THE PHYLOGENETIC POSITION OF ARCTICOMISOPHRIA BATHYLAPTEVENSIS GEN. ET SP. N. (CRUSTACEA: COPEPODA) A NEW MISOPHRIOID FROM HYPERBENTHIC DEEP-SEA WATERS IN THE LAPTEV SEA (ARCTIC OCEAN).

Pedro Martínez Arbizu & Sybille Seifried

SARSIA



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Arcticomisophria bathylaptevensis gen. et sp. n., the first record of Misophrioida from the high Arctic Ocean is described. The new genus belongs to the Misophria-group. It has retained a number of plesiomorphic characters, especially in the antennule, maxillule, and the fifth swimming leg. These affect the reconstruction of the groundpattern of the Misophrioida and Podoplea. A key to the genera of the Misophria-group is provided.

P. Martínez Arbizu & S. Seifried, FB7/AG. Zoomorphologie, Universität Oldenburg, D-26111 Oldenburg, Germany.

Keywords: *Arcticomisophria bathylaptevensis* gen. et sp. n.; Copepoda; Misophrioida; deep-sea; hyperbenthic community; Laptev Sea; Arctic Ocean; phylogenetic systematics.

INTRODUCTION

Misophrioida is a well defined order of Copepoda (Huys & BOXSHALL 1991) currently comprising one family and 12 genera. Its species inhabit mainly marine oligotrophic environments like anchialine caves and deep-sea hyperbenthic layers. A phylogenetic analysis of the family (Boxshall 1989) revealed two monophyletic groups, the Misophria-group and the Archimisophria-group. Species of basal genera of both groups within the cladogram inhabit deep-sea waters and within each group anchialine habitats have been colonized independently. This supports the hypothesis of a deep-sea origin of the order. The number of known species is very small as compared with most other copepod orders. This may be because the habitats in which misophrioids occur are less accessible and more difficult to sample. Investigations of a single anchialine cave, Jameos del Agua in Lanzarote (Canary Islands), have resulted in the discovery of at least three new genera and four new species (BOXSHALL & ILIFFE 1987). This indicates that the number of misophrioid species may be much larger than actually known. The deep-sea, one of the largest habitats in the world, is also difficult to sample and hence poorly investigated.

During a study of meiobenthic communities in the Arctic Ocean special attention was paid to the hyperbenthic fauna. At depths greater than 2000 m the hyperbenthic community becomes important in terms of abundance and diversity. This community is dominated by cyclopoid copepods belonging to the subfamily Cyclopininae, but Calanoida and Misophrioida are also found. A new genus and species of Misophrioida is described in the present contribution. This represents the first record of the order from the high Arctic Ocean. The retention of several plesiomorphic features in the new species is relevant to the discussion of misophrioid phylogeny.

MATERIAL AND METHODS

The material was collected during the German-Russian expedition to the Arctic Ocean ARK-IX/4 (6 Aug- 5 Oct 1993) on board of R/V *Polarstern* (Bremerhaven). Benthic samples were taken by biologists and geologists using different gears. The supernatant water of Multicorer and Giant Box Corer samples was extracted with a silicone tube and filtered with a $40~\mu m$ mesh sieve. The extracted organisms were fixed in 5 % buffered formalin immediately after collection. The new misophrioids were examined with a Leitz Dialux 20 interference microscope.

The type material is stored in the copepod collection of the Arbeitsgruppe Zoomorphologie, University of Oldenburg. DESCRIPTION

Family Misophriidae Brady

Genus Arcticomisophria nov.

Diagnosis. Misophrioida with 19-segmented antennule in female; 6-segmented antennary exopod bearing 2 setae on second segment; 14 setae on the maxillulary endopod; 11 setae on the maxillulary exopod; 8 setae on maxillulary coxal epipodite; only 1 seta in the middle endopod segment of the first swimming leg; fifth leg with coxa and basis, with a 2-segmented exopod (bearing 1 outer seta on the first segment and 3 slender setae on the second) and a discrete 1-segmented endopod bearing 2 well developed setae; seminal receptacles T-shaped, produced transversely and longitudinally.

Type species. Arcticomisophria bathylaptevensis sp. nov.

Holotype. One female, body length 590 μ m, collected in the Laptev Sea at 3 237 meters depth, 12 Sept. 1993 (79°13,64' N 122°51,29' E), dissected and mounted on six slides (Coll. No. 1996.24/1-1996.24/6).

