**; basis without outer seta; endopod **1-segmented** (char. 29: 0→1) with **6 setae** (char. 32: 0→1); exopod with **4 setae** (char. 32: 0→1). Maxilla with **syncoxa** (char. 33: 0→1) with **4 endites with 5, 3,**

**3, 3 setae**; allobasis bearing **1 tube pore on anterior surface** (char. 38: 0→1). Maxillipedal syncoxa without praecoxal seta and with incorporated coxal endites represented from proximal to distal by **I+1, I+2, I+1 spines and setae (X - 16)**; basis with 1 seta (9) and 1 spine (VIII); endopod with **3, II+2 setae and spines (1-7)**. P1-P4: coxae without inner seta (char. 51 + 57: 0→1); enp-3 of P1 and P2 with **2 inner setae**; formula of armature:

	coxa	basis	exopod	endopod
P1	0-0	I-I	I-1; I-1; III-I+1-2	0-1; 0-1; I-2-2
P2	0-0	I-0	I-1; I-1; III-I+1-2	0-1; 0-2; I-2-2
P3	0-0	I-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-3
P4	0-0	I-0	I-1; I-1; III-I+1-3	0-1; 0-2; I-2-2

P5 basis and endopod fused to baseoendopod (char. 59: 0→1).

*Male*. Antennule haplocer with 14 segments; armature formula: **1, 1, 12 + aes, 8 + aes, 2, 6 + aes, 2, 2, 4 / 3, 1, 2, 2, 6 + acrothek, aesthetasc on segment 6 fused at base with 1 seta, segments 1 and 2 with 1 seta each**; segments of Copepoda: 1-I, 2-(II), 3-(III-VIII), 4-(IX-XII), 5XIII, 6-(XIV-XVI), 7-XVII, 8-XVIII, 9-(XIX-XX), 10-(XXI-XXII), 11-XXIII, 12-XXIV, 13-XXV, 14-(XXVI-XXVIII).

#### ■ 4 Aegisthoidea

*Female*. Endopod of mandible with **1 spine** and 2 setae laterally (char. 19: 0→1). **Basis and endopod of maxillule fused; fused segment of characteristic rectangular shape, all setae at distal edge** (char. 30: 0→1). Endopodal armature of maxillar allobasis consisting of **displaced seta 10 between anterior and posterior surface** (char. 40: 0→1), **an additional seta closely set to seta 10** (char. 41: 0→1), **displaced seta 9 inserting near seta 10 but on anterior surface**, and seta 11 on posterior surface. P5 exopod more than twice as long as wide (char. 60: 1→3).

*Male*. P5 basis not separated from coxa (char. 70: 0→1) nor from endopod (char. 71: 0→1).

#### ■ 5 Rometidae (for further autapomorphies see also chapter 4.5)

First pedigerous somite **completely fused to dorsal cephalic shield** (char. 1: 0→1). Enp-2 of antenna with 1 spine (I) and **3 setae (2 - 4) laterally: element 1 forming a seta** (char. 12: 1→0). Maxilliped 3-segmented, comprising of syncoxa, basis and **1-segmented endopod, enp-1 and enp-2 fused** (char. 48: 0→1).

#### ■ 6 Aegisthidae (for further autapomorphies see also chapter 4.6)

*Female*. Antenna with **allobasis or incomplete basis** (char. 7: 0→1).

*Male*. Antennule 10-segmented, fusion of Oligoarthra segments 2 and 3, **10 and 11** (char. 63: 0→1), **12 to 14** (char. 64: 0→2).

#### ■ 7 Syngnathartha

*Female*. Prosome consists of **cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield** (char. 1: 0→1). Syncoxa maxilla with **(5 + 3), 3, 3 setae, the two proximal endites fused** (char. 34: 0→1). Coxa of maxilliped with incorporated endites represented from proximal to

distal by **I, I+2, I+1 spines and setae, seta 16 of proximal endite lost** (char. 43: 0→1); maxilliped with **joint with high degree of inward flexibility between basis and endopod** (char. 47: 0→1); enp-1 with 2 setae (6 + 7) and 1 thin claw (V); the **claw displaced to the posterior side of the distal end of enp-1** (char. 49: 0→1); **enp-2 reduced in size** (char. 48: 0→1) with 2 small outer seta (1 + 2) and 2 geniculated distal setae (3 + 4) (char. 50: 0→1). Proximal segment of exopod P1 without inner seta (char. 55: 0→1).

*Male* with 1 spermatophore (char. 5: 0→1).

■ 8 Neobradyidae (for further autapomorphies see also chapter 4.8)

Distal segment of female and male antennule with 1 subterminal and 6 terminal setae (char. 6 + 68: 0→1).

■ 9 N.N. 1

*Female*. Syncoxa of maxilliped with **not more than 4 setae (10 - 13), 2 spines (X, XII) transformed to setae** (char. 43: 0→1). Maxilliped with **joint with high degree of inward flexibility between syncoxa and basis** (char. 45: 0→1); basis with 2 setae inserting medially and distally on inner edge (8 + 9) (char. 46: 0→1); enp-1 with 1 large claw displaced to posterior side of the distal end (V), 1 thin claw (VI) and 1 seta (7) (char. 49: 0→3).

■ 10 Podogennonta (for further autapomorphies see also chapter 4.9)

*Female*. Endopod of mandible with 3 proximal lateral setae (from enp-1), 3 distal lateral setae (char. 20: 1→0) and 3 + 2 + 2 distal setae. P1 **enp-3 short** (char. 53: 0→1).

■ 11 N.N. 2

*Female*. Maxillular coxa with 4 inner setae (char. 27: 0→1). Allobasis maxilla **without tube pore from oligoarthran groundpattern** (char. 38: 1→0). **Exopodal seta 8 of female P5 missing** (char. 61: 0→1).

*Male*. Oligoarthran segments 12 to 14 of antennule **fused into one segment** (copepod segments XXIV to XXVIII) (char. 64: 0→2). Antennule **without an aesthetasc on oligoarthran segment 3** (char. 65: 0→1) and 4 (char. 66: 0→1). Endopod of P5 **fused to basis** (char. 71: 0→1).

■ 12 Chappuisiidae (for further autapomorphies see also chapter 4.10)

*Female*. Prosome consists of cephalosome and 4 free pedigerous somites; **first pedigerous somite completely separated from dorsal cephalic shield** (char. 1: 1→0). **No egg-sac** (char. 4: 2→0). Maxillula: **praecoxal seta 10 absent** (char. 23: 0→1); **2 long spinules of posterior distal spines of praecoxa missing** (char. 25: 1→0); **coxa and basis fused** (char. 28: 0→1). Maxillar allobasis **without setae of fused endopod segment** (char. 39: 0→1). Proximal endopod segment of maxilliped with 1 thin claw (V?), setae 6 and 7 lacking (char. 49: 3→1).

## ■ 13 N.N. 3

*Female.* Exopod of mandible **2-segmented, due to fusion of 3 proximal segments of Oligoarthra** (char. 21: 1→2). Syncoxa of maxilliped **with not more than 2 setae** (10 + 11) (char. 43: 2→3), **inserting at inner and outer border** (char. 44: 0→1).

*Male.* **Oligoarthran segments 6 to 9 of antennule fused to one segment** (copepod segments XIV to XX), **antennule subchirocer** (char. 62: 0→1); **oligoarthran segments 10 and 11 fused** (copepod segments XXI-XXII and XXIII) (char. 63: 0→1). **Coxa and basis of P5 fused** (char. 70: 0→1).

## ■ 14 Ectinosomatidae (for further autapomorphies see also chapter 4.11)

*Female.* **Praecoxal seta 10 of maxillula absent** (char. 23: 0→1). Distal endite of praecoxa (fused to proximal one) **with 2 setae** (char. 36: 0→1). Maxilliped: 1-segmented endopod **with 1 small claw (V) displaced to posterior side** (char. 49: 3→1), **1 small claw (VI) and 1 seta (7) from enp-1 lacking**.

## ■ 15 Exanechentera

*Female.* Distal border of antennal endopod **bevelled with an angle towards the exopod** (char. 13: 0→1). Gnathobase of mandible **with bulge at proximal border** (char. 16: 0→1).

*Male.* Antennule **with a claw with a pointed end formed by oligoarthran segments 10 to 14** (char. 67: 0→1).

## ■ 16 Idyanthidimorpha

*Female.* Coxal setae 10 and 11 of maxilliped **inserting subapical at inner and outer border** (char. 44: 1→2). The outer spine of the P1 enp-3 is **displaced terminally**; all exopodal spines of P1 **elongated and with very long spinules on one side**, but exp-3 not small and rounded (char. 56: 0→1).

*Male.* Enp-3 of P2 terminally **with modified bare spine (I) fused at base (originated from displaced outer spine)**, **1 middle hyaline seta (2) and 1 inner terminal seta** (char. 69: 0→1).

## ■ 17 Idyanthidae (for further autapomorphies see also chapter 4.14)

*Female.* **Enp-3 of P-1 small** (char. 53: 0→1).

## ■ 18 Zosimidae (for further autapomorphies see also chapter 4.15)

*Female.* **Lateral seta 2 of distal endopod segment of antenna missing** (char. 10: 0→1). Distal border of endopod antenna **not bevelled** (char. 13: 1→0). Mandible endopod **with 1 lateral seta** (char. 18: 0→1) and **3 distal setae** (char. 20: 1→2). Syncoxa of maxilliped **at most twice as long as wide** (char. 42: 0→1). Maxilliped **without joint between syncoxa and basis** (char. 45: 1→0), **neither between basis and endopod** (char. 47: 1→0).

■ 19 N.N. 4

*Female.* Maxillule: **2 long spinules of posterior distal spines of praecoxa missing** (char. 25: 1→0); endopod and all endopodal setae **directed inwards** (char. 31: 0→1). Allobasis of maxilla **without setae of fused endopod segment** (char. 39: 0→1). Syncoxa of maxilliped **with 1 seta (10)** (char. 43: 3→4).

■ 20 Paramesochridae (for further autapomorphies see also chapter 4.16)

*Female.* Distal endite of maxillar praecoxa (fused to proximal one) **with 2 setae** (char. 36: 0→1). P1 enp-3 **small** (char. 53: 0→1).

■ 21 N.N. 5

*Female.* **Lateral seta 2** of distal endopod segment of antenna **missing** (char. 10: 0→1). Maxillipedal enp-1 with 1 large claw displaced to posterior side of the distal end (V), and **2, 1 or 0 setae and spines; thin claw (VI) transformed to seta or spine (6) or reduced** (char. 49: 3→2).

*Male.* Antennule **with an aesthetasc on oligoarthran segment 4** (char. 66: 1→0).

■ 22 Tachidiidae (for further autapomorphies see also chapter 4.17)

*Female.* Body **dorso-ventrally flattened** (char. 2: 0→1).

■ 23 Palinarthra

*Female.* **Strongly developed, triangular labrum and fused lobes of paragnaths forming an oral cone** (char. 3: 0→1). Lateral element 1 of distal endopod segment of antenna **forming a seta** (char. 11: 1→0). Gnathobase of mandible **elongated and narrow** (char. 15: 0→1). Praecoxal arthrite of maxillula **elongated and narrow** (char. 22: 0→1); seta 10 of praecoxa **absent** (char. 23: 0→1). Maxilla: distal endite of praecoxa (fused to proximal one) **with 2 setae** (char. 36: 0→1). Syncoxa of maxilliped **at most twice as long as wide** (char. 42: 0→1). Seta 8 of exopod P5 **present** (char. 61: 1→0).

■ 24 Novocriniidimorpha

*Female.* Antennula: **1 subterminal and 6 terminal setae on oligoarthran segment 9** (char. 6: 0→1). Lateral element 3 of distal endopod segment of antenna **forming a seta** (char. 12: 1→0). Mandible endopod **with 1 lateral seta** (char. 18: 0→1); exopod **with 4 segments** (char. 21: 2→1). Coxa of maxillule **with 6 inner setae** (char. 27: 1→0). Proximal endite of maxillar coxa **with 1 seta** (char. 37: 0→1). Maxilliped **without joint between syncoxa and basis** (char. 45: 1→0). All pinnate spines of P2-P4 **swollen, flattened and spatulate** (char. 58: 0→1). Seta 12 of female exopod **missing**.

*Male.* Antennule: aesthetasc on oligoarthran segment 3 **present** (char. 65: 1→0); **some of the oligoarthran segments 6 to 9 separated, haplocer** (Copepod segments XIV to XX) (char. 62: 1→0); **without a claw formed by oligoarthran segments 10 to 14** (char. 67: 1→0); **1 subterminal and 6 terminal setae on oligoarthran segment 14** (char. 68: 0→1).

■ 25 Novocriniidae: for autapomorphies see chapter 4.20

■ 26 N.N. 6

*Female.* Antenna **with allobasis** (char. 7: 0→1). Gnathobase mandible **style-like** (char. 15: 1→2), **without bulge at proximal border** (char. 16: 1→0); endopod with **4 distal setae** (char. 20: 1→2). Praecoxal arthrite of maxillule **elongated, narrow, and cylindrical; 4 distal spines transformed to setae, all terminal elements tight together** (char. 22: 1→2); **setae 11 and 12 of praecoxa absent** (char. 24: 0→1). Syncoxa of maxilliped **without setae** (char. 43: 4→5).

*Male.* **Only oligoarthran segments 12 and 13 of antennule fused to one segment** (Copepod segments XXIV and XXV) (char. 64: 2→1).

■ 27 Superornatiremidae (for further autapomorphies see also chapter 4.21)

*Female.* Exopod P5 **more than twice as long as wide** (char. 60: 1→2).

*Male.* Antennule **without an aesthetasc on oligoarthran segment 3** (char. 65: 0→1).

■ 28 Rotundiclipeidae (for further autapomorphies see also chapter 4.22)

*Female.* P1-bearing somite **not fused to cephalothorax** (char. 1: 0→1). Exopod of mandible **missing** (char. 21: 1→2). Seta 8 of P5 exopod **missing** (char. 61: 0→1).

■ 29 Tisboidea

*Female.* Body **dorso-ventrally flattened** (char. 2: 0→1). Setae 11 and 12 of maxillular praecoxa **absent** (char. 24: 0→1). Coxa and basis of maxillule **fused** (char. 28: 0→1). Fused praecoxal endites of maxilla **displaced to the inner proximal corner of syncoxa** (char. 35: 0→1). P1: enp-2 **elongated** (char. 52: 0→1); exp-1 and exp-2 **elongated** (char. 54: 0→1); **exp-3 small and rounded, all spines of exp-3 elongated, with long spinules on one side** (char. 56: 0→2). Exopod of P5 **more than twice as long as wide** (char. 60: 1→2).

■ 30 Peltidiidae - Tegastidae (for further autapomorphies see also chapter 4.24)

*Female.* **No oral cone** (char. 3: 1→0). Mandible endopod **with 1 lateral seta** (char. 18: 0→1). Syncoxa of maxilliped **more than 3 times longer as wide** (char. 42: 1→0), **with 2 setae (10 + ?)** (char. 43: 4→3).

■ 31 N.N. 7

*Female.* Lateral seta 2 of distal endopod segment of antenna **present** (char. 10: 1→0). Praecoxa and coxa of maxillula **fused** (char. 26: 0→1); proximal endite of maxillar coxa **lost** (char. 37: 0→1). Enp-3 of P1 **small** (char. 53: 0→1). Antennule **without an aesthetasc on oligoarthran segment 4** (char. 66: 0→1). Seta II of caudal rami **displaced to dorsal surface** (char. 72: 0→1).



■ 32 Porcellidiidae (for further autapomorphies see also chapter 4.25)

*Female.* **No oral cone** (char. 3: 1→0). Lateral element 3 of distal endopod segment of antenna **forming a seta** (char. 12: 1→0). Maxilliped **without joint between syncoxa and basis** (char. 45: 1→0) and **basis and endopod** (char. 47: 1→0).

■ 33 Tisbidae *sensu strictu* (for further autapomorphies see also chapter 4.26)

*Female.* Lateral element I of distal endopod segment of antenna **forming a spine** (char. 11: 0→1). All pinnate spines of P2-P4 **swollen, flattened and spatulate** (char. 58: 0→1).

*Male.* **Some segments of oligoarthran segments 6 to 9 of antennule separated, haplocer** (Copepod segments XIV to XX) (char. 62: 1→0).

### 5.1.6 Evolution of Harpacticoida

The hypotheses about the evolution are always the corollary of the phylogenetic relationships and the autapomorphies of the taxa. The evolution within Harpacticoida can thus be reconstructed taking the phylogenetic relationships of Harpacticoida and the autapomorphies of the taxa as a basis (Fig. 4; chapter 5.1.5).

The evolution of the maxilliped follows the general oligomerization trend within Copepoda (chapter 5.2.6). Species of Polyarthra, Rometidae, and Aegisthidae have 16 to 23, species of N.N. 1 have maximally 12 (Fig. 48), and species of Palinarthra have maximally 10 maxillipedal setae and spines (Fig. 49). Many species of Harpacticoida have less setae and spines. The second evolutionary trend of the maxilliped within Harpacticoida goes from a leaf like to a prehensile appendage. Two claws were evolved and setae and spines were reduced.

The evolution of the P1 is marked by the transformation of the endopod. The elongation of the proximal endopodal segment is convergently evolved in Harpacticoida many times (e.g. Podogenonta, Paramesochridae, Superornatiremidae, Tisbidae, Porcellidiidae, Idyanthidae, within Neobradyidae, within Ectinosomatidae within Peltidiidae). The evolution of the endopod was otherwise unique in the ancestral line to each taxon. Very thick spines and claws were evolved (e.g. Podogenonta, Paramesochridae, Idyanthidae), segments were reduced or shortened (e.g. Paramesochridae, Zosimidae, Idyanthidae), and setae of the exopod and the endopod were reduced, transformed or displaced. Many transformations resemble each other, however small differences in details can be found (Fig. 50). With the phylogenetic system as background it can be said, that sometimes small differences in details refer to the fact that these character states are not the same but evolved independently.

First steps towards the characterisation of the evolution of Harpacticoida are made. Detailed descriptions and discussion of the evolutionary process are specified in the discussion of the characters (chapters 5.2.3 and 5.2.4). Additional conclusions on the evolution drawn from the phylogenetic system of Harpacticoida will be published elsewhere.

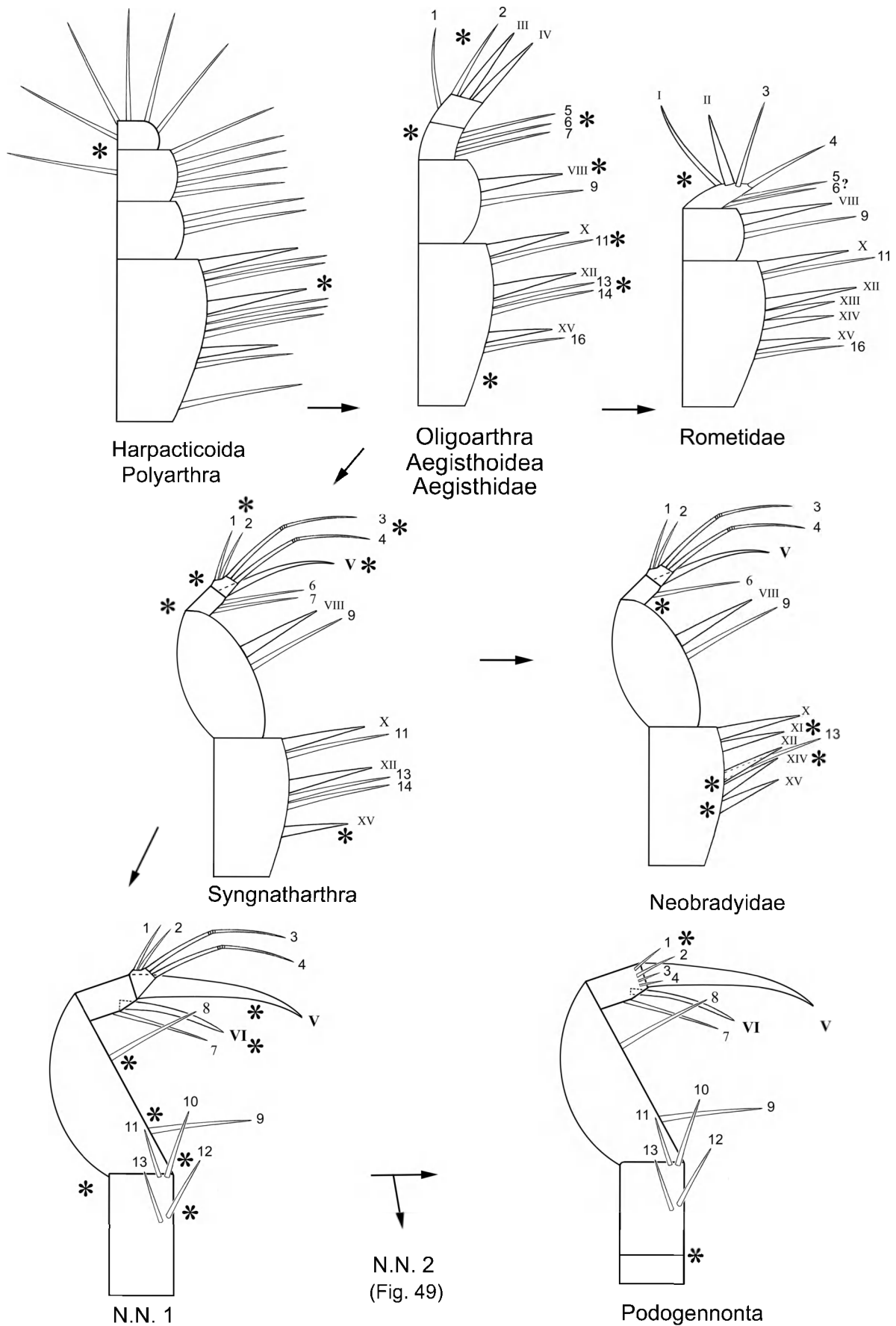


Fig. 48: Evolution of the maxilliped within Harpacticoida (groundpattern of the respective taxon; anterior view). Asterisks mark autapomorphies of the respective taxon with the higher systematic rank.

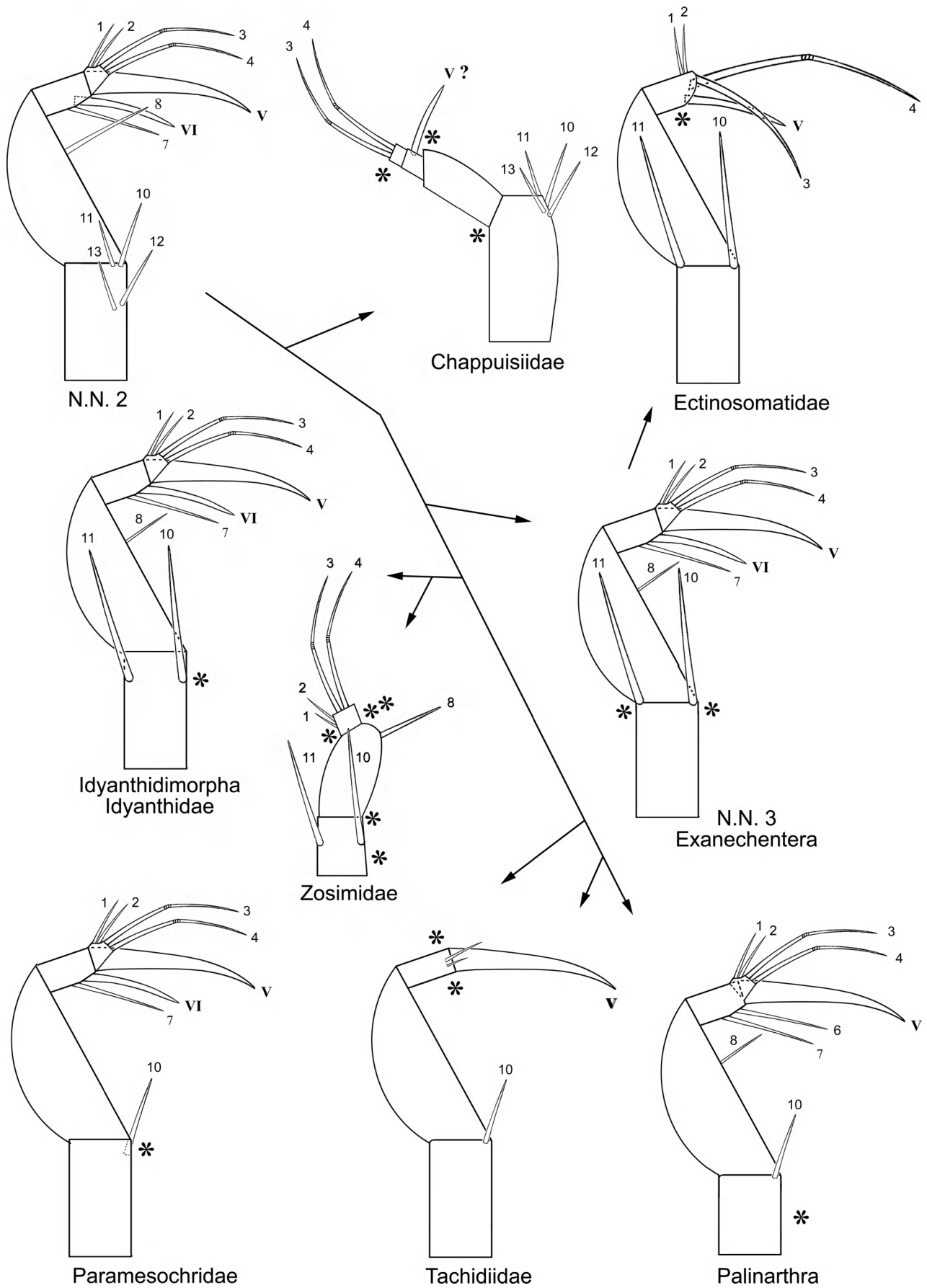


Fig. 49: Evolution of the maxilliped within Harpacticoida (groundpattern of the respective taxon; anterior view). Asterisks mark autapomorphies of the respective taxon with the higher systematic rank.

