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Phylogenetic relationships at the base of Oligoarthra (Copepoda, Harpacticoida) with a new species as the cornerstone**

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Abstract

Romete bulbiseta gen. et sp. nov. (Aegisthoidea Giesbrecht, 1892: Rometidae fam. nov.) is described from the Great Meteor Seamount, northeast Atlantic. An analysis of the phylogeny and evolution of the basal Harpacticoida Sars, 1903 is presented. Cerviniidae Sars, 1903 and Cervinioidea Sars, 1903 are respective junior synonyms of Aegisthidae Giesbrecht, 1892 and Aegisthoidea Giesbrecht, 1892. Rometidae fam. nov. is identified as sistertaxon of Aegisthidae. Rotundiclipeidae Huys, 1988 and Styracothoracidae Huys, 1993 are removed from Aegisthoidea and placed in Syngnatharthra tax. nov., sistergroup of Aegisthoidea. "Maxillipedasphalea" Lang, 1944 is polyphyletic and therefore not maintained here. A morphological analysis of taxa of Harpacticoida reveals the autapomorphies of Rometidae, Aegisthidae, Aegisthoidea, Syngnatharthra, and Oligoarthra Lang, 1944. Diagnoses for these taxa are given.

Key words: Rometidae, Aegisthidae, Cerviniidae, Syngnatharthra, autapomorphies, phylogeny

Introduction

Harpacticoida is a highly successful group of Copepoda Milne Edwards, 1840 in terms of speciosity and adaptive radiation. It has diversified mainly in marine but also in freshwater benthic habitats, where its species have a profound ecological impact. From these benthic origins a number of planktonic as well as parasitic forms have evolved independently. Lang (1944) divided Harpacticoida into Polyarthra Lang, 1944, containing Longipediidae Sars, 1903 and Canuellidae Lang, 1944, and Oligoarthra containing all other taxa. The monophyly of a taxon Harpacticoida containing Polyarthra and Oligoarthra was considered doubtful by some later authors (Tiemann 1984, Dahms 1990, Willen 2000, Seifried 2002). Instead, Polyarthra should possibly be separated from Harpacticoida, and as a consequence Oligoarthra would fall as identical with Harpacticoida. Oligoarthra is enormously rich in species. Wherever samples are taken new species are discovered. In the deep sea the proportion of new species described within Oligoarthra amounts to almost 100 percent.

One of these deep-sea species is described here because it exhibits an interesting combination of characters which sheds light on the phylogenetic relationships within Oligoarthra as a whole. There is as yet no phylogenetic system available to help understand their evolutionary success. The only comprehensive attempt so far to elucidate relationships within Harpacticoida was undertaken by Lang (1948), but his system is outdated because it was based not only on apomorphic but also on plesiomorphic characters. A few studies (Huys 1990, Huys & Lee 1999, Martínez Arbizu & Moura 1994, Willen 1999, 2000, 2002) have been published recently which will be complemented here. A character list, a data matrix (Table 1) and a diagram of the phylogenetic relationships at the base of Oligoarthra (Fig. 7) will be presented together with the autapomorphies of the taxa involved.

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Methods and material

Taxonomy

All specimens were preserved in 5% buffered formalin and subsequently transferred into glycerine. The dissected specimens are 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 descriptive terminology is adopted from Huys & Boxshall (1991). Abbreviations used in the text are: aes = aesthetasc; enp = endopod; enp-1(2, 3) = proximal (middle, distal) segment of endopod; exp = exopod; MUC = Multicorer; P1-P6 = first to sixth thoracopod.

Parsimony analysis and phylogeny

The methods of phylogenetic systematics were applied (Hennig 1950, 1966, 1982, Ax 1984, Wägele 2000) to infer phylogeny of Oligoarthra on the basis of morphological characters. In order to discern monophyletic taxa the study started at the species level. Calanoida Sars, 1903, Misophrioida Gurney, 1933 and Polyarthra were used as outgroups to polarise characters. Every group of species for which strong autapomorphies were found was recognized as a monophyletic group and its groundpattern was reconstructed. The groundpattern represents the hypothetical morphology of the last common population of the species group in question. The sistergroup of this 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.

Computer cladistics was used as a second technique to learn something about the relationships of species of Oligoarthra, but these investigations are published in additional papers (see Seifried 2002). A first analysis was made with species selected from the over 3000 species of Harpacticoida. Secondly, an analysis on the basis of reconstructed groundpatterns was made with all Oligoarthra, united in 17 monophyletic taxa characterised by strong autapomorphies, mainly traditional “families” (Seifried 2002). The Calanoida, Misophrioida and Polyarthra were again used as outgroups there to root the cladograms.

Species of Aegisthoidea examined for phylogenetic analysis

The following list includes material from museums of Oslo, Stockholm and Bergen. The Swedish Museum of Natural History in Stockholm keeps the K. Lang Collection, the Zoological Museum in Oslo the G. O. Sars Collection, and the Zoological Museum in Bergen stores some material collected by I. Drzycimski and F. D. Por. The present first author has visited these museums in the summer and autumn of 1997.

Romete bulbiseta gen. et sp. nov. (male, Great Meteor Seamount, M42/3, St. 451, 455 m, 01.09.1998); *Romete* spec. (male, Angola Basin, Diva 1, M48/1, 346/6, MUC 1, 5389 m, 27.07.2000).

Aegisthidae gen. spec. 1 (female, Antarctic, Weddell Sea, ANT V/3, 10/592, 1986); Aegisthidae gen. spec. 2 (female, Fiji Basin, SO-99, station 42, 1996); Aegisthidae gen. spec. 3 (male, Fiji Basin, SO-99, station 98, 1996); Aegisthidae gen. spec. 4 (male, Angola Basin, Diva 1, M48/1, St. 346/1, MUC 5, 27.07.2000); Aegisthidae gen. spec. 5 (female, Angola Basin, Diva 1, M48/1, St. 346/1, MUC 1, 27.07.2000); *Aegisthus* spec. (females, NE-Atlantic, M42/2, station 419, 1998); *Andromastax* spec. (females, NE-Atlantic, M42/2, station 419, 1998); *Brotskayaia* cf. *tenuiseta* (Brodskaya, 1963) (female, Angola Basin, Diva 1, M48/1, St. 346/4, MUC 5, 27.07.2000); *Cervinia bradyi* Norman, 1878 (females, male, Museum Bergen, Oslo, Stockholm); *Cervinia pilosa* Lang, 1948 (females, Museum Stockholm); *Cervinia synarthra* Sars, 1910 (females, Museum Bergen, Oslo, Stockholm); *Cervinia* spec. 1 (female, copepodite, Antarctic, Weddell Sea, ANT IX, 18/062, 1991); *Cervinia* spec. 2 (male, Angola Basin, Diva 1, M48/1, St. 346/1, MUC 5, 27.07.2000); *Cervinia* spec. 3 (female, New Ireland Fore-Arc, SO-133, St. 57, 1998); *Cervinia* spec. 4 (female, New Ireland Fore-Arc, SO-133, St. 65, 1998); *Cervinia* spec. 5 (female, New Ireland Fore-Arc, SO-133, St. 57, 1998); *Cerviniella* spec. 1 (female, Antarctic, Weddell Sea, ANT V/3, 10/563, 1986); *Cerviniella* spec. 2 (females, males, copepodites, Angola Basin, Diva 1, M48/1, St. 325, St. 346, 07.2000); *Cerviniopsis clavicornis* Sars, 1903 (females, males, copepodites, Museum Bergen, Oslo, Stockholm); *Cerviniopsis intermedia* Lang, 1936 (female, Museum Stockholm); *Cerviniopsis longicaudata* Sars, 1903 (females, Museum Oslo); *Eucanuella spinifera* T. Scott, 1900 (females, males, copepodites, Museum Bergen, Oslo, Stockholm); *Eucanuella* cf. *langi* Por, 1964 (male, Angola Basin, Diva 1, M48/1, St. 346/4, MUC 4, 27.07.2000); *Expansicervinia* spec. 1 (female, New Ireland Fore-Arc, SO-133, St. 59, 1998); *Expansicervinia* spec. 2 (female, New Ireland Fore-Arc, SO-133, St. 1, 1998); *Hemicervinia stylifera* (I. C. Thompson, 1893) (females, Museum Bergen, Oslo, Stockholm); *Pontostratiotes horrida* Brodskaya, 1959 (female, New Ireland Fore-Arc, SO-133, St. 57, 1998); *Stratiopontotes* spec. (female, Arctic, ARK IX/4, 27/022, 1993).

Systematics

Lang (1944, 1948), Bodin (1997) and all later articles that dealt with the systematics of Harpacticoida are the basis of the systematics presented below. The justifications for the systematic changes made here are given in the section dealing with the respective taxa. However, for reasons of clarity the new systematics is applied from here on.

The following changes and additions to harpacticoid systematics are introduced:

- Aegisthidae Giesbrecht, 1892 is the senior synonym of Cerviniidae Sars, 1903.
- 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.

- Aegisthoidea enclose only Rometidae fam. nov. and Aegisthidae, whereas Styracothoracidae Huys, 1993 and Rotundiclipeidae Huys, 1988 are integrated in Syngnatharthra tax. nov.
- Syngnatharthra tax. nov. is established to enclose all taxa of Oligoarthra except Aegisthoidea, which is the sistergroup of Syngnatharthra.
- “Maxillipedasphalea” Lang, 1944 is polyphyletic and therefore not maintained here. Chappuisiidae Chappuis, 1940, Darcythompsoniidae Lang, 1936, Ectinosomatidae Sars, 1903, Neobradyidae Olofsson, 1917, and Phyllognathopodidae Gurney, 1932 are integrated in Syngnatharthra tax. nov.

Descriptions

Rometidae fam. nov.

Type and only genus: *Romete* gen. nov.

Diagnosis (autapomorphies underlined)**:** Deep depressions with reticular ornamentations lateral in anterior half of cephalic shield. First pedigerous somite completely fused to dorsal cephalic shield. Enp-2 of antenna with 1 spine (I) and 3 setae (2–4) laterally: element 3 forming a seta. Distal segment of mandibular exopod extremely minute. Maxilliped 3-segmented, with syncoxa, basis and 1-segmented endopod, enp-1 and enp-2 fused. Two outer spines of exp-3 P1 elongate. Distal outer corner of enp-2 of P2–P3 produced into spinous process; enp-3 of P2–P4 becomes slender in distal half, the step strengthened by cuticular thickening.

Male. Exopod P5 3-segmented, with 1-0, 0-1, 1-3-1 or 1-0, 0-1, 1-2-1 setae.

Romete gen. nov.

Type and only species: *Romete bulbiseta* sp. nov.

Diagnosis: Identical to that of Rometidae fam. nov.

Etymology: An anagram of Meteor, the name of the research vessel and the seamount where the new species was discovered.

Gender: Feminine.

Romete bulbiseta sp. nov.

Type material: Holotype male, dissected and mounted on 13 slides, deposited in the Copepod Collection of the AG Zoosystematik und Morphologie, University of Oldenburg, Germany (UNIOL Coll. No. 2001.039/1-2001.039/13); Atlantic Ocean, Great Meteor Seamount, 30°08.4′N, 28°34.8′W, 455 m, Giant Box Corer; leg. Prof. Dr. P. Martínez Arbizu during expedition with RV “Meteor”, M42/3, St. 451, 01.09.1998.

Description from male holotype: Body length 360 µm, measured from anterior margin of cephalic shield to posterior margin of caudal rami; length of caudal rami 32.2 µm.

Body (Fig. 1A–D) without distinction between prosome and urosome. Prosome consists of cephalothorax and 3 free pedigerous somites; first pedigerous somite completely fused to dorsal cephalic shield; deep depressions lateral in anterior half of cephalic shield, cuticle with reticular ornamentation. Urosome 6-segmented, consists of somites bearing P5 and P6, and 4 free abdominal somites; 2 spermatophores. Cephalothorax and body somites, except penultimate one, with sensillae and pores. All hyaline frills plain; hyaline frills of cephalothorax and following 5 somites reticulated. P6-bearing somite and following 4 somites with rows of small spinules. Last three abdominal somites with one row of larger spinules ventrally and laterally.

Nauplius eye not confirmed.

Rostrum not defined at base (Figs. 1A, 2A).

Anal operculum (Fig. 1A, B) plain.

Caudal rami (Fig. 1) 2 times longer than wide, probably with 7 setae; seta III (Figs. 1E, 6B) presumably broken off on both sides.