Paratype. One female, body length $520\,\mu m$, collected at 2 332 meters depth, 11 Sept. 1993 (77°03,58' N 125°00,01'E), mounted on one slide (Coll. No. 1996.25/1)

Etymology. The generic name refers to the Arctic, where the specimens were collected. Gender feminine. The specific name refers to the bathyal depth and to the Laptev Sea.

Female. Prosome about twice as long as urosome (Fig. 1 A-B). First pedigerous somite entirely concealed beneath carapace-like expansion extending from posterior margin of maxilliped-bearing somite. Third and 4th pedigerous somites produced posteriorly. Urosome 5-segmented (Fig. 1 A); genital and 1st abdominal somites fused to form genital double somite. Genital field with two copulatory pores located at the ventromedian surface of the double somite and a T-shaped seminal receptacle. Caudal ramus (Fig. 7 B) with 7 setae. Rostrum posteroventrally produced, with 2 pairs of sensillae and a median pore (Fig. 2 B). Naupliar eye not observed.

Antennule (Fig. 2 A) 19-segmented. First segment proximally with a field of fine spinules on outer margin.

Setation formula as follows: 1, 10, 2, 2, 8, 2, 2, 2+aesthetasc, 2, 2+aesthetasc, 2, 2+aesthetasc, 1, 1, 2, 2+aesthetasc, 7+aesthetasc.

Antenna (Fig. 3 A): basis with 2 apical setae of unequal length. Endopod 3-segmented; segment 1 bearing 1 distal seta; segment 2 with 2 median and 3 distal setae on inner margin; segment 3 bearing 7 setae and two rows of spinules on the outer and inner distal margins. Exopod 6-segmented; setal formula: 0, 2, 1, 1, 1, 3.

Mandible (Fig. 2 C): Fine spinules present on anterior surface of mandibular gnathobase. Mandibular palp biramous; basis bearing 1 spinulose seta. Endopod 2-segmented; proximal segment with 2 inner terminal setae; distal segment with 8 setae. Exopod 5-segmented; 1st segment asetose; segments 2, 3 and 4 partly fused; setal formula as follows: 0, 2, 1, 1, 2.

Maxillule (Fig. 3 B): praecoxal arthrite with 7 strong spines and 7 setae, 2 of which arise from anterior surface; coxal endite with 6 setae terminally; epipodite of coxa with 8 setae of unequal length; proximal and distal basal endites with 4 setae. Endopod of one segment, representing fused 1st to 3rd segments; armature divided into groups of 4 inner medial, 4 inner subterminal and 6 terminal setae. Exopod 1-segmented, bearing 11 setae and long spinules on inner and outer margin.

Maxilla (Fig. 4 B-C): praecoxa partially fused with coxa, with 2 endites, proximal one armed with 7 setae, distal with 3 setae; coxa with 2 endites, each with 3 setae; allobasis derived from fusion of basis and 1st endopodal segment, produced into strong, curved claw and bearing 4 setae; rest of endopod 3-segmented, setal formula: 2, 2, 4.

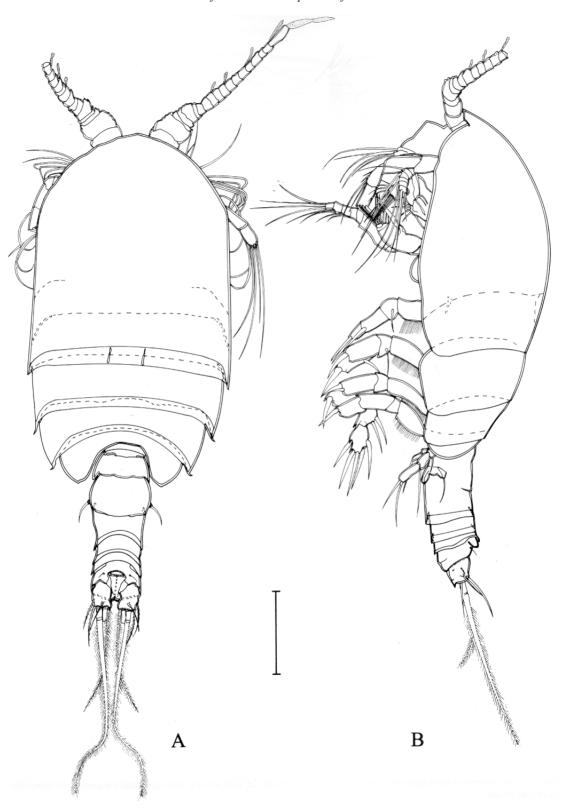
Maxilliped (Fig. 4 A) with 3 endites on syncoxa, setal formula: 1, 3, 2.; basis with 3 spinulose inner setae medially and a row of long spinules proximally; endopod 5-segmented, setal formula: 2, 2, 2, 2, 5.