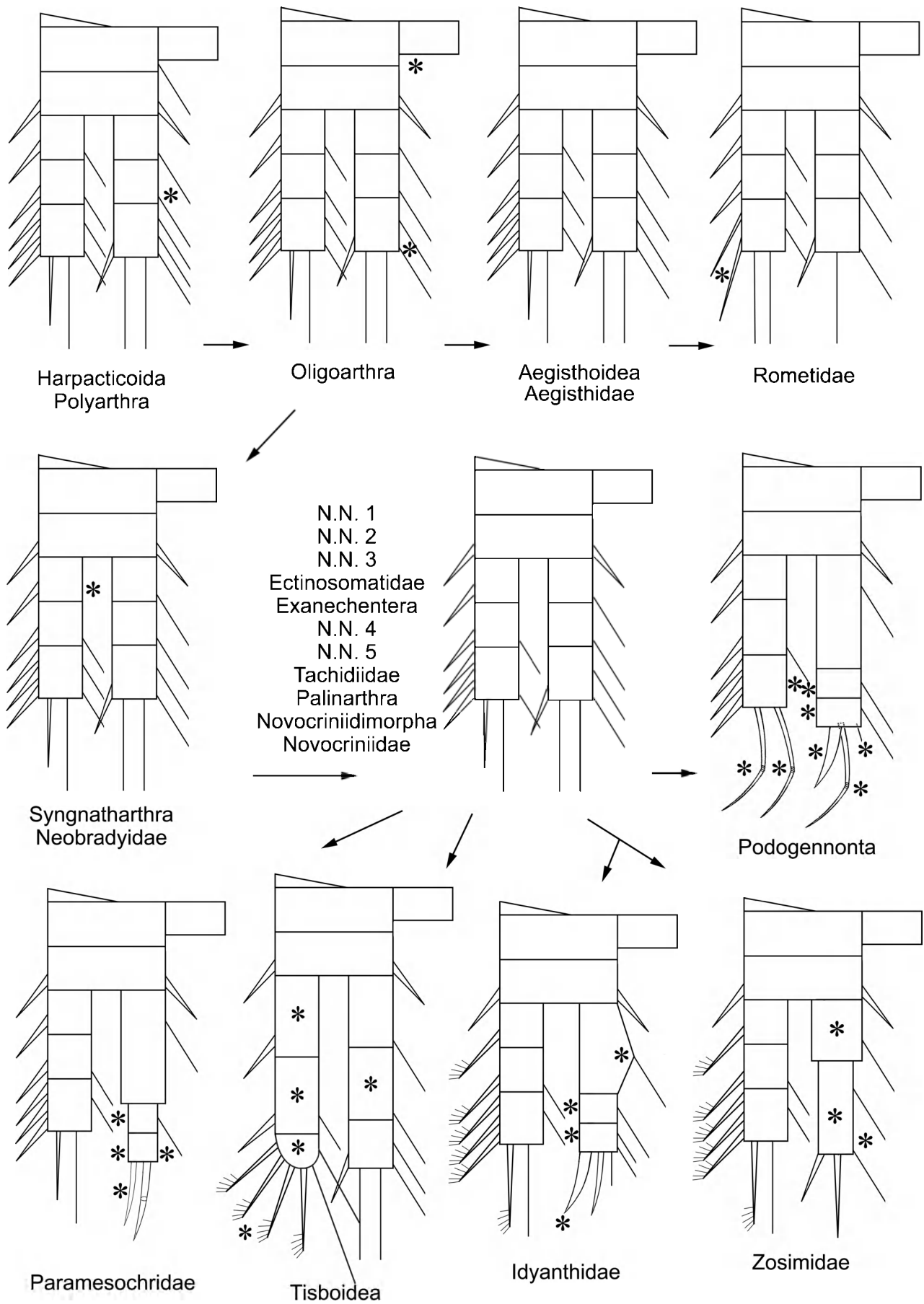


Fig. 50: Evolution of the P1 within Harpacticoida (groundpattern of the respective taxon). Asterisks mark autapomorphies of the respective taxon with the higher systematic rank.

## 5.2 Discussion

### 5.2.1 Selection of characters and their homology

For the analysis of phylogenetic relationships the character selection is crucial. It is essential, to select characters that have the right rate of evolution. Characters that did not visibly evolve within the time span in which the major evolutionary lines of the investigated taxa separated are not suitable. The evolutionary rate of these characters was and probably is too slow in the respective species group. As a consequence, recent taxa will not show enough differences to allow conclusive character states to be distinguished. Characters that have a very high rate of evolution are not suitable either for the systematic analysis. Such characters change so fast, that in recent taxa the state of a given character is often determined by recent evolutionary events. It follows that the autapomorphies of higher taxa cannot be observed any more. This holds true for various characters from morphology, anatomy, behaviour and molecular data. Therefore, not all recognised morphological differences between single taxa were coded as characters here. The number of segments and setae of the antennal exopod, for example, is highly variable within Oligoarthra. The exopod of an antenna can differ among sister species and is therefore only a valuable character to infer relationships between species or genera. Characters with an extremely high or low rate of evolution are thus not considered in the list of characters.

Anatomy (Hosfeld, 1997), larval morphology (Dahms, 1990, 1993), i.e. developmental pattern and the behaviour of Harpacticoida could not be used for the present phylogenetic analysis, either. To date the database in these fields is not large enough. The investigation of these characters depends on living material or cultures of species to a high degree. Most cultured species in the AG Zoosystematik and Morphologie (Universität Oldenburg) belong to Podogenonta. Living specimens were available only of six of the fifteen taxa besides Podogenonta analysed here. Species of only four of these taxa could be cultured (Chappuisiidae, Ectinosomatidae, Tachidiidae, Tisbidae *sensu strictu*). Species of all other taxa (except Podogenonta) are rare (also in the museum collections), not easy to culture, or live in rather inaccessible habitats like the deep sea. Because of the sizable collection in Oldenburg of deep sea and Antarctic samples collected by the German research vessels "R/V Meteor", "R/V Polarstern", and "R/V Sonne", I was lucky to obtain fixed material of nearly all of these taxa for morphological studies of the adults. However, it will be difficult to amass enough material of these tiny crustaceans (< 1 mm) for studies of larval morphology, anatomy, and molecular systematics.

A frequently quoted hypothesis about copepod evolution states that evolution in the course of time primarily leads to the reduction of somites, of segments of the appendages, and their setation (see chapter 5.2.6). Hence the complexity of copepod morphology tends to decrease, in contrast to the overall evolution of life. As a consequence of this trend, most characters that are given for a phylogenetic analysis are reduction characters. These characters are generally based on few mutations and are therefore not very useful for a well-supported hypothesis of phylogeny. Reductions can occur multiple times convergently, and at present there are no adequate means to detect them. In arthropods the number of setae seems to be regulated on a simple genetic basis (e.g. Wägele, 2000). As another consequence of ongoing

oligomerization, many characters that arose in the early evolution of Harpacticoida cannot be analysed in all taxa, because the respective segments or setae were reduced. If many of such characters were to be integrated in a character matrix, the percentage of missing character states would become too large and the analysis would be rendered doubtful.

Huys, & Boxshall (1991, p. 31) always regard the maximum number of segments as the most plesiomorphic state within a taxon: "In the construction of the ancestral character set we have searched for the maximum number of segments expressed within each order, for every appendage. As a general rule we have also listed, as the ancestral state, the maximum number of setation elements per segment of every appendage". The same assumption was used by Ho (1990) to develop the phylogeny of Copepoda and by Willen (2000) to reconstruct the phylogeny of Thalestridimorpha (Podogenonta) and the groundpattern of Podogenonta.

Because of lack of adequate knowledge about the genetic regulation of morphological characters, also because of the fact that the sister group of Harpacticoida is still not known with certainty and the circumstance that all recent phylogenetic hypotheses within Copepoda are based on the hypothesis of reduction of segments and setae, I attempted to find as complex characters as possible. The probability of homology is greater with complex characters compared to reduction characters (see below; e.g. Wägele, 2000). Due to the small number of complex characters available reduction characters were also used for the computer analysis. In the character list 44 % of the characters code reductions of segments, setae and aesthetascs (32 out of 72 characters; characters 1, 7, 8, 10, 14, 17, 18, 20, 21, 23, 24, 26, 27, 29, 32, 33, 36, 37, 39, 48, 51, 55, 57, 59, 61, 62, 63, 64, 65, 66, 70, 71), and 56 % code more complex characters, such as the form and the alignment of structural elements (40 out of 72 characters; characters 2, 3, 4, 5, 6, 9, 11, 12, 13, 15, 16, 19, 22, 25, 28, 30, 31, 34, 35, 38, 40, 41, 42, 43, 44, 45, 46, 47, 49, 50, 52, 53, 54, 56, 58, 60, 67, 68, 69, 72).

Ensuring the homology of compared structures is one of the most important conditions for phylogenetic reconstruction. There is a tremendous amount of literature about homology, however, the different concepts will not be discussed here in detail. Different methods conflict with one another. Phylogenetic Systematics demands to ascertain the homology of compared structures prior to a phylogenetic analysis, whereas in computer cladistics homology should be exclusively a result of the obtained cladogram. Indeed, hypotheses of homology are always necessary to draw up a character list and a character matrix, i.e. the homology of the respective structures, appendages, segments and setae, which are the carriers of the characters.

The homology of segments and setae in copepods as previously proposed by many copepodologists is applied here. Huys & Boxshall (1991) elaborated and summarised the homology of all appendages of Copepoda and Willen (2000) of Harpacticoida. The homology of setae of antenna, maxillula, maxilla and maxilliped of adult Harpacticoida is completed here (see chapters 4.1 and 4.3). Females of Oligoarthra have at most 277 homologous setae and males 282. Every segment and almost every seta could be homologised in many examined species of Harpacticoida (on the basis of adult morphology only). Merely some setae of the antennule, the mandibular endopod, the maxillular coxa, and the proximal coxal endite of maxilla eluded a homologisation to date. The use of total numbers of elements, however, may be misleading, because it

can conceal the true homology of elements. Nevertheless, for drawing up the character list and matrix presented here, all setae were homologised, with the exception of few setae mentioned in characters **18**, **20**, (mandibular endopod), **26** (maxillular coxa), and **37** (proximal coxal endite of maxilla).

### **5.2.2 Polarity of characters and choice of outgroups**

For an analysis according to the methods of Phylogenetic Systematics, the polarisation of characters of the character list has to be determined (e.g. Hennig, 1966; Wägele, 2000). As the monophyly of Harpacticoida is not beyond doubt (chapters 4.1 and 4.2), Polyarthra is used as outgroup in the present analysis of phylogeny and Oligoarthra is the ingroup. Calanoida and Misophrioida were used as additional outgroups to polarise the characters. The taxon Copepoda consists of ten taxa to date, traditionally classified as “orders”. Huys & Boxshall (1991) published a summary of the proposed phylogenetic relationships of Copepoda. Since Ho (1990) it has been accepted that Calanoida and Platycopioidea are the outgroups of the remaining copepods (Podoplea Giesbrecht, 1882). Calanoida is used here as an outgroup that represents relatively basal copepods. The phylogenetic relationships of Podoplea are in a state of flux to date. Siphonostomatoida Thorell, 1859 and Poecilostomatoida Thorell, 1859 are parasites or associates and in consequence, their morphology is diverse and derived. The mormonilloid species show extreme sexual dimorphism (Mormonilloidea Boxshall, 1979). The female has no fifth leg and the mouthparts are highly reduced in the male. The monstrilloids have non-feeding adults without feeding appendages and the gelyelloid species are found in subterranean waters. Therefore the morphology mainly of the swimming legs is characterised by many reductions. Only Cyclopoida and Misophrioida are taken into consideration for a second outgroup for Harpacticoida. As Misophrioida share some specific apomorphies with Harpacticoida, e.g. arrangement and shape of the setae and spines of the praecoxal arthrite of the maxillule (chapter 4.1), Misophrioida is an eligible candidate for the sister group of Harpacticoida. None of the newly proposed phylogenies of Copepoda mentioned Harpacticoida and Misophrioida as sister groups, however, Sars (1903) placed the species of Misophrioida as species of “Misophriidae” within Harpacticoida. Misophrioida is chosen here as second outgroup. The ancestral states of the taxa reconstructed in “Copepod Evolution” (Huys & Boxshall, 1991) are used here as groundpattern for Calanoida and Misophrioida. However, when the reconstruction of the phylogenetic relationships of a copepod taxon is made by the aid of groundpattern reconstruction, these groundpatterns have to be considered critically. For the reconstruction of a groundpattern of a taxon, the hypothesis of the phylogenetic relationships within the taxon is necessary. The character state with the most setae, aesthetascs, and segments is not always the plesiomorphic one. Therefore, also the morphology of the species of Calanoida and Misophrioida was always considered. For the discussion of the general oligomerization trend see chapter 5.2.1, 5.2.5 and 5.2.6.

The homology of the characters and character states used for the phylogenetic analysis and the polarity of characters were always checked after the analysis and corrected where necessary, i.e. when other, more complex characters contradicted the original homology or polarisation hypothesis (principal of reciprocal elucidation). All

characters were treated as unordered for cladistic computer analyses. Outgroup comparison was used to root cladograms. In all cases, the polarity of characters indicated by the cladistic analyses could be followed for the reconstruction of phylogeny and evolution (see chapters 5.1.3 to 5.1.5). The polarity of all 72 characters indicated by the cladistic analysis was the same as that determined for the analysis according to the methods of Phylogenetic Systematics.

### 5.2.3 Analysis and discussion of characters

The presented cladistic computer analysis is made with the groundpattern of the taxa as the starting point. For the investigation of the groundpattern the methods of Phylogenetic Systematics were applied (chapter 2. Material and Methods). The character states, especially the number of segments and setae in the groundpattern of most terminal taxa, were ascertained by additional cladistic computer analysis within the terminal taxa. When the maximum number of segments and setae is not regarded as the most plesiomorphic state within a taxon, it is discussed in the chapter of the respective taxon (see chapters 4, 5.2.5 and 5.2.6). For the groundpattern of Podogennonta see chapters 4.9 and 5.2.5.

In chapter 5.2.4 further remarks to the homology, the morphology of the outgroups, the polarisation, the amount of homoplasy, and the evolution of characters are added.

### Female

#### Body

**Char. 1:** first pedigerous somite

Most Oligoarthra have the first pedigerous somite fused to the cephalothorax. This is in contrast to the species of the outgroups, in which the first pedigerous somite is free. The fusion is an autapomorphy of Syngnatharthra (char. 1: 0→1; chapter 5.1). However, some species of Syngnatharthra have a first pedigerous somite that was secondarily separated from the cephalosome (char. 1: 1→0). Species of Chappuisiidae, Phyllognathopodidae, and some Latiremidae have a completely separated first pedigerous somite that has almost the original size and shape. The first pedigerous somite of species of Darcythompsoniidae, contrary to older descriptions, is always fused to the cephalosome (Huys et al., 1996, p. 60). *Atergopedia vetusta* (Novocriniidae), *Rotundiclipeus canariensis* (Rotundiclipeidae), and some species of Tachidiidae (e.g. *Tachidius (Tachidius) discipes*) have a P1 segment that is not completely separated from the cephalosome or has a different size or shape. For the last group of species it is unquestionable that the P1 segment is secondarily separated, as is indicated by its size and form and the phylogeny within Oligoarthra. In Chappuisiidae, Phyllognathopodidae, and Latiremidae the separation also took place secondarily, as can be deduced from the phylogenetic system of Harpacticoida. A completely or incompletely separated first pedigerous somite is probably more common in Oligoarthra, as can be seen in TEM observations (Hosfeld, pers. comm.). It seems that in some taxa of Oligoarthra the degree of fusion is a variable character (even between sister species), in phylogenetic analysis this character should therefore be used with care.

The P1 segment is fused to the cephalosome in Rometidae and in *Cerviniella*



(Aegisthidae). However, *Cerviniella* is highly derived within Aegisthidae. The more plesiomorphic state within Aegisthidae is a free P1 segment, so that the fusions in Syngnatharthra, Rometidae, and *Cerviniella* are not homologous. The alternative possibility would be that the fusion happened in the ancestor line of Oligoarthra, the P1 segment was secondarily separated from the cephalosome in Aegisthidae and that the fusion of the P1 segment evolved secondarily in *Cerviniella*.

**Char. 2:** body form

Most non-parasitic copepods have a body that is not considerably flatter than wide, as most species of Calanoida and Misophrioida. The interstitial harpacticoids are cylindrical, many epibenthic forms are fusiform and many planktonic forms are cyclopid-like. The phytal Harpacticoida are often dorso-ventrally flattened (char. 2: 0→1; chapter 5.1). The flattened body form evolved convergently in derived species of Ectinosomatidae (*Peltobradia bryozoophila* Médioni & Soyer, 1967) and Podogenmonta (some Harpacticidae as species e.g. of *Zaus* Goodsir, 1845; some Thalestridae as species e.g. of *Amenophia* Boeck, 1865). The body is dorso-ventrally flattened in the groundpattern of Tachidiidae, Peltidiidae - Tegastidae, and Tisbidae. However, species of Tegastidae are laterally compressed and within Tisbidae a more cylindrical body form evolved secondarily (chapters 4.24 and 4.26). All species of Porcellidiidae are extremely dorso-ventrally flattened, even shield-shaped (chapter 4.25). It is interesting that all these dorso-ventrally flattened harpacticoids favour habitats, where seaweeds are common. Most of them, as species of Porcellidiidae, Peltidiidae, *Zaus*, *Scutellidium*, and *Sacodiscus* (Tisbidae *sensu strictu*) are phytal species. The flattened body form certainly allows adhering to algae, when the current is strong. In the evolutionary line to Porcellidiidae, a sucker evolved mainly formed by the mandibular palp and the P1 aided by the body form.

**Char. 3:** oral cone

The lobes of the paragnaths are fused to form a labium in Novocriniidae, Superornatiremidae, Peltidiidae - Tegastidae, Porcellidiidae, and Tisbidae. It is very likely that *Rotundiclipeus canariensis* also has a labium (fused lobes of the paragnaths), but this is not known. The labrum is strongly developed, triangular and prominent in most species of Palinarthra, forming an oral cone with the also prominent labium (char. 3: 0→1; Figs. 36 + 37). The elongated gnathobases of the mandibles are able to move between labrum and labium thus forming with them a functional unit (Figs. 36 + 37). However, it is difficult to observe the whole oral cone in most cases. The labium is often completely covered by the elongated gnathobases of the mandibles and the praecoxal arthrite of maxillula, so that only the tip of the labium is visible. The fusion of the labium and the labrum is mostly also covered in not dissected specimens. When the mouthparts are dissected and mounted, the labium is often destroyed or “crumpled”. However, in drawings, where the oral cone is documented (e.g. Figs. 36 + 37) and in specimens, where an observation was possible, the oral cone shows the same general morphology as described above.

The morphology of the oral cone and the mandible gnathobase resemble those of siphonostomatoid copepods, with more plesiomorphic character states within Siphonostomatoida. However, the oral cones of Palinarthra and Siphonostomatoida

cannot be homologous and must have evolved convergently. In all siphonostomatoid copepods the oral cone has, in contrast to oligoarthran species, a more or less tubular structure. Within Harpacticoida the oral cone evolved in the derived taxon Palinarthra. The oral cone of Palinarthra formed by labrum and labium is reduced in the extremely dorso-ventrally flattened tsebids *Scutellidium* and *Sacodiscus*. It is also reduced in Peltidiidae and Porcellidiidae, the other taxa with an extremely dorso-ventrally flattened body-shape within Palinarthra. In them, the paragnaths are still fused medially (but are not prominent) and the gnathobase of the mandible and the praecoxal arthrite of maxillula are still elongated in Peltidiidae - Tegastidae, Porcellidiidae (Figs. 37 E + F), and *Scutellidium* - *Sacodiscus* (but not so extremely). In other Palinarthra these two elongated mouthparts belong to the functional unit of the oral cone comprising labrum and labium (Figs. 36 E + F). It is very likely that the complex oral cone evolved only once in Palinarthra and that it was reduced three times convergently in Peltidiidae - Tegastidae, Porcellidiidae, and *Scutellidium* - *Sacodiscus*. The reduction of the prominent oral cone may be a necessity for dorso-ventrally flattened animals that attach closely to the substrate, e.g. algae. The species of Tsebidae *sensu strictu* with a more slender habitus have a big prominent oral cone (Figs. 37 A + D) composed of labrum and labium, supported by the elongated gnathobase of the mandible and the praecoxal arthrite of maxillula. The remaining species of Palinarthra as Superornatiremidae exhibit an identical pattern.

A strongly developed, prominent labrum exists in some species of Ameiridae (Podogenonta). However, a prominent labrum fused to the labium could not be confirmed until now. As the taxon Ameiridae consists of many morphologically different species and as no strong autapomorphy exists for Ameiridae to date, it is possible, that some species of Ameiridae belong to Palinarthra. The other possibility is, that the strongly developed, prominent labrum evolved convergently in Palinarthra and Ameiridae.

#### **Char. 4: egg-sacs**

The females of Misophrioida and Calanoida produce no true egg sacs with a membranous cover. However, many copepods enclose their eggs in two egg-sacs (Huys & Boxshall, 1991). As Mormonilloida, Cyclopoida, Siphonostomatoida, and Poecilostomatoida have 2 egg-sacs as groundpattern character, it is probable that the ancestor of Harpacticoida also had 2 egg-sacs. As in Canuellidae, the number of egg-sacs in the groundpattern of Polyarthra is probably 2 (Fig. 1 A; char. 4: 0→1; chapter 5.1). The production of one egg-sac (char. 4: 0→1) obviously was convergently evolved in the ancestor line of Oligoarthra and Longipediidae. All basal Oligoarthra produce only 1 egg-sac as e.g. *Eucanuella spinifera* (Aegisthidae; Fig. 1 C). Within Oligoarthra, all females of Miraciidae and some of *Huntemannia* Poppe, 1884 (Huntemaniidae) produce 2 egg-sacs. It is very likely that this is a secondary phenomenon. Assuming that the production of 2 egg-sacs is part of the groundpattern of Oligoarthra would mean, that the production of only one egg-sac evolved many times. *Chappuisius singeri* and *Ch. inopinus* (Chappuisiidae), two groundwater species, have no egg sac secondarily.

**Char. 5:** spermatophore

The Misophrioida and Polyarthra produce two spermatophores simultaneously, but the Calanoida produce only one spermatophore at the same time. However, it is very likely that the plesiomorphic condition within Copepoda and Harpacticoida is that 2 spermatophores are produced simultaneously as in Aegisthidae (Hosfeld, 1997).

The existence of only one spermatophore at a time is characteristic for Syngnatharthra (char. 5: 0→1). However, *Nannopus palustris* Brady, 1880 (Podogenonta, Huntmanniidae) produces 2 spermatophores simultaneously (Hosfeld, 1997). The same is true for the males of *Harpacticella* spp., *Tigriopus* spp. and *Zaus goodsiri* Brady, 1880 (Podogenonta, Harpacticidae) as noted by Huys et al. (1996). Within Podogenonta the species with 2 spermatophores belong to two different evolutionary lines. All other Podogenonta and Syngnatharthra produce only 1 spermatophore simultaneously. The production of 2 spermatophores at the same time in *Nannopus palustris* and some Harpacticidae is interpreted as secondary.

Female antennule**Char. 6:**

The novocriniidimorph distal displacement of setae of oligoarthran segment 9 of female antennule (char. 6: 0→1) is also present in Neobradyidae. As indicated by the parsimony analysis, it is likely that the displaced setae are not homologous in these two groups.

Antenna**Char. 7:**

The outgroup species, all species of Rometidae and the species of the more plesiomorphic taxa of Syngnatharthra, have a separated basis and proximal endopod segment. All species of Aegisthidae have an allobasis or a basis that is incompletely fused with the proximal endopod segment (char. 7: 0→1). An allobasis has convergently evolved in N.N. 6 (Rotundiclipeidae - Superornatiremidae) and a few advanced taxa of Podogenonta (e.g. Cletodidae).

**Char. 8:**

The ancestral condition of the endopod of Calanoida is 4-segmented (Huys & Boxshall, 1991). Most Calanoida, however, have a 2-segmented endopod due to the fusion of the second, third, and fourth segments. In the basal Misophrioida and species of Polyarthra it is 3-segmented. All species of Oligoarthra have an antenna with a 2-segmented endopod or a basis that is fused with the proximal endopodal segment (allobasis) and one free distal endopodal segment (char. 8: 0→1). The distal endopodal segment of Oligoarthra is explained by the missing segment border between the two distal endopodal segments of Polyarthra. These segments are not separated in many species of Misophrioida and Calanoida, either. It is a typical situation when dealing with the phylogeny and evolution of Copepoda or Harpacticoida that segments are fused, that borders between segments are missing or that segments and setae are completely reduced within several taxa convergently. Sometimes segments or setae are even regained (chapters 5.2.1, 5.2.5 and 5.2.6). When the reconstruction of the phylogenetic relationships of a copepod taxon is made by the aid of groundpattern

reconstruction, these groundpatterns have to be considered critically. It is possible that the character state that codes the highest number of setae and segments is not the plesiomorphic one (chapter 2, 5.2.1, 5.2.5 and 5.2.6).

