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Sarsicopia polaris gen. et sp. n., the first Platycopioida (Copepoda: Crustacea) from the Arctic Ocean, and its phylogenetic significance

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Abstract

A new genus of Platycopioida is described from a box core sample taken at a depth of 534 m in the Arctic Barents Sea. This is the deepest record of Platycopioida so far. *Sarsicopia* gen. n. is the sistergroup of a taxon comprising *Platycopia* and *Nanocopia*; the sistergroup of these is *Antrisocopia*. *Sarsicopia* gen. n. is the only platycopioid to retain 2 inner setae on the second endopod segment P2–P4, and 8 setae in the third endopod segment of P2. The male antennule is remarkable in having a geniculation located between ancestral segments XX and XXI. It is suggested that this flexure zone was already present in the groundpattern of Copepoda. *Platycopia* and *Nanocopia* have secondarily lost this geniculation.

Introduction

The family Platycopiidae was created by G. O. Sars (1911) in order to accomodate a primitive new copepod species, *Platycopia perplexa* G. O. Sars, collected from a bottom sample at 60 fathoms depth off Korshavn (Norway). Sars included the new family in the Calanoida, and some years later added a second species to the genus collected at the same locality (Sars, 1921). Lang (1948) suggested that the peculiar shape of the mouthparts, together with the retention of several primitive characters where sufficient arguments to consider Platycopia a representative of a separate suborder of Copepoda, 'Progymnoplea', equal in rank with Gymnoplea (Calanoida), Propodoplea (Misophrioida) and Podoplea (Cyclopoida and Harpacticoida). Andronov (1985) corroborated Lang's opinion and considered Progymnoplea a valid suborder of Copepoda. One year later Fosshagen & Iliffe (1985) introduced the order Platycopioida, and placed it in the Gymnoplea together with the order Calanoida. Finally Huys & Boxshall (1991) regarded Platycopioida as the sister group of all other Copepoda, placing it in the infraclass Progymnoplea equal in rank with a new infraclass Neocopepoda.

The order Platycopioida consists of one family and three genera, *Platycopia*, *Nanocopia* Fosshagen and *Antrisocopia* Fosshagen. All species of Platycopioida have so far been found in shallow waters down to 120 m depth. The eight species of *Platycopia* are known from the North Sea (Sars, 1911, 1921), the eastern coast of North America (Wilson, 1946), Bahamas (Fosshagen, 1972), Mauritania (Andronov, 1985) and Japan (Ohtsuka & Boxshall, 1994) while both monotypic genera *Nanocopia* and *Antrisocopia* are known from one anchialine cave on Bermuda only (Fosshagen & Iliffe, 1985, 1988).

During summer 1993, meiobenthic samples were taken along the continental slope of the Barents Sea off northwestern Franz-Josef Land, as part of a German-Russian joint venture (ARK-IX/4) to better understand Arctic marine biocenoses. In one box core sample, taken at 534 m depth, the bottom was covered by a layer of sponge spicula about 2 cm thick. This sample yielded an extremely diverse hyperbenthic crustacean fauna, including no less than 1 species of Tantulocarida, 5 species of Cyclopoida (Cyclopinidae and Cyclopidae Euryteinae), 3 species of Misophrioida, 1 hyperbenthic species of Calanoida (Pseudocyclopiidae) and a new species of Platycopioida, to be described in the present contribution. The platycopioid belongs to a new genus

Sarsicopia. It represents the first record of Platycopioida from the Arctic Ocean, and the deepest sampling site where platycopioids have been found so far. It has retained some plesiomorphic characters affecting the reconstruction of the groundpattern of Platycopioida as a whole. The antennule of *Sarsicopia* gen. n. requires some comments on the evolution of sexually dimorphic male antennules within Copepoda.

Material and methods

Meiobenthic samples were taken during a German-Russian expedition to the Arctic Ocean ARK-IX/4 (Aug.–Oct. 1993), on board of RV *Polarstern* using a Multicorer and a Giant Box Corer. The supernatant water of the Giant Box Corer was extracted using a silicone tube, filtered through a 40 μm sieve, and the residue was fixed with formalin together with the first 5 cm of sediment from the Box Corer at a final concentration of 4%. Station 27/025, contained 5 specimens of a new species of Platycopioida (1 female, 3 males and 1 copepodid).

Drawings were made using a camera lucida on a Leitz Diaplan interference contrast microscope (antennules and mouthparts) or a Leitz Dialux phase contrast microscope.

Terminology is adopted from Huys & Boxshall (1991), except for the terms of phylogenetic systematics used according to Hennig (1982), and the term 'telson' used following Schminke (1976) instead of 'anal somite'. Abbreviations used in the text are: P1–P6: legs 1–6, ae: aesthetasc; enp.: endopod; exp.: exopod.

The material is stored at the Copepod Collection of the AG. Zoomorphologie, University of Oldenburg, Germany.

Description

Sarsicopia gen. n.

Diagnosis. Platycopioida with prehensile 16-segmented antennules in male, non-prehensile 18-segmented in female. Ancestral segments XV–XVI and XVIII–XX fused in both sexes. Antenna with 4-segmented exopod. Mandible with 3-segmented exopod. Maxillule with distal basal endite fused to rami bearing 6 setae in total. Maxilla with well developed proximal precoxal endite bearing 4 setae, distal precoxal endite missing, proximal coxal endite represented by 1 seta, distal coxal endite with 2 setae, with allobasis and 2 free endopodal segments. Maxilliped with 1 seta each on syncoxa and basis and with 5-segmented endopod, last endopodal segment bearing 2 setae. No intermaxillipedal process present. P1 with 2-segmented rami, enp.-2 with 6 setae, exp.-2 with 4 setae. P2-P5 with 3-segmented rami. P2-P4 with 2 inner setae on enp.-2

Type species. Sarsicopia polaris gen. et sp.n.

Sarsicopia polaris gen. et sp. n.

Type material. 1 male (holotype) dissected and mounted on 17 slides (Coll. No. 1996.1/1–1996.1/17); 1 female (allotype) dissected and mounted on 2 slides (Coll. No. 1996.2/1–1996.2/2); 2 males (paratype 1, Coll. No. 1996.3/1, and paratype 2, Coll. No. 1996.4/1) and 1 copepodid (paratype 3 Coll. No. 1996.5/1) mounted on one slide each.