Legs 1-4 biramous with 3-segmented rami; spine and seta formula:

	coxa	basis	endopod	exopod
leg 1	0-1	I-I	0-1; 0,1; 1,2,3	I-1; I-1; III,I,3
leg 2	0-1	1-0	0-1; 0-2; 1,2,3	I-1; I-1; III,I,5
leg3	0-1	1-0	0-1; 0-2; 1,2,3	I-1; I-1; missing
leg4	0-1	1-0	0-1; 0-2; 1,2,2	I-1; I-1; III,I,5

Leg 1 (Fig. 5 A-C): inner spine of basis reaching almost the end of the last endopodal segment; right limb: outer distal edge of 1st and 2nd endopod segment bifid, left limb: outer distal edge of 2nd endopod segment multidenticulate.

Leg 2, 3, and 4 (Figs 5 B, 6 A-B): inner distal margin of basis produced into small tip; outer distal angle of 1st



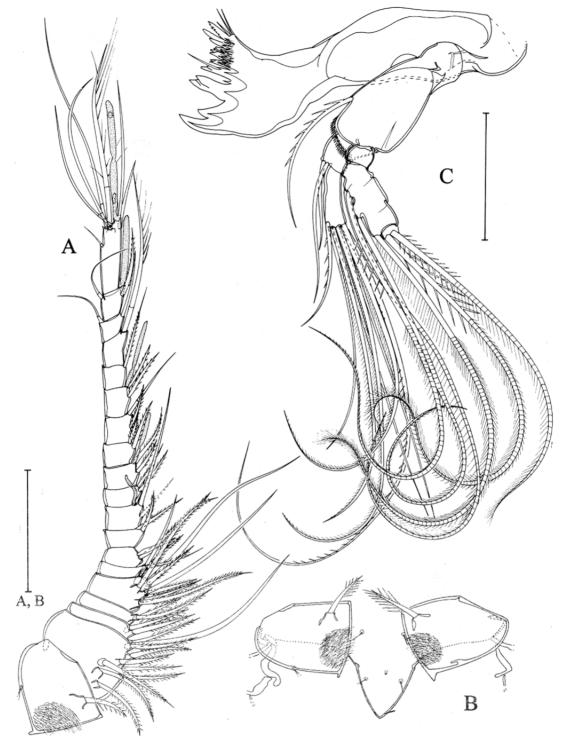
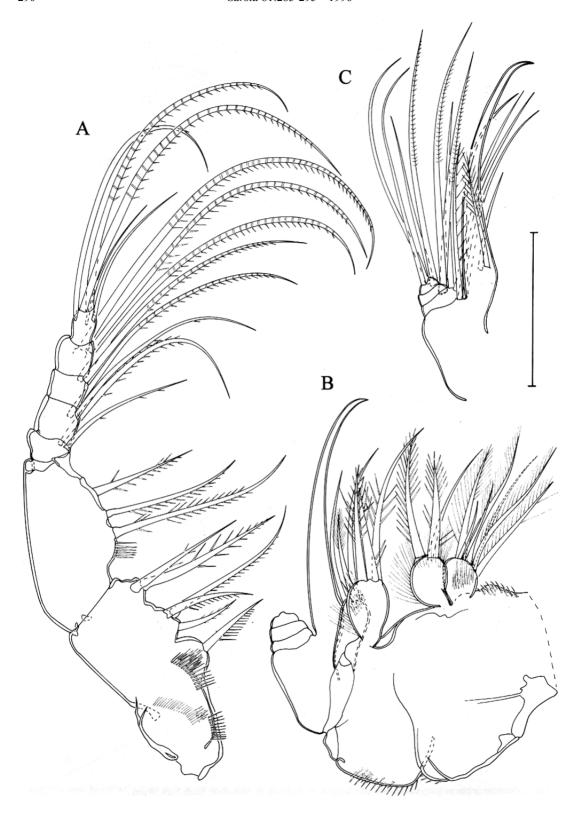


Fig. 2. $Arcticomisophria\ bathylaptevensis\ gen.\ et\ sp.\ n.\ A.\ Antennule.\ B.\ Rostrum\ and\ first\ antennulary\ segments.\ C.\ Mandible.\ Scale\ bars\ 50\ \mum.$



Fig. 3. Arcticomisophria bathylaptevensis gen. et sp. n. A. Antenna. B. Maxillule. Scale bars 50 μm .