#### **Chars. 9 to 12:**

The 4 lateral setae of the distal endopod segment antenna are derivable from the 5 setae of the middle endopod segment of Polyarthra (Figs. 6 - 7). All species of Oligoarthra miss seta 5 of Polyarthra, whereas Canuellidae lost seta 2. Seta 2 inserts between seta 1 and seta 3 in Oligoarthra as in Longipediidae (compare *Longipedia minor* in Huys & Boxshall, 1991, fig. 2.4.7). The basal Calanoida and Misophrioida have a 3- or 4-segmented endopod, with more than 5 setae on the second segment.

A homologous modification of the 4 subterminal setae of proximal endopod segment antenna is found in most Oligoarthra (char. 9: 0→1). The setation consists of 1 short proximal spine (I), 1 longer distal spine (III), 1 distal geniculate seta (4) and 1 bare, slender seta (2) (Willen, 2000). The outgroup species have no such transformation. Seta 2 inserts originally between spines I and III as in Polyarthra (Fig. 6). This condition is still found in Neobradyidae and Chappuisiidae (e.g. *Tachidiopsis* spec., *Marsteinia* spec. 2., *Chappuisius inopinus*). The position of seta 2 is otherwise variable. Seta 2 is reduced in N.N. 5 and Zosimidae convergently (char. 10: 0→1) and regained in N.N. 7. The lateral element 1 of the distal endopod segment of the antenna forms a seta in nearly all species of Palinarthra (char. 11: 1→0). This condition is also shown in the outgroups of Oligoarthra. Otherwise, the lateral element 1 forms a spine in species of Oligoarthra (char. 11: 0→1), with the exception of species of Tisbidae, where the spine is secondarily developed. All species of Aegisthidae have a maximum of 3 lateral elements on the distal endopod segment. One spine (spine I) is always lacking. In species of Rometidae, Porcellidiidae and Novocriniidimorpha element 3 is secondarily transformed to a seta (char. 12: 1→0; chapter 5.1).

#### **Char. 13:**

The bevelled distal border of the antennal endopod is very characteristic for species of Exanechentera (Figs. 24 A - E; char. 13: 0→1; chapter 5.1). Within Oligoarthra only species of this taxon have such an endopod. Evolution continued within Exanechentera, so that the angle of the slope became more acute. The end is marked by species of Tisbidae *sensu strictu*, where some of the distal setae insert at the same level as the lateral ones (Fig. 24 E). Only species of Zosimidae have a rectangular antennal endopod (char. 13: 1→0), as the outgroup species. This is not astonishing, because species of Zosimidae have an aberrant morphology in nearly all appendages.

#### **Char. 14:**

Species of Calanoida have at most a 10-segmented antennal exopod and Misophrioida and Polyarthra a 8-segmented one. The smallest number of exopodal segments in the species of these outgroups seems to be 6. The maximum number of segments found in Oligoarthra is 4 (char. 14: 0→1). However, most oligoarthran species have an exopod with fewer segments or no exopod at all.

Mandible**Char. 15:**

All species of Palinarthra have an elongated and narrow gnathobase of mandible (char. 15: 0→1). In *Rotundiclipeus canariensis* and Superornatiremidae, the gnathobase is stylet-like (char. 15: 1→2). In some parasitic copepods, especially in Siphonostomatoida, a stylet-like gnathobase is evolved convergently. In Misophrioida and Calanoida the gnathobase is wide, as in basal Harpacticoida.

**Char. 16:**

The bulge at the proximal border of the mandibular gnathobase is a distinctive character that supports the monophyly of Exanechentera (Figs. 24 G - F; 37 C, E, F; char. 16: 0→1). All species of Exanechentera, with the exception of the two taxa with the stylet-like mandible gnathobase (*Rotundiclipeus canariensis*, Superornatiremidae; char. 16: 1→0; Figs. 36 D + H) have this characteristic bulge. It is probable that with the extreme elongation of the mandible gnathobase in N.N. 6 and the accompanying functional change the bulge became a hindrance and therefore was reduced. Some species of Podogennonta have a bulge that looks like the bulge of exanechenteran species (*Cletodes macurata* Fiers, 1991; *Metahuntemannia spinipes* Dahms & Pottek, 1992; *Nannopus abyssii* Sars, 1921). In the case of *Nannopus abyssii* the membership to Exanechentera (Tachidiidae?) is possible. However, neither Cletodidae nor *Metahuntemannia* Smirnov, 1946 belong to Exanechentera nor do some of their species, as strong apomorphies indicate their membership to a derived group within Podogennonta. The bulge has probably evolved convergently in a few species of Podogennonta and the ancestral line to Exanechentera.

**Char. 17:**

The endopod of *Drescheriella glacialis*, *Novocrinia trifida*, and some species of Paramesochridae is 2-segmented, as in Polyarthra, Calanoida and Misophrioida. This led to the conclusion, that the groundpattern of all Oligoarthra is a 2-segmented endopod (Willen, 2000). In *D. glacialis* and *N. trifida* this is clearly a secondary phenomenon. The outgroup taxa of both genera have a 1-segmented endopod as nearly all oligoarthran species. Species of Paramesochridae have a 1-segmented or a “3-segmented” endopod. The distal “segment” of the “3-segmented” endopod is in fact the confluent base of the terminal setae (Huys & Boxshall, 1991). Nearly all species having this confluent base also show the separation of the enp-1 and enp-2 segment, like Polyarthra or Misophrioida species. It seems, that with the separation of the fused setal basis from the endopod, the separation of the 2 real segments is retained. The 1-segmented endopod is an autapomorphy for Oligoarthra (char. 17: 0→1) and the 2-segmented condition is secondary, and convergently evolved in *N. trifida*, *D. glacialis* and within Paramesochridae (char. 17: 1→0).

**Char. 18:**

The mandible endopod has only 1 lateral seta (char. 18: 0→1; chapter 5.1) in Zosimidae, Novocriniidomorpha, and Peltidiidae - Tegastidae. The groundpattern of Oligoarthra is a 1-segmented mandible endopod with 3 lateral setae from fused proximal segments. The Calanoida and Misophrioida have a 2-segmented endopod

with at most 4 setae on the proximal segment. The species of Polyarthra have 3 setae on the proximal segment.

**Char. 19:**

The large lateral spine at the 1-segmented mandibular endopod is very characteristic for Aegisthoidea (char. 19: 0→1; see also Seifried & Schminke, 2003). Such a spine is not described from any other harpacticoid or outgroup species. Nearly all species of Aegisthoidea have 2 setae and 1 spine. The descriptions of *Eucanuella spinifera*, *Stratiopontotes mediterraneus*, and of some but not all species of *Cerviniopsis* indicate an endopod with 3 lateral setae. Also *Stratiopontotes* spec. from the Arctic (see list of examined material) has 3 lateral setae. The museum material of *Eucanuella spinifera* originally collected by G.O. Sars (see list of examined material) clearly shows that the description of the mandible by Sars (1903) is not detailed enough. *E. spinifera* has the large lateral spine and two setae at the mandibular endopod. This can also be seen in the original description of *E. spinifera* by T. Scott (1901). In consequence, the more plesiomorphic Aegisthoidea such as *Romete bulbiseta* and *E. spinifera* have the lateral spine. It is probable, that the spine is secondarily transformed to a seta in the more advanced species of *Cerviniopsis* and *Stratiopontotes*. As most *Cerviniopsis* species have the spine (e.g. *C. clavicornis* Sars, 1903, *C. curviseta* Brodskaya, 1963, *C. obtusirostris* Brodskaya, 1963), the secondary transformation of the lateral spine of the mandibular endopod may be an indication of a closer relationship of some *Stratiopontotes* and some *Cerviniopsis* species.

**Char. 20:**

Species of Calanoida have at most 11 setae on the distal endopod segment of the mandible. Species of Polyarthra do not have more than 9 setae and species of Misophrioida not more than 8 setae.

Willen (2000) reconstructed 10 setae for the (fused) distal endopod segment as groundpattern of Oligoarthra and Podogennonta. Some species of Harpacticidae have 9 and some species of Pseudotachidiidae have 9 or 10 setae on the (fused) distal segment (Willen, 2000). However, this has to be a secondary phenomenon. The ancestor of Oligoarthra did not have more than 7 distal setae on the (fused) distal endopod segment of mandible (char. 20: 0→1). When the 2 or 3 additional setae of the (fused) distal segment of Harpacticidae and Pseudotachidiidae would be assumed for the groundpattern of Oligoarthra, they would have been reduced within Oligoarthra at least 5 times independently. It has to be proven, whether the 3 additional setae were really present in the groundpattern of Podogennonta or whether they evolved within Podogennonta.

In Superornatiremidae and Rotundiclipeidae the endopod of mandible has 4 distal setae as in Zosimidae (char. 20: 1→2).

**Char. 21:**

The plesiomorphic character state within Calanoida and Misophrioida is a 5-segmented mandibular exopod. The plesiomorphic character state within Polyarthra and Oligoarthra is a 4-segmented exopod. However, species of Polyarthra have the two distal segments and species of Oligoarthra two proximal segments fused (char. 21:

0→1; chapter 5.1). Willen (2000) reconstructed a 5-segmented exopod for the oligoarthran groundpattern. This is not followed here (chapter 4.3). The mandibular exopod is 3- or 4-segmented in the basal Oligoarthra. The “accelerated” optimisation of character 21 results in the single transformation of the 1-segmented exopod mandible of N.N. 3 (char. 21: 1→2) into the 4-segmented exopod mandible of Novocriniidimorpha (char. 21: 2→1). *Rotundiclipeus canariensis* has a 1-segmented exopod again (char. 21: 1→2).

### Maxillule

#### **Char. 22:**

The praecoxal arthrite of Calanoida, Misophrioida, Polyarthra, and the basal Oligoarthra is wide and relatively short, mostly quadratic or sometimes rather triangular as in some species of Polyarthra. In basal Palinarthra the elongation of the arthrite is visible in its initial stage (Fig. 35; char. 22: 0→1), which may be related with the evolution of the oral cone. In Superornatiremidae - Rotundiclipeidae (N.N. 6) the praecoxal arthrite is further elongated, narrow, and additional cylindrical; 4 distal spines are transformed into setae, and all terminal elements are situated tightly together (char. 22: 1→2; Fig. 41).

#### **Chars. 23 and 24:**

Seta 10 on anterior surface and setae 12 and 13 at the proximal corner of the praecoxa are present in Misophrioida, Polyarthra and the basal Oligoarthra. The praecoxa of Calanoida has 16 elements, more than that of Misophrioida (15) and Harpacticoida (14), but the homologisation of setae 10, 11, and 12 is not without doubt. However, it is very probable, that species of Calanoida have these setae.

Species of Chappuisiidae, Ectinosomatidae, and Palinarthra have convergently reduced seta 10 of the praecoxal arthrite of the maxillula (char. 23: 0→1; chapter 5.1). In Superornatiremidae and Rotundiclipeidae setae 11 and 12 of maxillular praecoxa are absent (char. 24: 0→1; chapter 5.1) as in most Tisboidea. In Tisbidae only seta 11 is absent and seta 12 is displaced towards the transition zone from arthrite to praecoxa. Within Podogennonta, setae 10, 11, and 12 are also reduced in advanced taxa. However, as the basal Podogennonta has these setae, the reduction is a convergence. The homologisation of the elements in Ectinosomatidae is very difficult as the aberrant syncoxa lacks 4 spines and 4 setae.

#### **Char. 25:**

The 2 long spinules of some posterior distal spines of the maxillular praecoxa (chapter 4.1) are missing in all species of N.N. 4 (char. 25: 1→0), but also in Chappuisiidae. The spinules are present in all other taxa of Harpacticoida and in some species of Misophrioida (e.g. *Arcticomisophria bathylaptevensis*).

#### **Char. 26:**

The praecoxa and the coxa of maxillule are separated in all outgroups and harpacticoid taxa except Tisbidae and Porcellidiidae. The fusion of praecoxa and coxa is an autapomorphy of N.N. 7 (char. 26: 0→1).

**Char. 27:**

All species of N.N. 2 except Novocriniidimorpha do not have more than 4 inner setae at the maxillular coxa (char. 27: 0→1). The Novocriniidimorpha has 6 inner coxal setae (char. 27: 1→0) as in the groundpattern of Harpacticoida. The coxa of Calanoida has 5 and that of Misophrioida 6 inner setae.

**Char. 28:**

The coxa and the basis are separated in all outgroups and harpacticoid taxa except Tisboidea and Chappuisiidae (char. 28: 0→1). The fusion of coxa and basis happened convergently in these two taxa.

**Chars. 29 and 30:**

The groundpattern of Calanoida shows a 3-segmented maxillular endopod with 6, 4, 7 setae and that of Misophrioida a 2-segmented one with 6, 6 setae. Species of Polyarthra have a 2-segmented endopod with 5, 6 setae. Species of Oligoarthra have at most one free endopod segment (char. 29: 0→1). All species of Aegisthoidea have a maxillule in which the basis and endopod are fused (char. 30: 0→1; see also Seifried & Schminke, 2003). The fused segment has a characteristic rectangular shape and all setae arise from the distal edge (Fig. 9). This is a very strong synapomorphy for Rometidae and Aegisthidae. There is no other harpacticoid or outgroup maxillule with such a fusion. The more plesiomorphic syngnatharthran species have a 1-segmented endopod with at most 6 setae. Many species of Syngnatharthra have an endopod that is fused with the basis and is only represented by some setae. Some even have no endopodal segment or setae at all.

**Char. 31:**

In all species of N.N. 4, but in no other taxon of Oligoarthra, the endopod and all endopodal setae of maxillule are directed inwards (char. 31: 0→1). Although the endopod is variable in the number of setae and the form of the segment within N.N. 4, the inward orientation is always visible. Only in most species of Porcellidiidae is the inward orientation somewhat modified. The overall morphology of the maxillula of Porcellidiidae (and all other mouthparts) is conspicuously modified to form the sucker. For example, the exopod of maxillula is outwards oriented, so it is understandable that also the orientation of the endopod has changed. However, in species like *Porcellidium sesquimaculata* (Harris, 1994) the inward direction of the endopod is still observable.

**Char. 32:**

The groundpattern of Misophrioida, Calanoida and Polyarthra shows a 1-segmented exopod with 11 setae. No oligoarthran species has more than 4 setae on the 1-segmented exopod of the maxillule (char. 32: 0→1). Rometid species and the more plesiomorphic syngnatharthran species have a 1-segmented exopod with 4 setae. Aegisthid and many exanechenteran species have 3 setae on the exopod. Some species of N.N. 2 have less setae or no exopod at all.



### Maxilla

#### **Char. 33:**

The maxilla of Calanoida consists of praecoxa, coxa, basis, and a 4-segmented endopod. Misophrioida and Polyarthra have a maxilla composed of praecoxa, coxa, allobasis, and a 3-segmented endopod. All Oligoarthra have a syncoxa due to the fusion of praecoxa and coxa (char. 32: 0→1), an allobasis and a 3-segmented endopod (chapters 4.1 and 4.3).

#### **Char. 34:**

The monophyletic group Syngnatharthra is characterized, among other characters, by the fused proximal endites of the syncoxa of the maxilla (char. 34: 0→1; Fig. 15; see also Seifried & Schminke, 2003). Species of Aegisthoidea have the more plesiomorphic character state: the endites of the praecoxa are not fused but clearly separate. In most Syngnatharthra a depression still marks the fusion zone of the maxillar endites. In Neobradyidae, the sister group of all other Syngnatharthra, the fusion appears in an initial state: the endites are fused, but the resulting endite is bilobed (Fig. 15). The cleft reaches almost to the syncoxa as in *Antarcticobradya tenuis*. In *Neobradya pectinifera* the cleft reaches right to the syncoxa. However, the endites are close together in all neobradyid species, and all other species of Neobradyidae possess the fusion of the proximal endites of the syncoxa of the maxilla (e.g. *Marsteinia typica*). The more plesiomorphic state with the proximal endites clearly apart is only found in Aegisthoidea and the outgroups of Oligoarthra. The fusion of proximal endites of the maxillar syncoxa is an autapomorphy of Syngnatharthra. In some taxa within Podogenonta the proximal endite is reduced to one small endite with no depression and less than 6 setae. According to the phylogenetic hypothesis developed here, this small endite is the result of the fusion of the two proximal endites and subsequent reduction in number of setae and size and is not due to the loss of one endite of the oligoarthran groundpattern.

#### **Char. 35:**

The fused praecoxal endites of maxilla are displaced to the inner proximal corner of the syncoxa in Tisboidea (Figs. 43 A - D; char. 35: 0→1). In other taxa of Harpacticoida and the outgroups the (fused) praecoxal endites insert more distally. The endites in Calanoida, Misophrioida, and Polyarthra insert in the middle of the inner border or at the distal inner edge of the praecoxa. In all Oligoarthra except Tisboidea, where the endites are not reduced, the (fused) endites insert in the middle of the inner border of the syncoxa or directly underneath. In Zosimidae the fused endites insert on the distal half of the syncoxa.

#### **Char. 36:**

The distal endite of praecoxa (fused to proximal one) has not conserved more than 2 setae in Ectinosomatidae, Paramesochridae and Palinarthra convergently (char. 36: 0→1; chapter 5.1). In the groundpattern of Calanoida, Misophrioida, Polyarthra and Oligoarthra the distal praecoxal endite has 3 setae.

#### **Char. 37:**

The proximal endite of coxa has conserved not more than 1 seta in

Novocriniidimorpha and Porcellidiidae - Tisbidae convergently (N.N. 7; char. 37: 0→1; chapter 5.1). In the groundpattern of Calanoida, Misophrioida, Polyarthra and Oligoarthra the proximal endite of coxa has 3 setae.

**Char. 38:**

The tube pore on the anterior side of the allobasis is present in Aegisthoidea (Seifried & Schminke, 2003: Fig. 3 E), Podogenmonta (Willen, 2000), and Neobrydiidae. The tube pore is not confirmed in any other copepod taxon. The tube pore is an autapomorphy of Oligoarthra (char. 38: 0→1). However, no species of N.N. 2 has this tube pore (char. 38: 1→0).

**Char. 39:**

No setae of the fused endopod segment inserting on the allobasis of maxilla remain in any species of N.N. 4 and convergently in Chappuisiidae (char. 39: 0→1; chapter 5.1). In all other taxa of Oligoarthra, 2 or 3 setae of the fused endopod segment are to be found on the maxillar allobasis. In some species of Calanoida the proximal segment of the 4-segmented endopod has 4 setae and Misophrioida and Polyarthra have an allobasis with 3 endopodal setae in the groundpattern.

**Chars. 40 and 41:**

Huys & Boxshall (1991) indicated a 4-segmented endopod of maxilla with 4 setae on the proximal endopod segment as in Calanoida for the groundpattern of Copepoda, and 3 setae for the groundpattern of Harpacticoida. As stated above (chapter 4.1), the plesiomorphic condition in Harpacticoida is an allobasis (fusion of proximal endopod segment and basis) and a 3-segmented endopod. The fused endopod segment can be recognized by 2 setae (9, 10) on the anterior surface of the allobasis situated between outer and inner edge of the free endopodal segments, and 1 seta (11) on the posterior surface. However, in Aegisthidae the situation is different. The displaced endopodal seta 10 of allobasis inserts between anterior and posterior surface (char. 40: 0→1), the displaced seta 9 inserts near seta 10 but on the anterior surface, and an additional seta is present very close to endopodal seta 10 (char. 41: 0→1; e.g. Aegisthidae gen. spec. 1., Aegisthidae gen. spec. 3, Aegisthidae gen. spec. 5, *Stratiopontotes* spec.; see also Seifried & Schminke, 2003). This additional seta is either the fourth seta of the proximal endopod segment of the groundpattern of Copepoda or a duplicate of seta 10. Until more information is available, the seta is regarded as an additional seta with the insertion point between anterior and posterior surface, probably a duplication of seta 10. Also rometid species have seta 10 and the additional seta, inserting very closely together between anterior and posterior surface (Seifried & Schminke, 2003). These parallel setae are very characteristic, although often visible only in undissected specimens. When the maxilla is separated, the setae are mostly covered by the endopodal setae and the insertion points of the setae are invisible. In addition to the posterior spine 11 and the anterior seta 9, Itô (1982, 1983) described three different cases of setation on the endopodal part of the allobasis in Aegisthidae (Seifried & Schminke, 2003). In all species of Aegisthoidea analysed for this study and where the insertion points of the setae were visible, more than two parallel setae could not be found inserting very closely together between the anterior and posterior side and

nearby seta 9 on the anterior side. However, it should be kept in mind that a further additional seta may be present and that sometimes the three setae are fused, as described by Itô (1982).

#### Maxilliped (Figs. 48 + 49)

##### **Char. 42:**

Praecoxa and coxa are separate in the groundpattern of Misophrioida, however, together they are more than 2 or 3 times longer than wide. Species of Calanoida and all basal Harpacticoida have a syncoxa that is more than 2 or 3 times longer than wide. It is conspicuous that all Palinarthra (with one exception) have a large maxilliped, but a relatively short syncoxa. The syncoxa of palinarthran species is at most twice as long as wide (char. 42: 0→1). Only species of Peltidiidae - Tegastidae have a secondary elongated syncoxa of the maxilliped (char. 42: 1→0; chapter 5.1). This is not astonishing, because these species have elongated the whole maxilliped with an unusual pedestal, situated between the syncoxa and the body (chapter 4.24). Species of Peltidiidae - Tegastidae seem to need an extremely long maxilliped in their phytal environment, as do species of other phytal taxa (e.g. Harpacticidae). Apart from Palinarthra, species of Zosimidae have a square syncoxa due to an overall shortened maxilliped.

##### **Chars. 43 and 44:**

Huys & Boxshall (1991) reconstructed 10 setae on the maxillipedal praecoxa and coxa in the groundpattern of Misophrioida and 11 setae in the groundpattern of Calanoida. The ancestral state of the syncoxal setation in Calanoida is 1, 2, 4, 4 setae and that of the praecoxal and coxal setation in Misophrioida 1, 2, 4, 3 setae. All setae insert at the inner border. As described here, the three spines of the maxillipedal syncoxa are an autapomorphy for Harpacticoida (chapter 4.1). The syncoxal formula is 1, I+1, I+3, I+2 as in species of Polyarthra. Three setae were reduced in the ancestral line to Oligoarthra (syncoxal formula: I+1, I+2, I+1). Seta 16 of the proximal endite of Aegisthoidea is missing in Syngnatharthra (char. 43: 0→1). Seta 16 is present in the more plesiomorphic species of Aegisthoidea, as e.g. species of *Romete* and *Eucamuella*. However, in very advanced taxa of Aegisthidae with many reductions in general (e.g. the benthopelagic *Andromastax* species), the seta of the proximal endite of the syncoxa is convergently lost.

The character state in the groundpattern of Podogennonta is 4 syncoxal setae as in the two species of Chappuisiidae. Spines X and XV are retransformed to setae here (char. 43: 1→2). All species of N.N. 3 (Ectinosomatidae - Exanechentera) have retained only 2 or fewer setae (char. 43: 2→3). Species of N.N. 3 with 2 setae always have 1 seta inserting at the inner border and 1 seta displaced towards the outer border of the syncoxa (char. 44: 0→1; Ectinosomatidae, Idyanthidae, Zosimidae and maybe Peltidiidae - Tegastidae, see below). In species of Oligoarthra with more than 2 setae and spines all setae insert at the inner border. For species of Idyanthidimorpha 2 subterminal syncoxal setae of the maxilliped are very characteristic (char. 44: 1→2). In some species of Idyanthidimorpha the setae even insert in the middle between the proximal and the distal border of the maxilliped (Figs. 29 B + C). All taxa of N.N. 4 (with one exception) have no outer distal setae on the syncoxa of the maxilliped and

display only 1 inner distal seta or none (char. 43: 3→4; Fig. 49; Paramesochridae, Tachidiidae, Palinarthra). Only some peltidiid species have 2 setae on the syncoxa of the maxilliped, 1 inner seta and 1 seta between the inner and outer edge (e.g. *Eupelte villosa*). This morphology of the maxillipedal syncoxa is recorded in the groundpattern of Peltidiidae - Tegastidae here. However, it is likely, that the middle seta evolved within Peltidiidae - Tegastidae. A complete phylogenetic system of this group on the species level is needed to clarify the evolution of setae of the maxillipedal syncoxa (and other characters) within Peltidiidae - Tegastidae. To date, the homology of the middle syncoxal seta of Peltidiidae - Tegastidae is uncertain. This seta could be the regained seta 11 or a duplicate of seta 10. Species of Superornatiremidae and Rotundiclipeidae are the only taxa within Harpacticoida without a single seta on the maxillipedal syncoxa in the groundpattern (char. 43: 4→5).

**Char. 45:**

Species of Misophrioida and Polyarthra have no joint between the syncoxa and the basis of the maxilliped. Some, but not all species of Calanoida have a maxilliped with a more or less flexible joint between the syncoxa and the basis. The character state in the data matrix is therefore “?” for Calanoida (Table 4). The parsimony analysis showed that the joint between the syncoxa and the basis of Oligoarthran species evolved in the ancestral line to N.N. 1 (Fig. 46; char. 45: 0→1). As a consequence, the plesiomorphic character within Copepoda and Harpacticoida seems to be a maxilliped without a joint. Within Calanoida and Oligoarthra, the joint apparently evolved convergently.

