



## A new species of Ancorabolidae (Crustacea: Copepoda: Harpacticoida) from the Campos Basin, Brazil, including a phylogenetic review of the taxon *Polyascophorus* George, 1998, and a key to its species

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### ABSTRACT

A new species of the genus *Polyascophorus* George, 1998 (Copepoda, Harpacticoida, Ancorabolidae), collected from the Grussaí Canyon (Campos Basin, Brazil, South Atlantic), is described in the present contribution, and increases the number of *Polyascophorus* species to three. A detailed phylogenetic analysis reveals that *Polyascophorus monoceratus* sp. nov. shares the following generic apomorphies: (i) lateral posterior cephalic processes bifurcate, (ii) significant diminution of leg 1 endopod, (iii) furcal rami rounded on outer apical margin, and (iv) furcal apical setae IV, V, VI displaced to inner apical edge of furcal ramus. Within the genus, *P. monoceratus* sp. nov. has five derived characters that justify its establishment as a distinct species: (a) first abdominal somite (genital double-somite in female) with single cuticular process dorsally at posterior margin, (b) branches of female lateral bifurcate cephalic processes of the same size, (c) furcal seta VII plumose on distal half, (d) male leg 1 lacking endopod and (e) apical setae of third exopodal segment of second leg bare and geniculate. While *P. gorbunovi* (Smirnov, 1946) and *P. martinezi* George, 1998 were collected from arctic areas, the finding of *P. monoceratus* sp. nov. off Brazil extends the generic distributional range to the South Atlantic ocean. A key to the species is provided.

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### 1. Introduction

Along the Brazilian coast, the Campos Basin oil field is the largest oil-prospecting and production area, with an average output of 1 million barrels per day (Rezende et al., 2002). Considering that more than 50% of Brazilian offshore exploration blocks are in water depths over 400 m, the characterization of the deepwater ecological communities is of primary concern.

The present report is part of a multidisciplinary environmental research project 'Campos Basin Environmental Heterogeneity – HABITATS' sponsored by the Brazilian petroleum company PETROBRAS, in the deepwater oil exploration and production area of the basin. The main objective of the HABITATS project is to characterize physically, chemically and biologically the different environments on the continental shelf and slope of the Campos Basin, in addition to building a model ecosystem to understand the ecological dynamics of this region in order to improve the quality of decisions about developmental activities.

The subfamily Ancorabolinae Sars, 1909 (Copepoda: Harpacticoida: Ancorabolidae) comprises 13 genera, most with a single

species, with a very characteristic body shape although with wide variation in body construction and ornamentation. The generally low abundance of Ancorabolinae in meiofaunal samples, together with the inaccessibility of the deep-sea habitat of most of its species, has led to an underestimation of their diversity (cf. Conroy-Dalton, 2001; George, 2006a; Wandeness et al., 2009). Examination of samples of harpacticoid copepods from the Grussaí Canyon (Campos Basin, Brazil) revealed the presence of a new species of *Polyascophorus* (Copepoda, Harpacticoida, Ancorabolidae). The description of the new species, which extends the known distribution range of the genus to the South Atlantic Ocean, and a phylogenetic review of the genus are the focus of the present contribution.

### 2. Material and methods

Sampling was carried out during the fourth cruise of R/V GYRE in the frame of the HABITATS project (May 2008). A total of 3 stations along the 700, 1000 and 1300 m isobaths were sampled at the Grussaí Canyon (Campos Basin, South Atlantic) (Fig. 1). Samples were taken with a box corer covering 0.25 m<sup>2</sup> of sediment subdivided into 25 subsamples. Each sample was transferred to a 1 l plastic flask and fixed in 10% formalin buffered with borax.

Meiobenthic organisms were extracted by colloidal silica flotation (Giere, 2009). The harpacticoid copepods found in the samples