Locus typicus. Northern Barents Sea, Arctic Ocean, 82° 07, 42′ N, 42° 32, 35′ E, 534 m depth, Box Corer sample from 28.8.93; muddy sediments covered by a mat of sponge spicula about 2 cm thick.

Male (holotype) – Body length without furca 338 μm. Prosome consisting of cephalosome, and first to fifth pedigerous somites (Figure 1A, B). First pedigerous somite incompletely fused to cephalosome. Tergite of fifth pedigerous somite completely separated from fourth pedigerous somite. Urosome 5-segmented. Genital somite small, latero-posteriorly produced (Figure 5C). Abdominal somites posteriorly with serrated and striated hyaline frill (Figure 1B). Frill on third abdominal somite dorsomedially produced forming pseudoperculum covering telson partially. Furca slightly longer than wide (Figure 5C), with 4 terminal and 2 lateral setae and ornamented with triangular frills. Rostrum produced anteriorly, fused to cephalosome, with paired sensilla at base (Figure 2A).

Antennule 16-segmented (Figure 2A), geniculate on both sides. Setal formula beginning with proximal segment (Figure 2B): 7 + 3 ae/ 2 + ae/ 2 + ae/ 2 + ae/ 2 + ae/ 3 + ae/ 2 + ae/ 1 + ae/ 2 + ae/ 2 + ae/ 0/ 2 + 2 ae/ 1 + ae/ 1/ 3 + 3 ae/ 4 + ae (Figure 2B).

Antenna small (Figure 3B), with unarmed coxa and basis, 3-segmented endopod with setal formula of 0/2/5 and indistinctly 5-segmented exopod with setal formula of 1/0/4/1/3.

Mandible (Figure 3) gnathobasis with 4 main teeth and some spinules, basis unarmed, endopod 1-segmented with 4 setae, exopod 3-segmented with a setal formula of 1/2/3.

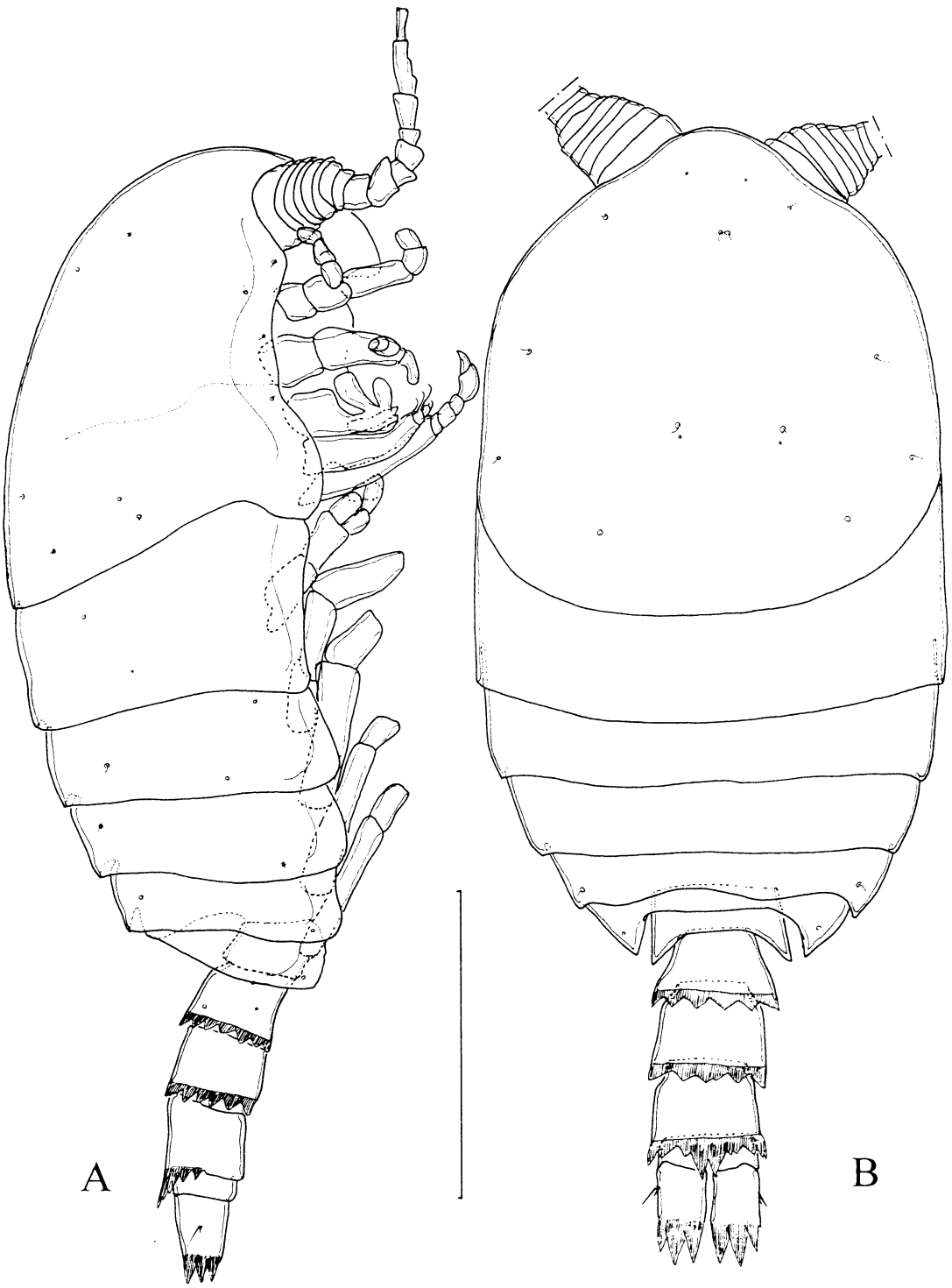

Figure 1. *Sarsicopia polaris* gen. et sp.n. Male habitus. A, lateral view. B, dorsal view. Scale bar 100 μm.