The joint evolved in the ancestor line of N.N. 1 and was independently reduced three times in Zosimidae, Peltidiidae and Novocriniidimorpha. The rigid connections between the syncoxa and the basis of the maxillipeds of Zosimidae, Peltidiidae and Novocriniidimorpha are not the plesiomorphic condition within Harpacticoida or the regained plesiomorphic condition, but independently evolved novelties. In species of Novocriniidimorpha there is no joint between syncoxa and basis (Figs. 39 A + B; char. 45: 1→0), and both segments are slender and cylindrical, having the same orientation. This unique form has no equivalent outside Novocriniidimorpha. The maxilliped of Zosimidae and Peltidiidae has no claw; that of Zosimidae is short (Fig. 31) that of Porcellidiidae is longer (Fig. 37 G) and the details of setation differ significantly. Therefore, the morphological differentiation of the maxilliped of Zosimidae and Peltidiidae is not homologous. As indicated by the parsimony analysis and the morphological details, the rigid connection between the syncoxa and the basis of the more basal Harpacticoida, Zosimidae, Peltidiidae, and Novocriniidimorpha is not homologous (see chapter 5.2.4).

**Char. 46:**

In the groundpattern of Misophrioida, Calanoida the endopod of the maxilliped has 3 setae. Polyarthra have only 2 basal setae. Species of Aegisthoidea and Neobryadyidae have an endopod with 1 spine and 1 seta in the middle of the inner endopodal border or in the distal half. In the evolutionary line to N.N. 1 the spine is retransformed to a seta and the 2 setae (8 + 9) insert medially and distally on the inner edge (char. 45: 1→0; Fig. 48). Species of N.N. 2 show only seta 8 or no seta.

**Char. 47:**

Species of Polyarthra and Aegisthoidea have no highly flexible joint between the basis and the endopod of the maxilliped (char. 47). Some but not all species of Calanoida and Misophrioida have a maxilliped with a more or less flexible joint between basis and endopod. The character state in the data matrix is therefore “?” for these taxa (Table 4). The parsimony analysis showed that the joint between the basis and endopod of Oligoarthran species evolved in the ancestral line leading to Syngnatharthra (Fig. 46; char. 47: 0→1). As a consequence, the plesiomorphic character state within Harpacticoida and maybe within Copepoda seems to be a maxilliped without a joint between basis and endopod. Within Calanoida, Misophrioida, and Oligoarthra, the joint apparently evolved convergently. However, in some taxa of Copepoda, such as Siphonostomatoida a joint between the basis and the endopod of the maxillipeds is also present. In caligiform taxa fused endopod segments, a terminal claw and a highly flexible joint between basis and endopod are evolved “to form a powerful compound subchela” (Huys & Boxshall, 1991) useful for grasping. The verification of the homology of the character states and the polarisation of character 47 can be made by an analysis of the maxillipedal morphology of all copepod taxa.

**Chars. 48 to 50:**

According to Huys & Boxshall (1991) a 6-segmented endopod with 2, 4, 4, 3, 3 + 1, 4 setae is the ancestral character state of the maxillipedal endopod of Calanoida and the 6-segmented endopod of Misophrioida has 2, 2, 2, 2, 2 + 1, 5 setae. Polyarthra has 5 + 1, 5 setae on the 2-segmented endopod, due to the fusion of the proximal endopodal segments. In the ancestral line to Oligoarthra some setae were lost and 2 setae were transformed to spines. The resulting setal formula in Aegisthoidea is 3, II + 2 setae and spines.

The endopod of syngnatharthran species is 1-segmented, indistinctly 2-segmented or 2-segmented. In the latter two cases, the distal endopod segment is always reduced in size as in *Tachidiopsis* species (Fig. 17 A; Figs. 48 + 49). A 1-segmented endopod is also present within some terminal taxa (Neobradidae, Podogennonta, Idyanthidae). As the segmentation of the endopod is too variable it is no good character for a phylogenetic analysis within Harpacticoida. However, the distal segment reduced in size, sometimes even partially fused to the proximal segment e.g. as in *Tachidiopsis* species is very characteristic (char. 48: 0→1; Fig. 17 A). One result of the parsimony analysis is, that the different 1-segmented endopods found within Syngnatharthra are derivations of the 2-segmented endopod with the small distal segment.

Species of Rometidae have a 1-segmented endopod, too. In the cladistic analysis, there are two most parsimonious possibilities of character evolution. The fusion of the 2 segments happened in the ancestral line to Oligoarthra and the segments of the maxillipedal endopod in Aegisthidae and many Syngnatharthra are secondarily separate (ACCTRAN optimization in chapter 5.1.3). The second possibility that the fusion of the endopodal segments convergently evolved in the ancestral line to Rometidae and to the Syngnatharthran taxa seems to be more likely (DELTRAN optimization in chapter 5.1.3). In this case the different 1-segmented endopods

evolved within Syngnathartha are derivations of the 2-segmented endopod with the small distal segment as discussed above, and the 1-segmented endopod in Rometidae is a derivation of the 2-segmented endopod of Aegisthidae with a larger distal endopodal segment.

The 2 geniculated distal setae (3 + 4) of the small distal endopod segment of the *Tachidiopsis* maxilliped are accompanied by 2 small outer setae (1 + 2) and can be found in many species of Oligoarthra (chapter 4.8; Fig. 17 A). They are an autapomorphy of Syngnathartha (char. 50: 1→0). For example, the two geniculated setae occur in Tisbidae, Idyanthidae, Paramesochridae, and Superornatiremidae. The hypothesis is that all species of Syngnathartha without geniculated setae on the maxilliped have lost them. It is very unlikely that this characteristic morphology, with the geniculated setae at the distal end of the small endopod accompanied by the two small lateral setae, has developed more than once within Oligoarthra (see chapter 5.1). As to the evolution of character 49 different results are obtained when applying Phylogenetic Systematics or and computer aided cladistics (chapter 5.1.5). However, it is much more likely to assume that the large, displaced claw (V) has evolved only once (char. 49: 1→3; ■ 9; N.N. 1) and was reduced to a smaller size (char. 49: 3→1) in Chappuisiidae (■ 12) and Ectinosomatidae (■ 14) respectively (chapter 5.1.5). There is no satisfactory reason to assume that the large, displaced claw (V) has evolved twice from a small claw like that of Neobradyidae. Especially an independent evolution of the exceptional innervation of claw V is unlikely. The reconstructed phylogeny of Harpacticoida with the evolution of character 49 is one step longer than the alternative indicated by the single minimum length cladogram (chapter 5.1).

The supposed evolution of the endopod of the maxilliped in N.N. 1 is somewhat dependent on the position of Podogennonta within Syngnathartha. As this position is uncertain, the following interpretation of the evolutionary transformation of the maxillipedal endopod is preliminary. The common ancestors of Neobradyidae and N.N. 1 had only a small claw and 2 setae on enp-1 (char. 49: 0→1; Fig. 48). Further evolution in the line to N.N. 1 led to the claw being enlarged (see above). Species of e.g. Podogennonta and Idyanthidae have a large claw at the terminal border of enp-1. Additionally, seta 6 is transformed to a second claw, which inserts laterally on enp-1 (char. 49: 1→3; Fig. 29 A). This second claw (VI) can only be observed in Podogennonta, Idyanthidae, and Paramesochridae (Figs. 48 + 49). All other taxa have lost or transformed claw VI. In N.N. 5 (Tachidiidae - Palinartha), claw VI is completely lacking (char. 49: 3→2), it also lacks in Ectinosomatidae and Chappuisiidae (char. 49: 3→1). The morphology of the maxillipedal endopod is different in N.N. 5, Chappuisiidae, and Ectinosomatidae (Fig. 49). Furthermore, the morphology of the maxillipedal endopod is variable within N.N. 5. Most taxa have lost claw VI (Tachidiidae, Novocriniidimorpha and Porcellidiidae). However, within Tisbidae *sensu strictu*, this claw is retransformed to a seta (6), and within Peltidiidae - Tegastidae 1 seta and 1 short strong spine appear on the posterior side of the endopod. The strong spine is probably the transformed claw VI. In the ancestral line to Porcellidiidae the size of claw V was secondarily reduced. Species of Zosimidae have no claw at all.

**Char. 51:**

No species of Oligoarthra has an inner coxal seta (char. 51: 0→1), which is present in species of Calanoida, Misophrioida, and Polyarthra.

**Chars. 52 and 53:**

The length of the endopodal segments of the P1 in Calanoida, Misophrioida, Polyarthra and the basal Oligoarthra is the same as depicted by Huys & Boxshall (1991) for the “basic copepod swimming leg”. Enp-1 and enp-2 are nearly square and enp-3 is twice as long as wide. Species of Tisboidea have an elongated middle endopodal segment (char. 52: 0→1). This segment is twice as long as wide or longer in most tisboidean species (Figs. 43 E + F). In Tisbidae *sensu strictu* and Porcellidiidae the enp-3 is small (N.N. 7; char. 53: 0→1; Fig. 43 F), as is also the case in Podogennonta, Paramesochridae and Idyanthidae (Fig. 50). The small enp-3 is not always clearly visible in all species of N.N. 7 (chapter 4.26). The length of the proximal endopodal segment is traditionally used as diagnostic character, for e.g. Podogennonta (Willen, 2000). However, the length of the proximal endopodal segment is extremely variable and is modified many times within Harpacticoida. The enp-1 is long in the groundpattern of Podogennonta, Paramesochridae, Idyanthidae, Superornatiremidae, Tisbidae, and Porcellidiidae. Also taxa with a square enp-1 in the groundpattern include species with an elongated enp-1 (e.g. Neobradidae, Ectinosomatidae, Peltidiidae). The elongated proximal endopod segment of the P1 is no adequate character for a phylogenetic analysis (chapter 5.2.1).

**Chars. 54 to 56:**

The inner seta of exp-1 P1 is the only seta that was lost only once in the evolution of all oligoarthran taxa (char. 55: 0→1). All other setae were lost several times. Every single species of Polyarthra and Aegisthoidea has this seta, whereas no species of Syngnatharthra has it. In the groundpattern of Calanoida and Misophrioida the seta is present.

The morphology of the P1 exopod in Calanoida, Misophrioida, Polyarthra and the basal Oligoarthra is the same as that described by Huys & Boxshall (1991) for the “basic copepod swimming leg”. The exp-1 and exp-2 are nearly square and the exp-3 is twice as long as wide. The outer elements are spines, the distal ones are spines and/or setae and the inner ones are setae. Only the number of spines and setae differ between taxa. The morphology of the exopod of P1 of Idyanthidimorpha is typical, although the P1 differs between Idyanthidae and Zosimidae, but the outer and distal spines of P1 exp-1 to exp-3 are elongated and ornamented terminally with long spinules in both taxa (char. 56: 0→1; Figs. 30 + 50). In Tisboidea the outer and distal spines of P1 exp-3 are also ornamented terminally with long spinules. However, the morphology of the P1 exopod of Tisboidea (char. 56: 0→2; Fig. 43) differs from that of Idyanthidimorpha. Species of Tisboidea have no transformed spine in exp-1 and in most cases also not in exp-2. Additionally, the exopod of Tisboidea has elongated exp-1 and exp-2 (char. 54: 0→1, Fig. 50) and a short and rounded exp-3 contrary to the form of the exopod of P1 of Idyanthidimorpha, which resembles that of Syngnatharthra. However, the typical tisbidimorph P1 is not always realized in all species of Tisbidae *sensu strictu* (chapter 4.26).

P2-P4 female**Char. 57:**

No species of Harpacticoida has an inner coxal seta on the P2, P3 and P4 (char. 57: 0→1) whereas it is present on these legs in Calanoida and Misophrioida.

**Char. 58:**

All pinnate spines of P2-P4 are swollen and spatulate in species of Novocriniidimorpha (Fig. 39 D; char. 58: 0→1). The peculiarity of these spines is that they are flattened. In other taxa of Harpacticoida the spines can be thick and round but not flattened. The difference between flattened and round is often not distinguishable in drawings. Spatulate spines are to be observed also in species of Tisbidae *sensu strictu*. The question arises, whether these spines evolved in the ancestor line of Palinarthra and were later reduced in Peltidiidae - Tegastidae and Porcellidiidae, the two taxa within Palinarthra that have elongated spines and setae of the swimming legs in the groundpattern. In this case, the spatulate spines would not be a convergent in Novocriniidimorpha and Tisbidae *sensu strictu*, but an autapomorphy of Palinarthra.

P5 female**Chars. 59 and 60:**

Calanoida have a 3-segmented exopod and a 3-segmented endopod in the groundpattern and Misophrioida a 3-segmented exopod and a 1-segmented endopod. *Longipedia minor* as a representative of Polyarthra has a 1-segmented endopod and a 1-segmented exopod. In nearly all species of Oligoarthra there is a 1-segmented exopod and an endopod fused to the basis (baseoendopod). The baseoendopod is assumed to be an autapomorphy of Oligoarthra (char. 59: 0→1), as all species with an endopod have no demarcation line between basis and endopod (for *Marsteinia bozici* see chapter 4.1). The 1-segmented exopod is an autapomorphy of Harpacticoida (char. 60: 0→1). In some females of Harpacticoida exopod, endopod, or the whole P5 are reduced. Species of Aegisthoidea, Superornatiremidae and Tisboidea have an exopod that is more than twice as long as wide (char. 60: 1→2). Some advanced Podogennonta have an elongated exopod too, especially argestid species.

**Char. 61:**

Calanoida have a 3-segmented exopod with 11 elements in the groundpattern of which 4 are outer spines. As Harpacticoida has 3 outer spines on a 1-segmented exopod in the groundpattern, the homology of the spines of Calanoida and Harpacticoida is difficult to establish. However, it is very likely that Calanoida have spine 8 as they have more spines than the basal Harpacticoida and it is improbable that new outer spines evolved within the ancestor line to Harpacticoida. In the groundpattern Misophrioida have a 3-segmented exopod with 3 outer elements. It is probable, that the same 3 outer elements are present in Misophrioida and Harpacticoida. Element 8 of the exopod is regained in Palinarthra (char. 61: 1→0), after having been suppressed in N.N. 2 (char. 61: 0→1). The female of Rotundiclipeidae has only 2 spines representing the whole P5. It is probable that none of these spines is element 8 (char.



61: 0→1).

## **Male**

### **Male antennule**

#### **Char. 62:**

In basal Calanoida the seven copepod segments XIV to XX are separated. In basal Misophrioida segments XIV to XVIII are separated and segments XIX and XX are fused. The basal Oligoarthra have all or some segments of the four oligoarthran segments 6 to 9 separated (copepod segments: 6-(XIV-XVI), 7-XVII, 8-XVIII, 9-(XIX-XX)). The character state of Polyarthra is doubtful (chapter 4.1). An autapomorphy of N.N. 3 (Ectinosomatidae - Exanechentera) is the fusion of all oligoarthran segments 6 to 9 to one segment (char. 62: 0→1), resulting in a subchirocer or chirocer antennule defined by Willen (2000). The unique pattern of the haplocer antennule of the male of Novocriniidimorpha is expressed in the fusion of only some but not all of the oligoarthran segments 6 to 9 (char. 62: 1→0) and by the displacement of some of the setae to the terminal end (Fig. 39 E; char. 68). The fusion patterns have no equivalent outside Novocriniidimorpha and the displaced setae probably either (chapter 5.2.4). The specific morphology of the male antennule is probably an autapomorphy of Novocriniidimorpha, which resembles the plesiomorphic character state in the groundpattern of N.N. 3, but nevertheless is secondarily acquired as evidenced by the parsimony analysis. In Tisbidae *sensu strictu* the antennule is haplocer too (Fig. 25 F). In Tisbidae *sensu strictu* the oligoarthran segments 6 and 7 are secondarily separated from fused segments 8 and 9 (char. 62: 1→0).

#### **Chars. 63 and 64:**

The copepod segments XXI to XXIII are separated in the male antennule of Calanoida without a geniculation. In basal Misophrioida and basal Calanoida the segments XXIV, XXV, and XXVI are free but segments XXVII and XXVIII are fused. In basal Misophrioida and basal Oligoarthra segments XXI and XXII are fused (oligoarthran segment 10) but separated from segment XXIII (oligoarthran segment 11). In the basal Oligoarthra the segments XXIV and XXV are free (oligoarthran segments 12 and 13) but segments XXVI to XXVIII are fused (oligoarthran segment 14). The character state of Polyarthra is doubtful (chapter 4.1).

The groundpattern of Aegisthidae is a 10-segmented male antennule due to the fusion of Oligoarthra segments 2 and 3, 10 and 11 (char. 63: 0→1), and 12 to 14 (char. 64: 0→2). The fusion of segments 10 and 11 took place convergently in the ancestral line to N.N. 3 (Ectinosomatidae - Exanechentera; char. 63: 0→1) and the fusion of segments 12 to 14 convergently evolve

d in the ancestral line to N.N. 2 (Chappuisiidae - N.N. 3; char. 64: 0→1). Only in Superornatiremididae and Rotundiclipeidae the fused oligoarthran segments 12 and 13 of the male antennule are secondarily separated from segment 14 (char. 64: 2→1).

**Chars. 65 and 66:**

The aesthetascs on oligoarthran segments 3 and 4 (copepod segments III-VIII and IX-XII) are present in the groundpattern of Calanoida, Misophrioida, Aegisthoidea, Neobradyidae and the basal Podogenonta. Both aesthetascs are reduced in the ancestral line to N.N. 2 (char. 65: 0→1, char. 66: 0→1) The “accelerated” optimisation of character 65 results in the single transformation of the male antennule without an aesthetasc on the oligoarthran segment 3 to an antennule with an aesthetasc on this segment in the groundpattern of Novocriniidimorpha (Fig. 39 E; char. 65: 1→0; chapter 5.1.3). *Rotundiclipeus canariensis* lost the aesthetasc again (char. 65: 0→1). The other possibility would be that the aesthetasc on the oligoarthran segment 3 was regained independently in Novocriniidae and Superornatiremidae (char. 65: 1→0). The appearance of the aesthetasc on the antennular oligoarthran segment 4 of the male is patchy. The aesthetasc was suppressed in N.N. 2, regained in N.N. 5 (char. 66: 1→0) and suppressed again in N.N. 7 (char. 66: 0→1). As indicated by this cladistic analysis an aesthetasc is not always a reliable indication of relationships of taxa (see chapter 5.2.5).

**Chars. 67 and 68:**

Very characteristic for Exanechentera is the male antennula with the claw and the pointed end (Fig. 25; char. 67: 0→1). In Idyanthidimorpha, Tachidiidae, Paramesochridae, Peltidiidae, Porcellidiidae and Tisbidae *sensu strictu* the antennula is formed differently, but the claw is always 2-segmented and evolved from the oligoarthran segments 10 to 14. It always has a pointed end, the setae insert on top of the last segment and the whole claw forms a functional unit with oligoarthran segments 6 to 9. Noticeable are also the setae inserting on top of the last segment of the claw. A claw formed by the same segments as in Exanechentera does to my knowledge not occur outside Harpacticoida. Within Exanechentera, only the species of Novocriniidimorpha do not have this claw (char. 67: 1→0; Fig. 39 E), but 6 setae insert at the distal end of the terminal segment, which is unusual (char. 68: 0→1; Fig. 39 E). These displaced setae are perhaps a trace of the setae that insert on top of the last segment of the claw. The novocriniidimorph distal displacement of setae of oligoarthran segment 14 of male antennule is also present in Neobradyidae (char. 68: 0→1). As indicated by the parsimony analysis it is likely that the displaced setae are not homologous in these two groups. Most described males of Cletodidae and *Leptopontia* T. Scott, 1902 also have hook-shaped segments behind the geniculation of the antennule (e.g. *Enhydrosoma parapropinquum* Gomez, 2003, *Metahuntemannia triarcticulata* Schriever, 1984, *Schizacron vervoorti* (Fiers, 1987); *Leptopontia punctata* Huys & Conroy-Dalton, 1996). At first sight most of these antennules look like those of Exanechentera as the claw has at pointed end and the setae insert on top of the last segment. However, the homology of the segments forming the different parts of the claw could not be affirmed. In some of the species of Cletodidae and *Leptopontia* the claw is 3-segmented and not 2-segmented as in all exanechenteran species. Cletodidae and *Leptopontia* do not belong to Exanechentera, as they do not share the other apomorphies with Exanechentera and as strong apomorphies indicate their membership to a derived group within Podogenonta. The claw-like antennule

probably convergently evolved in Cletodidae, *Leptopontia* and the ancestral line to Exanechentera.

#### P2 male

##### **Char. 69:**

Calanoida, Misophrioida, Polyarthra, and Oligoarthra have a male P2 that looks like the female P2 in the groundpattern. The sexual dimorphism of the male P2 of Idyanthidimorpha is unique (Figs. 29 B + C; char. 69: 1→2). It varies among the genera of Idyanthidae (Figs. 27 A - G), however the different developmental stages can be deduced from each other (chapter 4.14). Species of Idyanthidae have only 1 inner seta (4) reduced that is present in species of Zosimidae (Fig. 27 H). Some species of Tachidiidae have a transformed and displaced outer spine of the enp-3 and the middle terminal seta is short and sometimes broad (Figs. 34 A - C). However, not all species of Tachidiidae have this dimorphism (see chapter 4.17) and details of the 2 setae differ between Tachidiidae and Idyanthidimorpha, e.g. the displaced outer spine is fused and bare in Idyanthidimorpha, but delimited and pinnate in Tachidiidae. Furthermore, species of Tachidiidae have 2 inner setae on the male enp-3. These differences indicate that the dimorphisms of the P2 in Tachidiidae and Idyanthidimorpha are not homologous.

#### P5 male

##### **Chars. 70 and 71:**

Fusion of segments of the male P5 happened convergently in the ancestral line to Aegisthoidea and within Syngnatharthra. The fusion of the coxa and the basis (char. 70: 0→1) occurred in the ancestral line to Polyarthra, Aegisthoidea and N.N. 3 (Ectinosomatidae - Exanechentera). The fusion of the basis and the endopod (char. 71: 0→1) occurred in the ancestral line to Aegisthoidea and N.N. 2 (Chappuisiidae - N.N. 3). In species of Calanoida, Misophrioida, and the more basal Syngnatharthra (Neobradyidae, some Podogennonta) coxa, basis and endopod are separate.

#### Caudal rami

##### **Char. 72:**

The ancestral condition within Copepoda is that element II of the caudal rami inserts anterolaterally (Huys & Boxshall, 1991). This insertion is generally conserved in basal Calanoida, Misophrioida, Polyarthra, and Oligoarthra. In Porcellidiidae and Tisbidae *sensu strictu* the seta II is displaced to the dorsal surface (char. 71: 0→1). In Porcellidiidae the caudal rami are lamelliform, 5 of the 7 setae are very short apical setae (I, III, IV, V, VI) and 2 setae insert dorsally but not apically (II, VII). In Tisbidae *sensu strictu* the setation of the caudal rami is equivalent to the ancestral condition within Harpacticoida except that seta II is displaced to the dorsal surface. In *Tachidius discipes* and *Tachidius spec.* (Appendix I) and a few descriptions of Tachidiidae species (e.g. *Tachidius discipes* by Sars, 1910; *Microarthridion perkinsi* Bodin, 1970 by Bodin, 1970) seta II is displaced to the dorsal surface and is situated near seta VII. However, in most descriptions this character state is not documented. One possibility is that the descriptions are insufficient; the other possibility is that the displacement of seta II happened within Tachidiidae. The species material available for this study was

not sufficient to decide whether the displaced seta 2 was present in an ancestor of Tachidiidae or evolved within Tachidiidae.

#### 5.2.4 Monophyly of taxa

Arguments in support of the monophyly hypotheses of Harpacticoida, Polyarthra, Oligoarthra, Aegisthoidea, Syngnatharthra and the terminal taxa (“families” and Podogennonta) are given and discussed in chapter 4 and in Seifried & Schminke (2003). Arguments in support of the monophyly hypotheses of all other taxa and Syngnatharthra are given here. In the discussion of characters (chapter 5.2.3) additional remarks concerning the homology, morphology of the outgroups, polarisation, amount of homoplasy, and evolution of characters are made.

Taxa named with N.N. followed by a number (e.g. N.N. 1) are probably monophyletic taxa but the monophyly of these taxa has to be confirmed. N.N. stands for *nomen nominandum* (“name to be given”). The subordinated taxa belonging to these taxa are listed in chapter 3.1. Sister taxa or more than two taxa which together represent a monophyletic taxon are connected with a dash (e.g. Tachidiidae - Palinarthra).

#### Syngnatharthra (Fig. 14)

The monophyly of Syngnatharthra is beyond doubt (see also Seifried & Schminke, 2003). The monophyletic group Syngnatharthra is characterised by the first pedigerous somite being completely fused to the dorsal cephalic shield forming a cephalothorax (char. 1: 0→1), the fused proximal endites of the syncoxa of the maxilla (char. 34: 0→1, Fig. 15), the maxilliped with I, I+2, I+1 coxal spines and setae, a flexible joint between basis and endopod, the thin claw of enp-1 (V), the characteristic enp-2 (chars. 43, 47, 48, 49, 50: 0→1; Figs. 17 A + 48), the lack of the inner seta of exp-1 P1 (char. 55: 0→1), and the male with one spermatophore (char. 5: 0→1). The Bremer support of this clade is 6.