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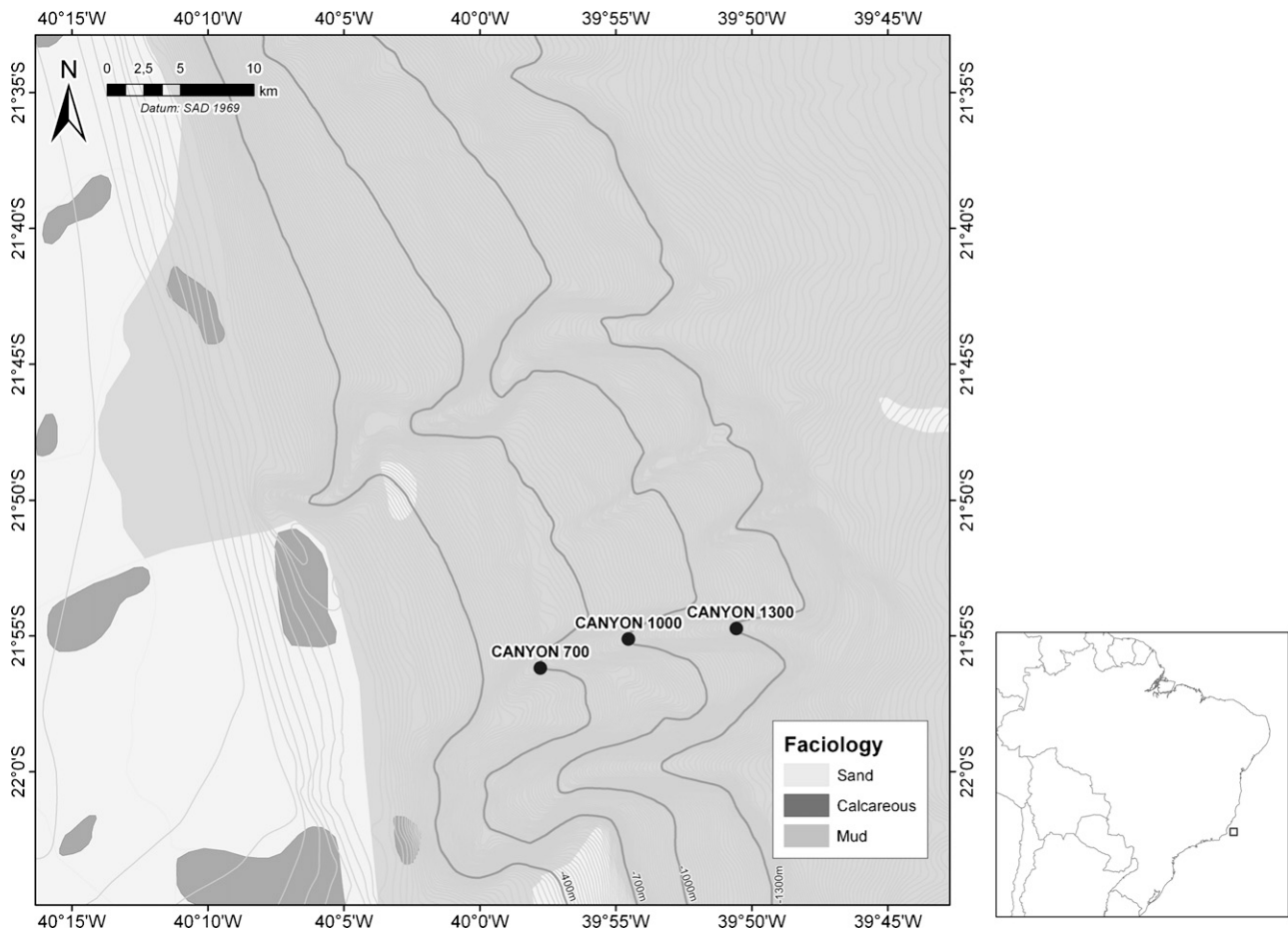


Fig. 1. Map showing the investigation area including the sampling locations.

were picked out and preserved in 70% ethanol for later identification to species level. For light microscopy, specimens were dissected in glycerin under a Leica MZ 9.5 stereomicroscope. Parts of the dissected holotype and allotype were mounted on several slides, using glycerol as the embedding medium and nail varnish for sealing. Drawings were made with the aid of a drawing tube on a Leica-DMR compound microscope equipped with a 100× interference-contrast objective. General terminology follows Lang (1948) and Huys and Boxshall (1991). Terminology referring to phylogenetic aspects follows Ax (1984); the terms “telson” and “furca” are adopted from Schminke (1976).

Abbreviations used in the text and figures: A1: antennula, A2: antenna, aes: aesthetasc, benp: baseopod, cphth: cephalothorax, enp: endopod, enp-1(2,3): proximal (middle, distal) segment of endopod, exp: exopod, exp-1(2,3): proximal (middle, distal) segment of exopod, GDS: genital double-somite, FR: furcal rami, md: mandible, mxl: maxillula, mx: maxilla, mxp: maxilliped, P1–P6: swimming legs 1–6.

The type specimens have been deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), Brazil. Scale bars in the figures are in  $\mu\text{m}$ .

### 3. Results

Harpacticoida Sars, 1903  
 Ancorabolidae Sars, 1909  
 Ancorabolinae Sars, 1909  
 Polyasphorus George, 1998

Generic diagnosis amended from George (1998) and Conroy-Dalton (2001):

Body slender, tapering posteriorly. Cephalothorax comprising approximately  $\frac{1}{4}$  of body length; rostrum fused to cephalothorax, very small or if enlarged, then Y-shaped; with long tube pore. Cephalothorax with a pair of large frontolateral processes in addition to paired lateral bifurcated processes, and with or without a pair of dorsal processes near its posterior margin. Thoracic somites bearing P2–P5 with paired dorsal processes on their posterior margins. First abdominal somite (posterior part of genital double-somite in female) with or without single, centred process on posterior margin. Cephalothorax, body somites, and furca with tube pores dorsally and/or laterally. Furcal rami at most 4 times longer than broad, rounded at their apical outer margin; with seven setae. Furcal setae I and II laterally on outer margin, set close together; III inserted subapically on outer margin; IV, V, VI displaced to inner apical margin of furcal ramus; VII subapically on dorsal side. A1 of female 4-segmented, with first segment elongated and bearing long spinules on inner margin, and with aesthetasc on third and fourth segment. Male A1 6-segmented, subchirocer, with swollen fourth segment that bears an aesthetasc; geniculation between fourth and fifth segment. First swimming leg with 2-segmented exp; exp-2 with 4 apical, geniculate setae and 1 outer spine; enp 1–2-segmented in female, 0–2-segmented in male, with at most 1 seta. P2–P4 with 3-segmented exps; exp-1 with 1 outer spine, exp-2 with 1 outer spine and 1 inner seta; exp-3 with 2 outer spines and 2 apical setae, and with 1 (P2, P4) or 2 (P3) inner setae. P2 enp 0–1-segmented, with at most 1 seta. P3 enp sexually dimorphic: in female 1–2-segmented, carrying 1–2 setae; in male 3-segmented with an elongate enp-2 that bears a curved apophysis on inner apical margin, and 2 apical setae on enp-3. P4 enp sexually dimorphic, at most 2-segmented: in female, distal (or only) segment with 1

seta; in male, distal segment with 2–3 setae. P5 with benp and exp fused; endopodal lobe completely reduced and represented by 1 seta and 1–2 tube pores in female, and by 1–2 setae and 1–2 tube pores in male. Female genital field with gonopore covered by genital operculum formed by the reduced P6, with 1 seta on each side.