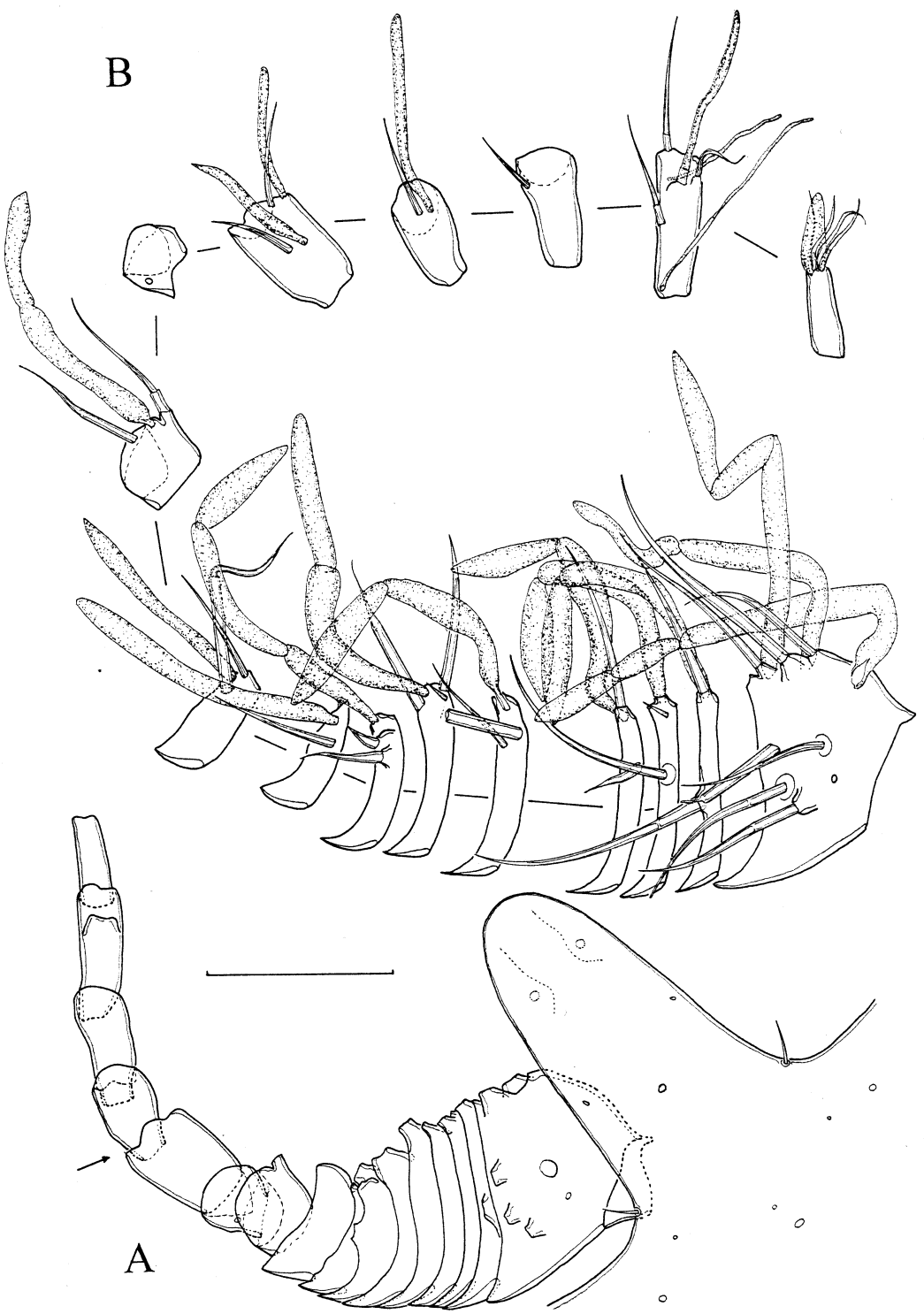

Figure 2. Sarsicopia polaris gen. et sp.n. Male antennule. A, antennule and rostrum; flexure zone between ancestral segments XX and XXI arrowed. B, antennulary segments separated. Scale bar 20 μm.