#### N.N. 1

The monophyly of N.N. 1 is supported by characters of the maxilliped only (Fig. 48). The Bremer support of this clade is 2. The lack of the syncoxal setae 14, 15 and 16 and the simultaneous transformation of the spines X and XII to setae (char. 43: 0→1) are considerably complex characters for an oligoarthran taxon. All species of Aegisthoidea and Neobradyyidae have 6 or 7 syncoxal setae and spines; all species of N.N. 1 have 0 to 4 syncoxal setae. Furthermore, the maxilliped has a joint between syncoxa and basis (char. 45: 0→1) and the 2 basis setae are inserted medially and distally as in Podogennonta (char. 46: 0→1). The proximal endopod segment has 1 large claw displaced to posterior side of the distal end (V), 1 thin claw (VI) and 1 seta (7) (char. 49: 0→3). This ancestral maxilliped is not preserved in a single taxon of N.N. 1. Only species of Chappuisiidae and Podogennonta have 4 syncoxal setae and most species have reduced 1 or 2 basis setae. Species of Novocriniidimorpha, Zosimidae and Peltidiidae have a rigid connection between syncoxa and basis. For detailed discussion of the morphology of the maxilliped see chapter 5.2.3.

### N.N. 2

All 7 characters supporting the monophyly of N.N. 2 are reduction characters, i.e. fusions of segments or reductions of setae, of a tube pore or of an aesthetasc. The Bremer support of this clade is 6. The existence of the tube pore of the maxillar allobasis is an autapomorphy of Oligoarthra, its lack an autapomorphy of N.N. 2 (char. 38: 1→0). Not a single species of N.N. 2 has this tube pore. All other six characters (chars. 27, 61, 65, 66, 71: 0→1; char. 64: 0→2) consist in the lack of structures that are regained in N.N. 5, Palinarthra, Novocriniidimorpha or N.N. 6 (chapter 5.2.3). For the discussion of irreversibility of characters see chapter 5.2.5. The best supported hypothesis to date is: the evolution towards N.N. 2 is characterised by the reduction of segments, setae, aesthetascs and a tube pore and the evolution within N.N. 5 and Palinarthra is characterised by regained segments, setae and aesthetascs (see chapter 5.2.5).

### N.N. 3

The number, the position and the morphology of the syncoxal setae of the maxilliped are good autapomorphies for N.N. 3 (Fig. 49). All species of this taxon have 2 or fewer setae (char. 43: 2→3), contrary to all other oligoarthran taxa that have 4 to 7 syncoxal setae and spines in the groundpattern. The species of N.N. 3 with 2 setae always have 1 seta inserting at the inner border and 1 seta displaced towards the outer border of the syncoxa (char. 44: 0→1; Ectinosomatidae, Idyanthidae, Zosimidae and Peltidiidae - Tegastidae). In species of Oligoarthra with more than 2 setae and spines all setae insert at the inner border. The fusion of oligoarthran segments 10 and 11 of male antennules (char. 63: 0→1) in all species of N.N. 3 is another support of the monophyly of N.N. 3. The only other species of Oligoarthra displaying the same fusion are species of Aegisthidae. Furthermore, all species of N.N. 3 have a fused coxa and basis of the male P5 (char. 70: 0→1). However, the same fusion also occurs in all Aegisthoidea and most species of Neobradyidae and Podogennonta. Additionally, a 1- or 2 segmented exopod of the mandible (char. 21: 1→2) and the (sub-) chirocer antennula of males (char. 62: 0→1) is characteristic for species of N.N. 3. However, within Palinarthra the exopod of the mandible becomes 4-segmented again and some of the fused segments of the (sub-) chirocer male antennule are secondarily separated. The monophyly of N.N. 3 is likely but not absolutely certain (see chapter 5.2.5). The Bremer support of this clade is 5.

### Exanechentera (Fig. 23)

The bevelled distal border of the antennal endopod is very characteristic for species of Exanechentera (Figs. 24 A - E; char. 13: 0→1). Within Oligoarthra only species of this taxon have such an endopod. The further evolution progressed within Exanechentera, the more acute the angle of the slope became. At the end there are species of Tisbidae *sensu strictu*, in which some of the distal setae insert at the same level as the lateral setae (Fig. 24 E). Only species of Zosimidae have a rectangular antennal endopod. This is not astonishing, because species of Zosimidae have an aberrant morphology in nearly all appendages. The bulge at the proximal border of the mandibular gnathobase is also a unique character that supports the monophyly of Exanechentera (Figs. 24 G -

F; 37 C, E, F; char. 16: 0→1). All species of Exanechentera, with the exception of the two taxa with the stylet-like mandible gnathobase (*Rotundiclipeus canariensis*, Superornatiremidae; Figs. 36 D + G), have this characteristic bulge. As discussed in chapter 5.2.3, some species of Podogennonta have a similar bulge, however it is probably a convergence. The male antennula with the claw and the pointed end is also very characteristic (Fig. 25; char. 67: 0→1). The antennula is formed differently in Idyanthidimorpha, Tachidiidae, Paramesochridae, Peltidiidae, Porcellidiidae and Tisbidae, but the claw is always 2-segmented and evolved from the oligoarthran segments 10 to 14. It always has a pointed end, the setae insert on top of the last segment and the whole claw forms a functional unit with oligoarthran segments 6 to 9. The species of Novocriniidimorpha do not have this claw, but 6 setae insert at the distal end of the terminal segment, which is unusual (Fig. 39 E). These displaced setae are perhaps a trace of the setae that insert on top of the last segment of the claw. For the discussion of the cletodid claw see chapter 5.2.3.

Hence, three distinctive characters support the monophyly of Exanechentera. All 3 characters are weakened by homoplasy and the Bremer support of the clade to Exanechentera is low (2). Nevertheless, the 3 characters together are complex enough to make the monophyly of Exanechentera a viable hypothesis.

#### Idyanthidimorpha (Fig. 26)

The monophyly of Idyanthidimorpha is highly probable, although the Bremer support of this clade is low (2). Zosimidae and Idyanthidae share three partly complex synapomorphies. That Zosimidae and Idyanthidae are sister taxa is beyond doubt. The sexual dimorphism of the male P2 is unique (Figs. 27 A + D; char. 69: 0→1). Species of Idyanthidae have only 1 inner seta (4) reduced that is present in species of Zosimidae (Fig. 27 H). Some species of Tachidiidae have a sexual dimorphism of the male P2 that resembles that of Idyanthidimorpha. However, the characteristics are not homologous (chapter 5.2.3). The 2 subterminal syncoxal setae of the maxilliped (Figs. 29 B + C; char. 44: 1→2) are also very characteristic for Idyanthidimorpha (Fig 49) and unique within Harpacticoida. In some species of Idyanthidimorpha the setae even insert in the middle between the proximal and the distal border of the maxilliped (Figs. 29 B + C). The morphology of the P1 is typical as well, although the P1 differs between Idyanthidae and Zosimidae. However, the outer and distal spines of P1 exp-1 to exp-3 are elongated and ornamented terminally with long spinules (char. 56: 0→1) and the outer spine of enp-3 is displaced terminally in species of both taxa (Figs. 30 + 50). The P1 of Podogennonta and Tisboidea have some convergent structures that resemble the P1 of Idyanthidimorpha (chapter 5.2.3).

#### N.N. 4

The monophyly of Paramesochridae - Tachidiidae - Palinarthra is likely, but the support is not unambiguous. The Bremer support of this clade is 3. The 2 long spinules of some posterior distal spines of the maxillular praecoxa are missing in all species of N.N. 4 (char. 25: 1→0), but also in Chappuisiidae. The spinules are present in all other taxa of Harpacticoida and in some Misophrioida.

In the species of N.N. 4, but in no other taxon of Oligoarthra the endopod and all endopodal setae of the maxillule are directed inwards (char. 31: 0→1), which is an

additional indication that they are monophyletic. Although the endopod is variable in the number of the setae and the form of the segment within N.N. 4, the inward orientation is always visible. Only in most species of Porcellidiidae the inward orientation is somewhat modified (chapter 5.2.3).

All setae of the fused endopod segment on the allobasis of the maxilla are lost in the species of N.N. 4 (char. 39: 0→1) nor convergently in Chappuisiidae. In all other taxa of Oligoarthra, 2 or 3 setae of the fused endopod segment are to be found on the maxillar allobasis. Furthermore, all taxa of N.N. 4 have no outer distal setae on the syncoxa of the maxilliped and display only 1 inner distal seta or no seta (char. 43: 3→4; Fig. 49). Only some peltidiid species have 2 setae on the syncoxa of the maxilliped, 1 inner seta and 1 seta between the inner and outer edge (e.g. *Eupelte villosa*). This seta could be the regained seta 11 or a duplicate of seta 10 (chapter 5.2.3).

#### N.N. 5

The monophyly of Tachidiidae - Palinarthra is weakly supported. The Bremer support of this clade is 2. Seta 2 of the antennal endopod is reduced in N.N. 5 and Zosimidae convergently (char. 10: 0→1) and regained in N.N. 7. The claw VI of the maxillipedal enp-1, which had evolved in the ancestor line of N.N.1 is lacking in all species of N.N. 5 (char. 49: 3→2), and also in Ectinosomatidae and Chappuisiidae (char. 49: 3→1). The morphology of the maxillipedal endopod is different in N.N. 5, Chappuisiidae, and Ectinosomatidae (Fig. 49; see above). Furthermore, the morphology of the maxillipedal endopod is variable within N.N. 5 (chapter 5.2.3). Accordingly, the evolution of the maxillipedal enp-1 setation is too variable to be a good character in support of the monophyly of Tachidiidae - Palinarthra. The appearance of the aesthetasc on the antennular oligoarthran segment 4 of the male is patchy. The aesthetasc was suppressed in N.N. 2., regained in N.N. 5 (char. 66: 1→0) and suppressed again in N.N. 7. An aesthetasc is not always a reliable indication of relationships of taxa (see chapter 5.2.5). Consequently, all three characters supporting the sister group relationship of Tachidiidae and Palinarthra are weakened by homoplasy or variability.

#### Palinarthra (Fig. 35)

The hypothesis of the monophyly of Palinarthra is strongly supported. Eight characters support the monophyly, 2 of them without homoplasy (chars. 15 + 22) and 4 characters are more complex than mere reductions of setae or segments (chars. 3, 15, 22, 42). The Bremer support of the clade to Palinarthra is 4. The presence of an oral cone (char. 3: 0→1; Figs. 36 A - F, 37 B + D), an elongated mandibular praecoxa (char. 15: 0→1; Figs. 36 + 37) and an elongated praecoxal arthrite of the maxillula (char. 22: 0→1) are characteristic for Palinarthra (chapters 5.2.3). Another character that supports the monophyly of Palinarthra is the shortened maxillipedal syncoxa (char. 42: 0→1). It is conspicuous that all Palinarthra (with one exception) have a large maxilliped, but a relatively short syncoxa. Only species of Peltidiidae-Tegastidae have a secondary elongated syncoxa of the maxilliped (chapters 5.2.3). Apart from Palinarthra, species of Zosimidae have a square syncoxa, but in contrast to species of

Palinarthra an overall shortened maxilliped. Species of Palinarthra additionally have reduced seta 10 of the praecoxal arthrite of the maxillula (char. **23**: 0→1) and 1 seta of the distal endite of the maxillar praecoxa (char. **36**: 0→1), but these setae are convergently reduced in other taxa of Oligoarthra.

In the ancestor line of and within Palinarthra the evolution of Oligoarthra appears to be unusual (as discussed in chapter 5.2.5, 5.2.6 and below). The lateral element 1 of the distal endopod segment of the antenna forms a seta in nearly all species of Palinarthra (char. **11**: 1→0). This condition is also shown in the outgroups of Oligoarthra. Otherwise, the lateral element 1 forms a spine in species of Oligoarthra. In species of Tisbidae, the spine is developed secondarily. Seta 8 of exopod P5 is regained in Palinarthra (char. **61**: 1→0), after having been suppressed in N.N. 2.

#### Novocriniidimorpha (Fig. 38)

All 13 characters supporting the hypothesis of the monophyly of Novocriniidimorpha are weakened by homoplasy. However, the Bremer support is 8 and some of the characters are noticeable. The distal displacement of setae of oligoarthran segment 9 of male (Fig. 39 E) and female antennule (chars. **6** + **68**: 0→1) is also present in Neobradynidae. As indicated by the cladistic analysis it is likely, that the displaced setae are not homologous in these two groups. As described above, the males of Novocriniidimorpha are the only ones in Exanechentera without a claw in the male antennule (char. **67**: 1→0) and the displaced setae are probably a trace of the setae that insert on top of the last segment of the claw in other Exanechentera (see chapter 5.2.3). The mandible endopod has only 1 lateral seta (char. **18**: 0→1), but this reduction also takes place convergently in two taxa with an exceptional morphology, the taxa Zosimidae and Peltidiidae - Tegastidae. On the proximal endite of the maxillar coxa only 1 seta inserts as in N.N. 7 (char. **37**: 0→1). All pinnate spines of P2-P4 are swollen, flattened and spatulate in species of Novocriniidimorpha (Fig. 39 D; char. **58**: 0→1). These characteristic spines are found in Tisbidae also. The question arises, whether these transformed spines evolved in the ancestor line of Palinarthra and were later reduced in Peltidiidae - Tegastidae and Porcellidiidae. In this case, the spatulate spines would not be an apomorphy for Novocriniidimorpha (see chapter 5.2.3).

The remaining seven character transformations that took place in the ancestor line of Novocriniidimorpha are all an apparent regain of relatively plesiomorphic character states. The lateral element 3 of the distal endopod segment of the antenna forms a seta (char. **12**: 1→0) as in the outgroups of Oligoarthra. The exopod of the mandible is 4-segmented (char. **21**: 2→1) as in the groundpattern of N.N. 2. The maxilliped has no joint between syncoxa and basis as in the groundpattern of Syngnathartha (Figs. 39 A + B; char. **45**: 1→0). The maxillular coxa has 6 inner setae (char. **27**: 1→0) and the aesthetasc on oligoarthran segment 3 of the male antennule is present (char. **65**: 1→0) as in the groundpattern of N.N. 1. The male antennule is haplocer and forms no claw (char. **67**: 1→0; Fig. 39 E) as in the groundpattern of N.N. 3. Some of these seemingly plesiomorphic character states were recognized as secondary, because a trace of the evolutionary process is still visible. The unique pattern of the haplocer antennule of the male of Novocriniidimorpha is expressed in the fusion of only some and not all of the oligoarthran segments 6 to 9 (char. **62**: 1→0) and by the displacement of some of the



setae to the terminal end (Fig. 39 E). The fusion patterns have no equivalent outside Novocriniidimorpha and the displaced setae probably either (see above and chapter 5.2.3). The specific morphology of the male antennule is probably an autapomorphy of Novocriniidimorpha, which resembles the plesiomorphic character state in the groundpattern of N.N. 3, but nevertheless is secondarily acquired as evidenced by the cladistic analysis.

The same is true for the rigid connection of syncoxa and basis of the novocriniidimorph maxilliped. The maxilliped is characteristic in all species of Novocriniidimorpha (Figs. 39 A - C): there is no joint and consequently no flexibility between syncoxa and basis, and both segments are slender and cylindrical, having the same orientation. Additionally, the syncoxa is short and the basis is long, the endopod is elongated and flexible because of a joint between the endopod and the basis. This unique form has no equivalent outside Novocriniidimorpha. In taxa within Harpacticoida with a more plesiomorphic maxilliped without a joint between syncoxa and basis it has a long and often wide syncoxa with many setae and spines, a short basis and mainly a rigid endopod (Fig. 48: Polyarthra, Aegisthidae, Rometidae, Neobradyidae). The maxillipeds of Zosimidae and Peltidiidae - Tegastidae both have a unique morphology, which is an autapomorphy of each respective taxon (chapter 5.2.3). As indicated by the cladistic analysis and the morphological details, the rigid connection between the syncoxa and the basis of the more basal Harpacticoida, Zosimidae, Peltidiidae - Tegastidae and Novocriniidimorpha is not homologous. The joint evolved in the ancestor line of N.N. 1 and was independently reduced three times in Zosimidae, Peltidiidae and Novocriniidimorpha. The rigid connections between the syncoxa and the basis of the maxilliped in Zosimidae, Peltidiidae - Tegastidae and Novocriniidimorpha are not the plesiomorphic condition within Harpacticoida or the regained plesiomorphic condition, but independently evolved novelties.

Four character states of Novocriniidimorpha seem to be a regain of the plesiomorphic condition: the lateral element 3 of the distal endopod segment of the antenna forming a seta as in the outgroups of Oligoarthra, the exopod of the mandible being 4-segmented as in the groundpattern of N.N. 2, the coxa of the maxillule having 6 inner setae and the aesthetasc on oligoarthran segment 3 of the male antennule being present as in the groundpattern of N.N. 1. These character states of Novocriniidimorpha are not distinguishable from the plesiomorphic ones. However, some species indicate that the evolution of Novocriniidimorpha is indeed exceptional: *Atergopedia vetusta* has an incompletely fused P1 segment and a setoid tuft laterally on enp-2 (multiplication of setae), *Novocrinia trifida* has an indistinctly 2-segmented mandibular endopod (oligoarthran groundpattern: 1-segmented endopod), species of Superornatiremidae have “supernumerary” setae on the P1 and the first pedigerous somite of *Rotundiclipeus canariensis* is completely separated from the dorsal cephalic shield. These character states are certainly all multiplications of setae or secondary separations of segments as discussed in chapter 4 and 5. As a consequence “the regain of character states” within Novocriniidimorpha and Palinarthra appears not to be unusual. The hypothesis of a secondary reappearance of character states within Palinarthra is also supported by the cladistic analysis (see chapter 5.1.3). However, as discussed in chapter 5.2.5 these character states are not really the older states but new states that merely resemble the older ones.

To sum up it can be said that the taxon Novocrinidomorpha is monophyletic. Many details of different appendages support this conclusion.

#### N.N. 6

As discussed above it is highly probable that Palinarthra is characterised by the presence of the oral cone, the elongated gnathobase of the mandible and the elongated praecoxal arthrite of the maxillule. In Superornatiremidae and Rotundiclipeidae the evolution continued towards extraordinary feeding appendages. The praecoxal arthrite of the maxillule is elongated, narrow, and cylindrical, 4 distal spines are transformed into setae, and all terminal elements are situated tightly together (char. **22**: 1→2). The gnathobase mandible is stylet-like (char. **15**: 1→2) and consequently the bulge at the proximal border is reduced (char. **16**: 1→0; Figs. 36 D + H). This morphology is sufficiently complex to support the monophyly of N.N. 6. Furthermore, species of Superornatiremidae and Rotundiclipeidae are the only taxa within Harpacticoida without a single seta on the maxillipedal syncoxa in the groundpattern (char. **43**: 4→5). Superornatiremidae and Rotundiclipeidae also have an antenna with an allobasis (char. **7**: 0→1) as in Aegisthidae, the endopod of the mandible has 4 distal setae as in Zosimidae (char. **20**: 1→2), and setae 11 and 12 of the maxillular praecoxa are absent (char. **24**: 0→1) as in Tisboidea. Only in Superornatiremidae and Rotundiclipeidae the fused oligoarthran segments 12 and 13 of the male antennule are secondarily separated from segment 14 (char. **64**: 2→1). The membership to Palinarthra is expressed by this unique regain, as in all the other species of N.N. 1, segments 12 to 14 are completely fused to one segment. The Bremer support of this clade is 6. Superornatiremidae and Rotundiclipeidae are probably sister taxa.

#### Tisboidea (Fig. 42)

The monophyly of Tisboidea is supported by four complex autapomorphies, which show no homoplasy in the cladistic analysis. The fused praecoxal endites of the maxilla are displaced to the inner proximal corner of the syncoxa (Figs. 43 A - D; char. **35**: 0→1), the enp-2, exp-1 and exp-2 of the P1 are elongated (chars. **52** + **54**: 0→1), the exp-3 is small and rounded and all spines of exp-3 are elongated or transformed, with long spinules on one side (char. **56**: 0→2; Figs. 43 E + F). However, some of these characters are not always clearly visible in all tisboidean species. The exp-3 is not always small and rounded in tisbid species (chapter 4.26) and the long spinules on one side of the spines of exp-3 P1 are not always present in peltidiid species (Figs. 43 E + F). Four more character states are shared by species of Tisboidea, but also by other taxa: the body is dorso-ventrally flattened (char. **2**: 0→1) in Tisboidea and Tachidiidae. The body resumes also a more cylindrical shape within Tisbidae *sensu strictu* (see chapter 4.26). Setae 11 and 12 of maxillular praecoxa are absent in Tisboidea (char. **24**: 0→1) as in N.N. 6, coxa and basis of maxillule are fused (char. **28**: 0→1) as in Chappuisiidae, and the exopod of female P5 is more than twice as long as wide (char. **60**: 1→2) as in Superornatiremidae and Aegisthidae.

To sum up: there is no doubt that Tisboidea is monophyletic. The Bremer support of this clade is 4.

N.N. 7

Porcellidiidae and Tisbidae *sensu strictu* are connected by 2 autapomorphies without homoplasy: The seta II of the caudal rami is dislocated to the dorsal surface (char. 72: 0→1; chapter 5.2.3) and praecoxa and coxa of the maxillula are fused (char. 26: 0→1). Additionally, the (fused) enp-3 of the P1 is small (char. 53: 0→1) and has 2 terminal, densely unipinnate claws in this diverse group (Figs. 37 G + 43 F). Podogenmonta, Idyanthidae and Paramesochridae also have a small enp-3 of the P1, but the morphology of P1 endopod is not homologous in these four taxa (Fig. 50; chapters 5.1.3 to 5.1.5, and 5.2.3). The lateral seta 2 of the distal endopod segment of the antenna is regained (char. 10: 1→0), and the aesthetasc on the oligoarthran segment 4 of the male antennule is secondarily reduced (char. 66: 0→1). Furthermore, the proximal endite of the maxillar coxa is lost (char. 37: 0→1) as in Superornatiremidae and Rotundiclipeidae. Species of Novocriniidae and Peltidiidae-Tegastidae have this endite. The Bremer support of this clade is 5. The hypothesis that Porcellidiidae and Tisbidae *sensu strictu* are sister taxa is relatively well supported.

**5.2.5 Irreversibility of character transformation**

There are cases in literature where all characters for a cladistic analysis within Harpacticoida are coded as irreversible (e.g. Huys et al., 1997, Conroy-Dalton & Huys, 2000, Conroy-Dalton, 2001; see chapter 4.4). When the apomorphic state of a character is a novelty, the irreversibility of the character would mean, that once a character evolved it can never be reduced. Evolutionary theory does not exclude that previously evolved characters cannot be lost. If an apomorphic state were to represent the reduction of a feature (setae, segments, aesthetasc), coding this character as irreversible would mean that once a character is reduced, it could never reappear. There is not enough knowledge about gene expression and epigenetics to confirm this assumption. In many textbooks of evolution examples of atavistic characters are mentioned. Developmental mechanisms are sometimes completely maintained over very long periods of time, even if they are not expressed phenotypically. Ferrari (1988, p. 618) remarked “that for evolutionary transformations among crustaceans, Dollo’s Law should not be strictly applied nor should hypotheses about loss-and-redevelopment of characters be excluded from consideration.” Fiers (1990) found evidence, in ontogeny and in the form of the sixth legs, that the separation of genital and first abdominal somites in adult *Abscondicola humesi* Fiers, 1990 (as in Platycopioidea) was a secondary state resulting from heterochrony. Boxshall & Huys (1998; p. 784): “Evolutionary changes in the setation patterns of all copepod appendages, including the antennules, appear to proceed predominantly by reduction and losses (Huys & Boxshall, 1991). Exceptions to this empirical oligomerization principle are rare, with very few known examples of secondary gains in setal number from the presumed ancestral condition. However, our studies indicate that aesthetascs are an exception. They are much more labile than setae, being gained and/ or lost along an evolutionary lineage with relative ease. ... Caution should be exercised in the use of aesthetascs as characters in phylogenetic analysis although those that appear in the earliest stages (particularly CoI and CoII) appear to be relatively less labile”. Furthermore, it is clear that a newly emerged character state can resemble a

plesiomorphic state, but this is not simply a regain of the older state, but instead a new state that merely resembles the older plesiomorphic one. Nevertheless it is possible that the new state is based on the genetic basis of the plesiomorphic state. It is often difficult to distinguish between a plesiomorphic state and a new state that merely resembles the plesiomorphic one. In short: it is possible within taxa that states evolve looking like formerly reduced ones. Consequently, it is inconsiderate to code all characters as irreversible. This procedure can lead to faults. This does not mean that coding of characters as irreversible is wrong principally. In particular cases it can be reasonable to do so but not in all cases and these particular cases must be well-founded.

To test the opinion that it is inconsiderate to code all characters as irreversible, an analysis of the data in table 4 with all characters coded as irreversible was made. Four cladograms with a length of 196 were computed (CI=0,44). These cladograms are 42 steps longer than the single minimum length cladogram. It could hardly be a good choice to opt for one of these cladograms 42 steps longer than the minimum length cladogram. The evolution of characters is decayed by convergently evolved novelties and large numbers of parallel losses of segments and setae. Hence, a different approach is necessary.

As discussed above, in the analysis with all characters coded as unordered, none of the more complex characters that code e.g. the form and details of structures, undergo evolutionary transformations that are unlikely. It is reduction characters that cause the problems in this approach. Following the optimisation of the single minimum length cladogram, some setae, segments or aesthetascs are lost and regained (Fig. 46; chapters 5.1.5, 5.2.3 and 5.2.4). For some of them it could be shown that their reappearance does not mean the resurrection of the plesiomorphic state, but the evolution of a new state merely resembling the plesiomorphic one (see chapters 5.2.3 and 5.2.4). For other character states this could only not be demonstrated satisfactorily. Nevertheless, for the phylogenetic relationships of Oligoarthra (Fig. 4) it is accepted here that these character states are new, despite resembling plesiomorphic ones and that it is possible that they evolved from the genetic basis of the plesiomorphic character states.