Type species: *Polyascophorus martinezi* George, 1998. Additional species: *Polyascophorus gorbunovi* (Smirnov, 1946), *Polyascophorus monoceratus* sp. nov. (present contribution).

### 3.1. *Polyascophorus monoceratus* sp. nov.

Type locality: Grussaí Canyon, Campos Basin, Brazil, at 21.91S/39.91W, 1000 m depth.

Holotype: female, collected on May 28th, 2008 at type locality, mounted on 8 slides, and labelled MZUSP Coll. no. 24559. Paratype (allotype): male, collected on May 28th, 2008 at type locality, mounted on 6 slides, and labelled MZUSP Coll. no. 24560.

Etymology: the specific epitheton *monoceratus* refers to the single cuticular process that is present dorsally on the first abdominal somite (posterior part of GDS in female).

### 3.2. Description of the female holotype

Habitus (Fig. 2A) cylindrical, long and slender. Body length (rostrum to FR) about 470  $\mu\text{m}$ . Rostrum (Figs. 2A and 3A) elongate and bifurcated, with few spinules, 1 sensillum on each tip, and 1 tube pore ventrally on its distal margin. Cphth frontally with peak that bears a pair of long frontolateral processes with 1 sensillum on each of their tips and accompanied by 1 tube pore basally. Posterior part with pair of large and furcated lateral processes carrying sensilla on the tips and bases. Cphth with few pairs of sensilla. Dorsal posterior margin of cphth and P2–P5-bearing thoracic somites each with pair of long processes with sensillum on top, cephalothoracic processes basally accompanied by tube pores. Additionally with pair of sensilla (2 pairs on P2-bearing somite along dorsal posterior margin). P2–P6-bearing somites dorsally with single tube pore; distal margin of GDS and following abdominal somite dorsally with paired tube pores. GDS bearing on posterior margin, 1 centred cuticular process carrying a sensillum on its tip. Abdominal part of GDS and following abdominal somites including telson laterally with long spinules. Abdominal somites except telson with row of spinules dorsally on posterior margin. Telson small, broader than long. Anal operculum flanked by pair of sensilla, apical margin with row of fine spinules, and with 1 tube pore ventrally near each FR insertion (Fig. 2B).

FR (Fig. 2B and C) about 2.7 times longer than broadest width, with outer distal margin rounded, and with 7 setae: I and II set close together, I bare, II bipinnate; III inserted subapically, bipinnate; IV very small, bare; V longest, approximately 1.5 times longer than FR, bipinnate; VI longer than IV, bare; VII subapically on dorsal side, triarticulate and biplumose on its distal half. One small tube pore on proximal outer margin of FR, a second long tube pore arising subapically on ventral side.

A1 (Fig. 3A) 4-segmented. First segment longest, with 1 biplumose seta and several long spinules on inner margin. Remaining segments of almost same length. Second segment with 3 bare and 4 bipinnate setae and covered with several long spinules. Third segment bearing 8 bare setae, two of which arise from apical pedestal together with long aes (\* in Fig. 3A). Fourth segment with 10 bare setae and 1 aes. Setal formula: 1-1; 2-7; 3-8+aes; 4-10+aes.

A2 (Fig. 3B) with allobasis carrying 2 abexopodal setae (the proximal one uni-, the distal one bipinnate) and row of spinules. Exp absent. Enp with row of spinules, subapically with 2 cuticular dentate frills; at  $\frac{3}{4}$  of margin with 2 bipinnate setae, apically with 5

**Table 1**

Setation of swimming-legs 2–4, female (outer spines in roman numerals).

	Exopod			Endopod	
	1	2	3	1	2
P2	I;0	I;1	II;2;1	–	–
P3	I;0	I;1	II;2;2	0;0	0;2;0
P4	I;0	I;1	II;2;1	0;0	0;1;0

bare setae, 2 of which geniculate. Additionally with 1 small tube pore.

Md (Fig. 4A) with strong gnathobase bearing 5 teeth and 1 bipinnate seta. Md palp 1-segmented, without spinules, with 3 bipinnate apical and 2 lateral setae (both broken in Fig. 4A).

Mxl (Fig. 4B). Praecoxal arthrite apically with 6 strong spines, subapically with 2 bare setae, additionally with 2 bare surface setae with bifurcate tips. Coxal endite with 1 strong unipinnate and 1 bare seta. Basis, enp and exp fused, forming single lobe that carries 5 marginal bare setae and 2 apical setae, one of which unipinnate.

Mx (Fig. 4C). Syncoxa and allobasis fused, with 2 endites. Proximal endite with 2 spines, the larger one unipinnate and fused to segment, the other smaller and bare. Distal endite with 2 pinnate spines apically. Allobasis apically with 2 pinnate spines, the larger one unipinnate and fused to segment; additionally with 2 subapical bare setae. Enp represented by 2 bare setae.

Mxp (Fig. 4D) prehensile. Syncoxa with 1 apical biplumose seta and 2 rows of small spinules. Basis with numerous long spinules. Enp produced into long bare claw, accompanied by small bare seta.

P1 (Fig. 5A) not prehensile, with 2-segmented enp and exp. Basis transversely elongate, with inner and outer biplumose seta, anteriorly with several long spinules and 1 tube pore. Exp-1 with 1 bipinnate outer spine. Exp-2 longer than exp-1, with few spinules on inner margin, all elements located apically, consisting of 1 bipinnate outer spine and 4 long geniculate setae, the innermost unipinnate. Enp shorter than exp. Enp-1 as long as enp-2, bare, enp-2 apically with 1 long bipinnate seta (broken).