Antennule (Fig. 2A) 13-segmented; with geniculation between segments 8 and 9; 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 (Fig. 2B, C) 4-segmented, composed of 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.

Mandible (Fig. 3A, B) with coxa bearing well-developed gnathobase; cutting edge with 1 seta at proximal corner; palp consists of basis, endopod and exopod; basis with 3 spines and 1 seta; endopod 1-segmented bearing 1 spine and 2 setae laterally and 6 distal setae, 2 distal setae fused at base; exopod with 2, 1, 1, 2 setae, distal segment extremely minute, difficult to observe.

Maxillule (Fig. 3C) composed of praecoxa, coxa, exopod, and basis fused with endopod; praecoxal arthrite: anterior surface in outer half with 2 juxtaposed setae (1 + 2), apically 2 rows of spines with 3 anterior and 4 posterior spines (2 posterior spines with 2 long spinules), as well as 1 smaller, flexible seta (10) inserting on anterior surface, apical inner margin with 2 plumose setae (11 + 12), posterior surface with 2 proximal setae (13 + 14); coxa with 6 setae, epipodite represented by 4 setae; basis and endopod of maxillule are fused to one segment with characteristic rectangular shape, all 14 setae insert at distal edge; exopod with 4 setae.

Maxilla (Fig. 3D, E) composed of syncoxa, allobasis, and 3-segmented endopod; syncoxa with 4 endites with 4, 3, 3, 3 setae; allobasis fused with strong claw (I); ac-

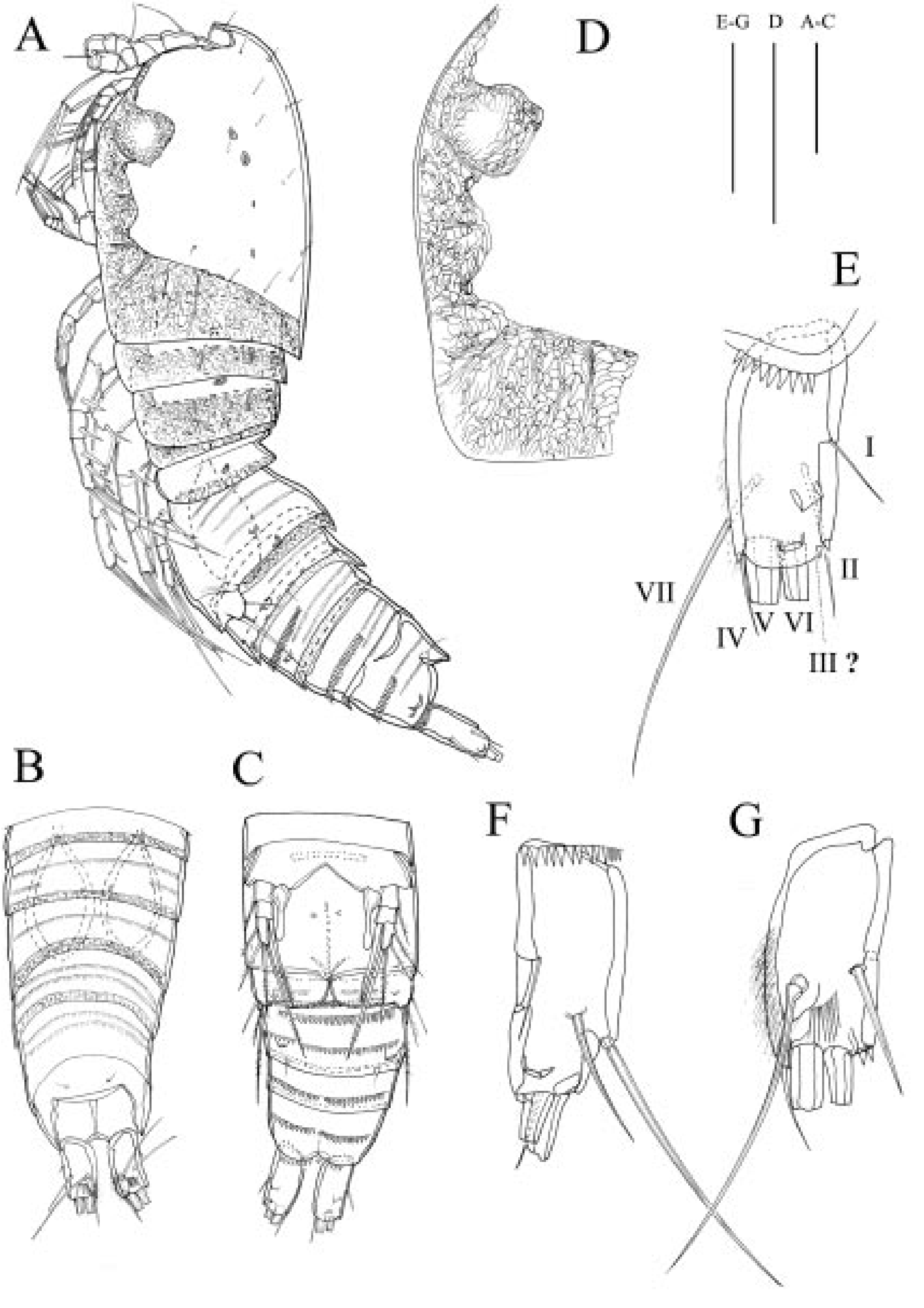

Fig. 1. *Romete bulbiseta* gen. et sp. nov., holotype male. A. Habitus, lateral. B. Urosome, dorsal. C. Urosome, ventral. D. Cephalothorax, lateral. E. Caudal ramus, ventral. F. Caudal ramus, lateral. G. Caudal ramus, dorsal. Scale bars: A–D 50 µm; E–G 20 µm.

Fig. 2. *Romete bulbiseta* gen. et sp. nov., holotype male. A. Antennule and rostrum. B. Antenna, lateral setae of distal endopod segment omitted. C. Antenna, distal endopod segment with lateral setae, distal setae omitted. D. Maxilliped. Scale bars: 20 µm.

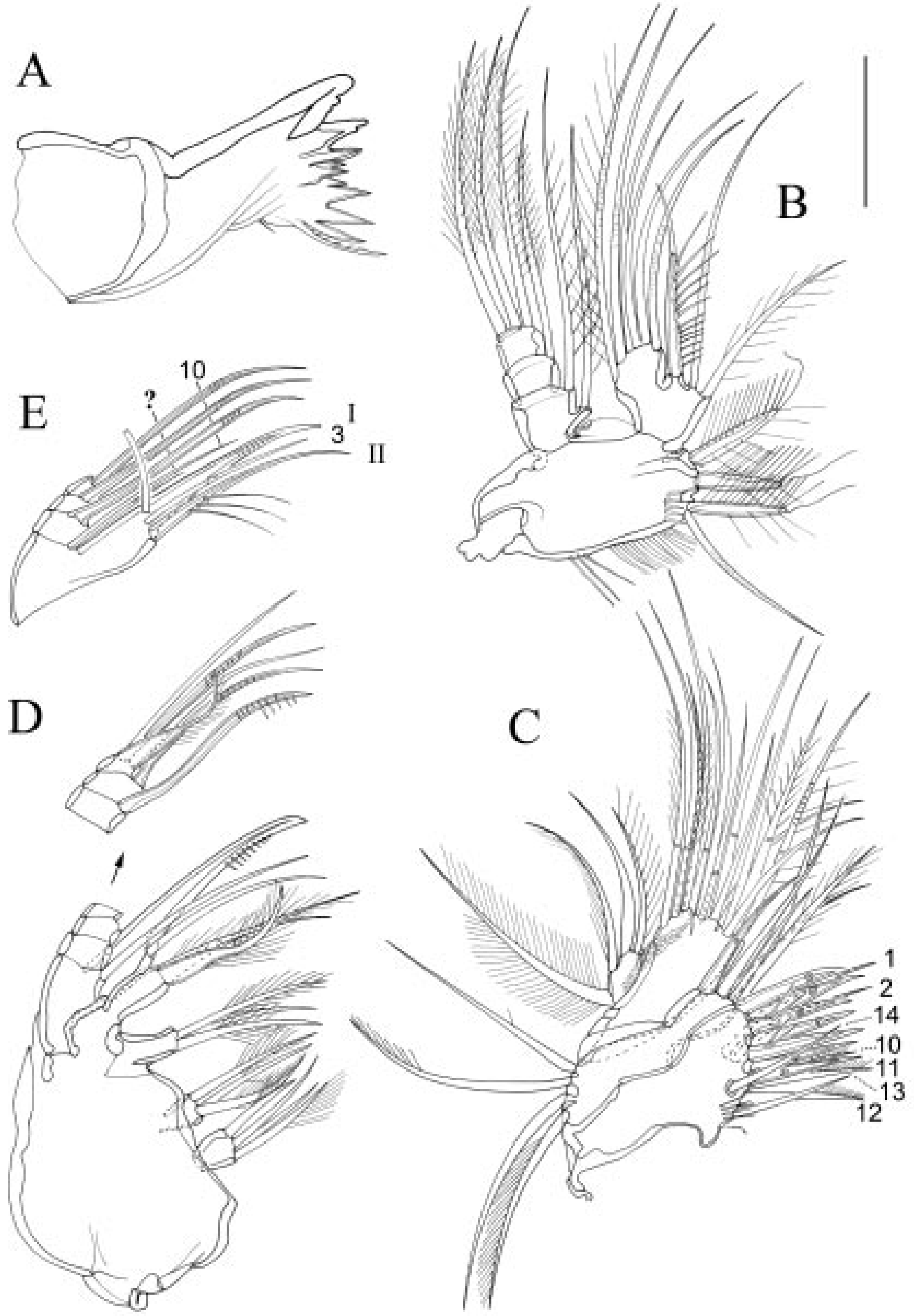

Fig. 3. *Romete bulbiseta* gen. et sp. nov., holotype male. A. Coxa of mandible. B. Palp of mandible. C. Maxillule. D. Maxilla, posterior. E. Maxilla, allobasis and endopod, anterior. Scale bar: 20 µm.

cessory armature of fused basis consisting of 1 curved spine (II), 1 seta (3) and 1 long hyaline tube pore on anterior surface, and a seta (4) on posterior surface; endopodal armature of allobasis consisting of displaced seta 10 between anterior and posterior surface, an additional seta closely set to seta 10, and seta 11 on posterior surface; endopod with armature formula: 2, 2, 4.

Maxilliped (Fig. 2D) 3-segmented, composed of syncoxa, basis and 1-segmented endopod; syncoxa with incorporated coxal 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 inwards with 4 setae and 2 spines.

P1–P4 (Figs. 4, 5) with 3-segmented rami, distal inner corner of endopod-2 P2–P3 produced into