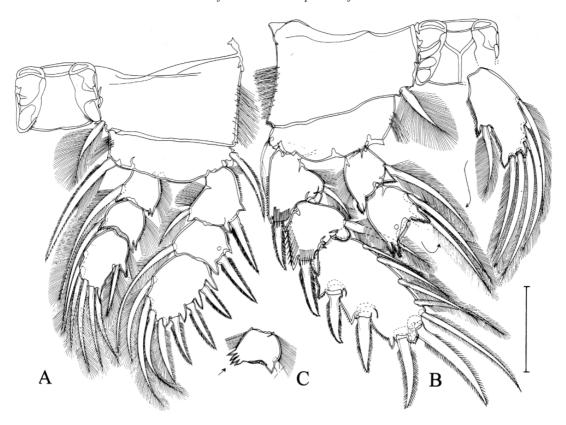


Fig. 5. Arcticomisophria bathylaptevensis gen. et sp. n. A. First leg. B. Second leg. C. Endopod 2 of left leg 1. Scale bar 50 µm.

and 2nd endopod segment bifid; intercoxal sclerite of leg 4 relatively small compared with intercoxal sclerites of legs 1, 2 and 3.

Leg 5 (Fig. 7 D) biramous, comprising a small unarmed coxa, a basis armed with one outer angle seta, 1-segmented endopod with 2 terminal setae, and a 2-segmented exopod. Exopod segment 1 with an outer seta, segment 2 bearing 3 slender setae; exopod, endopod and outer margin of basis covered with fine spinules; intercoxal sclerite not clearly discernible.

Leg 6 (Fig. 7 D) represented by genital operculum bearing an outer seta on a low cylindrical process.

Paratype. No differences in setation were noticed between the paratype and the holotype. The exopod 3 of leg 3 was also missing in the paratype, so that the setation

of this podomere remains unknown. Internal structures of the reproductive system were better preserved in the paratype than in the holotype. Fig. 8 A-B shows the genital field and an interpretation of the observed structures. The copulatory pores (1) are situated on the medioventral surface of the genital double somite. Paired copulatory tubes (2) run into a single T-shaped seminal receptacle (5). The transversely produced part of the seminal receptacle is connected by a duct on each side with a common antrum (4) in which the paired gonoducts end (dotted circles). On the outer side of the copulatory tubes there is a structure (3) that may be a gland opening into the seminal receptacle.

Male. Unknown.

Fig. 4. Arcticomisophria bathylaptevensis gen. et sp. n. A. Maxilliped. B. Maxilla. C. Maxilla, basis and endopodal segments. Scale bar 50 μm.

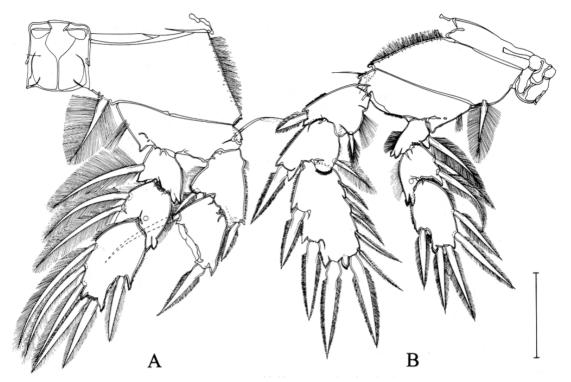


Fig. 6. Arcticomisophria bathylaptevensis gen. et sp. n. A. Third leg. B. Fourth swimming leg. Scale bar 50 µm.

Key to the subgroups of Misophrioida (based on females only).

1.	Antennule with 19 segments at most (fusion of segments II-VI and IX-XII); antennulary segment XII without aesthetasc
_	Antennule with more than 19 segments (segments II-VI and IX-XII free); antennulary segment XII with aesthetasc
Ke	y to genera of the Misophria-group (based on females only).
1.	Female antennule 19-segmented
_	Female antennule 18-segmented or less
2.	Maxillulary exopod with 4 setae; endopod 2 of swimming leg 1 with 2 setae; fifth leg without endopod
-	Maxillulary exopod with 11 setae; endopod 2 of swimming leg 1 with 1 seta; fifth leg with 1-segmented endopod bearing 2 setae
3.	Fifth leg exopod 2-segmented; middle of 3 terminal setae exopod 2 of fifth leg transformed as a spine; antennary exopod 6-segmented
-	Fifth leg exopod 1-segmented at most; all exopod setae of fifth leg slender; antennary exopod 5-segmented Benthomisophria SARS, 1909
4.	Antennule 18-segmented
_	Antennule 17-segmented
5.	Fifth leg with distinct coxa and basis; intercoxal sclerite present; proximal exopod segment with outer seta; endopod
	represented by 1 seta
_	Fifth leg with fused coxa and basis; intercoxal sclerite absent; proximal exopod segment without outer seta; endopod,