P2–P4 (Figs. 5B and 6A and B) with strongly transversely prolonged bases, each bearing several long spinules and 1 tube pore on its anterior margin. Exps 3-segmented, setation as in Tab. 1. P2 and P3 exp-3 subapically with long tube pore on anterior surface and 1 outer bare seta. P2 lacking enp but with its original position shown by slight elevation; P3 and P4 enps 2-segmented, small, not reaching end of respective exp-1; enp-1 without ornamentation. P3 enp-2 slightly longer than enp-1, apically with 2 setae, the inner small and bare, the outer long and biplumose. P4 enp-2 as long as enp-1, with 1 apical biplumose seta (Table 1).

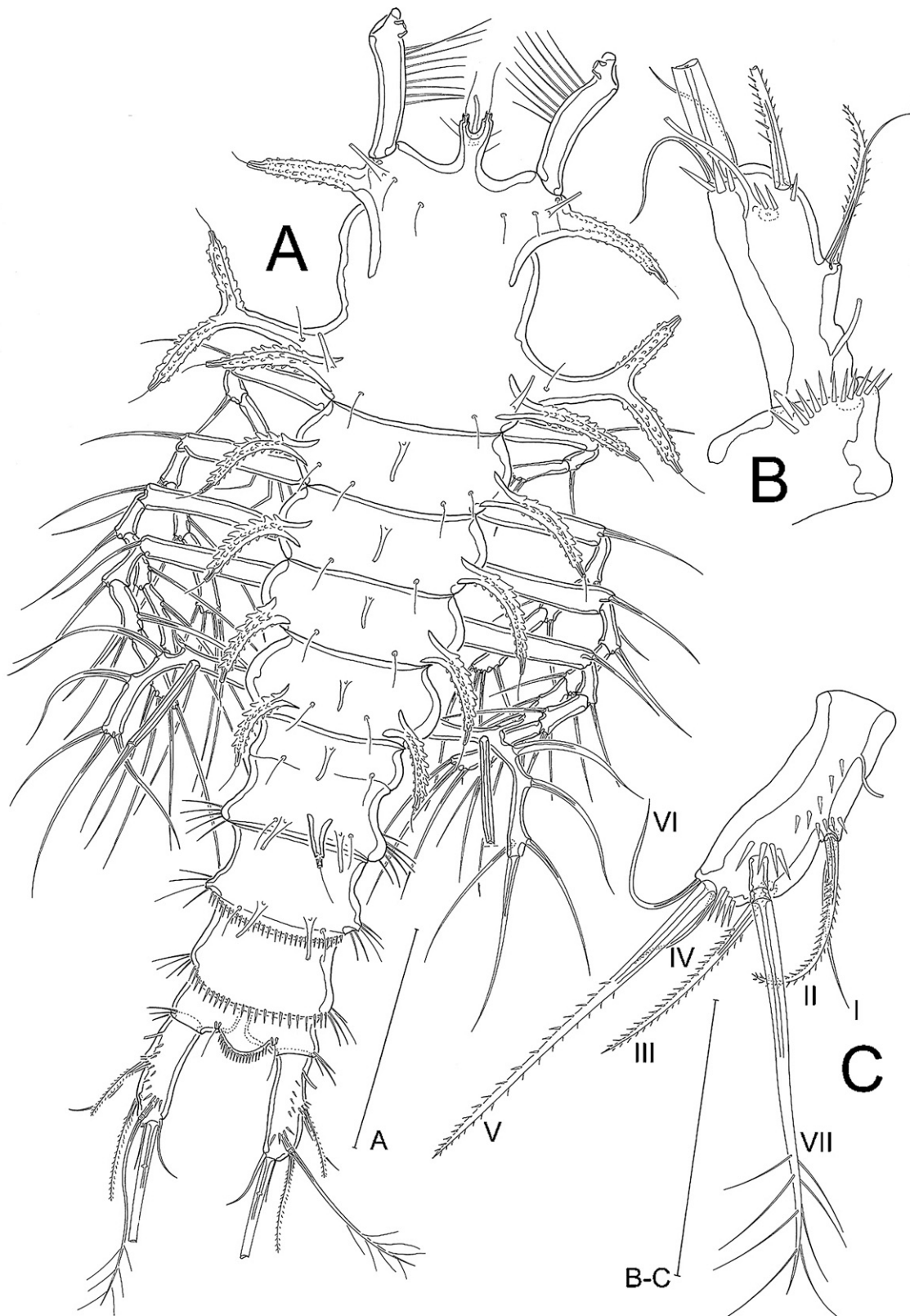
P5 (Fig. 6C) basis and enp fused, forming a benp that bears 1 long setophore (seta broken) and 1 strong tube pore. Enp represented by 1 bare seta accompanied by 1 tube pore. Exp fused to benp, with 3 lateral and 1 apical triplumose setae, and 1 inner bipinnate seta, whose remarkably long pinnae are set very closely together, giving a feather-like impression. Additionally with long spinules on inner margin, and with 1 long tube pore subdistally.

Genital field (Fig. 4E) small, with P6 fused to form single genital operculum, bearing 1 bare seta on each lobe.