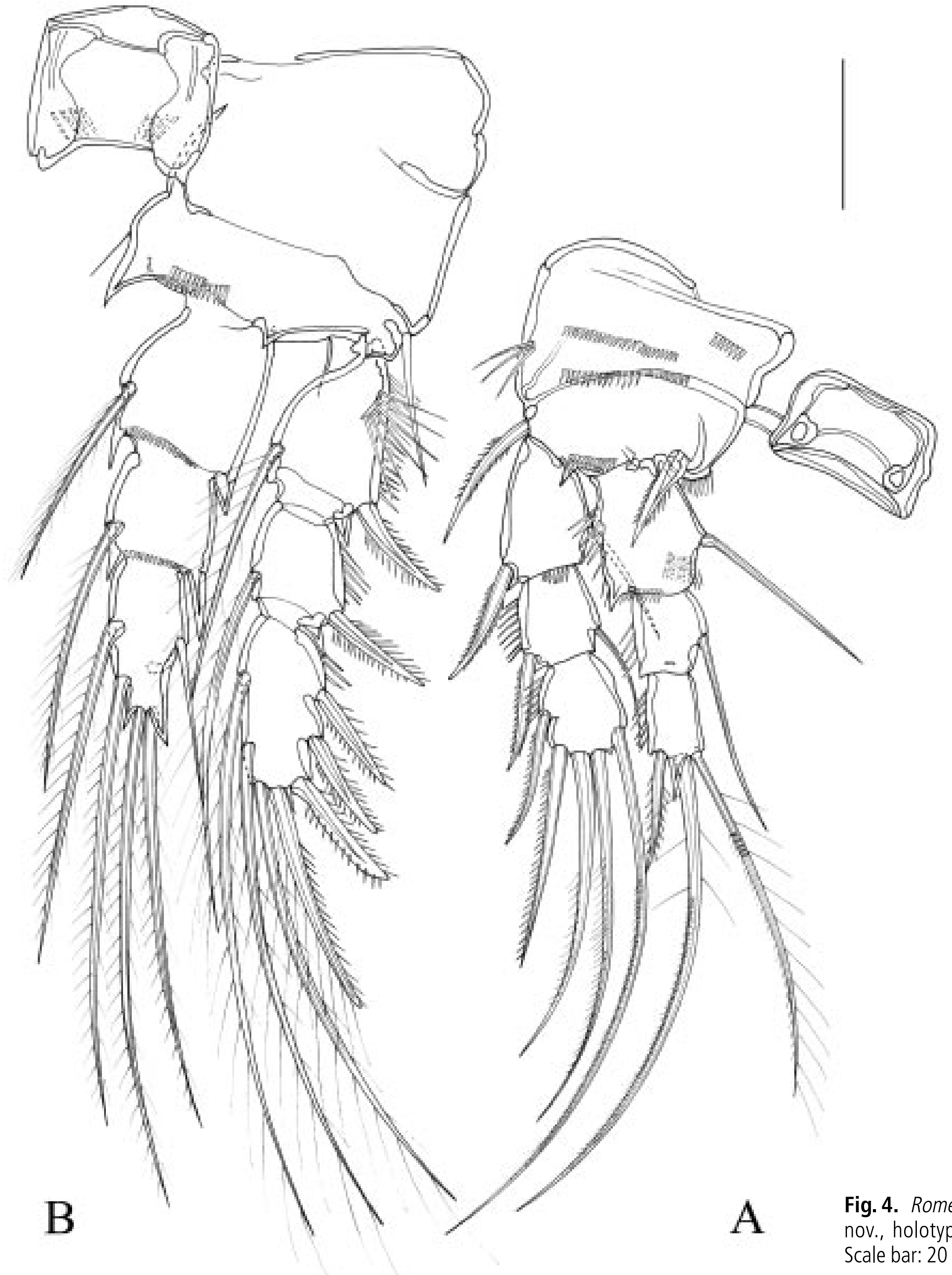

Fig. 4. *Romete bulbiseta* gen. et sp. nov., holotype male. A. P1. B. P2. Scale bar: 20 µm.

spinous process; enp-3 of P2–P4 becomes slender in distal half, the step strengthened by cuticular thickening; two outer spines of exp-3 P1 elongate; 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; II-I+1-2	0-1; 0-1; 1-2-3
P4	0-0	1-0	I-1; I-1; II-I+1-2	0-1; 0-1; 1-2-2

P5 (Fig. 6A) fused medially; endopodal lobe with 1 seta, which is broad and hyaline at the apex and bulbous at the base; 3-segmented exopod with 1-0, 0-1, 1-2-1 setae.

P6 (Fig. 6A) symmetrical with 3 setae.

Female unknown.

Etymology: The species name alludes to the bulbous base of the endopodal seta of the male P5.

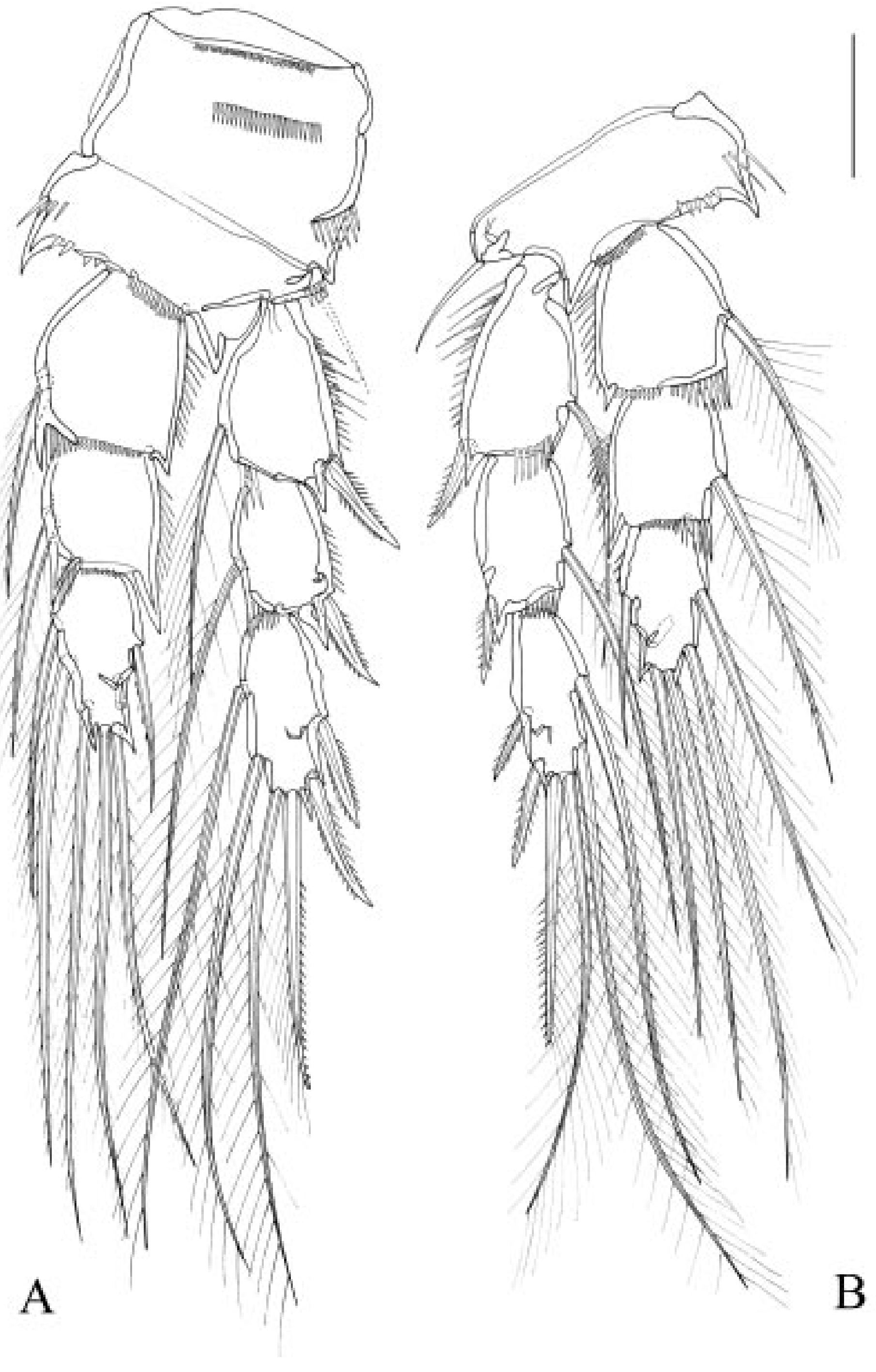

Fig. 5. *Romete bulbiseta* gen. et sp. nov., holotype male. A. P3. B. P4. Scale bar: 20 µm.

Remarks: Another single male of a different species of Rometidae was found in the deep sea of the Angola Basin (*Romete* spec.; DIVA 1, see list of material; Fig. 6B). As the sorting of the rich material is still in progress, it is hoped that females will soon be found to allow description.

It is highly probable that *Romete bulbiseta* does possess seta III on the caudal ramus. On both caudal rami the typical hole can be seen which results when a seta is broken off (Fig. 1E). Seta III is visible in *Romete* spec. (Fig. 6B).

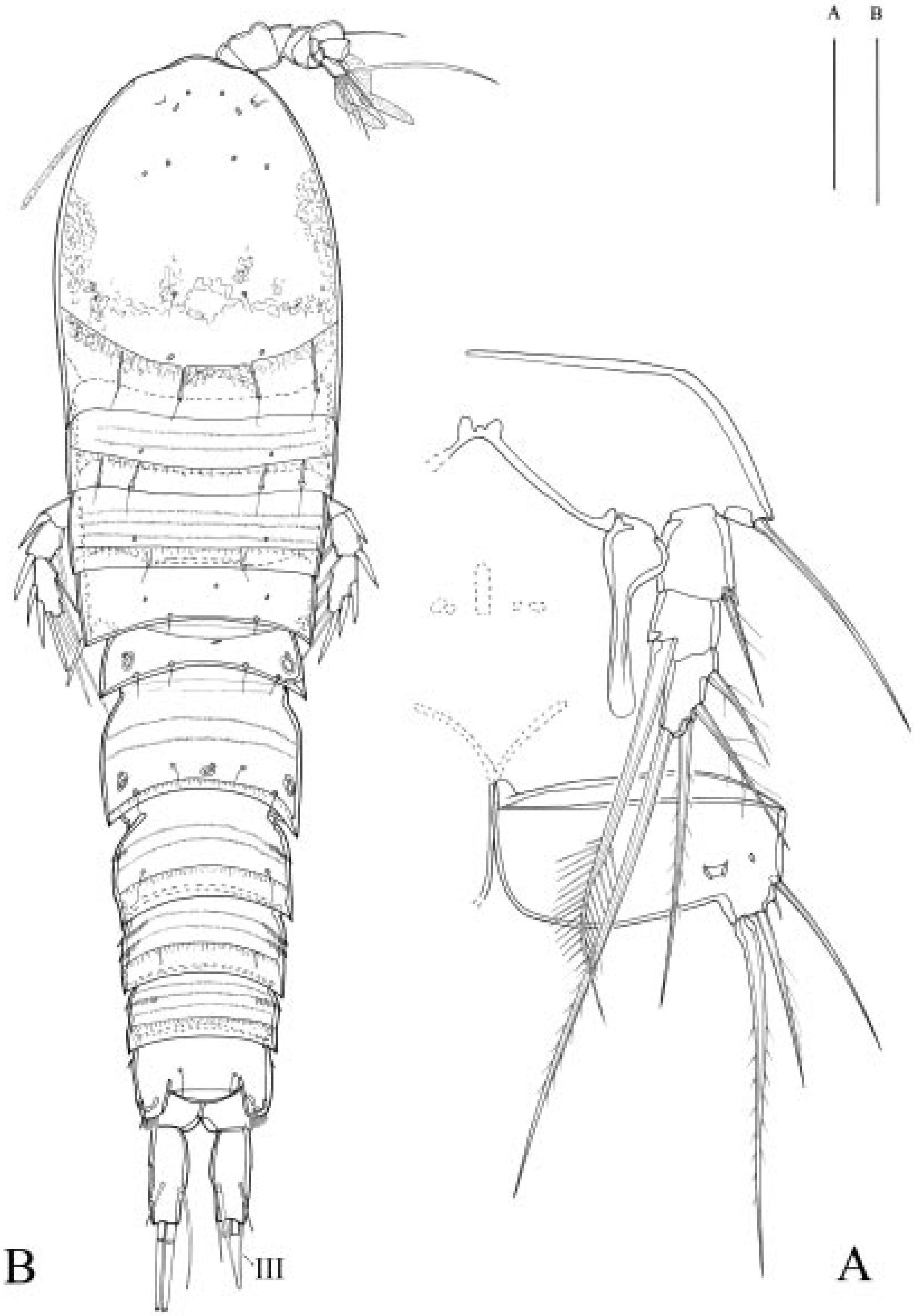

Fig. 6. A. *Romete bulbiseta* gen. et sp. nov., holotype male; P5 and P6. B. *Romete* spec.; habitus, dorsal. Scale bars A: 20 µm; B: 100 µm.