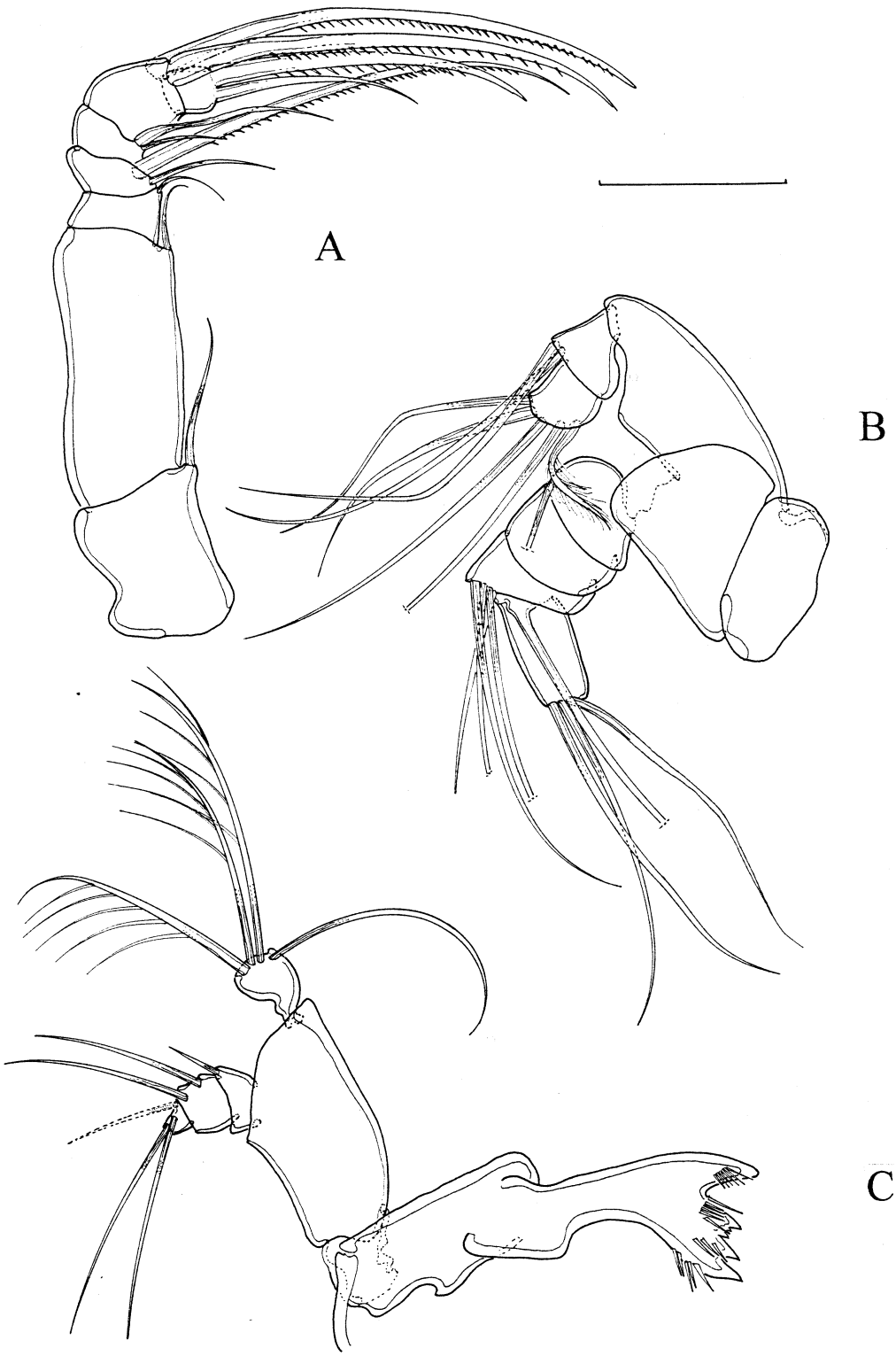

Figure 3. *Sarsicopia polaris* gen. et sp.n. A, maxilliped. B, antenna. C, mandible. Scale bar 20 μm.

Maxillule (Figure 4A), precoxal arthrite with 8 spines and 5 setae, coxal endite with 3 setae, basal exite with 2 setae, proximal basal endite with 3 setae, distal basal endite fused to rami, with 6 setae in total.

Maxilla (Figure 4B) precoxal endite with 4 setae, proximal coxal endite represented by minute seta, distal coxal endite with 2 setae, allobasis with 2 setae on endite and 2 distal inner strong seta, free endopod 2-segmented, proximal segment with 2 setae, distal segment with 3 setae.

Maxilliped (Figure 3A) syncoxa with 1 seta, basis with 1 seta on distal inner margin, endopod 5-segmented, setal formula 1/2/2/2/2.

Leg 1 (Figure 5A) coxa unarmed, basis with inner seta, exopod 2-segmented bearing 0 and 4 setae, endopod 2-segmented, proximal segment with 1 inner seta, distal with 6 setae.

Legs 2–5 (Figures 6A-B, 5B) most probably with 3-segmented rami (distal segments of legs partially missing). All legs with well developed intercoxal sclerite. Seta and spine formula:

	Coxa	Basis	Exopod	Endopod
leg 1	0-0	0-1	0-0; 0, 0, 4	0-1; 0,2,4
leg 2	0-0	I-1	II-0; I-0; missing	0-1; 0-2; II, II, II2
leg 3	0-0	I-1	II-0; I-0; missing	0-1; 0-2; II,II,II1
leg 4	0-0	I-1	II-0; missing	0-1; missing
leg 5	0-0	I-0	II-0; I-1; missing	0-1; 0-1∗; missing

Segment marked with asterisk present in paratype 1 only.

Genital somite without any seta representing leg 6.

Female (allotype) differs from male only in following characters:

Body length 390 μm. Antennule non-geniculate, 18-segmented (Figure 4C). Setal formula beginning with proximal segment: 11 + 4 ae/2 + ae/2/2 + ae/1/2/2 + ae/2 + ae/0/2/1 + ae/0/1/ 1/2 + 2 ae/2/2/4 + ae.

Labrum as in male tripartite (Figure 7E). Genital somite as in male completely separated from first abdominal somite (Figure 7A). No genital apertures discernible. P6 represented by 1 seta?

Variability. Male paratypes slightly bigger than holotype (paratype 1: 351 μm; paratype 2: 354 μm). Paratype 1 with aberrant right P3 consisting of fused coxa and basis and 2-segmented exopod, first segment with two outer spines and inner seta, second segment with 6 elements in total. No endopod. Left P3 of normal shape.

Etymology. The genus is named after the Norwegian zoologist G. O. Sars, first describer of Platycopioida. The specific name refers to the polar region.

Discussion

Sarsicopia polaris gen. et sp.n. represents the first record of Platycopioida from the Arctic Ocean and increases the depth range considerably (from 120 to 534 m) in which the order has been found so far. It would not be surprising to find Platycopioida even in the deep sea, when an intensive exploration of this vast ecosystem is finally undertaken.

Sarsicopia gen. n. differs from other genera in the family by the presence of fused ancestral antennulary segments XV-XVI and XVIII-XX in both sexes, the presence of 2 inner setae on P2-P4 enP.-2, and the presence of 8 elements on P2 enp.-3.

The new genus represents the sistergroup of a taxon including *Platycopia* and *Nanocopia*. *Nanocopia* requires redescription and re–examination of several features. Pending this the synapomorphies of *Nanocopia* and *Platycopia* are tentatively determined as (i) a non prehensile male antennule, while it is prehensile in *Antrisocopia* and *Sarsicopia* gen. n., (ii) sexually dimorphic male fifth legs, while they are not sexually dimorphic in *Antrisocopia* and although these legs are partially damaged in the *Sarsicopia* material, they seem to lack any modifications, (iii) P1 enp-2, or homologous, with three setae, while no less than 6 setae are present in the other platycopioid genera, and (iv) loss of inner seta on P1 enp.-1, while this seta is present in *Antrisocopia* and *Sarsicopia* gen. n.