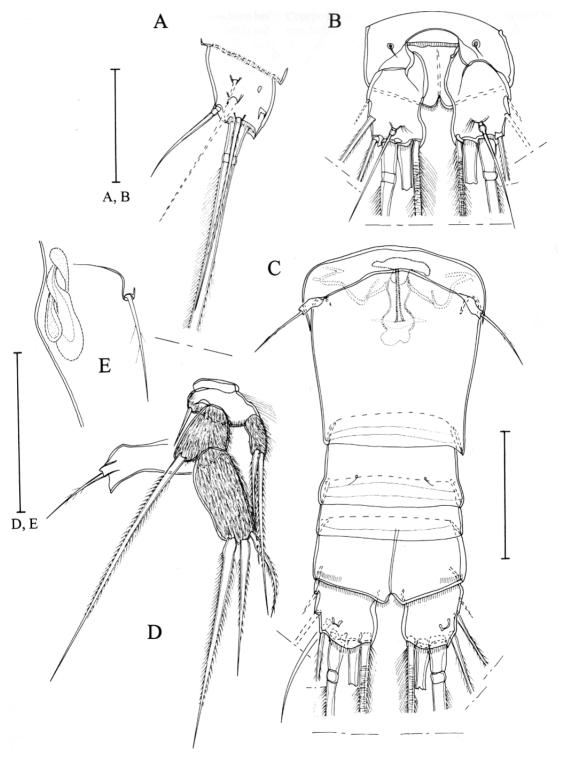


Fig. 7. Arcticomisophria bathylaptevensis gen. et sp. n. A. Furca, lateral view. B. Telson, dorsal view. C. Urosome, ventral view. D. Fifth and sixth swimming legs. E. Genital field, lateral view. Scale bars 50 µm.

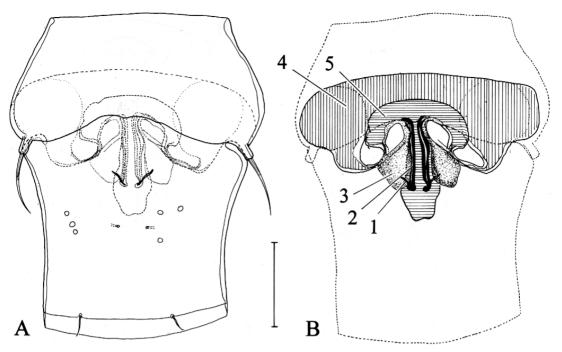


Fig. 8. Arcticomisophria bathylaptevensis gen. et sp. n. Paratype. A. Genital field, ventral view. B. Same, homology of structures, 1: copulatory pore; 2: copulatory tube; 3: gland ?; 4: antrum; 5: seminal receptacle. Scale bar 20 μm.

DISCUSSION

The new species differs from all other known *Misophrioida* in the setation formula of the maxillulary endopod. The retention of a 4/4/6 formula corresponding to the fused first to third endopodal segments of this appendage is unique among Misophrioida. It is also the highest number found in any Podoplea and should be taken into consideration when reconstructing the groundpattern of the superorder. In addition *Misophriopsis dichotoma* BOXSHALL and *Arcticomisophria bathylaptevensis* gen. et sp.n. are the only podopleans with 8 setae representing the epipodite of the maxillulary coxa.

Within Misophriidae, the new genus belongs to the *Misophria*-group as defined by Boxshall (1989) the other genera of which are *Misophria*, *Misophriella*, *Misophriopsis*, *Benthomisophria*, and *Stygomisophria*. Accepting the homology of the antennulary segments proposed by Huys & Boxshall (1991), the *Misophria*-group is characterized by the following autapomorphic characters: 1) fusion of antennulary segments IX-XII and 3) loss of aesthetasc on antennulary segment XII in female and 4) antennary exopod with only 6 segments (setation formula 0/2/1/1/1/3). In the

following only the genera belonging to the *Misophria*-group will be considered for further discussion.