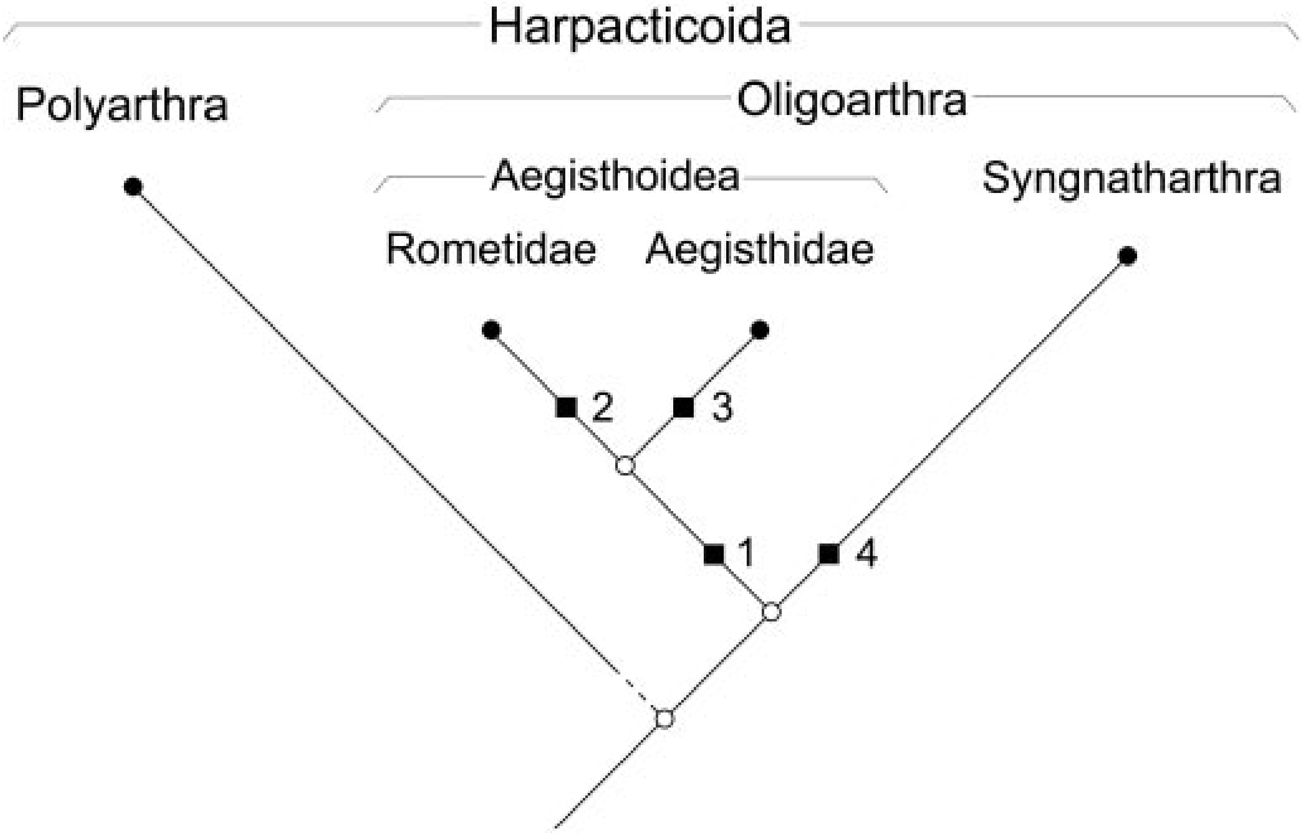

Fig. 7. Diagram of phylogenetic relationships within Harpacticoida. Character set 1: char. 9: 0→1, char. 14: 0→1, char. 17: 0→1, char. 30: 0→1, char. 33: 0→1, char. 34: 0→1. Character set 2: char. 1: 0→1, char. 2: 0→1, char. 8: 1→0, char. 12: 0→1, char. 21: 0→1, char. 25: 0→1, char. 26: 0→1, char. 27: 0→1, char. 36: 0→1 or 2→1. Character set 3: char. 3: 0→1, char. 5: 0→1, char. 6: 0→1, char. 7: 0→1, char. 10: 0→1, char. 11: 0→1, char. 13: 0→1, char. 15: 0→1, char. 18: 0→1, char. 28: 0→1, char. 29: 0→1, char. 31: 0→1, char. 32: 0→1, char. 35: 0→1, char. 37: 0→1. Character set 4: char. 2: 0→1, char. 4: 0→1, char. 13: 0→1, char. 16: 0→1, char. 19: 0→1, char. 20: 0→1, char. 21: 0→1, char. 22: 0→1, char. 23: 0→1, char. 24: 0→1.

Table 1. Data matrix of characters of Oligoarthra. Same characters as in the character list. ? = missing data. No autapomorphies of Oligoarthra are added.

Taxon Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Calanoida	0	0	0	1	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	?
Polyarthra	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0
Rometidae	1	1	0	0	?	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0
Aegisthidae	0	0	1	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0	0
Syngnatharthra	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	1

Taxon Character	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Calanoida	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	1	0
Polyarthra	0	0	0	0	0	0	0	0	0	?	?	?	1	0	0	3	0
Rometidae	1	0	0	0	1	1	1	?	?	1	0	0	1	1	0	1	0
Aegisthidae	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	1
Syngnatharthra	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0

Phylogenetic relationships at the base of Oligoarthra

The new species shows an interesting combination of characters. To assess its phylogenetic relationships a comprehensive study of the basal Oligoarthra was advantageous (Fig. 7).

List of characters

This character list contains only abbreviated representations of the individual character states. More detailed descriptions can be found below (Discussion of characters and Taxa of Oligoarthra sections) and in Seifried (2002). Character states are here given as (0) to (3). Characters and their states according to the character list and the character matrix (Table 1) are marked in the text as follows: transformation of, e.g., character 1 from character state (0) to state (1) is symbolized by char. 1: 0 →1. The autapomorphies supporting the phylogenetic relationships within Harpacticoida are summarized in character sets carrying the number of the branch leading to the respective taxon (Fig. 7). For example, the autapomorphies of Syngnatharthra are summarized in character set 4 which contains characters 2, 4, 13, 16, 19, 20, 21, 22, 23, and 24 (see section on Syngnatharthra below). The most plesiomorphic state of a character within Copepoda and Oligoarthra is marked with P (= plesiomorphy). The more derived character states within Copepoda and Oligoarthra are marked with A (= apomorphy).

Body

Char. 1. (0) No deep depressions laterally in anterior half of cephalic shield; reticular ornamentation of cuticula of cephalic shield and following somites sometimes present; P. (1) Deep depressions with reticular ornamentation laterally in anterior half of cephalic shield; A.

Char. 2. (0) P1-bearing somite not fused to cephalosome; P. (1) P1-bearing somite and cephalosome fused forming a cephalothorax; A.

Char. 3. (0) Anal somite not longer than wide, and not tapering; P. (1) Anal somite elongate, tapering posteriorly; A.

Char. 4. (0) Male with 2 spermatophores; P. (1) Male with 1 spermatophore; A.

Antennule of female

Char. 5. (0) Oligoarthran segments 3 and 4 separate (copepod segments III–VIII and IX–XIV); P. (1) Oligoarthran segments 3 and 4 fused (copepod segments III–VIII and IX–XIV); A.

Antenna

Char. 6. (0) Basis and proximal endopod segment separate; P. (1) Allobasis or basis and proximal endopod segment incompletely fused; A.

Char. 7. (0) Second endopodal segment with more than 4 setae (3- or 4-segmented endopod), or distal endopod segment with 4 or more lateral setae and spines (2-segmented endopod); P. (1) Distal endopod segment laterally with 1 spine and 2 setae, spine I lacking (2-segmented endopod); A.

Char. 8. (0) Lateral element 3 of distal endopod segment forming a seta; P. (1) Lateral element III of distal endopod segment forming a spine; A.

Mandible

Char. 9. (0) 2-segmented endopod with setae on enp-1, or 1-segmented endopod with setae laterally; P. (1) Endopod with 1 spine and 2 setae laterally; A.

Char. 10. (0) 2-segmented endopod, or 1-segmented endopod considerably smaller than basis and at most 1.5 times longer than wide; P. (1) Endopod of one large segment, at least 2 times longer than wide; A.

Char. 11. (0) Exopod 5-segmented, or 4-segmented and proximal segment not much longer than wide; P. (1) Proximal segment of exopod elongate, considerably longer than remaining segments and at least 3 times longer than wide; A.

Char. 12. (0) Distal segment of exopod not minute, maybe small but segment clearly visible; P. (1) Distal segment of exopod extremely minute; A.

Maxillula

Char. 13. (0) Epipodite of coxa represented by more than 3 setae; P. (1) Epipodite of coxa represented by 2 or 3 setae; A.

Char. 14. (0) Endopod not fused with basis; P. (1) Endopod fused with basis, forming a rectangular segment, and all setae inserting at distal edge; A.

Char. 15. (0) Exopod well developed, with more than 3 setae; P. (1) Exopod reduced in size, with 3 setae; A.

Maxilla

Char. 16. (0) Endites of praecoxa not fused; P. (1) Endites of praecoxa fused; A.

Char. 17. (0) Proximal endopod segment of Copepoda free, with 4 setae; or fused with basis, with 2 anterior setae and 1 posterior seta; P. (1) Proximal endopodal segment of Copepoda fused with basis; endopodal element 11 on posterior side; endopodal seta 10 of allobasis inserting between anterior and posterior surface, seta 9 absent or inserting near seta 10 but on anterior surface, an additional seta very closely set to endopodal seta 10; A.

Char. 18. (0) All elements of proximal endopod segment of Copepoda developed as setae, sometimes proximal endopod segment fused with basis to form an allobasis; P. (1) Posterior endopodal element 11 of allobasis developed as large, strong spine; A.

Maxilliped

Char. 19. (0) Syncoxa, or praecoxa and coxa combined, with 11, 10 or 7 setae and spines on inner border; P. (1) Syncoxa with 6 setae and spines, one seta of proximal endite lost; A.

Char. 20. (0) Without joint between basis and endopod; P. (1) With highly flexible joint between basis and endopod; A.

Char. 21. (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, or indistinctly 2-segmented, or 1-segmented; A.

Char. 22. (0) Endopod without a claw; P. (1) Endopod 2-segmented and enp-1 with a small claw displaced to posterior side of distal end, and with 2 lateral setae; A.

Char. 23. (0) Enp-2 or distal endopod segment with 4 spines and setae, or with more than 4 setae; no geniculated setae; P. (1) Enp-2 with 2 geniculated distal setae (3 + 4) and 2 small outer setae (1 + 2); A.

P1

Char. 24. (0) Exp-1 with 1 inner seta; P. (1) Exp-1 without inner seta; A.

Char. 25. (0) No outer spines of exp-3 of P1 elongate; P. (1) Only 2 outer spines of exp-3 of P1 elongate; A.

P2–P4

Char. 26. (0) Distal outer corner of enp-2 of P2-P3 not produced into spinous process; P. (1) Distal outer corner of enp-2 of P2-P3 produced into spinous process; A.

Char. 27. (0) Distal end of enp-3 of P2-P4 not slender, or the whole enp-3 long and slender; P. (1) Enp-3 of P2-P4 becomes slender in distal half, the step strengthened by cuticular thickening; A.

P5 of female

Char. 28. (0) With endopod or endopodal lobe; P. (1) Without endopodal lobe; A.

Char. 29. (0) Exopod 3-segmented, or exopod 1-segmented and less than 1.5 times as long as wide; P. (1) Exopod 1-segmented, more than twice as long as wide; A.

Antennule of male

Char. 30. (0) Oligoarthran segments 2 and 3 separate (copepod segments II and III–VIII); P. (1) Oligoarthran segments 2 and 3 fused (copepod segments II and III–VIII); A.

Char. 31. (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.

Char. 32. (0) Oligoarthran segments 12 to 14 separated (copepod segments XXIV to XXVIII); P. (1) Oligoarthran segments 12 to 14 fused to one segment (copepod segments XXIV to XXVIII); A.

P5 of male

Char. 33. (0) Coxa and basis separate; P. (1) Coxa and basis fused; A.

Char. 34. (0) Endopod separate from basis; P. (1) Endopod fused to basis; A.

Char. 35. (0) With endopod or endopodal lobe; P. (1) Without endopodal lobe; A.

Char. 36. (0) 3-segmented exopod with 1-0, 1-1, 1-3-1 or more setae; P. (1) 3-segmented exopod with 1-0, 0-1, 1-3-1 setae; A. (2) 3-segmented exopod with 1-0, 1-1, 1-2-1 setae; A. (3) Exopod 1-segmented; A.

Caudal rami

Char. 37. (0) Caudal rami not more than twice as long as wide; P. (1) Caudal rami clearly more than twice as long as wide; A.

Discussion of characters

Char. 1 (cephalic shield): Rometidae is characterized by the deep lateral depressions with reticular ornamentations in the anterior half of the cephalic shield (Fig. 1A, D). These structures are unique within Harpacticoida. In some species of Aegisthidae, the cuticula of the cephalic shield and the following somites is also reticulated. This ornamentation is well presented in the descriptions of Aegisthidae by Itô (1982, 1983), Conroy-Dalton & Huys

(1999) and Lee & Huys (2000); e.g. *Cervinia plumosa* Itô, 1983, *Andromastax muricatus* Conroy-Dalton & Huys, 1999, *Jamstecia terazakii* Lee & Huys, 2000. In many other descriptions of Aegisthidae this reticulation is not mentioned, despite its presence in species of most aegisthid genera. The reticular ornamentation may be a further autapomorphy of Aegisthoidea. However, the deep, round lateral depressions of Rometidae specimens are not mentioned in any description of Aegisthidae and could not be found on any investigated specimen.