### 3.3. Description of the male allotype

The male differs from the female in the following characteristics:

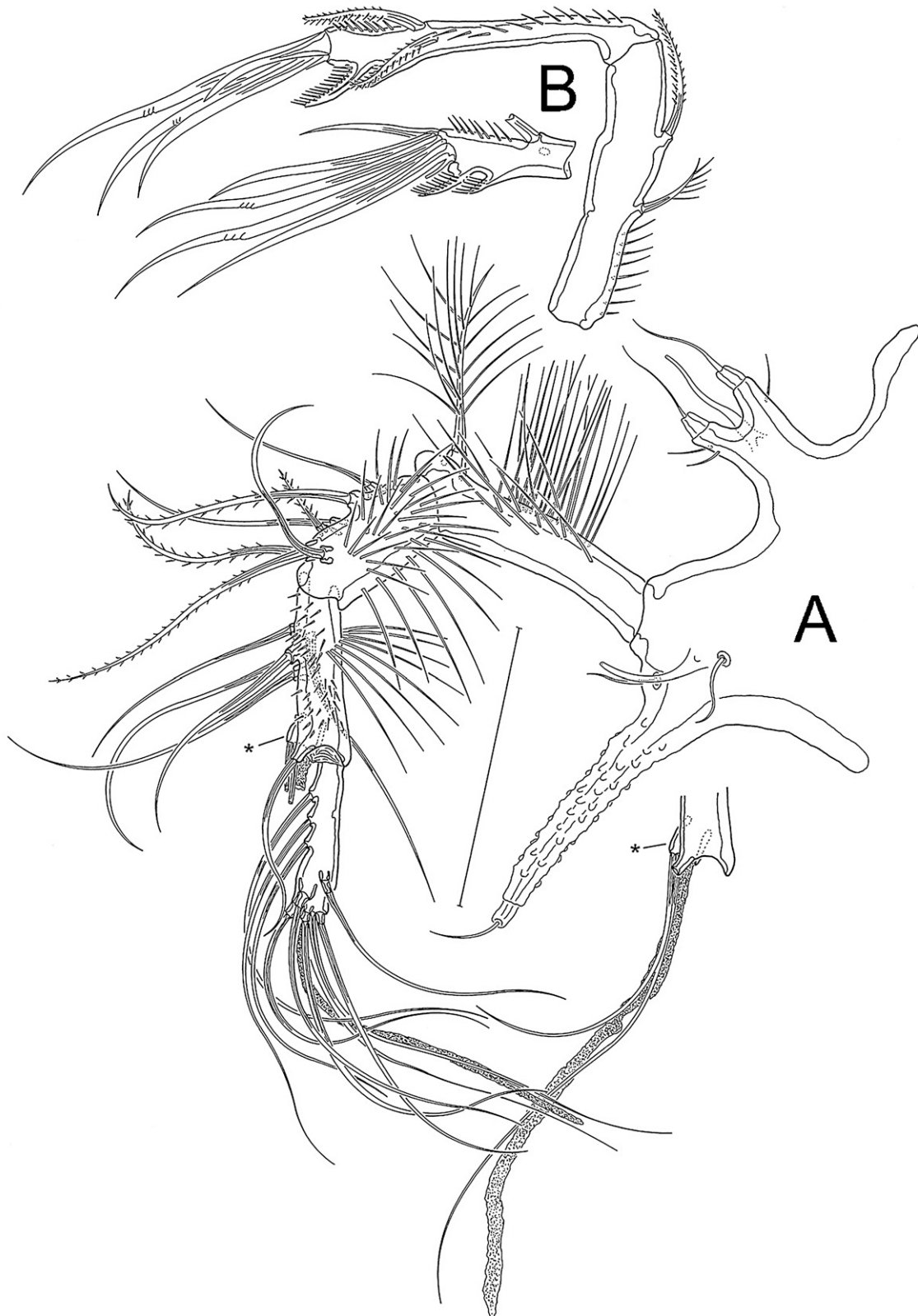
Habitus (Fig. 7A): slightly longer than the female (rostrum to FR: 496  $\mu\text{m}$ ). Also the cephalothoracic peak, the rostrum (Fig. 8A) and the dorsal and lateral body processes are longer and/or more pronounced (the processes appearing to be more elastic) than in the female. On the other hand, the abdominal somites are generally smaller than in the female, being considerably broader than wide,



**Fig. 2.** *Polyascophorus monoceratus* sp. nov., female. (A) Habitus, dorsal view, (B) right FR, ventral view, (C) right FR, dorsal view, roman numbers I–VII naming corresponding furcal setae. Scales: (A) 100  $\mu$ m, (B and C) 50  $\mu$ m.

while tending towards quadrate in the female (cf. Fig. 2A). Last thoracic and first abdominal somite separate. Abdominal somites laterally without spinules. The FR are more compact than in the female, being only 2.0 times longer than broad. The single dorsal