An alternative possibility seems to be to code only the 32 reduction characters as irreversible (see chapter 5.2.1), so that the reappearance of setae and segments is assumed as impossible, but the reduction of novelties is not excluded. This leads to 15 cladograms with a length of 172 (CI=0,51). These cladograms are 18 steps longer than the single minimum length cladogram. The strict consensus of the 15 cladograms shows many collapsed clades, but Ectinosomatidae, Idyanthidimorpha and Paramesochridae are together in one clade. Setting the majority-rule consensus to 50%, Ectinosomatidae, Idyanthidimorpha, Paramesochridae and Tachidiidae are one clade; the sister group is Tisboidea and the sister group of all together Novocriniidimorpha. However, in this consensus cladogram the evolutionary transformations of the more complex characters are very unlikely. For instance both claws of the maxilliped, the big (V) and the small claw (VI) would have evolved twice convergently. The oral cone and all other related characters would also have developed twice independently. Some of the segments and setae would have been reduced 5 or 6 times. Therefore, it is not acceptable either to code only the 32 reduction characters as

irreversible. To choose only some but not all reduction characters and code them as irreversible is also impossible, because there is no criterion to decide, which segment, seta or aesthetasc can be reduced but has not the potential to reappear again.

To date, the best-supported hypothesis is that there are rare cases in which a character state can evolve that resembles a formerly reduced one. This applies to the reappearance of segments, setae and aesthetascs. The evolution of Harpacticoida includes steps that are exceptions of Dollo's Law (cf. Dollo, 1893) which states "... anything that has been lost in evolution will never be regained in that same form...".

Willen (2000) accepted the maximum number of segments and setae that can be found as the ancestral state in Podogennonta and integrated it in the podogennontan groundpattern. This groundpattern reconstruction is quoted here (chapter 4.9). However, this groundpattern seems to consist of too many plesiomorphic character states. Some of the setae and segments (e.g. setae 1 and 14 of female P5) can only be found in advanced taxa within Podogennonta. To suppose that these elements were present in the members of the last common population of Podogennonta would require to accept many multiple reductions within Podogennonta. The groundpattern of Podogennonta has to be revised considering the possibility of the reappearance of single segments and setae.

### 5.2.6 Oligomerization

It was one purpose to test the hypothesis of oligomerization in Oligoarthra, i.e. the reduction in the number of segments of the body and the appendages. Due to the lack of knowledge about genetic regulation of morphological characters, to the uncertainty of the identity of the sister group of Harpacticoida and to the circumstance that all recent phylogenetic hypotheses of Copepoda are based on the hypothesis of reduction of segments and setae, the aim here was to find mainly complex characters for which the probability of homology is higher (see chapter 5.1). In the character list, 44 % of the characters code reductions of segments, setae and aesthetascs (32 of 72 characters) and 56 % code more complex characters, like the form, the arrangement and the details of structures (40 of 72 characters; see chapter 5.2.1). A computer analysis was conducted, in which only the more complex characters were used; this means that the resulting cladograms were based only on the form and the composition of details of structures rather than on reductions of segments and setae. The result was a single minimum length cladogram with a length of 85 (CI=0,61; RI=0,80; RC=0,49). It exactly resembles the single minimum length cladogram computed with all 72 characters (Fig. 46). When the reduction characters are mapped on the cladogram, the hypothesis of oligomerization is confirmed in general. There is, however, as described above, the exception of rare evolutionary events leading to the reappearance of segments, setae and aesthetascs (chapters 5.1.5, 5.2.3, and 5.2.5).

One consequence of oligomerization is that many characters relevant for a phylogenetic analysis are reduction characters. Such characters are generally based on few mutations only and therefore hardly useful for a well-supported hypothesis of phylogeny. Another consequence of ongoing oligomerization is, that many characters acquired in the early phase of evolution of a taxon, cannot be analysed in all groups of this taxon, because these characters (segments or setae) are subsequently lost. When

many such characters are integrated in the character matrix the percentage of missing character states becomes too large and the analysis doubtful. These circumstances sometimes complicate the analysis of phylogenetic relationships in groups that are marked by oligomerization.

Oligomerization was elaborated for the first time by Dogiel in the late the 1920s and summarised in Dogiel (1954). However, the idea was introduced before by the carcinologists G.O. Sars and W. Giesbrecht. Monchenko & von Vaupel Klein (1999) have described this phenomenon in Cyclopoida and discussed the literature. The authors show e.g. a high correlation of body size and numbers of segments in P2-P4 in *Diacyclops*. Oligomerization and reduction of setae in small Crustacea often occur simultaneously with a decrease in body length and a paedomorphic origin of taxa (for Copepoda see Serban, 1960, Marcotte, 1982). It can also concur with the adaptation to a parasitic existence (e.g. Kabata, 1981). The primary evolutionary processes in copepods proceed towards fusion of body somites, and towards reductions in the segmentation and armature of the appendages (Boxshall et al., 1984). "However, ... at least two distinct mechanisms are involved in generating this trend towards oligomerization. One mechanism is progressive reduction and eventual loss of a character state in adults, the other is the heterochronic displacement of the time of appearance or transformation of characters during ontogeny, resulting in the total loss of a character state in the adult descendant" (Huys & Boxshall, 1991, p. 369). It seems that the oligomerization and decrease in body size in copepods is often also accompanied by a decrease in size of appendages, by a reduction of structures and sometimes even a simplification of the function of appendages (Monchenko & von Vaupel Klein, 1999).

### 5.3 Final remarks

A hypothesis of the phylogeny of Harpacticoida, in particular of Oligoarthra is presented. The only taxa that have an uncertain position within Oligoarthra are Podogennonta, Ectinosomatidae, and Paramesochridae. No strong synapomorphy connects Ectinosomatidae to any other oligoarthran taxon. There is a vague possibility indicated by the cladistic analysis that Ectinosomatidae is the sister group of N.N. 4 (chapter 3.1) and Idyanthidimorpha is the sister group of Ectinosomatidae - N.N. 4. As a consequence, Exanechentera would be polyphyletic. However, no strong apomorphy supports these relationships. To date the most parsimonious hypothesis is that Ectinosomatidae is the sister group of Exanechentera. The relationship of Paramesochridae and Tachidiidae is also uncertain. As indicated by the cladistic analysis, it is possible that Paramesochridae rather than Tachidiidae is the sister group of Palinarthra. Paramesochridae has all autapomorphies of Exanechentera. However, no apomorphy that is not also present in Tachidiidae connects Paramesochridae with Palinarthra. The most parsimonious hypothesis to date is: Tachidiidae is the sister group of Palinarthra and Paramesochridae is the sister group of Tachidiidae - Palinarthra (N.N. 5).

If for Harpacticoida the hypothesis is accepted that setae, aesthetascs, and segments can evolve in a state that resembles a formerly reduced state, the phylogenetic relationships within Oligoarthra (with exception of the position of Podogennonta) and

the autapomorphies of taxa as presented here are very likely (Fig. 4; chapter 5.1.5). It is now necessary to test the monophyly, the phylogeny and the groundpattern of Podogenonta on the basis of adult morphology. As a next step, the presented hypothesis of the phylogeny of Harpacticoida has to be tested by further characters, e.g. anatomy, larval morphology, developmental pattern or molecular characters. It would also be a great step forward if the sister group of Oligoarthra and of Harpacticoida could be ascertained.

## 6. SUMMARY

- A hypothesis of phylogenetic relationships within Harpacticoida is presented as a result of the application of Phylogenetic Systematics and cladistic computer analysis.
- The result of the cladistic analysis of the data matrix of the taxa of Oligoarthra (16 taxa) and 3 outgroup taxa and 72 characters was one minimum length cladogram of a length of 154 (indices: CI = 0.57; RI = 0.77; RC = 0.44).
- The diagram of the phylogenetic relationships within Harpacticoida shows the same relationships as obtained from the cladistic analysis. Only the assumed evolution of the oral cone and the maxilliped is different in the two techniques.
- Hierarchical presentation of the phylogenetic system of Harpacticoida:
  - Harpacticoida Sars, 1903
    - Polyarthra Lang, 1944
      - Longipediidae Sars, 1903
      - Canuellidae Lang, 1944
    - Oligoarthra Lang, 1944
      - Aegisthoidea Giesbrecht, 1892
        - Rometidae Seifried & Schminke, 2003
        - Aegisthidae Giesbrecht, 1892
      - Syngnatharthra Seifried & Schminke, 2003
        - Neobradyidae Olofsson, 1917
    - N.N. 1
      - Podogennonta Lang, 1944
    - N.N. 2
      - Chappuisiidae Chappuis, 1940
    - N.N. 3
      - Ectinosomatidae Sars, 1903
      - Exanechentera Lang, 1944
        - Idyanthidimorpha tax. nov.
          - Idyanthidae Lang, 1944
          - Zosimidae tax. fam.
    - N.N. 4
      - Paramesochridae Lang, 1944
    - N.N. 5
      - Tachidiidae Sars, 1909
      - Palinarthra tax. nov.
        - Novocriniidimorpha tax. nov.
          - Novocriniidae Huys & Iliffe, 1998
    - N.N. 6
      - Superornatiremidae Huys, 1996
      - Rotundiclipeidae Huys, 1988
    - Tisboidea Stebbing, 1910
      - Peltidiidae Sars, 1904
      - Tegastidae Sars, 1904
    - N.N. 7
      - Porcellidiidae Boeck, 1865
      - Tisbidae Stebbing, 1910



- Oligoarthra is monophyletic. Many autapomorphies support this hypothesis. The groundpattern of Oligoarthra is completed here. Some character states that are traditionally considered as plesiomorphic within Oligoarthra could be described as secondarily evolved or apomorphic within Oligoarthra (e.g. the separated first pedigerous somite, 2 egg-sacs, 2 proximal setae on the cutting edge of the mandible, the 2-segmented endopod of the mandible, setation of P5 within Podogennonta). Sometimes a different character state as hitherto maintained has to be assumed for the groundpattern of Oligoarthra; e.g. an allobasis and a 3-segmented endopod of maxilla is the plesiomorphic condition; the strong claw (I) of the maxilla is not fused with the endite of the basis and the praecoxa and the coxa of the maxilliped are fused to a syncoxa in the groundpattern of Oligoarthra.
- “Maxillipedasphalea” (Aegisthidae, Chappuisiidae, Darcythompsoniidae, Ectinosomatidae, Neobradysiidae, Phyllognathopodidae) is polyphyletic and therefore not maintained here. Darcythompsoniidae and Phyllognathopodidae are integrated in Podogennonta.
- A cladistic analysis demonstrates: *Neocervinia* and *Pseudocervinia* are synonyms of *Cervinia* and *Brotzkayaia* is a synonym of *Expansicervinia*.
- “Neobradysiidea” (Chappuisiidae, Darcythompsoniidae, Neobradysiidae, Phyllognathopodidae) is polyphyletic and therefore not maintained here.
- *Paramesochra australis* belongs to Ameiridae (Podogennonta) as *Psammoleptomesochra australis*.
- Ectinosomatoidea is synonymized with Ectinosomatidae, as both taxa embrace the same species.
- The monophyly of Exanechentera is confirmed. The exanechenteran species share a bevelled antennal endopod, a bulge at the proximal border of the mandibular gnathobase and the claw with the pointed end of the male antennule. Thompsonulidae is excluded from Exanechentera and is transferred to Podogennonta. Novocriniidae, Paramesochridae, Rotundiclipeidae, and Superornatiremidae are integrated in Exanechentera.
- Idyanthidimorpha tax. nov. contains Zosimidae tax. fam. and Idyanthidae. They mainly share the displaced coxal setae of the maxilliped, the morphology of the P1 and the sexual dimorphism of P2.
- Lang (1944) established Idyanthinae. Idyanthinae is excluded from Tisbidae *sensu strictu* and is raised to family rank. The species of Idyanthidae are mainly characterised by the elongated exopod of the maxillula, the characteristic endopod of P1, and the lack of the inner setae of the P2 enp-3 in male. *Dactylophia* together with *Idyanthe*, *Idyella*, *Idyellopsis*, *Styracothorax*, and *Tachidiella* represents the taxon Idyanthidae. *Tachidiopsis* is excluded from Idyanthidae and transferred to Neobradysiidae mainly on the basis of the shape and arrangement of the syncoxal setae of the maxilliped, and the sexual dimorphism in P2 and P3. *Tachidiopsis bozici*, *T. ibericus*, *T. laubieri*, *T. parasimilis*, and *T. sarsi* are moved from *Tachidiopsis* to *Marsteinia*. *Styracothoracidae* is synonymized with Idyanthidae, as *Styracothorax gladiator* has the autapomorphies of Idyanthidae. *Neoscutellidium* is excluded from Idyanthidae and is transferred to Cholidiinae (Tisbidae *sensu strictu*).
- *Zosime*, *Peresime*, and *Pseudozosime* are excluded from Idyanthidae and are combined in Zosimidae tax. fam. This monophyletic species group is characterised by many

autapomorphies.

- *Idyanthopsis psammophila* belongs to Paramesochridae as *Diarthrodella psammophila*.
- As Harpacticidae was integrated in Podogenonta, “Tachidioidea” is polyphyletic and therefore not maintained here.
- The monotypic Euterpinidae is synonymized with Tachidiidae, as *Euterpina acutifrons* has all autapomorphies of Tachidiidae.
- The taxon Palinarthra tax. nov consists of Novocriniidimorpha tax. nov. (Novocriniidae - Superornatiremidae - Rotundiclipeidae) and Tisboidea (Peltidiidae - Tegastidae - Porcellidiidae - Tisbidae *sensu strictu*). The species of Palinarthra mainly share the oral cone, the elongated and narrow gnathobase mandible and praecoxal arthrite of the maxillula, the ornamentation of the distal syncoxal endite of the maxilla, and the short syncoxa of the maxilliped. Novocriniidimorph species share at least 13 autapomorphies. Tisboidea is mainly characterised by the proximally displaced fused praecoxal endites of the maxilla, the elongated enp-2, exp-1 and exp-2 of P1, and the rounded small exp-3 of P1 with the transformed spines.
- Clytemnestridae is synonymized with Peltidiidae, because the eight species of *Clytemnestra* - *Goniopsyllus* belong to an advanced taxon within Peltidiidae. A complete revision of Peltidiidae - Tegastidae on species level is needed to clarify whether Tegastidae is either the sister taxon of Peltidiidae or a monophyletic taxon within Peltidiidae probably related to *Clytemnestra* - *Goniopsyllus*.
- The hypothesis of oligomerization in Oligoarthra, i.e. the reduction in the number of segments of the appendages and the body and additionally their ornamentation was tested and confirmed in general.
- In the evolution of Harpacticoida it is rare but possible, that a character state evolves resembling a formerly reduced state. For some character states it could be shown that it is not the recovered plesiomorphic state, but a new state resembling the plesiomorphic one. These rare evolutionary events lead mainly to the reappearance of segments, setae and aesthetascs.
- Every segment and almost all setae could be homologised in all examined adult species of Harpacticoida. The homology of setae of antenna, maxillula, maxilla, and maxilliped is completed here.
- First steps towards the characterisation of the evolution of Harpacticoida are made.

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## 8. APPENDICES

### 8.1 Appendix I. List of examined species

The morphology of all listed species was analysed. Nearly all specimens are stored in the Copepod Collection of the AG Zoosystematik und Morphologie, Universität Oldenburg, Germany. Species of which characters were used for the groundpattern reconstruction of a taxon will be completely described elsewhere. These species are marked with an asterisk \*. A survey of species that were part of a museum collection can be found in Appendix II. The sampling localities are listed in Appendix III.

#### Copepoda

##### Calanoida

*Pseudocyclops spec.* ff, mm Varadero, Cuba, 1998, culture,  
09.1999

##### Misophrioida

*Arcticomisophria bathylaptevensis* Martínez ff Arctic, 1993, ARK IX/4, Laptev See,  
Arbizu & Seifried, 1996 coll. no. UNIOL 1996.24/1-6,  
1996.25/1  
*Misophriella schminkei* Martínez f Antarctic, Weddell Sea, 1986, ANT  
Arbizu & Jaume, 1999 V/3, 10/528  
*Misophriopsis australis* Martínez ff Antarctic, Weddell Sea, 1986, ANT  
Arbizu & Jaume, 1999 V/3, 10/585

##### Harpacticoida

#### Polyarthra

##### Canuellidae

*Canuella perplexa* T. & A. Scott, ff, mm Helgoland, 13.6.1991  
1893  
*Canuella spec.* f Fiji Islands, CAM 1, 20.08.1984

##### Longipediidae

*Longipedia minor* T. & A. Scott, m Baltrum, 21.09.1992  
1893

**Oligoarthra****Rometidae**

<i>Romete bulbiseta</i> Seifried & Schminke, 2003	m	Great Meteor Seamount, M42/3, St. 451, 01.09.1998
<i>Romete</i> spec.*	f, m	Angola Basin, 2000, M48/1, DIVA 1, 346/6, MUC 1, MUC 8

**Aegisthidae**

Aegisthidae gen. spec. 1	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/592
Aegisthidae gen. spec. 2	f	Fiji Basin, 1996, SO-99, Station 42
Aegisthidae gen. spec. 3	m	Fiji Basin, 1996, SO-99, Station 98
Aegisthidae gen. spec. 4 *	m	Angola Basin, 2000, M48/1, DIVA 1, 346/1, MUC 5
Aegisthidae gen. spec. 5	f	Angola Basin, 2000, M48/1, DIVA 1, 346/1, MUC 1
<i>Aegisthus</i> spec.	ff	NE-Atlantic, 1998, M42/2, Station 419
<i>Andromastax</i> spec.	ff	NE-Atlantic, 1998, M42/2, Station 419
<i>Cervinia bradyi</i> Norman, 1878	ff, m	Museum Bergen, Oslo, Stockholm
<i>Cervinia pilosa</i> Lang, 1948	ff	Museum Stockholm
<i>Cervinia synarthra</i> Sars, 1910	ff	Museum Bergen, Oslo, Stockholm
<i>Cervinia</i> spec. 1	f, c	Antarctic, Weddell Sea, 1991, ANT IX, 18/062
<i>Cervinia</i> spec. 2	m	Angola Basin, 2000, M48/1, DIVA 1, 346/1, MUC 5
<i>Cervinia</i> spec. 3	f	New Ireland Fore-Arc, St. 57, SO-133, 1998
<i>Cervinia</i> spec. 4	f	New Ireland Fore-Arc, St. 65, SO-133, 1998
<i>Cervinia</i> spec. 5	f	New Ireland Fore-Arc, St. 57, SO-133, 1998
<i>Cerviniella</i> spec. 1	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/563
<i>Cerviniella</i> spec. 2	ff, mm, cc	Angola Basin, 2000, M48/1, DIVA 1, 325, 346
<i>Cerviniopsis clavicornis</i> Sars, 1903	ff, mm, cc	Museum Bergen, Oslo, Stockholm
<i>Cerviniopsis intermedia</i> Lang, 1936	f	Museum Stockholm

<i>Cerviniopsis longicaudata</i> Sars, 1903	ff	Museum Oslo
<i>Eucanuella spinifera</i> T. Scott, 1901	ff, mm, cc	Museum Bergen, Oslo, Stockholm
<i>Eucanuella</i> cf. <i>langi</i>	m	Angola Basin, 2000, M48/1, DIVA 1, 346/4, MUC 4
<i>Expansicervinia</i> cf. <i>tenuiseta</i>	f	Angola Basin, 2000, M48/1, DIVA 1, 346/4, MUC 5
<i>Expansicervinia</i> spec. 1	f	New Ireland Fore-Arc, St. 59, SO-133, 1998
<i>Expansicervinia</i> spec. 2	f	New Ireland Fore-Arc, St. 1, SO-133, 1998
<i>Hemicervinia stylifera</i> (Thompson, 1893)	ff	Museum Bergen, Oslo, Stockholm
<i>Pontostratiotes horrida</i> Brodskaya, 1959	f	New Ireland Fore-Arc, St. 57, SO-133, 1998
<i>Stratiopontotes</i> spec.	f	Arctic, 1993, ARK IX/4, 27/022
<b>Neobradyyidae</b>		
Neobradyyidae gen. spec. 1 *	ff, mm, cc	Antarctic, Weddell Sea, 1986, ANT V/3, 10/504, 10/ 508, 10/ 520, 10/528, 10/561, 10/566, 10/ 580, 10/589
Neobradyyidae gen. spec. 2	m	Peru-Trench, Discol 3, MC 357, 16.02.1992
Neobradyyidae gen. spec. 3	ff, mm, cc	Angola Basin, 2000, M48/1, DIVA 1, stations 325, 331, 342, and 346.
<i>Antarcticobradyya tenuis</i> (Brady, 1910)	ff, mm, cc	Antarctic, Weddell Sea, 1986, ANT V/3, 10/520, 10/528, 10/561, 10/580, 10/586, 10/615; Great Meteor Seamount, M42/3, St. 451
<i>Antarcticobradyya</i> spec.	ff, mm, cc	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528, 10/580, 10/586, 10/615
<i>Marsteinia</i> spec. 1	f, m	Peru-Trench, Discol 3, MC 348
<i>Marsteinia parasimilis</i> (Dinet, 1974)	f	Angola Basin, 2000, M48/1, DIVA 1, 346/2; MUC 3
<i>Marsteinia</i> spec. 2*	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528
<i>Marsteinia</i> spec. 3	m, c	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528
<i>Marsteinia</i> spec. 4	m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/589

<i>Marsteinia</i> spec. 5	f	Angola Basin, 2000, M48/1, DIVA 1, 346/1, MUC 4
<i>Marsteinia</i> spec. 6	f	Angola Basin, 2000, M48/1, DIVA 1, 346/2; MUC 3
<i>Marsteinia</i> spec. 7	m	Angola Basin, 2000, M48/1, DIVA 1, 346/3, MUC 1
<i>Marsteinia</i> spec. 8*	f	Angola Basin, 2000, M48/1, DIVA 1, 346/2, MUC 10
<i>Tachidiopsis cyclopoides</i> Sars, 1911	ff	Museum Oslo
<i>Tachidiopsis</i> spec. *	ff, mm	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528, 10/560

### Phyllognathopodidae

<i>Phyllognathopus viguieri</i> (Maupas, 1892)	ff, mm, cc	Echthausen, 12.05.1992; Sardinia, 1996
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### Darcythompsoniidae

<i>Leptocaris</i> spec.	f	Fiji Islands, Viti-Lem, 12.1993
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### Chappuisiidae

<i>Chappuisius inopinus</i> Kiefer, 1938	ff, mm	Aschaffenburg, 09.1999
<i>Chappuisius singeri</i> Chappuis, 1940	ff, mm	Aschaffenburg, 09.1999

### Ectinosomatidae

<i>Bradya (Bradya)</i> spec. 1 *	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528
<i>Bradya (Bradya)</i> spec. 2	m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/592
<i>Bradya (Parabradya)</i> spec. 3	f	Angola Basin, 2000, M48/1, DIVA 1, 346/7, MUC 8

Innumerable species of *Arenosetella*, *Bradya*, *Bradyellopsis*, *Ectinosoma*, *Microsetella*, *Halectinosoma*, *Halophytophilus*, *Hastigerella*, *Klieosoma*, *Pseudobradya* and undescribed higher taxa of Ectinosomatidae.