Sarsicopia gen. n. shares with the taxon *Platycopia + Nanocopia* the fusion of the ancestral male antennulary segments IV–VI and XXI–XXII, while these segments are separated in *Antrisocopia* (Figure 8). Other synapomorphies of *Sarsicopia* gen.n. and *Platycopia + Nanocopia* are (i) presence of at most 7-segmented antennary exopod, while an indistinctly 8-segmented exopod is present in *Antrisocopia*, (ii) presence of an indistinctly 3- or 4-segmented mandibular exopod, while a 5-segmented exopod is present in *Antrisocopia*, (iii) presence of a total of only 6 setae on the maxillulary baso-ramal complex (comprising the distal endite and rami fused to it), 8 setae being present in *Antrisocopia*, (iv) retention of at most 6 setae in P1 enp.-2, 7 setae being the plesiomorphic state, (v) loss of inner seta on P5 exp.-1, this seta being present in *Antrisocopia*, (vi) presence of only 6 furcal setae

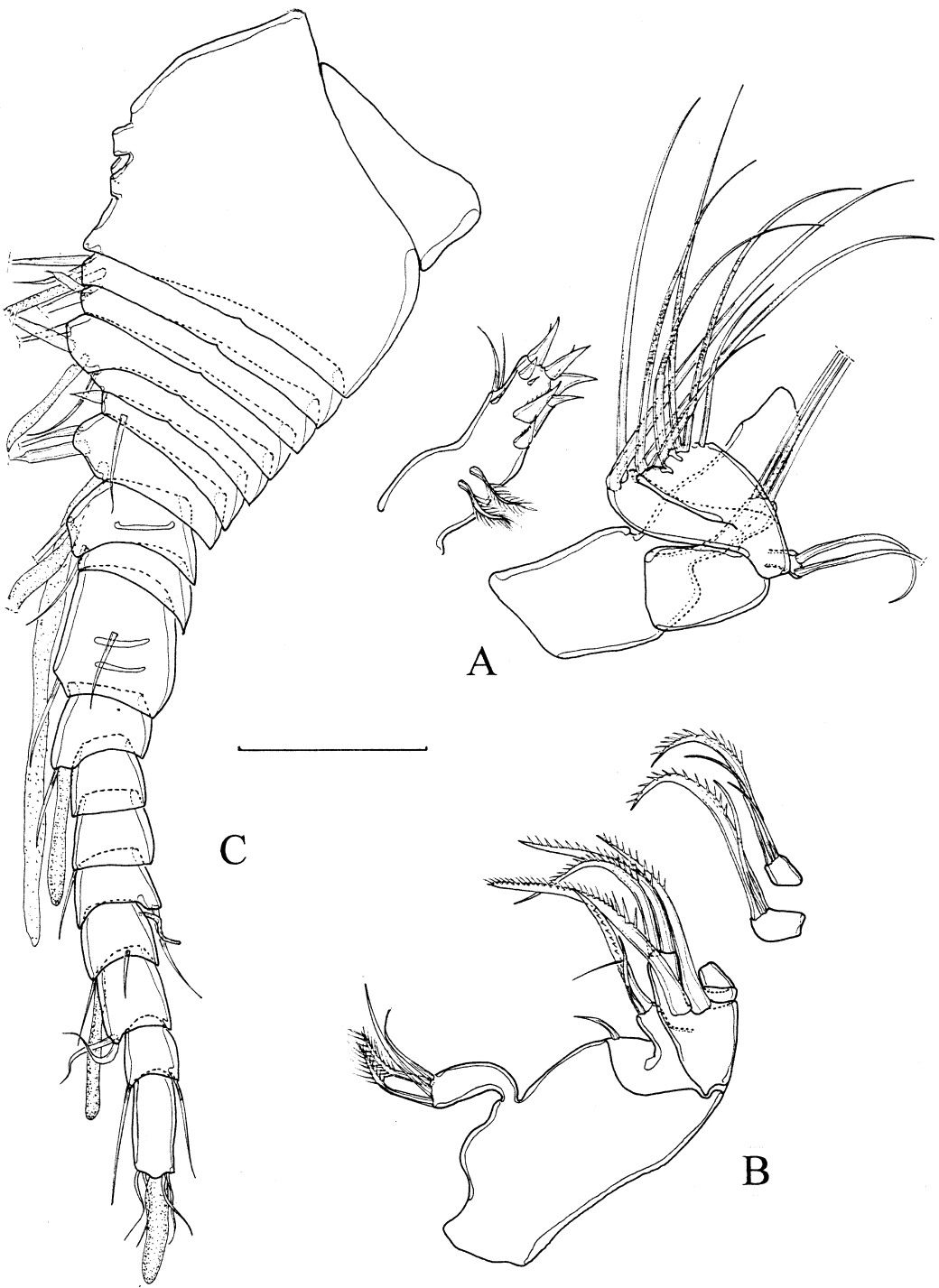

Figure 4. *Sarsicopia polaris* gen. et sp.n. A, maxillule, precoxal arthrite separate. B, maxilla, free endopodal segments separated. C, female antennule. Scale bar 20 μm.