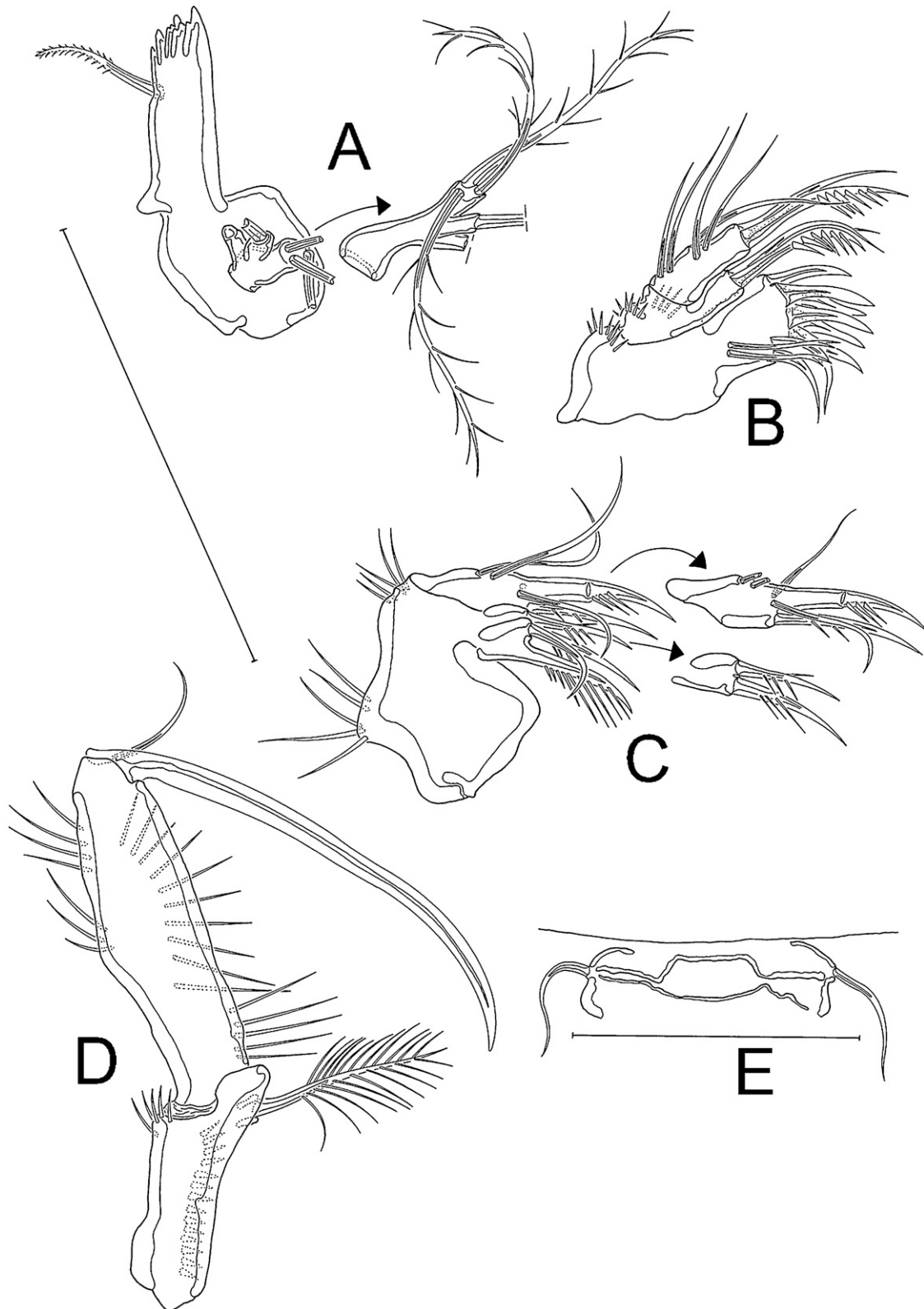
process on the first abdominal somite extends beyond the border of the following somite and bears 2 small but clearly developed subapical spikes. The second abdominal somite lacks the dorsal row of spinules on its posterior margin.



**Fig. 3.** *Polyascophorus monoceratus* sp. nov., female. (A) Rostrum and A1, asterisk (\*) showing acrothek and (B) A2, together with A2 enp distal part of counterpart. Scale: 50  $\mu$ m.

A1 (Fig. 8B) subchirocer, 6-segmented. As it is damaged, most setae are broken. First segment longest, with 1 seta and several long spinules on inner margin. Second segment with long spinules on posterior margin, equipped with 8 setae (7 of which

broken). Third segment smaller than preceding ones, with 7 setae (4 broken). Fourth segment slightly swollen, with 7 setae, one strong and carrying a subapical extension on its tip; additionally with aes. Fifth segment smallest, without setae. Sixth



**Fig. 4.** *Polyascophorus monoceratus* sp. nov., female. (A) md, (B) mxl, (C) mx, (D) mxp and (E) P6 and GF. Scales: 50  $\mu$ m.

segment long, tapering apically, with 8(?) setae; aes not discernible.

Setal formula: 1-1; 2-8; 3-7; 4-7+aes; 5-0; 6-8(?; aes not discernible).

P1 (Fig. 8C) sexually dimorphic, with 2-segmented exp, but no enp. Basis with several spinules along posterior margin in addition

to the long spinules on the anterior margin. Additionally with outer (broken) and inner biplumose seta. Subapical outer seta of exp-2 bare and geniculate. Original position of enp shown by slight elevation with thin cuticle.

P3 enp (Fig. 7B): 3-segmented, first segment small, bare; second segment elongate, with 2 spinules on inner margin, apically with