Char. 2 (first pedigerous somite): Most Oligoarthra have a cephalothorax, as the first pedigerous somite is fused to the cephalosome (Fig. 1A).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. However, some species of Syngnatharthra have a first pedigerous somite that was secondarily separated from the cephalosome. Species of Chappuisiidae, Phyllognathopodidae, and some Latiremidae Bozic, 1969 have a completely separate 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* Martínez Arbizu & Moura, 1998 (Novocriniidae Huys & Iliffe, 1998), *Rotundiclipeus canariensis* Huys, 1988 (Rotundiclipeidae), and some species of Tachidiidae Sars, 1909 (e.g. *Tachidius (Tachidius) discipes* Giesbrecht, 1881) 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 separate, 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 (Seifried 2002). A completely or incompletely separated first pedigerous somite is probably more common in Oligoarthra, as can be seen in TEM observations (B. 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 males of Rometidae and in males and females of *Cerviniella* Smirnov, 1946 (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. 3 (anal somite): Only species of Aegisthidae have an elongate and posteriorly tapering anal somite. This form is a consequence of the form of the caudal rami and can be found in all species of Aegisthidae. The outer edges of the caudal rami are always the continuation of the outer edges of the anal somite. As the caudal rami of Aegisthidae are not only elongate but also thin (see below) and inserting side by side, the anal somite is not as wide posteriorly as anteriorly. Other Oligoarthra and the outgroup species have caudal rami with a greater width, which do not insert side by side. Accordingly they have anal somites with nearly the same width anteriorly and posteriorly (Fig. 6B).

Char. 4 (spermatophore): The existence of only one spermatophore at a time is characteristic for Syngnatharthra. *Nannopus palustris* Brady, 1880 (Podogennonta Lang, 1944, Huntemanniidae Por, 1986) produces 2 spermatophores simultaneously (Hosfeld 1997). The same is true for the males of *Harpacticella* spp., *Tigriopus* spp. and *Zaus goodsiri* Brady, 1880 (Podogennonta, Harpacticidae Sars, 1904), as noted by Huys et al. (1996). This is interpreted as a secondary development (Seifried 2002). Within Podogennonta the species with 2 spermatophores belong to two different evolutionary lines.

The Misophrioida and Polyarthra produce two spermatophores simultaneously, but the Calanoida produce only one spermatophore at a time. However, it is very likely that the plesiomorphic condition within Copepoda and Harpacticoida is 2 spermatophores produced simultaneously as in Aegisthidae (Hosfeld 1997).

Char. 5 (female antennule): In aegisthid species the oligoarthran segments 3 and 4 of the female antennule are fused (copepod segments III–VIII and IX–XIV). For Rometidae the female is not known. The species of the Calanoida and Misophrioida and the more plesiomorphic species of Syngnatharthra have these segments separate.

Char. 6 (antenna): All species of Aegisthidae have an allobasis or a basis that is incompletely fused with the proximal endopod segment. The outgroup species, all species of Rometidae, and the species of the more plesiomorphic taxa of Syngnatharthra have the basis and proximal endopod segment separate (Fig. 2B). An allobasis has convergently evolved in advanced taxa of Syngnatharthra (e.g. Rotundiclipeidae; Superornatiremidae Huys, 1993; Cletodidae T. Scott, 1905).

Chars 7 and **8** (antenna): A homologous modification of the 4 subterminal setae of the proximal antennal endopod segment 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 (Seifried 2002). The outgroup species have more than 4 setae and no such transformation. In the species of Rometidae element 3 is secondarily transformed to a seta (Fig. 3C). All species of Aegisthidae have a maximum of 3 lateral elements on the distal endopod segment. One spine (spine I) is always lacking. Many of the more advanced species of Syngnatharthra also have only

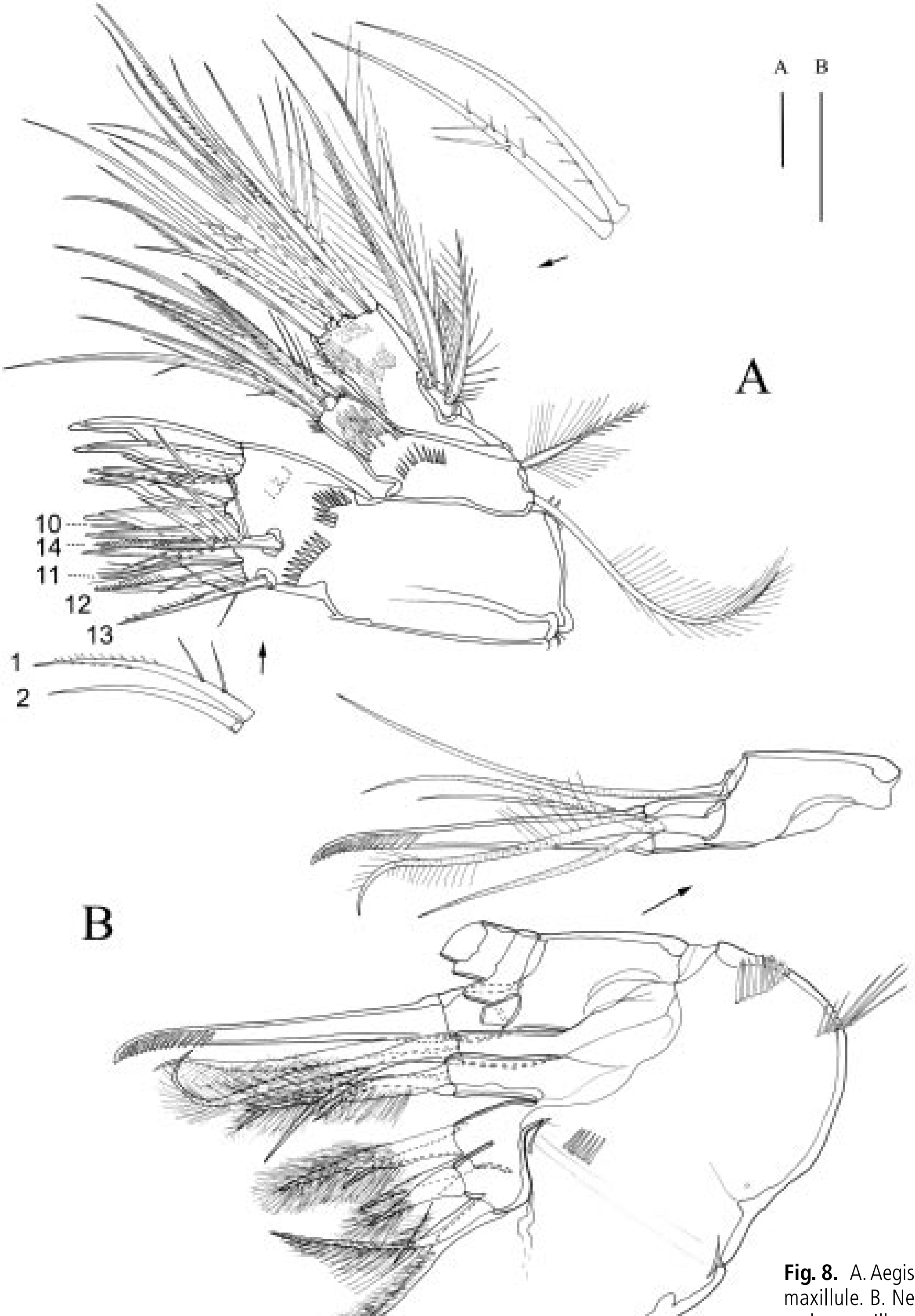

Fig. 8. A. Aegisthidae gen. spec. 1, female; maxillule. B. Neobradyidae gen. spec., female; maxilla, without setae of free endopodal segments. Scale bars: 20 µm.

3 lateral elements on the distal endopod segment. In the evolution of Oligoarthra, spine I and other elements are lost more often than once. However, the outgroup species and the more plesiomorphic syngnatharthran species have 4 or more lateral elements on the distal endopod segment. The evolution of these lateral elements was described in detail by Seifried (2002).

Char. 9 (mandible): The large lateral spine on the 1-segmented mandibular endopod is very characteristic for Aegisthoidea (Fig. 3B). 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* Soyer, 1970, and some but not all species of *Cerviniopsis* Sars, 1909 indicate an endopod with 3 lateral setae. *Stratiopontotes* spec. from the Arctic (see Methods and material) also has 3 lateral setae. The museum material of *Eucanuella spinifera* originally collected by G. O. Sars (see Methods and 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 on the mandibular endopod. This can also be seen in the original description of *E. spinifera* by T. Scott (1900). Thus, the more plesiomorphic Aegisthoidea such as *Romete bulbiseta* and *E. spinifera* have the lateral spine. It is probable that the spine has been secondarily transformed to a seta in the more advanced species of *Cerviniopsis* and *Stratiopontotes* Soyer, 1970. 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 *Stratiopontotes* and some *Cerviniopsis* species.

Chars 10 to **12** (mandible): 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 the endopod are unique for aegisthid species. With the exception of the proximal exopod segment, the more plesiomorphic character state within Harpacticoida is visible in *Romete bulbiseta* (Fig. 3B). 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 subsp. *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 large as the other exopodal segments, e.g. in *Eucanuella spinifera*, *Cerviniopsis muranoi* Itô, 1982, and *Expansicervinia glaceria* Montagna, 1981.

Char. 13 (maxillule): *Romete bulbiseta* has a maxillule with 4 setae representing the epipodite of the coxa (Fig. 3C). *Neobradya pectinifera* Scott, 1892 and *Antarcticobradya tenuis* (Brady, 1910) have 3 setae. All other described Oligoarthra never have more than 2 setae. In the ancestral lines to Aegisthidae and to Syngnatharthra the reduction of 1 or 2 epipodal setae happened convergently.

Chars 14 and **15** (maxillule): All species of Aegisthoidea have a maxillule in which the basis and endopod are fused (Figs. 3C, 8A). The fused segment has a characteristic rectangular shape, and all setae arise from the distal edge. This is a very strong synapomorphy for Rometidae and Aegisthidae. There is no other harpacticoid with a maxillule fused in this way. In addition, the maxillular exopod is always reduced in size with at most 3 setae in aegisthid species. Other taxa of Oligoarthra and the outgroup taxa have a free endopod segment in the groundpattern. Species of Polyarthra have a relatively large, 1-segmented exopod with at most 11 setae and a 2-segmented endopod with 5, 6 setae. The more plesiomorphic syngnatharthran species have a 1-segmented exopod with at most 4 setae and a 1-segmented endopod with at most 6 setae. The groundpattern of Misophrioida is a 1-segmented exopod with 11 setae and a 2-segmented endopod with 6, 6 setae. The groundpattern of Calanoida is a 1-segmented exopod with 11 setae and a 3-segmented endopod with 6, 4, 7 setae.

Char. 16 (maxilla): The monophyletic group Syngnatharthra is characterized, among other features, by the fused proximal endites of the syncoxa of the maxilla (Fig. 8B). Species of Aegisthoidea have the more plesiomorphic character state (Fig. 3D): 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 sistergroup of all other Syngnatharthra (Seifried 2002), the fusion appears in an initial state: the endites are fused, but the resulting endite is bilobed (Fig. 8B). 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 *Neobradya*, and all other species of Neobradyidae possess the fusion of the proximal endites of the maxillar syncoxa (e.g. *Marsteinia typica* Drzycimski, 1968). The more plesiomorphic state with the proximal endites clearly apart (Fig. 3D) is only found in Aegisthoidea and the outgroups of Oligoarthra. The fusion of proximal endites of the maxillar syncoxa is an autapomorphy of Syngnatharthra.