**Idyanthidae**

Idyanthidae gen. spec. 1	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 10/561, 10/589
Idyanthidae gen. spec. 2	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/566
Idyanthidae gen. spec. 3	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528
Idyanthidae gen. spec. 4	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528
Idyanthidae gen. spec. 5	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528
Idyanthidae gen. spec. 6	m	Antarctic, King George Island, Potter Cove, Station I, 16.03.1996
Idyanthidae gen. spec. 7	f	Peru-Trench, Discol 3, MC 362, 17.02.1992
Idyanthidae gen. spec. 8 *	ff, mm, cc	Angola Basin, 2000, M48/1, DIVA 1, stations 325, 331, 342, and 346.
description by Karin Bröhlidick		
Idyanthidae gen. spec. 9	ff, mm, cc	Angola Basin, 2000, M48/1, DIVA 1, stations 325, 331, 342, and 346.
Idyanthidae gen. spec. 10	ff, m, cc	Angola Basin, 2000, M48/1, DIVA 1, 346/2; MUC 3
Idyanthidae gen. spec. 11	f	Angola Basin, 2000, M48/1, DIVA 1, 325/4; MUC 2
Idyanthidae gen. spec. 12	f, m, cc	Angola Basin, 2000, M48/1, DIVA 1, 346/2; MUC 3
Idyanthidae gen. spec. 13 *	ff, m	Great Meteor Seamount, M42/3, St. 515, 09.1998
description by Kai George		
<i>Idyanthe dilatata</i> (Sars, 1905)	ff, mm, cc	Museum Bergen und Oslo
<i>Idyanthe</i> spec. 1	f, m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/539, 10/586
<i>Idyanthe</i> spec. 2 *	ff, mm, c	Antarctic, Weddell Sea, 1986, ANT V/3, 10/ 508, 10/520, 10/528, 10/580
<i>Idyella exigua</i> Sars, 1905	f	Museum Stockholm
<i>Idyella major</i> Sars, 1920	ff, mm	Museum Bergen, Oslo und Stockholm
<i>Idyella pallidula</i> Sars, 1905	ff	Museum Oslo und Stockholm
<i>Idyella</i> spec. 1	ff, mm, cc	Antarctic, Weddell Sea, 1986, ANT V/3, 10/504, 10/528, 10/539, 10/560, 10/585, 10/586

<i>Idyella</i> spec. 2 *	ff, m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/561, 10/520, 10/528
<i>Idyella</i> spec. 3	f, m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528, 10/561
<i>Idyella</i> spec. 4	ff, m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/586; 1991, ANT IX/2, 18/062
<i>Idyella</i> spec. 5	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528
<i>Idyella</i> spec. 6	ff, m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/508, 10/520, 10/528
<i>Idyella</i> spec. 7	m	Peru-Trench, Discol 3, MC 348
<i>Idyellopsis typica</i> Lang, 1944	ff, mm, cc	Antarctic, Potter Cove, E2/1; Museum Bergen und Stockholm
<i>Idyellopsis</i> spec. 1	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 10/615, 1989, ANT VII/4, 14/241
<i>Idyellopsis</i> spec. 2	m	Antarctic, Weddell Sea, 1989, ANT VII/4, 14/234
<i>Idyellopsis</i> spec. 3	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 10/520
<i>Styracothorax gladiator</i> Huys, 1993	f, m	Angola Basin, 2000, M48/1, DIVA 1, 346/2; MUC 5, 346/5; MUC 2
<i>Tachidiella minuta</i> Sars, 1909	ff	Museum Stockholm
<i>Tachidiella parva</i> Lang, 1965	ff	Museum Oslo und Stockholm
<i>Tachidiella</i> spec.	ff, m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528

### Zosimidae

<i>Pseudozosime browni</i> T. Scott, 1912	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/539
<i>Zosime bergensis</i> Drzycimski, 1968	ff, m, c	Museum Bergen und Stockholm
<i>Zosime gisleni</i> Lang, 1948	ff, m	Museum Stockholm
<i>Zosime incrassata</i> Sars, 1910	ff	Museum Bergen, Oslo und Stockholm
<i>Zosime major</i> Sars, 1921	ff, mm	Museum Oslo und Stockholm
<i>Zosime pacifica</i> Fiers, 1991	ff	Museum Stockholm
<i>Zosime typica</i> Boeck, 1872	ff, mm	Museum Bergen, Oslo und Stockholm
<i>Zosime valida</i> Sars, 1919	f	Museum Oslo

<i>Zosime</i> spec. 1	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/539
<i>Zosime</i> spec. 2	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 10/520, 17/528
<i>Zosime</i> spec. 3	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 17/592, 10/594, 10/615
<i>Zosime</i> spec. 4	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/594
<i>Zosime</i> spec. 5	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/594
<i>Zosime</i> spec. 6	ff, m, c	Antarctic, King George Island, 03.1998, ANT XV/3, 48/301.4
<i>Zosime</i> spec. 7	ff, m	Angola Basin, 2000, M48/1, DIVA 1, station 325, 346
<i>Zosime</i> spec. 8	f	Angola Basin, 2000, M48/1, DIVA 1, 346/1, MUC 4
<i>Zosime</i> spec. 9	f	Angola Basin, 2000, M48/1, DIVA 1, 346/7, MUC 2

Many undescribed species of *Zosime*.

#### **Paramesochridae**

<i>Apodopsyllus</i> spec. 1	f, m	Fiji Islands, CAM1, 20.08.1984
<i>Kliopsyllus</i> spec. 1	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 10/592
<i>Kliopsyllus</i> spec. 2	ff, mm	Fiji Islands, CAM1, 20.08.1984
<i>Kliopsyllus</i> spec. 3	ff	Papua New Guinea, PNG M4, 11.11.1984
<i>Paramesochra</i> spec.	f	Papua New Guinea, PNG M11, 11.11.1984
<i>Scottopsyllus</i> ( <i>Sc.</i> ) <i>praecipuus</i> Veit-Köhler, 2000	ff, mm, cc	Antarctic, King George Island, Potter Cove, Transect 1 + 2, 1994-1996



**Tachidiidae**

<i>Euterpina acutifrons</i> (Dana, 1848)	mm	Borkum, 07.1996.
<i>Tachidius discipes</i> Giesbrecht, 1881	ff, mm, cc	Deutschland: Banter See, Wilhelmshaven, 13.07.1991, Cridumer Siel, 02.03.1994; Spiekeroog, 06.07.1994, Dangast, 19.05.1996. France: Concarneau, 08.1996
<i>Tachidius</i> spec.	ff, mm, c	White Sea, Russia, 21.08.1986

**Peltidiidae**

<i>Alteutha oblonga</i> (Goodsir, 1845)	f	Helgoland, Deutschland, 6.1994
<i>Peltidium</i> spec. 1	ff, c	Antarctic, King George Island, Potter-Cove, Station 1: 22.11.1996, 15.11.96; Punta Elephante: 24.02.1996
<i>Peltidium</i> spec. 2	f	Antarctic, King George Island, Potter cove, Transect 1, 1996, 06.02.1996

**Tegastidae**

<i>Parategastes</i> spec.	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 10/528, 10/561
<i>Tegastes</i> spec. 1	ff	Antarctic, Weddell Sea, 1986, ANT V/3, 10/563, 10/566
<i>Tegastes</i> spec. 2	f	Fiji Islands, CAM1, 20.08.1984

**Porcellidiidae**

<i>Porcellidium</i> spec. 1	ff, c	Sri Lanka, SL 35
<i>Porcellidium</i> spec. 2	ff	Papua New Guinea, PNG M12, 21.11.1984
<i>Porcellidium</i> spec. 3	ff, c	Fiji Islands, CAM1, 20.08.1984
<i>Porcellidium</i> spec. 4	f, m	Antarctic, Weddell Sea, 1989, ANT VII/4, 14/295; Potter Cove, Punta Elephante, 01.03.1996

**Tisbidae**

Tisbidae gen. spec. 1	ff, m	Fiji Islands, Viti-Lem, 12.1993
Tisbidae gen. spec. 2	f	Antarctic, Weddell Sea, 1986, ANT V/3, 10/504
<i>Tisbe bulbisetosa</i> Volkmann-Rocco, 1972	ff, mm, cc	Oostende, Belgium, culture: 1997
<i>Tisbe holothuriae</i> Humes, 1957	ff, mm, cc	Venice, Italy, 1985, culture: 1997
<i>Tisbe</i> spec. 1	ff, mm, cc	Valencia, Spain, culture: 1997
<i>Tisbe</i> spec. 2	m	Antarctic, King George Island, Potter Cove, Punta Elephante, 24.02.1996.
<i>Tisbe</i> spec. 3	f	Cullera, Spain, 01.1995
<i>Tisbe</i> spec. 4	ff, mm	Papua New Guinea, PNG M4, 11.11.1984
<i>Tisbe</i> spec. 5	ff	Fiji Islands, Viti-Lem, 12.1993
<i>Tisbe</i> spec. 6	ff, mm	Antarctic, Weddell Sea, 1986, ANT V/3, 10/520, 10/528, 10/573, 10/592
<i>Tisbe</i> spec. 7	ff, m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/508, 10/561, 10/566, 10/573
<i>Tisbe</i> spec. 8	m	Antarctic, Weddell Sea, 1986, ANT V/3, 10/520, 10/586, 10/592
<i>Tisbella</i> spec.	f	Papua New Guinea, PNG M4
<i>Sacodiscus fasciatus</i> (Norman, 1868)	ff, mm	Museum Bergen, Oslo und Stockholm
<i>Sacodiscus littoralis</i> (Sars, 1904)	ff, mm, cc	Museum Oslo und Stockholm
<i>Scutellidium antarcticum</i> (Lang, 1936)	ff, cc	Museum Stockholm
<i>Scutellidium longicauda</i> (Philippi, 1840)	ff	Museum Stockholm

## 8.2 Appendix II. Museum material.

The following list of material includes all species of Oligoarthra (Harpacticoida) from museums in Oslo, Stockholm and Bergen, that were studied for the present analysis. The Swedish Museum of Natural History in Stockholm keeps the K. Lang Collection, the Zoological Museum in Oslo keeps the G.O. Sars Collection, and the Zoological Museum in Bergen stores some material collected by I. Drzycimski and F. D. Por. I visited these museums in the summer and autumn of 1997. Material on loan at that time may have been returned in the meantime.

### Remarks

#### **Zoological Museum in Oslo**

- All species are in the Harpacticoida Collection of G.O. Sars.
- Specimens with the remark ‘★ Syntype’ can be found in the type card index.
- Specimens covered with crystals can be restored with 80 % CaCl<sub>2</sub>.
- Specimens in alcohol with air inside the body can be restored by alcohol: glycerine = 1:1.
- Some species especially of *Ectinosoma*, *Pseudobradya*, *Arenosetella* and *Hastigerella* are very difficult to determine without dissection. The determination is only as certain as can be expected from undissected specimens.

#### **Swedish Museum of Natural History in Stockholm**

- All species are in the Harpacticoida Collection of K. Lang.
- Specimens with the remark ‘★ Syntype’ are labelled with ‘Syntype’ on the index card.
- Specimens with the remark type?/ type material? are probably types. We have to wait for publications on these species.
- Specimens on slides that are dried out and not dissected can be restored with glycerine. After some hours they are mostly in good condition.
- Specimens in alcohol with air inside the body can be restored by glycerine: alcohol = 1:1.
- Some species, especially of *Ectinosoma* and *Halectinosoma* are very difficult to determine without dissection. The determination is only as certain as can be expected from undissected specimens.

#### **Zoological Museum of the University of Bergen**

- I. Drzycimski or F. D. Por collected all species. They are in the Harpacticoida Collection.
- Specimens with the remark ‘★ Holotype/ Paratype’ are type material in the original description.

## Aegisthidae

Species	Reg. No. Harp.	Type Reg. No.	Number	Location	Preservation	Original species	Comments
<i>Cervinia bradyi</i> Norman, 1878	F20067 Oslo		0	Norway	Alcohol		No specimen found, decayed pieces?
	F20068 Oslo		(19) ♀♀ + Cop. Comments	Norway	Alcohol		2 species in F 20068: see also <i>C. synarthra</i>
	16 Stockholm		0	Gullmarfjorden 40 m, 1937	Alcohol		No specimen found!
	18 Stockholm		1 ♀	Måseskär, 145 m 1936	Alcohol		Crystals
	19 Stockholm		1 ♀	Bohuslän 222-249 m, 1936	Alcohol		Broken
	53136 Bergen		1 ♂	Raunefjorden, 145 m 1966, Drzycimski	Formalin		
<i>Cervinia pilosa</i> Lang, 1948	28 Stockholm	* Syntype 2242	1 ♀	Type location: Koster 210 m, 1936	Alcohol/ glycerine		
	29 Stockholm	* Syntype 2243	1 ♀	Type location: Koster 260 m, 1936	Alcohol/ glycerine		
<i>Cervinia synarthra</i> Sars, 1903 det.: S. Seifried, 1997	F20068 Oslo		(19) ♀♀ + Cop. Comments	Norway	Alcohol	<i>C. bradyi</i> Norman, 1878	2 species in F 20068: see also <i>C. bradyi</i>

	F 20069 Oslo	Type location? type material?	75 ♀♀ + Cop.	Bukken, south-west coast	Alcohol		First description as <i>C. bradyi</i> Norman, 1878 in Sars, 1903. Type location: some ♀♀ off the west coast of Norway and some of Lofoten Islands
det.: S. Seifried, 1997	F 20085 Oslo		1 ♀	Risør	Alcohol	<i>Zosime incrassata</i> Sars, 1910	2 species in F 20085: see also <i>Zosime incrassata</i>
det.: S. Seifried, 1997	F 20788 Oslo		15 ♀♀ + Cop.	Norway	Alcohol	<i>C. stumosa</i> Sars, Manuscript name	Only 5 ♀♀ determined. + 1 Longipediidae
	23 Stockholm		0	Gullmarfjorden, 60 m 1937	Alcohol		No specimen found!
	24 Stockholm		1 ♀	Gullmarfjorden, 60 m 1936	Alcohol		Crystals
	53131 Bergen		1 ♀	Korsfjorden, 515 m 1966 Drzycimski	Formalin	<i>Bradya (P.) dilatata</i> Sars, 1904	
?	53137 Bergen		1 ♀	Fanafjorden, 155 m 1966 Drzycimski	Formalin		Specimen in bad condition
	53275 Bergen		1 ♀	Korsfjorden, 690 m 1962 Por	Formalin		

<i>Cerviniopsis clavicornis</i> Sars, 1903	F 7266 MP 384 F 10747 MP 425 Oslo	Type?	1 ♀!	?	Slides	<i>Eucanuella clavicornis</i> Sars	One female (type?) under two different numbers on two slides!
	F 7436 MP 393 Oslo		3 ♂♂	?	Slide		Not dissected, dried out
	F 7437 MP 393 Oslo		1 ♂	?	Slide		Dissected, dried out
	F 20071 Oslo	Type material of ♂ in Sars, 1919? Location of ♂	17 ♀♀ + ♂♂ + Cop.	Risør	Alcohol		
	F 20075 Oslo	Type material of ♂ in Sars 1919?	11 ♀♀ 1 ♂	Norway	Alcohol		No index card!
	38 Stockholm		6 ♀♀	Gullmarfjorden 110 m, 1936	Alcohol		Crystals, 3 ♀♀ broken. + 1 Harpacticidae
	53138 Bergen		1 ♂?	Korsfjorden, 515 m 1966 Drzycimski	Formalin		Not opened
<i>Cerviniopsis intermedia</i> Lang, 1936	44 Stockholm	* Syntype 2244	1 ♀	Type location: Spitsbergen 2700 m, 1898	Alcohol/ glycerine		The only specimen left is completely broken! Crystals
<i>Cerviniopsis longicauda</i> Sars, 1903	F 20074 Oslo	Type location, type material?	2 ♀♀	Norway	Alcohol		

<i>Cerviniopsis stylicauda</i> Lang, 1936	?								No type material left (1 ♀, Lang, 1948)!
<i>Eucanuella spinifera</i> T. Scott, 1901; det.: S. Seifried, 1997	Stockholm F 20073 Oslo		1 Cop.	Norway	Alcohol	<i>Cerviniop- sis longi- cauda</i> Sars			+ 1 Laophontidae ♂
	F 20076 Oslo		31 ♀♀ + Cop	Norway	Alcohol				
	F 20077 Oslo		13 ♀♀ + ♂♂ + Cop.	Lyndalsfjord	Alcohol				
	46 Stockholm		1 ♂?	Gullmarfjorden, 120 m 1936	Alcohol				♂ or ♀?
	47 Stockholm		1 ♂	Gullmarfjorden, 45 m 1937	Alcohol				Broken
	53154 Bergen		1 ♀?	Husnesfjorden, 520 m, 1967, Drzycimski	Formalin				Not opened
	53155 Bergen		2 ♀♀ 1 ♂	Bømlafjorden, 340 m 1967, Drzycimski	Formalin				
	53277 Bergen		1 ♀	Raunefjorden, 240 m 1962, Por	Formalin				Broken
<i>Hemicervinia styliifera</i> (Thompson, 1893)	30 Stockholm		1 ♀	Gullmarfjorden 120 m, 1934	Alcohol	<i>Herdmania styliifera</i> Thompson, 1893			Broken
	31 Stockholm		1 ♀	Gullmarfjorden, 90 m 1948	Alcohol	<i>Herdmania styliifera</i> Thompson, 1893			

## Neobradiidae

Species	Reg. No. Harp.	Type Reg. No.	Number	Location	Preservation	Original species	Comments
<i>Marsteinia similis</i> Drzycimski, 1968	49323 Bergen	* Holotype	1 ♀	Raunefjorden 242 m, 1966 Drzycimski	Formalin		R. Huys, London
<i>Marsteinia typica</i> Drzycimski, 1968	49321 Bergen	* Holotype	1 ♀	Marsteinen, 300 m 1967, Drzycimski	Formalin		R. Huys, London
	49322 Bergen	* Paratypes	2 ♀♀ 1 ♂	Marsteinen, 300 m 1967, Drzycimski	Formalin		R. Huys, London
	53228 Bergen		5 Cops.	Korsfjorden, 450 m 1967, Drzycimski	Formalin		
<i>Neobradya pectinifera</i> T. Scott, 1892	85 Stockholm		♀♀ ♂♂, Cop.	Gullmaren, 1937	Alcohol		
<i>Tachidopsis cyclopoidea</i> Sars, 1911	F 20350 Oslo	Type location type material?	18 ♀♀	Korshavn	Alcohol		see Huys & Boxshall (1991)

## Darcythompsoniidae

Species	Reg. No. Harp.	Type Reg. No.	Number	Location	Preservation	Original species	Comments
<i>Leptocaris armatus</i> Lang, 1965	562 Stockholm	* Syntype 2204	0	Monterey Bay, 1960	Alcohol/ glycerine		Empty
<i>Leptocaris doughertyi</i> Lang, 1965	563 Stockholm	* Syntype 2205	0	Monterey Bay, 1960	Alcohol/ glycerine		Empty
<i>Leptocaris pori</i> Lang, 1965	564 Stockholm	* Syntype 2206		Monterey Bay, 1960	Alcohol/ glycerine		R. Huys, London



**Harpacticidae**

Species	Reg. No. Harp.	Type Reg. No.	Number	Location	Preservation	Original species	Comments
<i>Harpacticus trisetosus</i> Lang, 1948	? Stockholm	?					No type material left (1 ♀, Lang, 1948)?
<i>Perissocope litoralis</i> Lang, 1934	? Stockholm	?					No type material left (1 ♀, Lang, 1948)?
<i>Zausopsis mirabilis</i> Lang, 1934	155 Stockholm	? * Syntypes 2246	2 ♀♀	Süd-Georgien, 190? No type location!	Alcohol/ glycerine		No type location, male lost! Specimens from type location lost!
<i>Zausodes sextus</i> Lang, 1965	? Stockholm	?					No type material left (many ♀♀ + ♂♂, Lang, 1965)?
<i>Zausodes septimus</i> Lang, 1965	? Stockholm	?					No type material left (many ♀♀ + ♂♂, Lang, 1965)?

**Ectinosomatidae**

Species	Reg. No. Harp.	Type Reg. No.	Number	Location	Preservation	Original species	Comments
<i>Arenosetella kaiseri</i> Lang, 1965	593 Stockholm	* Syntypes 2237	5 ♀♀	Type location: Monterey Bay 1960	Alcohol/ glycerine		
<i>Bradya (B.) cladiofera</i> Lang, 1965	500 Stockholm	* Syntype 2217	1 ♀	Type location: Monterey Bay 26 m, 1960	Alcohol/ glycerine		1 ♀ in three pieces, no legs

<i>Bradya (B.) furcata</i> Sars, 1920	F 7425 MP 392 Oslo	Type location type material?	1 ♀	Risør	Slide	Not dissected, dried out
	F 7426 MP 392 Oslo	Type location type?	1 ♀	Risør	Slide	Dissected
	F 20043 Oslo	Type location	0	Risør	Alcohol	No specimen found!
	112 Stockholm		3 ♀♀	Gullmaren, 30 m 1937	Alcohol	
<i>Bradya (B.) congera</i> Sars, 1920	? Oslo					No type material left (Several specimens Sars, 1920)! See also <i>B.</i> <i>(B.) typica</i>
	107 Stockholm		1 ♀	Gullmaren, 40 m, 1937	Alcohol	Completely broken, species?
<i>Bradya (B.) macrochaeta</i> Sars, 1920 det.: S. Seifried, 1997	F 7430 MP 392 Oslo	Type?	1 ♀	?	Slide	Dissected, dried out
det.: S. Seifried, 1997	F 20777 Oslo	Type location type material?	1 ♀	Risør	Alcohol	Broken
						<i>B. longisetosa</i> Sars Manuscript name
						<i>B. longisetosa</i> Sars Manuscript name

det.: S. Seifried, 1997	F 20778 Oslo	Type location type material?	2 ♀	Risør	Alcohol	<i>B. longisetosa</i> Sars Manuscript name	Completely broken
?	109 Stockholm		1 ♀	Gullmaren, 70 m 1937	Alcohol		Broken, species?
	110 Stockholm		1 ♀	Väster, 140 m, 1937	Alcohol		Squeezed but not broken. + 2 Podogenmonta
	53132 Bergen		1 ♀	Korsfjorden, 518 m 1966, Drzycimski	Formalin		
<i>Bradya (B.) scotti</i> Sars, 1920	F 20042 Oslo	Type location type material?	7 ♀♀	Risør	Alcohol		Specimens in bad condition, some broken
det.: S. Seifried, 1997	F 20044 Oslo	Type location type material?	(10) ♀♀ see Com- ments	Risør	Alcohol	<i>B. typica</i> Boeck, 1872	3 species in F 20044: see also <i>B. (B.) typica</i> and <i>Halectinosoma</i> sp.
det.: S. Seifried, 1997	F 20045 Oslo		1 ♀	Norway	Alcohol	<i>B. armifera</i> (T. & A. Scott)	3 species in F 20045: see also <i>B. (B.) typica</i> and <i>Halectinosoma</i> <i>armiferum</i>
det.: S. Seifried, 1997	F 20062 Oslo		2 ♀♀	Norway	Alcohol	<i>B. typica</i> Boeck, 1872	2 species in F 20062: see also <i>B. (B.) typica</i>
det.: M. Clément	F 21181 Oslo		0	Norway	Alcohol	<i>Ectinosoma</i> <i>sarsi</i> Boeck, F 20038	No specimen found!

	111 Stockholm		1 ♀	Väster, 140 m, 1937	Alcohol	2 species in 111: see also <i>B. (B.) typica</i>
<i>Bradya (B.) simulans</i> Sars, 1920	F7427 MP 392 Oslo	Type location type?	1 ♀	Risør	Slide	Dissected
	F7428 MP 392 Oslo	Type location type material?	1 ♀	Risør	Slide	Not dissected, dried out
	F7429 MP 392 Oslo	Type location type material?	1 ♀	Risør	Slide	Not dissected, dried out
<i>Bradya (B.) typica</i> Boeck, 1872	F20044 Oslo		(10) ♀♀ Comments	Risør	Alcohol	3 species in F 20044: see also <i>B. (B.) scotti</i> and <i>Halectinosoma</i> sp.
det.: S. Seifried, 1997	F20045 Oslo		1 ♀	Norway	Alcohol	3 species in F 20045: see also <i>B. (B.) scotti</i> and <i>Halectinosoma</i> <i>armiferum</i>
	F20062 Oslo		2 ♀♀	Norway	Alcohol	2 species in F 20062: see also <i>B. (B.) scotti</i>
	F20064 Oslo		3 ♀♀	Risør	Alcohol	
	F20834 Oslo		2 ♀♀	2. Fram exp., 1900	Alcohol	

	102 Stockholm		9 ♀♀	Gullmaren, 20-60 m 1937	Alcohol		Only 2 ♀♀ determined.
	103 Stockholm		4 ♀♀	Spitsbergen, 210 m, 1898	Alcohol		Crystals
det.: S. Seifried	108 Stockholm		4 ♀♀	Gullmaren, 120 m, 1937	Alcohol	<i>B. congera</i> Sars, 1920	
det.: S. Seifried	111 Stockholm		1 ♀	Väster, 140 m, 1937	Alcohol	<i>B. scotti</i> Sars, 1920	2 species in 111: see also <i>B.(B.) scotti</i>
det.: S. Seifried	186 Stockholm		1 ♀	Gullmaren, 110 m, 1937	Alcohol/ glycerine	<i>Idyellopsis</i> <i>typica</i> Lang, 1948; type- card-index: 2251	
	53133 Bergen		1 ♀?	Fanafjorden, 155 m 1966, Drzycimski	Formalin		Not opened
	53274 Bergen		1 ♀?	Raunefjorden, 1962, Por	Formalin		Not opened
<i>Bradya (Parabradya)</i> <i>confluens</i> Lang, 1936	? Stockholm						No type material left (1 ♀, Lang, 1948)!
<i>Bradya (Parabradya)</i> <i>dilatata</i> Sars, 1904	F20063 Oslo	Type location? type material?	16 ♀♀	Norway	Alcohol	<i>B. dilatata</i> Sars	Type location: Oslo Fjord. Only 3 ♀♀ determined See <i>Cervinia synarthra</i>
<i>Ectinosoma</i> <i>breviarticulatum</i> Lang, 1965	542 Stockholm	* Syntypes 2183	4 pieces of ♀♀	Type location: Monterey Bay tidal pool, 1960	Alcohol/ glycerine		1 cephalothorax, 2 thorax pieces and 1 abdomen without P5

<i>Ectinosoma californicum</i> Lang, 1965	544 Stockholm	* Syntypes 2185	6 ♀♀ 3 abdomen 1 ♂!	Type location: Monterey Bay, 1960	Alcohol/ glycerine	<i>E. dentatum californicum</i> Lang, 1965	No ♂ in the original description
<i>Ectinosoma compressum</i> Sars, 1921	57 Stockholm		1 ♀	Gullmarfjorden 60m, 1936	Alcohol		Broken
?	58 Stockholm		1 ♀	Gullmarfjorden 60m, 1936	Alcohol		Broken
<i>Ectinosoma melaniceps</i> Boeck, 1865	59 Stockholm		1 ♀	Gullmarfjorden, 120m 1936	Alcohol		
<i>Ectinosoma obstusum</i> Sars, 1921	F 20832 Oslo		2 ♀♀	2. Fram exp.	Alcohol		Impossible to determine without dissection
<i>Ectinosoma normani</i> T.+ A. Scott, 1894	F 7475 MP 394 Oslo	Type location type?	1 ♀	Korshavn	Slide		Dissected, dried out, mouthparts not complete
	49 Stockholm		1 ♀	Gullmarfjorden 100 m, 1936	Alcohol		
	53 Stockholm		1 ♀	Gullmarfjorden, 8 m 1936	Alcohol		Broken
	55 Stockholm		0	Gullmarfjorden 100 m, 1936	Alcohol		No specimen found!
<i>Ectinosoma paranormani</i> Lang, 1965	543 Stockholm	* Syntypes 2184	3 pieces of ♀♀	Type location: Monterey Bay tidal pool, 1960	Alcohol/ glycerine		2 abdomen and 1 cephalothorax of ♀♀
" <i>Ectinosoma pusilla</i> " Sars	F 20791 Oslo		1 ♀	Risør, Korshavn	Alcohol		Manuscript name