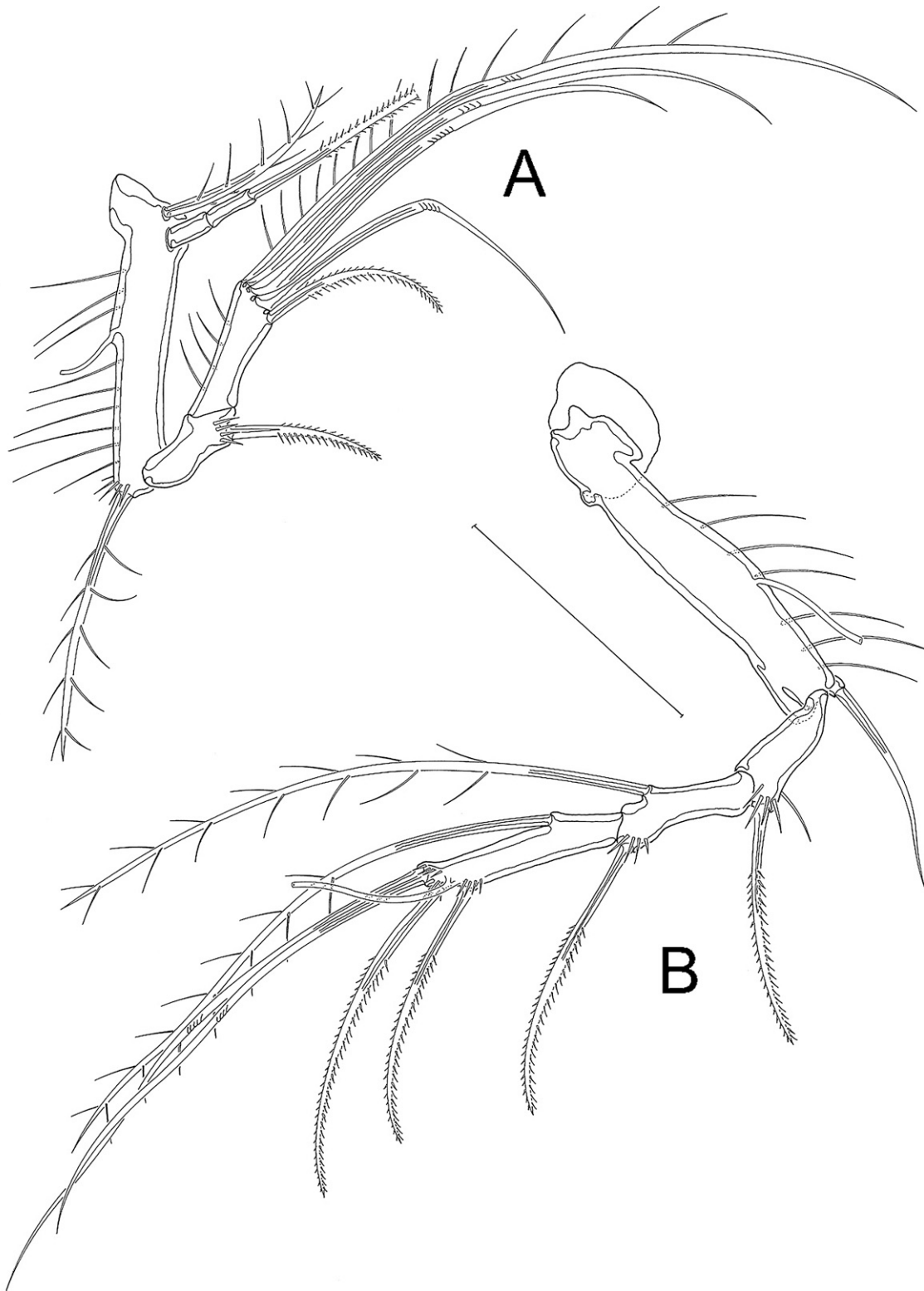


Fig. 5. *Polyascophorus monoceratus* sp. nov., female. (A) P1 and (B) P2. Scale: 50  $\mu$ m.

curved, inner apophysis extending beyond apical margin of third segment; third segment as long as first, apically with 1 small inner and 1 long bare, outer seta.

P4 enp (Fig. 7C) 2-segmented, second segment 2 times longer than first, with 1 bipinnate outer seta and 2 apical setae, the inner small and bare, the outer long and biplumose.

P5 (Fig. 7D): exp broken. Benp with subdistal tube pore, being very broad at its base, and with 1 seta arising from setophore

(broken). Endopodal lobe almost absent, represented by small socle bearing 2 bare setae accompanied by 2 tube pores.

#### Diagnostic key to the species of *Polyascophorus*

1. Rostrum elongate, bifurcated, Y-shaped; posterior margin of first abdominal somite (in male) or posterior half of genital double-somite (in female) dorsally with single cuticular process; cphth