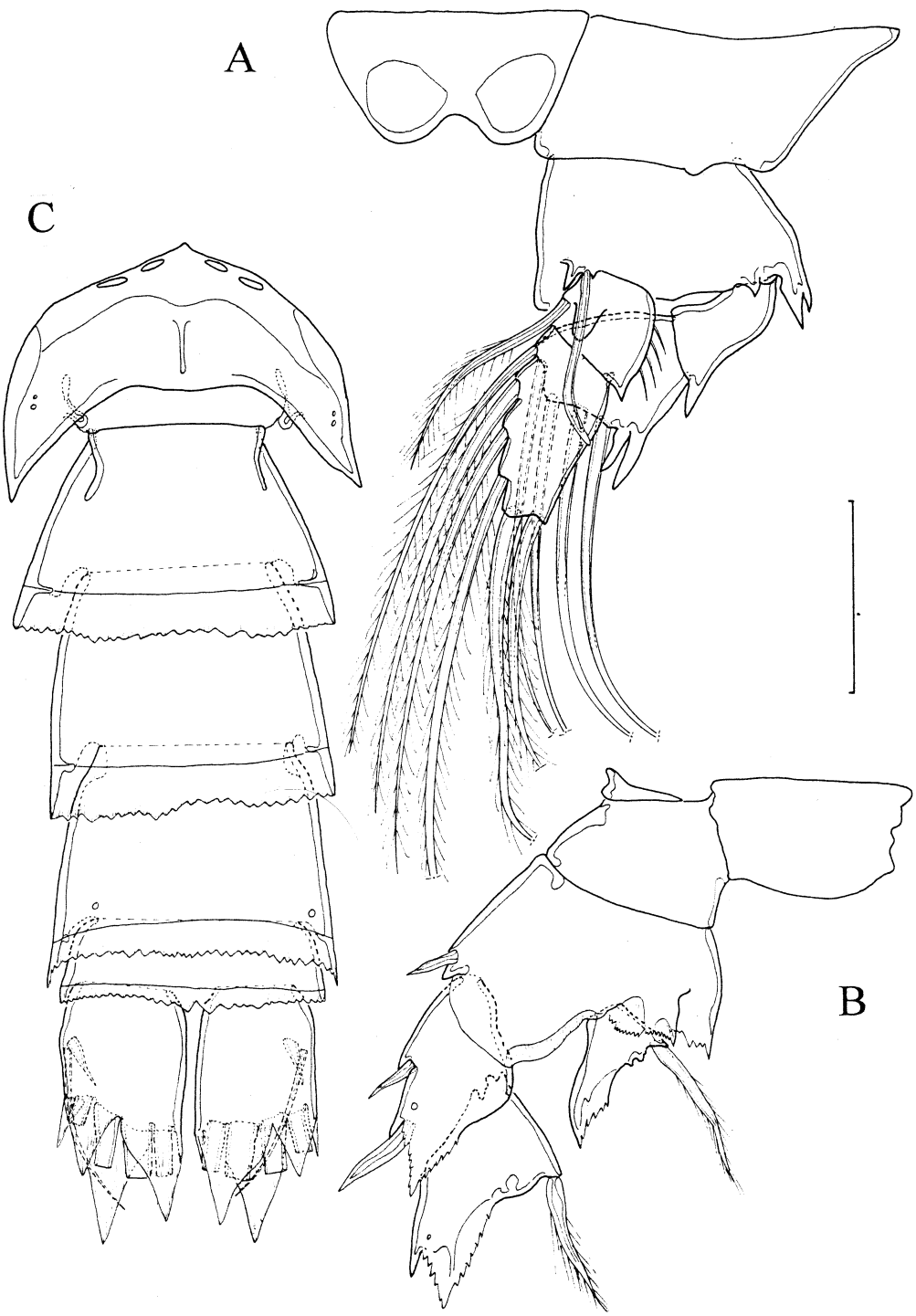

Figure 5. *Sarsicopia polaris* gen. et sp.n. A, first leg. B, male fifth leg (distal segments missing). C, male urosomite, ventral view. Scale bar 20 μm.

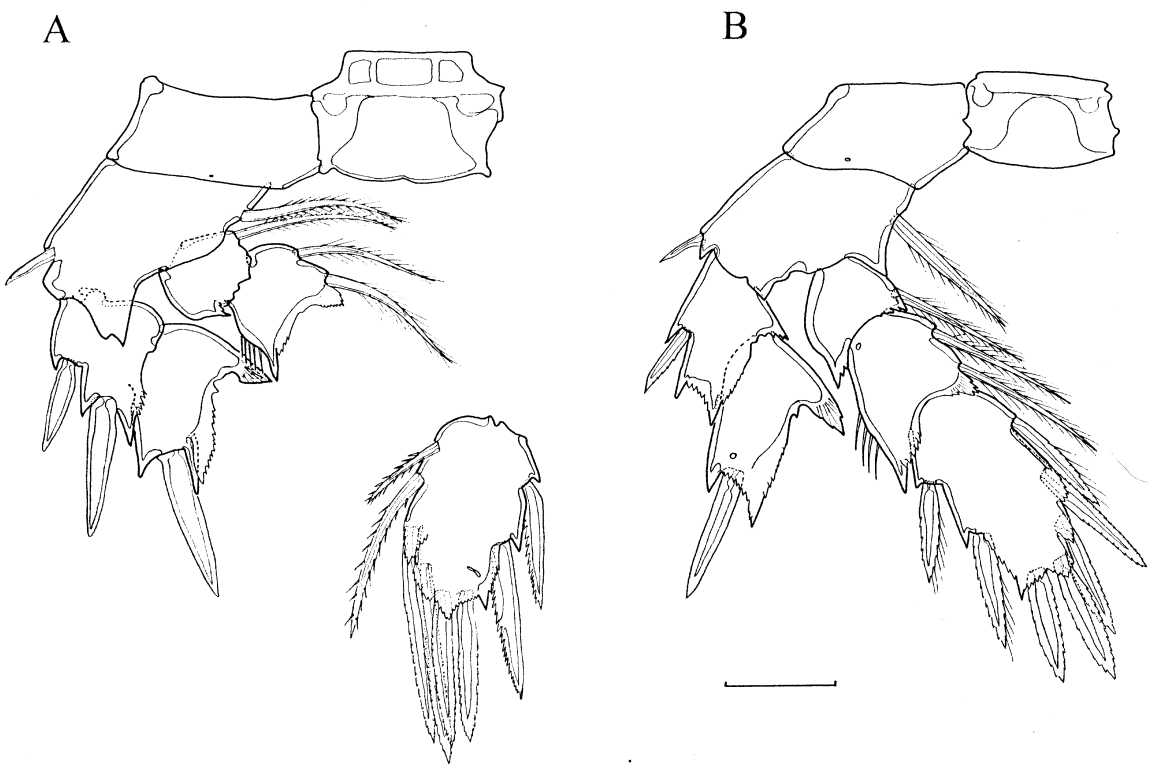

Figure 6. Sarsicopia polaris gen. et sp.n. A, second leg, and enp.-3 of opposite leg. B, third leg. Scale bar 20 μm.

(loss of setae VII), 7 setae being present in *Antrisocopia*, and (vii) abdominal ornamentation including serrated hyaline frills at the distal ends of somites, that of third abdominal somite forming a pseudoperculum and presence of characteristic triangular frills on the distal part of the furca (these frills have not been described for *Nanocopia* by Fosshagen & Iliffe (1988), but may have been overlooked due to the minute size of the specimens), while plain abdominal frills, no pseudoperculum and no frills on the furca are present in *Antrisocopia*. Unfortunately the swimming legs of all 5 *Sarsicopia* specimens were damaged, so that the reconstruction of the setation pattern of the swimming legs is only partial. However, *Sarsicopia polaris* gen. et sp.n. is the only platycopioid that has retained two inner setae in the second endopod segments P2-P4 and 8 elements on the third endopod segment P2. There are some typing errors in the reconstruction of the platycopioid setation formula presented by Huys & Boxshall (1991) as regards the basis P1 and P5. The spine and setation formula of the groundpattern of Platycopioida has to be emended as follows:

	Coxa	Basis	Exopod	Endopod
leg 1	0-0	0-1	0-0; 0-0; 0,I,5	0-1; 1,2,4
leg 2	0-0	I-1	II-I; I-1; III,I,4	0-1; 0-2; 2,2,4
leg 3	0-0	I-1	II-I; I-1, III,I,4	0-1; 0-2; 2,2,3
leg 4	0-0	I-1	II-I; I-1; III,I,4	0-1; 0-2; 2,2,2
leg 5	0-0	I-0	II-1; I-1; III,2,1	0-1; 0-1; 1,2,2

The absence of an intermaxillipedal process in *Sarsicopia* gen n. is regarded here a plesiomorphic character. The interpretation of the intermaxillipedal process as an autapomorphy of Platycopioida (Huys & Boxshall, 1991) has to be reconsidered. This structure is neither present in *Antrisocopia*, nor in *Nanocopia*. It also lacks in most *Platycopia* species, e.g. *Platycopia orientalis* Ohtsuka & Boxshall (Othsuka & Boxshall, 1994). In my opinion this structure should be regarded merely as a synapomorphy of *Platycopia perplexa* Sars and *Platycopia inornata* Fosshagen, the only species from which an intermaxillipedal process has been reported.

The male antennule of *Sarsicopia* gen n. is remarkable because of its sexual dimorphism that includes not

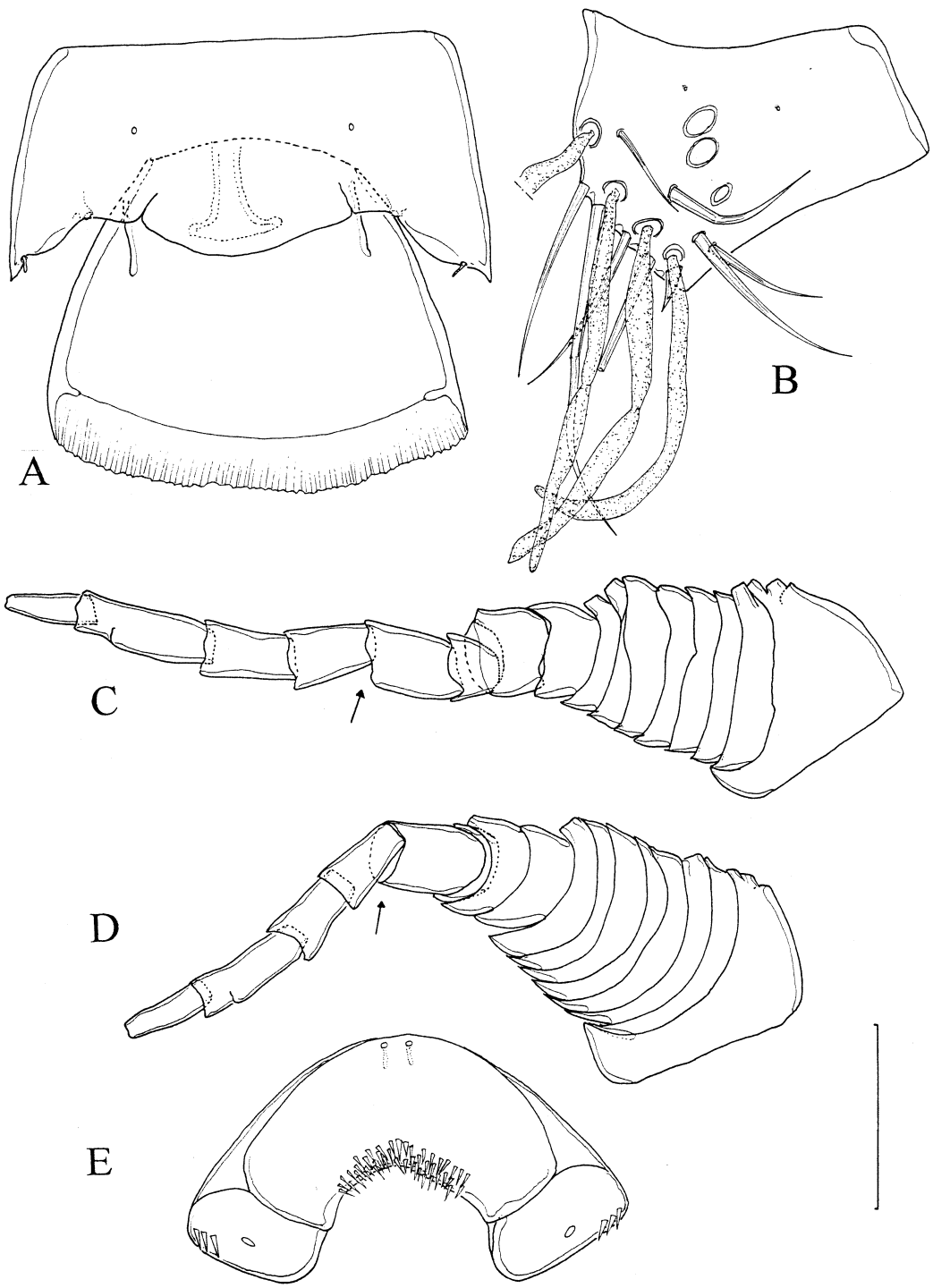

Figure 7. Sarsicopia polaris gen. et sp.n. A, female genital and first abdominal somites, ventral view. B, female first antennulary segment. C, male antennule, paratype 1. D, male antennule, paratype 2. C-D, flexure zone between ancestral segments XX and XXI arrowed. E, labrum, ventral view. Scale bar 20 μm.