<i>Ectinosoma tenuipes</i> T. + A. Scott, 1894	56 Stockholm		0	Öresund, 15-18 m 1934	Alcohol		No specimen found!
<i>Ectinosomella nitidula</i> Sars, 1910	F 7552 MP 398 Oslo	Type location? type?	1 ♀	Korshavn: Farsund or Oslo Fjord?	Slide	Slide: <i>Pseudo- bradya nitidula</i>	Dried out. Type location from <i>E. nitidula</i> : Farsund
	F 20790 Oslo	Type location type material?	2 ♀♀	Farsund	Alcohol	Manuscript name: <i>Ectinosoma nitidulum</i> Sars	
<i>Halectinosoma armiferum</i> (T. & A. Scott, 1894) ?	F 20045 Oslo		5 ♀♀ 1 ♂	Norway	Alcohol	<i>Bradya armifera</i> (T. & A. Scott)	3 species in F 20045: see also <i>Bradya</i> (B.) <i>scotti</i> and <i>Bradya</i> (B.) <i>typica</i>
<i>Halectinosoma</i> sp. det.: S. Seifried, 1997	New number Oslo		1 ♀	Risør	Alcohol	<i>Bradya typica</i> F20044	
<i>Halophytophilus similis</i> Lang, 1948	80 Stockholm	* Syntype 2245	0	Type location: Gullmaren 20 m, 1937	Alcohol/ glycerine		Last type material lost!
<i>Halophytophilus spinicornis</i> Sars, 1920; det.: S. Seifried, 1997	F 7556 MP 399 Oslo	Type?	1 ♀	?	Slide	<i>Pseudo- bradya spinicornis</i> Sars	Dissected, dried out, mouthparts not complete
	79 Stockholm		1 ♀	Gullmaren, 80-90 m 1937	Alcohol		

	585 Stockholm	* Syntypes 2228	3 ♀♀ 2 ♂♂	Type location: Monterey Bay tidal pool, 1960	Alcohol/ glycerine	Partly broken
<i>Hastigerella abbotti</i> Lang, 1965	Stockholm	2228	3 ♀♀ 2 ♂♂	Monterey Bay tidal pool, 1960	Alcohol/ glycerine	Partly broken
<i>Pseudobradya cornuta</i> Lang, 1965	? Stockholm	?				No type material left (many ♀♀ + ♂♂, Lang, 1965)?
<i>Pseudobradya crassipes</i> Lang, 1965	? Stockholm	?				No type material left (many ♀♀ + ♂♂, Lang, 1965)?
<i>Pseudobradya maxima</i> Lang, 1935	? Stockholm	?				No type material left (1 ♀ + 1 ♂, Lang, 1948)?
<i>Pseudobradya pectinifera</i> Lang, 1965	? Stockholm	?				No type material left (1 ♀, Lang, 1965)?
<i>Pseudobradya pulchra</i> Lang, 1965	575 Stockholm	* Syntypes 2218	50 ♀♀ + ♂♂ + Cop.	Type location: Dillon Beach, 1960	Alcohol/ glycerine	Only 1 ♀ and 1 ♂ determined

## Idyanthidae

Species	Reg. No. Harp.	Type Reg. No.	Number	Location	Preser- vation	Original species	Comments
<i>Idyanthe dilatata</i> (Sars, 1905)	F 7491 MP 395 Oslo	Location of ♂ type ♂ ?	1 ♂	Risør	Slide		Not dissected, dried out; description of ♂: Sars, 1909
	F 12729 Oslo	* Syntypes	0	Norway	Alcohol		No specimen found decayed pieces
	F 20354 Oslo	Type location? type material?	0	Norway	Alcohol		No specimen found decayed pieces



	F 20842 Oslo		2 ♀♀ 1 ♂	Polar Island, 2. Fram exp., 1900	Alcohol		
	53165 Bergen		3 ♀♀ 4 ♂♂ Cop.	Marsteinen, 60 m 1967, Drzycimski	Formalin	Bergen list: <i>Idyaea dilatata</i> Sars	
<i>Idyanthe pusilla</i> (Sars, 1905)	F 12728 Oslo	* Syntypes	0	Norway	Alcohol		No specimen found decayed pieces of <i>Idyella</i> sp. No type material left!
<i>Idyella exigua</i> Sars, 1905	F 7492 MP 395 Oslo	Type material ♂?	1 ♂	?	Slide		Not dissected. Description of the ♂: Sars, 1920
	F 7493 MP 395 Oslo	Type ♂?	1 ♂	?	Slide		Dissected. Description of the ♂: Sars, 1920
	F 12730 Oslo	* Syntypes	11 ♀♀ 1 ♂	Bukken, Stavangerfjord	Alcohol		Only 3 ♀♀ determined
	F 20099 Oslo		2 ♀♀	?	Alcohol		
?	188 Stockholm		2 ♀♀	Gullmaren, 30 m 1934	Alcohol		Probably <i>I. major</i> ! and <i>I. pallidula</i>
	53166 Bergen		1 ♀	Korsfjorden, 50 m 1967 Drzycimski	Formalin		Wrong number (53165) on Bergen list
<i>Idyella major</i> Sars, 1920	? Oslo						No type material found (1 ♀, Sars 1920)!
	187 Stockholm		1 ♀	Gullmaren, 70 m 1934	Alcohol		Completely covered with crystals. See also

										<i>I. exigua</i>
" <i>Idyella mixta</i> " Sars	F7495 M395 Oslo									R. Huys, London
" <i>Idyella mixtus</i> " Sars	F7494 M395 Oslo									R. Huys, London
<i>Idyella pallidula</i> Sars, 1905	F7496 MP 396 Oslo					1 ♀	Risør	Slide		Not dissected completely dried out
	F7497 MP 396 Oslo					0	Risør	Slide		No specimen found
	F 12731 Oslo									Not examined!?
	F20100 Oslo					10 ♀♀	Risør	Alcohol		Only 4 ♀♀ determined
	190 Stockholm					13 ♀♀ + Cop.	Gullmaren, 60 m, 1948	Alcohol		Only 5 ♀♀ determined
<i>Idyellopsis typica</i> Lang, 1944	182 Stockholm					1 ♀?: see comments	Type location: Gullmaren 60 m 1937	Slide		1 ♀?: -A1 and A2 of one ♀ on one slide, dissected and mounted by J.M. Gee, 1985  -same ♀ ? without A1 and A2 in alcohol glycerine; broken legs

	Coll. by J. M. Gee! No. ? Stockholm		1 ♀	Antarctica, Bory Bay Signy Island 15 m, 1983.	Slide	see Gee & Fleegeer, 1984
	53167 Bergen			Korsfjorden, 515 m 1967, Drzycimski	Formalin	R. Huys, London?
<i>Tachidiella minuta</i> Sars, 1909	F20389 Oslo	Type location type material?	7 ♀♀	Skutesnas, south- west coast	Alcohol	
	183 Stockholm		1 ♀	Gullmaren 30 m, 1934	Alcohol	Covered with detritus
	184 Stockholm		3 ♀♀	Gullmaren, 10 m, 1937	Alcohol	+ 1 ♀ Podogennonta
<i>Tachidiella parva</i> Lang, 1965	501 Stockholm	* Syntypes 2229	3 ♀♀	Type location: Monterey Bay 26 m, 1960	Alcohol/ glycerine	2 ♀♀ broken + 1 ♀ Podogennonta

## Zosimidae

Species	Reg. No. Harp.	Type Reg. No.	Number	Location	Preser- vation	Original species	Comments
<i>Zosime bergensis</i> Drzycimski, 1968 det.: S. Seifried, 1997	178 Stockholm		1 ♀	Gullmaren, 90 m 1937	Alcohol/ glycerine	<i>Z. gisleni</i> Lang, 1948 * Syntype 2248	Another broken female, squeezed by cotton
det.: S. Seifried, 1997	179 Stockholm		1 ♂ 1 Cop.	Gullmaren, 50 m 1937	Alcohol/ glycerine	<i>Z. gisleni</i> Lang, 1948 * Syntype 2249	3 species in 179: see also <i>Z. gisleni</i> and <i>Z. typica</i>

	48234 Bergen	* Holotype	1 ♀	Korsfjorden, 518 m 1966 Drzycimski	Formalin		R. Huys, London
	48235 Bergen	* Paratypes		Korsfjorden and Norwegian sea near Bergen, 105-680 m 1966-1967 Drzycimski	Formalin		R. Huys, London
	53233 Bergen			Korsfjorden, 515 m 1966 Drzycimski	Formalin		R. Huys, London?
	53234 Bergen			Raunefjorden, 324 m 1966, Drzycimski	Formalin		R. Huys, London?
	53235 Bergen			Korsfjorden, 680 m 1966 Drzycimski	Formalin		R. Huys, London?
	53236 Bergen			Korsfjorden, 1966 Drzycimski	Formalin		R. Huys, London?
	53237 Bergen			Bømlafjorden, 340 m 1967, Drzycimski	Formalin		R. Huys, London?
	53238 Bergen			Husnesfjorden, 520 m, 1966, Drzycimski	Formalin		R. Huys, London?
	53239 Bergen	Type location		Marsteinen, 105 m, 1967 Drzycimski	Formalin		R. Huys, London?
<i>Zosime gisleni</i> Lang, 1948?	179 Stockholm	* Syntypes 2249	3 ♀♀ 1 ♂	Type location: Gullmaren 50 m, 1937	Alcohol/ glycerine		3 species in 179: see also <i>Z. bergensis</i> and <i>Z. typica</i>
	53220 Bergen			Korsfjorden, 515 m 1966 Drzycimski	Formalin		R. Huys, London?

<i>Zosime incrassata</i> Sars, 1910	F 20085 Oslo		2 ♀♀	Risør No type location	Alcohol	No type material left. 2 species in F 20085: see also <i>Cervinia</i> <i>synarthra</i>
	180 Stockholm		1 ♀	Gullmaren, 100 m 1937	Alcohol	+ 2 ♀♀ <i>Idyella</i> sp.
	181 Stockholm		1 ♀	Gullmaren, 60 m 1937	Alcohol	Without abdomen
	53221 Bergen			Bømlafjorden, 340 m 1967, Drzycimski	Formalin	R. Huys, London?
	53222 Bergen			Husnesfjorden, 220 m, 1967, Drzycimski	Formalin	R. Huys, London?
<i>Zosime major</i> Sars, 1921	F 7603 MP 401 Oslo	Type location type material?	1 ♀ 2 ♂♂	Risør	Slide	Not dissected, dried out. No male in the species description!
	F 7404 MP 401 Oslo	Type location type material?	2 ♂♂	Risør	Slide	Not dissected, dried out. No male in the species description!
	F 7605 MP 401 Oslo		1 ♂	?	Slide	Not dissected, dried out
	F 7606 MP 401 Oslo		1 ♀	?	Slide	Not dissected, dried out
	F 7607 MP 401 Oslo		1 ?	?	Slide	Not dissected, dried out

	F 7608 MP 401 Oslo	Type?	1 ♀	?	Slide	Only dissected female!
	175 Stockholm		2 ♀♀	Gullmaren, 30 m 1934	Alcohol	
	176 Stockholm		2 ♀♀	Gullmaren, 70 m 1937	Alcohol	
	177 Stockholm		3 ♀♀	Gullmaren, 40 m 1937	Alcohol	
	53223 Bergen			Korsfjorden, 680 m 1966 Drzycimski	Formalin	R. Huys, London?
<i>Zosime pacifica</i> Fiers, 1991 det.: S. Seifried, 1997	170 Stockholm		3 ♀♀	Gullmaren, 20 m 1934	Alcohol	<i>Z. typica</i> Boeck, 1872  + broken ♀ species?
det.: S. Seifried, 1997	172 Stockholm		♀♀	Gullmaren, 60 m 1937	Alcohol	2 species in 172: see also <i>Z. typica</i>
det.: S. Seifried, 1997	173 Stockholm		3 ♀♀	Gullmaren, 1934	Alcohol	<i>Z. valida</i> Sars, 1919  <i>Z. valida</i> Sars, 1919
<i>Zosime typica</i> Boeck, 1872	F 20082 Oslo		5 ♂♂	Farsund	Alcohol	Covered with detritus, species?
	F 20083 Oslo		≥ 40 ♀♀ + ♂♂	Farsund	Alcohol	Only 5 specimens determined
	171 Stockholm		3 ♀♀ 3 ♂♂ 1 Cop.	Gullmaren, 60 m 1937	Alcohol	
det.: S. Seifried, 1997	172 Stockholm		♀♀ Cop.	Gullmaren, 60 m 1937	Alcohol	2 species in 172: see also <i>Z. pacifica</i>

det.: S. Seifried, 1997	179 Stockholm		1 ♂	Gullmaren, 50 m 1937	Alcohol/ glycerine	<i>Z. gislæni</i> Lang, 1948 * Syntype 2249	3 species in 179: see also <i>Z. bergensis</i> and <i>Z. gislæni</i>
	53224 Bergen			Husnesfjorden, 220 m, 1967, Drzycimski	Formalin		Not opened
	53284 Bergen			Korsfjorden, 690 m, 1962 Por	Formalin		Not opened
<i>Zosime valida</i> Sars, 1919	F 7609 MP 401 Oslo	Type location type?	1 ♀	Hvalør	Slide		Dissected
	174 Stockholm		1 ♀	Öresund, 22 m 1935	Alcohol		Broken
<i>Zosime</i> sp.	F 7878 MP ?, Oslo		1 ♂				R. Huys, London

### Paramesochridae

Species	Reg. No. Harp.	Type Reg. No.	Number	Location	Preser- vation	Original species	Comments
<i>Apodopsyllus</i> <i>vermiculiformis</i> Lang, 1965	594 Stockholm	* Syntypes 2238		Monterey Bay 1960	Alcohol/ glycerine		R. Huys, London
<i>Leptopsyllus</i> (L.) <i>reductus</i> Lang, 1948	354 Stockholm	* Syntypes 2261		Gullmaren, 70 m 1937	Alcohol/ glycerine		R. Huys, London
<i>Scottopsyllus</i> (Sc) <i>pararobertsoni</i> Lang, 1965	523 Stockholm	* Syntypes 2241		Monterey Bay 1960	Alcohol/ glycerine		R. Huys, London

## Tisbidae

Species	Reg. No. Harp.	Type Reg. No.	Number	Location	Preservation	Original species	Comments
<i>Sacodiscus fasciatus</i> (Norman, 1868) ?	F20211 Oslo		5 ♀♀ 4 ♂♂	Norway	Alcohol	<i>Aspidiscus fasciatus</i> Norman, 1868	<i>S. littoralis</i> ?
?	F20212 Oslo		4 ♀♀ 4 ♂♂	Norway	Alcohol	<i>Aspidiscus fasciatus</i>	<i>S. littoralis</i> ?
	169 Stockholm		1 ♀	Ireland, Blacksod Bay, Coll. Farran	Alcohol		<i>S. littoralis</i> ? Crystals
	53201 Bergen		1 ♀	Fanafjorden, 55 m 1967 Drzycimski	Formalin		
<i>Sacodiscus littoralis</i> (Sars, 1904)	F12727 Oslo	* Syntypes	15 ♀♀ 4 ♂♂ 3 Cop.	Norway	Alcohol	<i>Aspidiscus littoralis</i> Sars, 1904	Only 2 ♀♀ determined
	F20213 Oslo		1 ♀ 1 Cop.	Norway	Alcohol	<i>Aspidiscus littoralis</i>	
	191 Stockholm		1 ♀	Gullmaren, 10m, 1934	Alcohol		Crystals, broken
<i>Scutellidium antarcticum</i> (Lang, 1936)	167 Stockholm	* Syntypes 2247	33 ♀♀ 2 Cop.	Type location: Sydgeorgien, 1902	Alcohol/ glycerine	<i>S. antarcticum</i> Lang, 1936	Crystals
<i>Scutellidium longicauda</i> (Philippi, 1840)	168 Stockholm		1 ♀ ♀♀	Bonden, Bohuslän? 1936	-Slide -Alcohol		-Dissected by T. Itô -Not dissected
<i>Tisbe gurneyi</i> (Lang, 1934)	? Stockholm						No type material left (many ♀♀ + ♂♂ Lang, 1948)?



### 8.3 Appendix III. Sampling localities

#### Antarctica

##### Weddell Sea

ANT V/3, 1986, expedition by "R/V Polarstern", samples collected by Dr. habil. Hans-Uwe Dahms.

- Station 10/504, 12.10.1986, 70°30,4'S/8°02,5'W, 300 m
- Station 10/508, 15.10.1986, 72°49,3'S/19°25,0'W, 485 m
- Station 10/520, 20.10.1986, 72°53,3'S/19°34,7'W, 470 m, AGT
- Station 10/528, 22.10.1986, 72°28,0'S/17°23,5'W, 300 m
- Station 10/539, 25.10.1986, 74°06,1'S/24°39,7'W, 519 m
- Station 10/560, 02.11.1986, 73°47'S/24°49,6'W, 500 m
- Station 10/561, 03.11.1986, 72°52,4'S/19°31,2'W, 430 m, AGT
- Station 10/563, 03.11.1986, 72°49,4'S/19°42,8'W, 727 m
- Station 10/566, 04.11.1986, 73°16,3'S/21°05,3'W, 541 m, AGT
- Station 10/573, 06.11.1986, 73°07,9'S/20°14,7'W, 393 m, BG
- Station 10/580, 08.11.1986, 72°59,2'S/19°57,3'W, 460-475 m
- Station 10/585, 11.11.1986, 76°00,9'S/28°15,9'W, 323 m
- Station 10/586, 11.11.1986, 76°08,5'S/28°38,2'W, 324 m
- Station 10/589, 12.11.1986, 75°50,9'S/27°10,6'W, 320 m, AGT
- Station 10/592, 14.11.1986, 73°55,8'S/23°04,0'W, 228-235 m, GSN
- Station 10/594, 15.11.1986, 73°33,0'S/21°50,7'W, 467-445 m, GSN
- Station 10/615, 22.11.1986, 72°51,4'S/19°23,3'W, 404 m, AGT

ANT VII/4, 1989, Epos 3, expedition by "R/V Polarstern", samples collected by Dr. habil. Hans-Uwe Dahms.

- Station 14/234, 30.01.1989, 75°52,5'S/27°45,6'W, 416 m, AGT
- Station 14/241, 01.02.1989, 75°07,1'S/27°59,5'W, 462 m, AGT
- Station 14/295, 21.02.1989, 71°06,6'S/13°31,0'W, 2012 m

ANT IX/2, 1991, expedition by "R/V Polarstern", samples collected by Dr. Barbara Hosfeld.

- Station 18/062, 01.12.1991, 66°03,3'S/32°32,7'W, 4769 m

#### South Shetlands, King George Island, Potter Cove, Jubany Base, 62°14'S/58°40'W

Collected by Dr. Gritta Veit-Köhler:

Transect 1, centre of the cove near Dallmann laboratories:

- 1994: E1: 13.11.-30 m.
- 1995: E1: 06.11.-20 m, 16.11.-20 m, 01.12.-20 m, 16.12.-20m.
- 1996: E1: 05.01.-20 m, 06.01.-29 m, 13.01.-20 m.
- TRCB: 01.02.-20 m, 06.02.-5 m, 06.02.-10 m.

Transect 2, Punta Elephante, entrance of the cove:

- 1994: 23.11.-15m.
- 1995: 30.10-intertidal, algae.
- 1996: TRPE: 22.1.-12 m, 09.02.-20 m, 09.02.-30m.

Collected by Kerstin Elwers, plankton net, vertical:Station I: centre of the cove near Dallmann laboratories

16.03.1996; 18.03.1996; 18.06.1996; 15.11.1996, 24 m; 22.11.1996, 22 m;  
27.11.1996, 22 m; 27.02.1997, 33 m

Punta Elephante, entrance of the cove:

20.02.1996; 24.02.1996; 01.03.1996; 20.03.1996; 24.02.1996

Collected by Lee Hong Jee:

ANT XV/3, 03.1998, expedition by "R/V Polarstern"

Station 48/301.4, 62°16,6'S/58°42,0'W, 398 m, MUC

**Peru-Trench, Discol 3 expedition**

Collected by Dr. Gerd Schriever

MC 348, 08.02.1992, 07°05,019'S/88°26,985'W, 4176 m

MC 357, 16.02.1992, 07°04,406'S/88°27,849'W, 4135 m

MC 362, 17.02.1992, 07°04,532'S/88°27,611'W, 4166 m

**Papua New Guinea**

Collected by Prof. Dr. Horst Kurt Schminke

PNG M4, Ednago Island, near Kavieng, New Ireland, 11.11.1984,  
2°35'S/150°5'E, 1m

PNG M11, Motopure Island, Marine Biological Station University of Papua  
New Guinea, 21.11.1984, 0,5 m, sediment

PNG M12, Motopure Island, Marine Biological Station University of Papua  
New Guinea, 21.11.1984, 0,5 m, 21.11.1984, *Zostera*

**New Ireland Fore-Arc**

SO-133, expedition by "R/V Sonne", 10.07-10.08.1998, near New Ireland;  
samples collected by Dr. Michael Türkay.

Station 1, NW of Simbiri Island, 2°07,17'S/151°33,98'E, 1716 m,  
foraminiferal ooze.

Station 57, base of horst structure South of Edison SMT,  
3°19,37'S/152°35,31'E, 1610 m, sand.

Station 59, top of horst structure South of Edison SMT,  
3°19,34'S/152°35,46'E, 1573 m, sand.

Station 65, NE of Lihir, 2°38,96'S/153°01,92'E, 2040 m.

**Fiji Islands**

CAM1, Viti Levu, Joske Reef west of Suva, 20.08.1984, Grid reference 60K XE  
4093, 3m, collected by Prof. Dr. Horst Kurt Schminke

VL9, Viti-Lem, Coral Coast near Korotogo, 12.1993, collected by Johannes  
Dürbaum.

**Northern Fiji-Basin**

SO-99, 1996, expedition by "R/V Sonne", samples collected by Dr. Michael  
Türkay.

Station 42, no hydrothermal vent, 16°57.72'S/173°57.48'E, 2062 m

Station 93, hydrothermal vent, 16°59.44S/173°54.82E, 1984 m

Station 98, hydrothermal vent, 16°59.49S/173°54.83E, 1992 m

**Sri Lanka,**

SL 35, SL36, Unawatuna, coral Reef, intertidal, 1 m, collected by Dr. H.G. Müller

**Cuba**

Varadero, 1998, culture 09.1999

**USA**

Elliot Bay, Seattle, Washington, 04.1995, collected by Dr. J. Cordell.  
WBN, sand with algae; BM6, stones and sand, with algae; AM, stones with alga,  
BM, stones with algae

**Angola Basin**

Diva 1, M 48/1, 07.2000-08.2000, expedition by "R/V Meteor", collected by Dr. Elke Willen and Dr. Kai George

Station 325/1-7, 19° 58,4' S 002° 59,8' E, 5447 - 5505 m, 14.07.2000

Station 346/1-8, 16° 17,0' S 005° 27,0' E, 5388 - 5390 m, 27.07.2000

**Great Meteor Seamount**

Expedition by "R/V Meteor"

", 1998, M42/3, collected by Prof. Dr. P. Martínez Arbizu

Station 451: GKG, 455 m, 30°08,4'N, 28°34,8'W, 01.09.1998.

Station 515, 09.1998.

**Italy**

Sardinia, collected by Thorsten D. Künnemann

Venice, 1985, collected by Dr. B. Battagliai, culture: 1997

**Spain**

Valencia, 1994, collected by Prof. Dr. P. Martínez Arbizu, culture: 1997

Cullera, 01.1995, collected by Prof. Dr. P. Martínez Arbizu

**France**

Concarneau, 4°00'W, 47°59'N, 08.1996, collected by Thorsten D. Künnemann.

**Belgium**

Oostende, culture: 1997

**Germany**

Collected by Sybille Seifried:

Baltrum, 21.09.1992

Borkum, 04.07.1996

Cridumer Siel, 02.03.1994

Dangast, 19.05.1996

Helgoland, 13.06.91, 06.1994

Spiekeroog, 06.07.1994

Wilhelmshaven, Banter See, 13.07.1991

Collected by Dr. Peter Rumm:

Echthausen, 12.05.1992

Collected by James T. Enright:  
Aschaffenburg, 09.1999

### **NO-Atlantic**

Expedition by FS Meteor, 1998, M42/2, collected by Dr. Bernd Christiansen  
St. 419, 4853 m, 48°58'N, 16°27,9'W, 14.8.1998, hyperbenthos, Hol04,  
MOC4; L3, mab 10,2-17,4.

### **White Sea**

21.08.1986, collected by Dr. L. L. Chislenko, St. Petersburg

### **Arctic Ocean**

ARK IX/4, 1993, expedition by "R/V Polarstern", samples collected by Prof. Dr.  
Pedro Martínez Arbizu.

Barents Sea, Station 27/022, 21.08.1993, 82°09,7'N/42°02,7'E, 1024 m, GKG

Vilkitsky Strait, Station 27/028, 26.08.1993, 78°01,99'N/102°01,99'E, 149 m

Laptev Sea, Station, 27/052, 11.09.1993, 77°03,58'N/125°00,01'E, 2332 m,  
GKG

Laptev Sea Station, 27/053, 12.09.1993, 79°13,64'N/122°51,29'E, 3237 m,  
MUC

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