Chars 17 and **18** (maxilla): Huys & Boxshall (1991) indicated a 4-segmented maxillar endopod with 4 setae on the proximal segment for the groundpattern of Copepoda, and with 3 setae for the groundpattern of Harpacticoida. Seifried (2002) came to the conclusion that 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 detected through 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 (Seifried 2002). However, in Aegisthidae the situation is different. The displaced endopodal seta 10 of the allobasis is inserted between anterior and posterior surface, the displaced seta 9 is near seta 10 but on the anterior surface, and an additional seta is present very close to endopodal seta 10 (e.g. Aegisthidae gen. spec. 1., Aegisthidae gen. spec. 3, Aegisthidae gen. spec. 5, *Stratiopontotes* spec.). In addition, the posterior endopodal element 11 of the allobasis is developed as a large, strong spine. This striking spine constitutes a very good autapomorphy and a perfect diagnostic character, as it can be found in all species of Aegisthidae but not in species of Rometidae. However, the rometid species have the 2 setae, inserting very closely together between anterior and posterior surface (Fig. 3E: 10, ?). These parallel setae are very characteristic, although often only visible 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. One of these setae is displaced seta 10; the other is either the fourth seta of the proximal endopod segment of the groundpattern of Copepoda or a duplication 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. Often 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: he illustrated "three basally fused fine setae on distal edge close to inner base of endopodite" for *Pontostratiotes pacificus* Itô, 1982, *P. abyssicola* Brady, 1883, and *P. sixtorum mindanaoensis*, "three juxtaposed setae on distal edge close to inner base of endopodite" for *P. unisetosus* Itô, 1982, *Eucanuella longirostrata* Itô, 1983, and *Cerviniopsis minutiseta* Itô, 1983, and "two separate slender setae ... attached onto distal end close to anterior base of endopodite" for *P. robustus* Itô, 1982. In all species of Aegisthoidea analysed for this study and where the insertion points of the setae were visible, not more than two parallel setae could be found inserting very closely together between anterior and posterior side and nearby seta 9 on the anterior side. However, it should be kept in mind that a further additional seta could be present and that sometimes the three setae are fused, as described by Itô (1982).

Chars 19 to **23** (maxilliped): The evolution of the maxillipedal endopod will only be touched briefly here. Refer to Seifried (2002) for a discussion in more detail. The species of Syngnatharthra show a characteristic maxilliped: a 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) on enp-1, and an enp-2 which is reduced in size. The species with a more plesiomorphic morphology within Syngnatharthra have preserved this ancestral form of the maxilliped (Seifried 2002). Huys & Boxshall (1991) reconstructed 10 setae at the maxillipedal praecoxa and coxa in the groundpattern of Misophrioida and 11 setae in the groundpattern of Calanoida. The fusion of praecoxa and coxa and the transformation of 3 setae to spines are groundpattern characters of Harpacticoida (Seifried 2002). The groundpattern of Polyarthra is 1, I+1, I+3, I+2 spines and setae on the syncoxa of the maxilliped, that of Oligoarthra is I+1, I+2, I+1. The species of Syngnatharthra have a maximum of 6 syncoxal setae and spines, the seta of the proximal endite is lost. The latter seta is present in the more plesiomorphic Aegisthoidea, e.g. species of *Romete* and *Eucanuella* T. Scott, 1900. However, in very advanced taxa of Aegisthidae with many reductions in general (e.g. the benthopelagic species of *Andromastax* Conroy-Dalton & Huys, 1999), the seta of the proximal endite of the syncoxa is convergently lost.

The species of the outgroups and of Aegisthoidea have no highly flexible joint between basis and endopod of the maxilliped. The joint evolved in the ancestral line leading to Syngnatharthra. However, in some taxa of Copepoda, such as Siphonostomatoida Thorell, 1859, a joint between basis and endopod of maxillipeds is convergently developed. In caligiform taxa fused endopod segments, a terminal claw and a highly flexible joint between basis and endopod are convergently evolved "to form a powerful compound subchela" (Huys & Boxshall 1991) useful for grasping.

The 2 geniculated distal setae (3 + 4) of the small distal endopod segment are accompanied by 2 small outer setae (1 + 2) and can be found in many species of Syngnatharthra (Seifried 2002). They are an element of the groundpattern of Syngnatharthra, as is the small claw (V) displaced to the posterior side of the distal end of the proximal endopod segment. The hypothesis is that all species of Syngnatharthra 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 endopod accompanied by the two small lateral setae has developed more than once within Oligoarthra (Seifried 2002).

Char. 24 (P1): The inner seta of exp-1 P1 is the only seta that was lost only once in the evolution of all oligoarthran taxa. All other setae were lost several times. Every single species of Polyarthra and Aegisthoidea has this seta, and no Syngnatharthra species has it. In the groundpattern of Calanoida and Misophrioida the seta is present.

Char. 25 (P1): The 2 outer spines of exp-3 of P1 are elongate in both rometid species. The more plesiomorphic species of Aegisthidae and Syngnatharthra and the species of the outgroups have short, robust outer spines on the whole exopod P1. Species of some advanced taxa of Aegisthidae and Syngnatharthra, such as *Pontostratiotes* Brady, 1883 and Tisbinae Lang, 1944, also have elongate spines. However, in these cases all spines of all swimming legs or of the whole exopod P1 are elongate. In the advanced, very large, mainly planktonic Aegisthidae the elongation of many segments, setae and spines of the mouthparts and legs accompanies this. In Rometidae the elongation concerns only the 2 outer spines of exp-3 of P1. Rometidae are small, compact, benthic animals without any elongation apart from the discussed setae.

Chars 26 and **27** (P2–P4): The species of Rometidae have characteristic swimming legs. The distal outer corner of enp-2 of P2–P3 is produced into a spinous process and the enp-3 of P2–P4 becomes slender in the distal half, the step is strengthened by cuticular thickening (Figs. 4B and 5). The two proximal endopod segments of P2–P3 of rometid species are as wide as long, without apparent elongation. Some aegisthid species have elongate, slender legs. However, here the whole leg is slender, and there is no step in the distal half of the enp-3 strengthened by cuticular thickening as in Rometidae. The distal outer edge of enp-2 of P2–P3 is produced into a spinous process in rometid species. These outer edges are somewhat projecting in some species of Aegisthidae, e.g. in *Eucanuella spinifera*, a relatively plesiomorphic aegisthid. This character may therefore be an apomorphy for a group of species within Aegisthoidea or a convergence. Projecting outer edges of the endopod segments evolved more than once in Harpacticoida, thus this is not a very strong character. However, wherever in species of Aegisthidae the distal outer edge of enp-2 of P2–P3 is projecting, it is also projecting on enp-1 and the projection is not longer than a fourth of enp-3. In contrast, species of Rometidae have no outer spinous process on enp-1 of P2–P3. In addition, the outer spinous process of enp-2 in P2 is nearly half as long as enp-3, and one third of enp-3 in P3. The most parsimonious hypothesis presently is: species of Rometidae are characterized, among other features, by a long spinous process at the distal outer corner of enp-2 of P2–P3 and an enp-3 of P2–P4 that becomes slender in the distal half, with the step being strengthened by cuticular thickening (Figs. 4B, 5).

Chars 28, 29 and **35** (P5 of female and male): The evolution of the antennule and the P5 of Oligoarthra will only be briefly touched here, Seifried (2002) has discussed this in more detail. Both sexes of all outgroups, Polyarthra, Oligoarthra and Syngnatharthra have an endopod or an endopodal lobe in the groundpattern of the P5. As the males of Rometidae have an endopodal lobe with a seta (Fig. 6A), it could be that the female has one as well. Aegisthid species have no endopod and no endopodal lobe, but an elongate exopod in both sexes. *Styracothorax gladiator* Huys, 1993 and *Rotundiclipeus canariensis* have no endopodal lobe either, but a different general morphology of P5 (see below). Some advanced Podogennonta have reduced endopodal lobes, sometimes represented only by one seta (species of Argestidae Por, 1968, Cletodidae, Canthocamptidae Sars, 1906). Some of them have no P5 at all, like some Canthocamptidae, and some of them have a long P5 exopod like species of Aegisthidae, especially argestid species. The general morphology and the phylogenetic analysis shows that in the evolution of Harpacticoida the reduction of the endopod P5 of male and female happened more than once (Seifried 2002). However, except for Aegisthidae, all Harpacticoida with a more plesiomorphic general morphology have an endopodal lobe with setae, at least in the male.

Chars 30 to **32** (male antennule): The groundpattern of Oligoarthra is a 14-segmented male antennule. The species of Calanoida and Misophrioida have many more antennule segments. The antennule morphology of Polyarthra needs to be reviewed (Willen 2000). The groundpattern of Aegisthidae is a 10-segmented male antennule through the fusion of Oligoarthra segments 2 and 3, 10 and 11, and 12 to 14. As species of Rometidae and some species of Syngnatharthra (Neobradyidae, Chappuisiidae, Novocriniidae, Rotundiclipeidae, Tisboidea Stebbing, 1910, and some advanced Podogennonta) also show the fusion of segments 2 and 3, this is not a strong character. The fusion of segments 10 and 11 and of 12 to 14 also evolved convergently within Syngnatharthra, but not as frequently as the fusion of segments 2 and 3. In contrast to Aegisthidae, species of Rometidae and the more plesiomorphic species of Syngnatharthra (Neobradyidae, Chappuisiidae, partly Ectinosomatidae, the more plesiomorphic Podogennonta) have free segments 10 to 14 in the male antennule (Willen 2000, Seifried 2002).

Chars 33, **34** and **36** (male P5): As in the male antennule, the fusion of segments of the male P5 happened convergently in Aegisthoidea and Syngnatharthra. Fusions occurred even in the outgroups (e.g. Polyarthra). However, the species of Aegisthoidea have the coxa, basis and endopod of the male P5 fused, whereas species of Calanoida, Misophrioida and the more basal Syngnatharthra (Neobradyidae, some Podogennonta, Chappuisiidae) have coxa, basis and endopod free (Seifried 2002).

The male exopod P5 of *Romete* spec. (see Methods and material) 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. It is probable that this is the most plesiomorphic character state within Oligoarthra, as 3 distal setae are present in Calanoida and Misophrioida, and that the reduction of this seta occurred more than once. However, the possibility exists that one terminal seta of the male exp-3 P5 was regained in *Romete* spec. (Seifried 2002). Species of Rometidae and Misophrioida have no outer seta on enp-2. This is a convergence.

Char. 37 (caudal rami): Within Aegisthidae caudal rami that are longer than in *Romete* are plesiomorphic. The caudal rami in species of *Romete* are 2 times longer than wide (Fig. 1). The groundpattern of Aegisthidae is represented by caudal rami that are at least 5 times longer than wide. In females of *Eucanuella spinifera*, a very plesiomorphic aegisthid, the caudal rami are 3 times longer than wide. However, those of the males are much more elongate. The caudal rami in Aegisthidae are otherwise elongate in both sexes (with the exception of *Cerviniella langi* Bodin, 1968 and *Paracerviniella denticulata* Brodskaya, 1963, see below), sometimes extremely so, and either slightly to markedly divergent or juxtaposed and fused along the entire length. Comparing caudal rami with other characters such as the morphology of the mouthparts, P2 and P3, it is obvious that the extreme elongation of the caudal rami evolved within Aegisthidae. The extremely elongate caudal rami are therefore not characteristic for all Aegisthidae. *Cerviniella langi* have caudal rami that are 3 times longer than wide. In these advanced species it is obvious why the caudal rami are secondarily shortened: species of *Cerviniella* in general have a morphology adapted to burrowing. The short caudal rami are therefore advantageous. *Paracerviniella denticulata* has caudal rami that are not quite quadratic, but slightly elongate. These barely elongate caudal rami are interpreted as secondarily shortened.

Taxa of Oligoarthra, their diagnoses and autapomorphies

In the following, the diagnoses and autapomorphies of the discussed taxa are given. The autapomorphies are underlined. In addition, all subtaxa belonging to the discussed taxa are listed. The reconstructed groundpatterns are given and illustrated in Seifried (2002).

Rometidae fam. nov.

Taxa belonging to Rometidae: *Romete bulbiseta* gen. et sp. nov.

Diagnosis and autapomorphies of Rometidae (Fig. 7: character set 2): Deep depressions with reticular ornamentation lateral in anterior half of cephalic shield (char. 1: 0→1). First pedigerous somite completely fused to dorsal cephalic shield (char. 2: 0→1). Enp-2 of antenna with 1 spine (I) and 3 setae (2-4) laterally: element 3 forming a seta (char. 8: 1→0). Distal segment of mandibular exopod extremely minute (char. 12: 0→1). Maxilliped 3-segmented, with syncoxa, basis and 1-segmented endopod, enp-1 and enp-2 fused (char. 21: 0→1). Two outer spines of exp-3 P1 elongate (char. 25: 0→1). Distal outer corner of enp-2 of P2–P3 produced into spinous process (char. 26: 0→1); enp-3 of P2–P4 becomes slender in the distal half, the step strengthened by cuticular thickening (char. 27: 0→1).

Male. Exopod P5 3-segmented, with 1-0, 0-1, 1-3-1 setae (char. 36: 0→1 or 2→1).