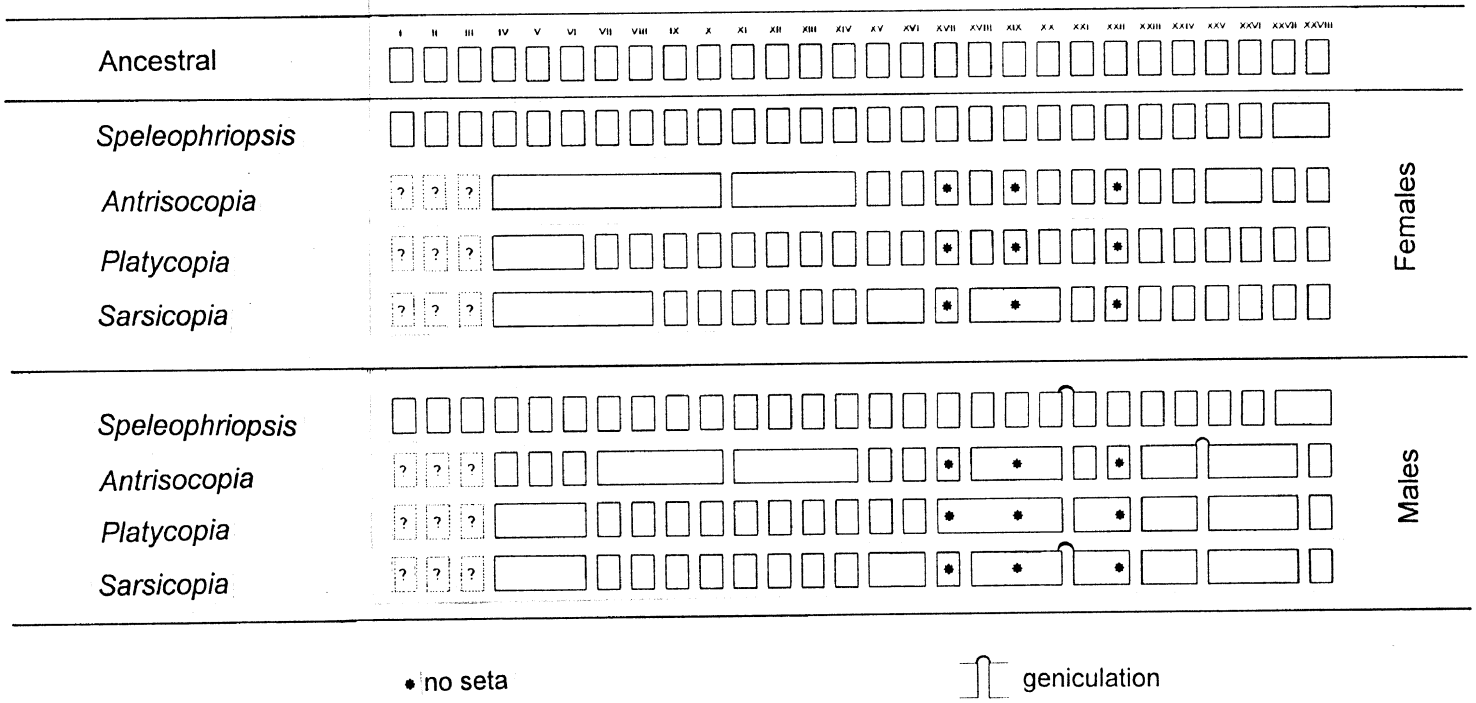

Figure 8. Homology of antennulary segments in Platycopioida compared with the misophrioid *Speleophriopsis balearicus*. Modified after Huys & Boxshall (1991).

only the fusion of some segments, but also the modification of the whole antennule as a grasping organ. It has been postulated that Platycopioida primitively lack geniculate male antennules (Huys & Boxshall, 1991), as non-prehensile male antennules are present in *Platycopia* and *Nanocopia*. The non-prehensile male antennules are interpreted here as apomorphic and the prehensile antennules of *Sarsicopia* gen. n. as plesiomorphic due to following reasons. The evolution of the male antennule in copepods as an organ used for grasping the female during mating involves two major modifications: (I) formation of geniculations that allow some segments to move inwards, and (II) fusion of segments to give robustness to those parts of the antennule where it is required. It seems logical to assume that a step by step evolution of the male antennule first requires the capability to grasp. Therefore the inward geniculation has to evolve first and then segments have to fuse to give robustness to the grasping organ. This sequence is supported by what is found in the misophrioid *Speleophriopsis balearicus* Jaume & Boxshall. This species exhibits the most primitive condition found in any of the Copepoda (Jaume & Boxshall, 1996), yet the male antennule clearly shows the 'neocopepodan' geniculation between segments 20 and 21. No fusion is involved in the evolution of the grasping capability of males of *Speleophriopsis balearicus*, as the antennule is 27-segmented in both sexes (Figure 8). Fusion of segments is a secondary event and within Platycopioida is not completely homologous in all the genera (Figure 8). The male antennule of *Platycopia* and *Nanocopia* shows no geniculation, but segments are fused in a very similar pattern as in the geniculate antennule of *Sarsicopia* gen. n. This shows that the non-geniculate antennule of *Platycopia* and *Nanocopia* represents the apomorphic condition, i.e. secondary loss of geniculation, evidenced by the retention of fused segments. The loss of the antennulary capability to grasp is in this genera replaced by the modification of male fifth legs probably to a grasping function. Sexually dimorphic grasping fifth legs are also known from male Calanoida, which use them to grasp the spermatophore during mating and attach it to the female copulatory pore. By anology the male P3 of the harpacticoid family Parastenocarididae is also highly modified as an organ used by the males to grasp the females during copulation (Glatzel & Schminke, 1996). Geniculation in male antennules has also secondarily been lost on both sides in some Calanoida (Pseudocyclopiidae) (Fosshagen & Iliffe, 1985) and in the copepod order Poecilostomatoida. Male Poecilostomatoida have developed very robust maxillipeds to grasp the female during mating, replacing the antennulary grasping mechanism of other copepods. Genetically the loss of geniculation in males is not a very complicated event. The antennulary geniculation appears in the final moult to the adult stage. The fifth male copepodid shows no geniculation, but it already shows the fusion of antennulary segments present in the adult. The condition present in male *Platycopia* and *Nanocopia* therefore can easily be interpreted as a delay in the formation of geniculation during ontogeny, the adult having retained the condition of the previous copepodid stage.

The condition present in male *Antrisocopia* is also remarkable because of the presence of a sexually dimorphic strong claw on the ancestral antennulary segment XXII and of a shift of the major geniculation to a position between segments XXIV and XXV (Figure 8) As to the question of the male antennule in the groundpattern of Copepoda, my opinion is that it is 28-segmented with capability of inward flexion between segments XX and XXI.

The flexure zone between ancestral antennulary segments XX and XXI as present in *Sarsicopia* gen. n. (Figures 2A, 7C–D) should be interpreted as a first step in a transformation series leading to the true 'neocopepodan' geniculation. The autapomorphy of Neocopepoda consisting in the modification of male antennulary segment XXI having its insertion point in the distal inner part of segment XX, and having a plain inner and a strongly convex proximal outer margin, as well as little arthrodial menbrane. All this allows the segment to flex in one plane only.

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