The new genus can easily be distinguished from all other genera of the group by the combination of the following characters: 19-segmented antennula in the female, 6-segmented antennary exopodite bearing 2 setae on second segment, 14 setae on the maxillulary endopod, 11 setae on the maxillulary exopod, 8 setae on maxillulary coxal epipodite, only 1 seta on the middle endopod segment of the first swimming leg and the retention of a discrete coxa and basis on female fifth leg, with a 2-segmented exopod (bearing 1 outer seta on the first segment and 3 slender setae on the second) and a discrete 1-segmented endopod bearing 2 well-developed setae.

The polarity of the characters mentioned can be assessed by the following comparison. We accept that there is an evolutionary trend within copepods consisting of the reduction of the number of segments and armature elements. This means that high numbers of segments and setae are relatively plesiomorphic and fewer segments and setae, relatively apomorphic. A high number of segments tends to correlate with plesiomorphic conditions in other characters.

The female antennula is 19-segmented in the groundpattern of the Misophria-group. This condition has been retained only in Misophriella (Boxshall 1983) and Arcticomisophria gen.n.. Stygomisophria and Misophriopsis both have 18 segments, Misophria has only 17 segments (Ohtsuka & al. 1992), and Benthomisophria has either 18 or 16 antennulary segments (Boxshall & Roe 1980). The antennary exopod is 6-segmented in the groundpattern of the *Misophria*-group. Its primitive setation formula of 0/2/ 1/1/1/3 has been retained only by Stygomisophria, Misophriopsis and Arcticomisophria gen.n.. The retention of 14 setae on the maxillulary endoped and of 8 setae on the maxillulary epipodite are sym-plesiomorphies of Podoplea. The maxillulary exopod bears 11 setae in the groundpattern of Misophrioida (Huys & Boxshall 1991). Within the Misophria-group this condition is retained only by Arcticomisophria gen. n., other genera having less setae (10 in Misophria and Stygomisophria, 9 or less in Benthomisophria and Misophriopsis, and 4 in Misophriella). The fifth leg of the new genus has also retained a great number of plesiomorphies such as a discrete coxa and basis. A discrete 1-segmented endopod bearing 2 well developed setae also is a character of the groundpattern of Misophrioida and has been reported so far only for an as yet undescribed genus referred to as *Misophriopsis* sp. in Huys & Boxshall (1991). Misophria also has 2 setae, but the outermost seta is very reduced and the endopod is partially fused with the basis. Within the Misophria-group the middle of the 3 terminal setae of the second exopod segment is usually modified as a short and strong spine. This is the case in all genera except for Benthomisophria. The new genus carries 3 slender terminal setae on this podomere. It is difficult to assess the polarity of this character, but comparison with species of the Archimisophria-group suggests that the slender setae represent the plesiomorphic and the spine the apomorphic state. Finally, all known species within the Misophria-group bear 2 setae on first leg endopod 2, while the new species has only 1 seta, this being the autapomorphic condition.

The condition of the mandibular exopod as present in *Arcticomisophria bathylaptevensis* gen. et sp. n. must be discussed in detail. As described above, the new species has a 5-segmented mandibular exopod, segments 2-4 being partially fused. Exactly the same arrangement of segments and setae are present in *Misophria pallida* (Huys & Boxshall 1991, fig. 2.3.5.c). According to Huys & Boxshall (1991) a 5-segmented exopod with a setation formula of 1/1/1/2 is present in the groundpattern of Copepoda. Within Misophrioida, this condition has been retained by *Speleophria bivexilla* Boxshall & Iliffe, 1986. However, the new species bears 2 setae on the second exopodal segment instead of 1. Assuming that in the stem species of

Copepoda each segment carried only one seta, it must be concluded that the second segment of the new species is the result of a fusion of two segments. This means that a 6 segmented exopod with a 0/1/1/1/1/2 setation formula was present in the groundpattern of Copepoda. We interpret the more proximal sclerite present in the exopod of the mandible in the new species and in *Misophria pallida* as of a real segment, and not just a pedestal arising from the basis.

After having discussed the polarity of the characters, it is clear that the new species from the Laptev Sea should belong to a separate genus as proposed above. To include this species in one of the genera already known would result in unjustifiable extension of the generic concept. Phylogenetically, *Arcticomisophria* gen. et sp. n. occupies a basal position within the *Misophria*-group.

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