Remarks on morphology of Rometidae: Species of Rometidae have the autapomorphies of Aegisthoidea and reductions of few setae of the swimming legs and mouthparts, but otherwise they match the groundpattern of Oligoarthra, so that it is difficult to find real autapomorphies for this taxon.

However, Rometidae is characterized by the deep lateral depressions with reticular ornamentation in the anterior half of the cephalic shield (char. 1), the reduction of the distal exopodal segment of the mandible to an extremely minute segment (char. 12), the spinous process at the distal inner corner of enp-2 P2–P3 (char. 26) and the characteristically slender distal end of enp-3 (char. 27; see Discussion of characters). The maxilliped of rometid species is also exceptional because it became 1-segmented before the two claws evolved (char. 21). In the groundpattern the species of Aegisthidae have a 2-segmented maxillipedal endopod without a claw, and all 7 endopodal setae of the Oligoarthran groundpattern. In basal species of Syngnatharthra, one seta of the proximal endopod segment is transformed into a claw, the distal endopod segment is reduced in size (char. 21), and the 2-segmented endopod is inwardly directed. In the further evolution a second seta is transformed to an additional claw (Seifried 2002). Then, the endopod becomes 1-segmented. Advanced species of Ectinosomatidae and Neobradyidae have a phyllopodial maxilliped with a 1-segmented endopod. However, some species of these taxa with a more plesiomorphic morphology show that the claws were lost (Seifried 2002). In consequence they have only 4 setae on the endopod, fewer than the rometid species. In summary: the species of Rometidae are the only ones within Oligoarthra with 6 setae on a 1-segmented endopod. In the planktonic evolutionary line of Aegisthidae, where the mouthparts of the males are reduced, the basis is fused to the syncoxa and the endopod of the maxilliped has become 1-segmented as well. However, species like *Andromastax muricatus* always have reduced numbers of setae on the protopod and endopod (down to 4 setae).

Besides these autapomorphies, the losses of single setae of the mandible, maxilla and pereiopods also characterize Rometidae. However, the same setae are lost also in some species of Aegisthidae and Syngnatharthra. Loss of single setae in mouthparts and pereiopods takes place independently several times within Harpacticoida and is therefore only a weak apomorphy to characterize a taxon (Seifried 2002). The discussion of single lost setae in the groundpattern of taxa is therefore omitted here in most cases. Nevertheless, when setae are reduced only once or twice within Harpacticoida, they are valuable for phylogenetic analysis (see below).

Romete bulbiseta has a maxillule with 4 setae representing the epipodite of the coxa (Fig. 3C). *Neobradya pectinifera* and *Antarcticobradya tenuis* have 3 setae. All other described Oligoarthra have not more than 2 setae (char. 13).

The exopod P5 male of *Romete* spec. has 1-0, 0-1, 1-3-1 setae (char. 36). Compared with all other Oligoarthra there is one additional terminal seta on the distal segment of the exopod (see Discussion of characters).

Basis and endopod of the maxillule are fused in *Romete bulbiseta* like in all species of Aegisthidae (char. 14; Figs. 3C, 8A). 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 sistergroup of Oligoarthra, still have a 2-segmented endopod.

The above reveals that the new species is most closely related to Aegisthidae. To include *Romete bulbiseta* in Aegisthidae would have meant to expand the diagnosis of Aegisthidae. Instead, a new taxon Rometidae is proposed. Another single male of a different species of Rometidae was found in the deep sea of the Angola Basin (*Romete* spec., DIVA 1; see Methods and material; Fig. 6B). As the sorting of the rich material is still in progress, it is hoped that females will soon be found to allow description.

Aegisthidae Giesbrecht, 1892

Type genus: *Aegisthus* Giesbrecht, 1891

Type species: *Aegisthus mucronatus* Giesbrecht, 1891

Taxa belonging to Aegisthidae: 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 (*Brodskaya* Huys, Møbjerg and Kristensen, 1997; *Cervinia* Norman, 1878; *Cerviniella* Smirnov, 1946; *Eucanuella* T. Scott, 1900; *Expansicervinia* Montagna, 1981; *Neocervinia* Huys, Møbjerg and Kristensen, 1997; *Paracerviniella* Brodskaya, 1963; *Pseudocervinia* Brodskaya, 1963).

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

Diagnosis and autapomorphies of Aegisthidae (Fig. 7: character set 3): *Female.* Anal somite elongate, tapering posteriorly (char. 3: 0→1). Caudal rami more than twice as long as wide (char. 37: 0→1). Antennule 8-segmented, Oligoarthra segments 3 and 4 fused (copepod segments III-VIII and IX-XIV) (char. 5: 0→1). Antenna with allobasis or incomplete basis (char. 6: 0→1); enp-2 laterally with 1 spine (III) and 2 setae (2 + 4), spine I lacking (char. 7: 0→1). Endopod of mandible of one large segment and at least 2 times longer than wide (char. 10: 0→1); proximal segment of exopod elongate, considerably longer than remaining segments and at least 3 times longer than wide (char. 11: 0→1). Epipodite of maxillular coxa represented by 2 setae (char. 13: 0→1); exopod of maxillule reduced in size with 3 setae (char. 15: 0→1). Endopodal element 11 of allobasis of maxilla developed as large, strong spine inserted on posterior surface (char. 18: 0→1). P5 without endopodal lobe (char. 28: 0→1); exopod more than twice as long as wide (char. 29: 0→1).

Male. Antennule 10-segmented through fusion of Oligoarthra segments 2 and 3 (as in all Aegisthoidea), 10 and 11 (char. 31: 0→1), and 12 to 14 (char. 32: 0→1). P5 without endopodal lobe (char. 35: 0→1).

Remarks on systematics of Aegisthidae: Aegisthidae Giesbrecht, 1892 as characterised here includes the taxa of the former Aegisthidae (now Aegisthinae) and of Cerviniidae Sars, 1903, because the species of both taxa share all autapomorphies (see below and Discussion of characters). Furthermore, Cerviniidae without Aegisthinae is paraphyletic because species of Aegisthinae are derived Cerviniidae (see below). Aegisthidae is the senior and therefore valid name (ICZN = International Commission on Zoological Nomenclature 1999: Art. 23.1 and 23.3). In consequence, Aegisthoidea Giesbrecht, 1892 is the senior synonym of Cervinioidea Sars, 1903. (ICZN 1999: Art. 36.1).

Published references to "Cerviniinae Brodskaya, 1963" are incorrect. Following ICZN (1999: Art. 36.1), the correct name is Cerviniinae Sars, 1903 as Sars (1903) erected Cerviniidae.

Species of Aegisthinae are derived "Cerviniopsinae" (see below) and therefore "Cerviniopsinae" is paraphyletic. However, until a phylogenetic analysis within Aegisthidae has been accomplished at species level (77 species until now), Aegisthinae, Cerviniinae and "Cerviniopsinae" are maintained.

Remarks on morphology of Aegisthidae: Aegisthidae is characterized by 15 autapomorphies. Six of the autapomorphies are strong (chars 1, 10, 11, 15, 18, 37). There is very good support for the hypothesis that the 5 genera of Aegisthinae (former Aegisthidae) belong to a monophyletic taxon with Cerviniinae and "Cerviniopsinae" (the latter two groups formed former Cerviniidae). The species show a unique form of the anal somite, and the change of posterior seta 11 of the maxilla into a strikingly large spine is visible in all species of Aegisthidae. The morphology of *Andromastax muricatus* fits the groundpattern of Aegisthidae and shows the striking spine (11) on the posterior side, if anterior and posterior in the text of the description of the maxilla in Conroy-Dalton & Huys (1999: p. 415, fig. 10B) are reversed. If Conroy-Dalton & Huys (1999) were correct the position of several setae and the tube pore of the allobasis in *A. muricatus* would be different from those in other Harpacticoida (Huys & Boxshall 1991), and there would be an additional spine on the posterior surface. *Aegisthus*, *Andromastax, Jamstecia, Nudivorax*, and *Scabrantenna* (Aegisthinae) represent an advanced, may be monophyletic group within Aegisthidae. Especially the unique spinous processes of the cephalothorax and the extremely elongate caudal rami show that species of these five genera are derived members of Aegisthidae as characterised here and belong to the same evolutionary line within "Cerviniopsinae" as *Pontostratiotes*. The mandible is significantly reduced in species of these five genera, so that it is not possible to recognize whether or not they share the respective apomorphies with species of the former Cerviniidae (chars 10, 11**)**. The loss of setae and the elongation and fusion of segments in antennule, antenna, maxillule and P5 even in the groundpattern indicate the long-isolated evolution of the ancestors of Aegisthidae.

Species of Aegisthidae have no nauplius eye (Lang 1944, 1948: 117–118). However, the nauplius eye is not confirmed for species of Rometidae. Consequently, its lack could be an autapomorphy for Aegisthidae or for Aegisthoidea.

At least 3 species (*Cervinia brevipes* Brodskaya, 1963; *C. langi* Montagna, 1981; *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* or *Pontostratiotes scotti* Brodskaya, 1959, but most species have an allobasis (char. 21).

The exopod of P5 is elongate in most species of Aegisthidae (char. 29), but not in all. Some have an extremely elongate exopod, some a square one. Only a complete phylogenetic analysis of Aegisthidae will answer the question of whether the ancestor of all Aegisthidae really had an elongate P5. The P5 of the outgroups gives no clear indication of polarisation.

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* (Conroy-Dalton & Huys 1999, Huys 1988a, Lee & Huys 2000). Different forms of dimorphism exist in different evolutionary lines within Aegisthidae.

Aegisthoidea Giesbrecht, 1892

Taxa belonging to Aegisthoidea: Aegisthidae Giesbrecht, 1892; Rometidae fam. nov.

Diagnosis and autapomorphies of Aegisthoidea (Fig. 7: character set 1): *Female.* Endopod of mandible with 1 spine and 2 setae laterally (char. 9: 0→1). Basis and endopod of maxillule fused, fused segment of characteristic rectangular shape, all setae at distal edge (Figs. 3C, 8A; char. 14: 0→1). 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 (char. 17: 0→1), and seta (11) on posterior surface.

Male. Antennule 13-segmented, fusion of Oligoarthra segments 2 and 3 (char. 30: 0→1). P5 basis not separated from coxa (char. 33: 0→1) nor from endopod (char. 34: 0→1).

Remarks on systematics and morphology of Aegisthoidea: Lang (1944) established the taxon Cerviniidimorpha Lang, 1944 to unite the former Cerviniidae Sars, 1903 and the former Aegisthidae Giesbrecht, 1892. Bowman & Abele (1982) changed Lang's "superfamily"-endings "-idimorpha" to "superfamily"-endings "-oidea" (see ICZN 1999: Art. 29.2) and introduced Cervinioidea Sars, 1903. As described below Cerviniidae is synonymized with Aegisthidae and in consequence Aegisthoidea is the synonym of Cervinioidea. Rometidae shows several synapomorphies with Aegisthidae and belongs to Aegisthoidea as the sistertaxon of Aegisthidae.

There are clear morphological indications that *Romete bulbiseta* from the Great Meteor Seamount and *Romete spec.* from the Angola Basin represent the sistergroup of the Aegisthidae within a monophyletic Aegisthoidea (see also Discussion of characters). In these taxa the basis and endopod of maxillule are fused (Figs. 3C, 8A). The fused segment has a characteristic rectangular shape and all setae arise from the distal edge (char. 14). There is no other harpacticoid with a maxillule fused in this way. The endopod of the mandible is 1-segmented, and one lateral seta is transformed into a large spine (Fig. 3B; char. 9). No description of any oligoarthran species outside of Aegisthoidea shows 2 setae and 1 spine laterally on the mandibular endopod. The apomorphic endopodal setation of the allobasis of maxilla is also characteristic for Aegisthoidea (chars 17, 18). The allobasis has as groundpattern character a displaced endopodal seta 10 inserted between anterior and posterior surface, a displaced seta 9 inserted near seta 10 but on the anterior surface, an additional seta very close to endopodal seta 10, and a posterior seta 11. The parallel setae between anterior and posterior surface (10 and one additional seta) are very characteristic and with careful examination could be seen in most aegisthid species and the two analysed rometid species, *Romete bulbiseta* and *Romete* spec.. The displacement of seta 10 is also an autapomorphy of Aegisthoidea. The rometid species lost seta 9, and species of Aegisthidae show the posterior seta 11 developed as a strikingly large spine. In both taxa the caudal rami are at least two times longer than wide.

Besides the few autapomorphies of Rometidae all characters of *Romete bulbiseta* and *Romete* spec. are more plesiomorphic compared with those of species of Aegisthidae which are very advanced and specialized.

Aegisthidae and Rometidae combined to Aegisthoidea (77 species) are the sistergroup of all remaining Oligoarthra, which can be united in a new monophyletic taxon being characterized by the autapomorphies described below.

Syngnatharthra tax. nov.

Etymology: Derived from Greek *syn* = together and *gnathos* = jaw, alluding to the two fused proximal endites of the maxillar syncoxa. Pronunciation: Syn-gnatharthra.

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; Clytemnestridae A. Scott, 1909; Cristacoxidae Huys, 1990; Dactylopusiidae Lang, 1936; Darcythompsoniidae Lang, 1936; Ectinosomatidae Sars, 1903; Euterpinidae Brian, 1921; Harpacticidae Sars, 1904; Huntemanniidae 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; 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; Styracothoracidae Huys, 1993; Superornatiremidae Huys, 1996; Tachidiidae Sars, 1909; Tegastidae Sars, 1904; Tetragonicipitidae Lang, 1944; Thalestridae Sars, 1905; Thompsonulidae Lang, 1944; Tisbidae Stebbing, 1910; 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; *Pyrocletodes* Coull, 1973; *Tisemus* Monard, 1928.

Diagnosis and autapomorphies of Syngnatharthra tax. nov. (Fig. 7: character set 4): *Female.* Prosome consisting of cephalothorax and 3 free pedigerous somites, first pedigerous somite completely fused to dorsal cephalic shield (char. 2: 0→1). Epipodite of maxillular coxa represented by 3 setae (char. 13: 0→1). Syncoxa of maxilla with (5 + 3), 3, 3 setae, the two proximal endites fused (char. 16: 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. 19: 0→1); maxilliped with joint with high degree of inward flexibility between basis and endopod (char. 20: 0→1); enp-1 with 2 setae (6 + 7) and 1 thin claw (V); the claw displaced to posterior side of distal end of enp-1 (char. 22: 0→1); enp-2 reduced in size (char. 21:

0→1) with 2 small outer setae (1 + 2) and 2 geniculated distal setae (3 + 4) (char. 23: 0→1). Proximal segment of exopod P1 without inner seta (char. 24: 0→1).

Male. With 1 spermatophore (char. 4: 0→1).

Remarks on morphology of Syngnatharthra: The monophyletic group Syngnatharthra is characterized above all by the fused proximal endites of the maxillar syncoxa (Fig. 8B; char. 16) and by the lack of the inner seta of exp-1 P1 (char. 24). In most Syngnatharthra a depression still marks the fusion zone of the maxillar endites (Fig. 8B; see discussion of char. 16). In some taxa the proximal endite is reduced to one small endite with no depression and less than 6 setae. According to our phylogenetic hypothesis, this small endite is the result of the fusion of the two proximal endites and subsequent reduction in number of setae and size, and not due to the loss of one endite of the oligoarthran groundpattern. The inner seta of exp-1 P1 is the only seta that is lost only once in the evolution of all oligoarthran taxa. All other setae are lost more than once. Every single species of Polyarthra and Aegisthoidea has this seta, and no species of Syngnatharthra has it. The loss of 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. 4). Only *Nannopus palustris* and some (but not all) Harpacticidae produce 2 spermatophores simultaneously (see discussion of char. 4); this is interpreted as a secondary development.

Syngnatharthra and Aegisthoidea together constitute Oligoarthra, which is characterized by the following autapomorphies.

Oligoarthra Lang, 1944

Taxa belonging to Oligoarthra: Aegisthoidea Giesbrecht, 1892; Syngnatharthra tax. nov.

Diagnosis and autapomorphies of Oligoarthra: *Female*. With 1 egg-sac; genital double somite with 1 copulatory pore. Antennule 9-segmented; armature formula: 1, 13, 10, 6 + aes, 3, 4, 2, 2, 6 + acrothek, characteristic arrangement and shape of setae, antennule paedomorphic (Willen 2000); 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; enp-1 with 1 seta; enp-2 with 4 subterminal setae; subterminal setation of enp-2 consisting of 1 short proximal spine (I), 1 longer distal spine (III), 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. Mandible endopod 1-segmented due to fusion of enp-1 and enp-2; endopod with 3 proximal lateral setae (from enp-1) and 3 + 2 + 2 apical setae, each group of apical setae basally fused (Willen 2000); exopod 4-segmented due to fusion of two proximal segments of Polyarthra, with 2, 1, 1, 2 setae. Epipodite of maxillular coxa represented by 4 setae; basis without outer seta; endopod 1-segmented with 6 setae; exopod with 4 setae. Maxilla with syncoxa with 4 endites with 5, 3, 3, 3 setae; allobasis bearing 1 tube pore on anterior surface. 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; basis with 1 seta and 1 spine; endopod with 3, II+2 setae and spines. P1-P4: coxae without inner seta; 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.

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, characteristic arrangement and shape of setae, aesthetasc on segment 6 fused at base with 1 seta, segments 1 and 2 with 1 seta each (Willen 2000); segments of Copepoda: 1-I, 2-II, 3-(III–VII), 4-(IX–XII), 5-XIII, 6-(XIV–XVI), 7-XVII, 8-XVIII, 9-(XIX–XX), 10-(XXI–XXII), 11-XXIII, 12-XXIV, 13-XXV, 14-(XXVI–XXVIII).

Remarks on morphology of Oligoarthra: The morphology and monophyly of Oligoarthra is discussed in detail in Seifried (2002).

Discussion

Reduction characters are generally based on few mutations. Reductions can occur multiple times convergently, and at present there are no adequate means to detect them. Because of the ongoing oligomerization within Copepoda and Harpacticoida (Huys & Boxshall 1991, Seifried 2002), 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 strong apomorphies. However, the oligomerization, i.e. the reduction of characters, cannot be ignored in the evolution of Harpacticoida. Our list of characters therefore also contains reductions of segments and setae.

The monophyly of Oligoarthra is an hypothesis well supported by many autapomorphies (Dahms 1990, Martínez Arbizu & Moura 1998, Willen 2000, Seifried 2002). On the other hand, Huys et al. (1996: 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 recognized by Lang (1948), Oligoarthra is a monophyletic taxon and the present analysis supports this.

Lang (1944) united former Cerviniidae, former Aegisthidae, Chappuisiidae, Phyllognathopodidae, Neobradyidae, and Darcythompsoniidae in the taxon "Maxillipedasphalea" on the basis of plesiomorphies (Seifried 2002). As discussed above, Cerviniidae is assigned to Aegisthidae. Chappuisiidae, Phyllognathopodidae, Neobradyidae and Darcythompsoniidae can be united with all Oligoarthra except Aegisthoidea as Syngnatharthra on the basis of the discussed autapomorphies (Seifried 2002) (Fig. 7: character set 4). "Maxillipedasphalea" is polyphyletic and therefore not maintained here.

Huys (1988b) added Rotundiclipeidae to Aegisthoidea (synonym Cervinioidea). He characterised a taxon containing Aegisthidae (Aegisthinae, Cerviniinae and "Cerviniopsinae") and Rotundiclipeidae on the basis of 4 characters: "(1) loss of endopodite P5, (2) antennula 8-segmented in female; 10-segmented in male (with 4 aesthetascs), (3) maxillula with reduced exopodite, (4) rostrum fused with cephalosoma." According to Huys (1993), character (2) cannot be regarded as an autapomorphy, because the fusion patterns of the female antennule of former Cerviniidae and Rotundiclipeidae are not the same, and 4 aesthetascs in the male antennule are a plesiomorphic feature. The exopod of the maxillule is present in Aegisthidae (and Rometidae). Indeed, the endopod is fused to the basis (char. 14). Consequently, character (3) of Huys (1988b) cannot be used to unite Rotundiclipeidae and the taxa of Aegisthoidea. Characters (1) and (4) apply to many taxa of Syngnatharthra. They are not unique, nor is the combination of these 2 unspecific characters particular in any way. Moreover, the shape of P5 and the rostrum differ in detail. The P5 of Rotundiclipeidae, for example, is completely reduced to two (exopodal?) setae. Neither an endopod nor an exopod are visible. In Aegisthidae the exopod is still present and has many setae. Huys (1993) placed the Styracothoracidae in the Aegisthoidea (synonym Cervinioidea) on the basis of the above-mentioned characters (1), (3) and (4) and "the reduction in setation (3 setae) on lateral margin of the second antennary endopod." Many Oligoarthra have 3 setae on the lateral margin of the distal antennary endopod. The setae have to be homologised to verify the apomorphy for the different species (char. 7). No autapomorphy supports the monophyly of a taxon containing Aegisthidae, Rometidae, Rotundiclipeidae, and Styracothoracidae. Rotundiclipeidae and Styracothoracidae are part of the Syngnatharthra on the basis of the autapomorphies of Syngnatharthra (Fig. 7: character set 4: char. 2, 4, 13, 16, 19, 20, 21, 22, 23, and 24) (Seifried 2002).

Hypotheses about evolution

In the case that Oligoarthra and Polyarthra are sistertaxa, the evolution within Harpacticoida begins with a significant change in morphology, which is accompanied by many reductions of setae and segments. Oligoarthra is characterized by many autapomorphies in relation to its sistertaxon Polyarthra.

The ancestor of all Oligoarthra, and may be of all Harpacticoida, was a fusiform crustacean living in or on the sediment, and not a large, hyperbenthic animal like the members of Aegisthidae. This is the most parsimonious conclusion to be drawn from the morphology and life style of Polyarthra, Rometidae and the more plesiomorphic Syngnatharthra (Seifried 2002). Calanoida are large, planktic copepods with the typical body form and morphology. However, Calanoida is a relatively plesiomorphic copepod taxon and not the sistergroup of the relatively advanced Oligoarthra. Species of Misophrioida, a taxon that is more closely related with Oligoarthra than Calanoida, are mainly hyperbenthic copepods; only some are planktic or live in anchialine caves. They are not fusiform, but instead have a wide prosome and a slender urosome. However, members of Polyarthra, the potential sistergroup of Oligoarthra, are large (> 1 mm), fusiform, and epibenthic animals. *Romete bulbiseta* and *Romete* spec. help to understand what the ancestor of Oligoarthra may have looked like, because the whole morphology of these species is more plesiomorphic than that of Aegisthidae. The known Rometidae are fusiform and smaller (360–640 µm) than the species of Aegisthidae (> 1 mm). The fusiform body is conducive to a burrowing or epibenthic life style (Fig. 6B). The more plesiomorphic Syngnatharthra, such as Neobradyidae (Seifried 2002), are small (< 1 mm), fusiform, and benthic, too. The more plesiomorphic Aegisthidae with a nearly fusiform habitus, e.g. the benthic *Eucanuella spinifera*, appear to have an in- or epibenthic life style as well. The more advanced species of Aegisthidae are always longer than 1 mm and not fusiform. They show a clear distinction between prosome and urosome, have elongate mouthparts and swimming legs. There is an evolutionary trend within Aegisthidae to very large body size (> 1.5 mm) and a life in the hyperbenthic zones of the deep sea, the habitat of most Misophrioida. The very derived Aegisthidae have secondarily adapted to a life in the plankton and are found in all oceans. In summary, it can be said that in the ancestral line towards Oligoarthra, or may be all Harpacticoida, the life style of the animals changed from a planktic or hyperbenthic to a benthic one, and that the habitus changed from a body with a wide prosome and a slender urosome to a fusiform shape. Lang (1948) and Becker (1972) also assumed the plesiomorphic condition within Harpacticoida to be fusiform, but had no phylogenetic support for this assertion.

It is highly probable that the ancestor of Oligoarthra lived in the lower sublittoral (at depths > 50 m), may be even in the deep sea. Polyarthra as the potential sister-group of Oligoarthra contain some deep-sea species, but they live mainly in the littoral. On the other hand, all species of the plesiomorphic taxa of Oligoarthra live in the lower sublittoral or even in the deep sea. All Aegisthoidea and the more basal Syngnatharthra (Seifried 2002) live in the deep sea and rarely occur on the continental shelf, never above 50 m depth. If we assume that the lower continental shelf and the deep sea are no refuge, it is highly probable that the ancestor of Oligoarthra lived in this zone. Within the more derived Syngnatharthra the littoral was colonized several times, with some lines returning to the sublittoral and the deep sea. Within Aegisthoidea a very large body size and a hyperbenthic life style has evolved secondarily, and the nauplius eye was lost. The more advanced Aegisthidae have adapted to a life in the plankton.

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