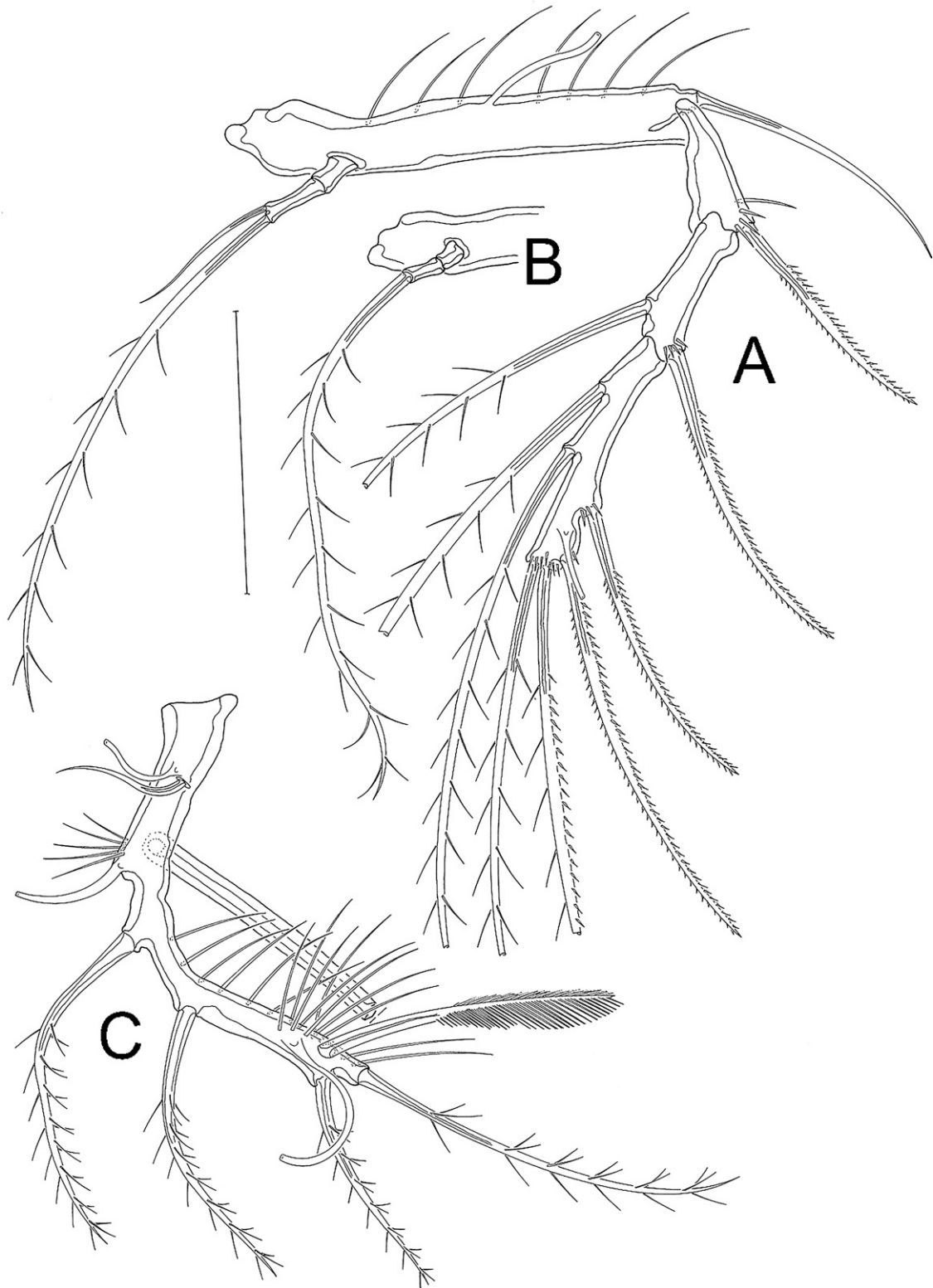


Fig. 6. *Polyascophorus monoceratus* sp. nov., female. (A) P3, (B) P4 enp and (C) P5. Scale: 50  $\mu$ m.

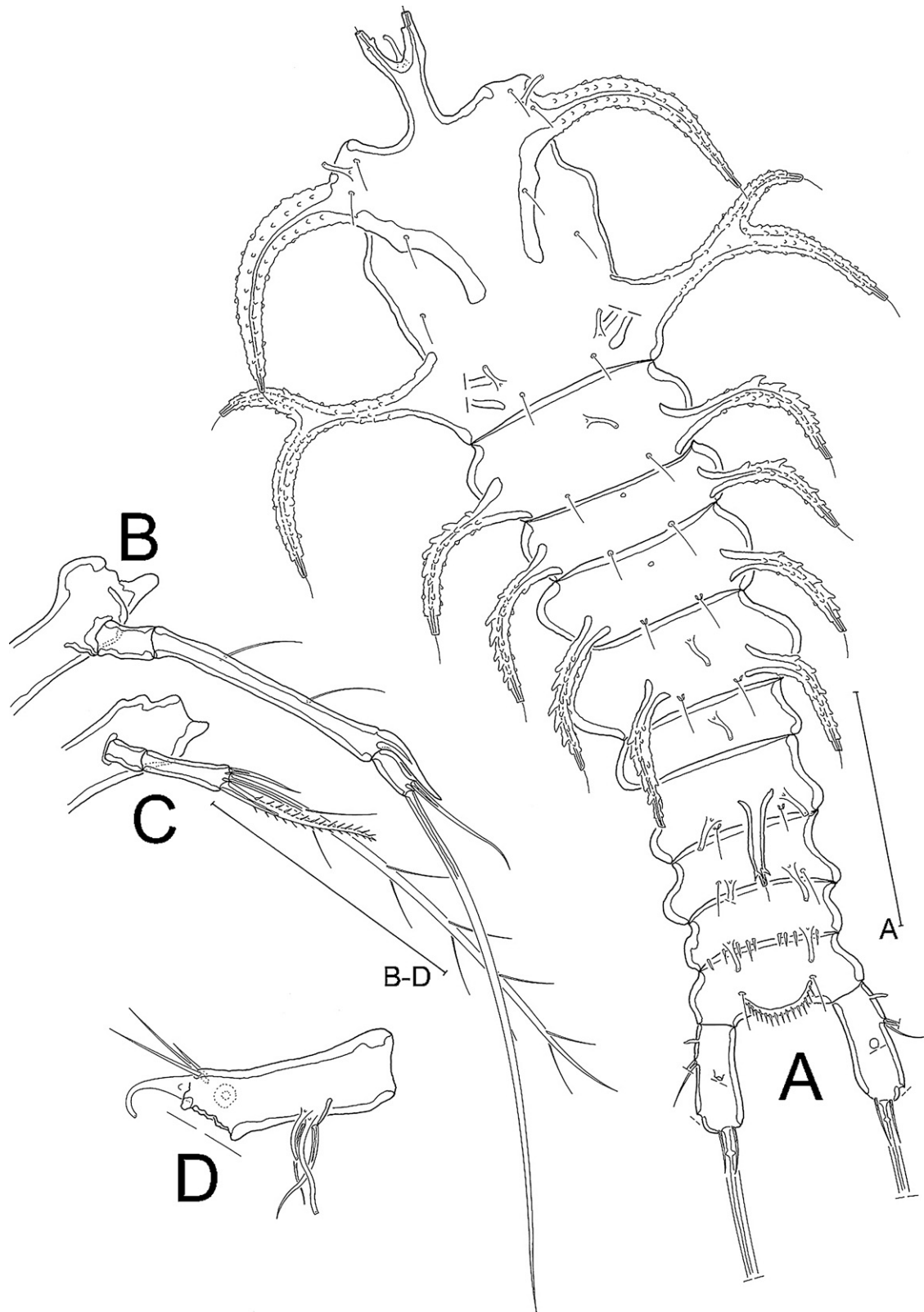
with pair of processes dorsally on posterior margin; male P1 lacking enp. . . *P. monoceratus* sp. nov.

– Rostrum very small; first abdominal somite (in male) or genital double-somite (in female) without single cuticular process; cphth lacking dorsal processes on posterior margin . . . 2

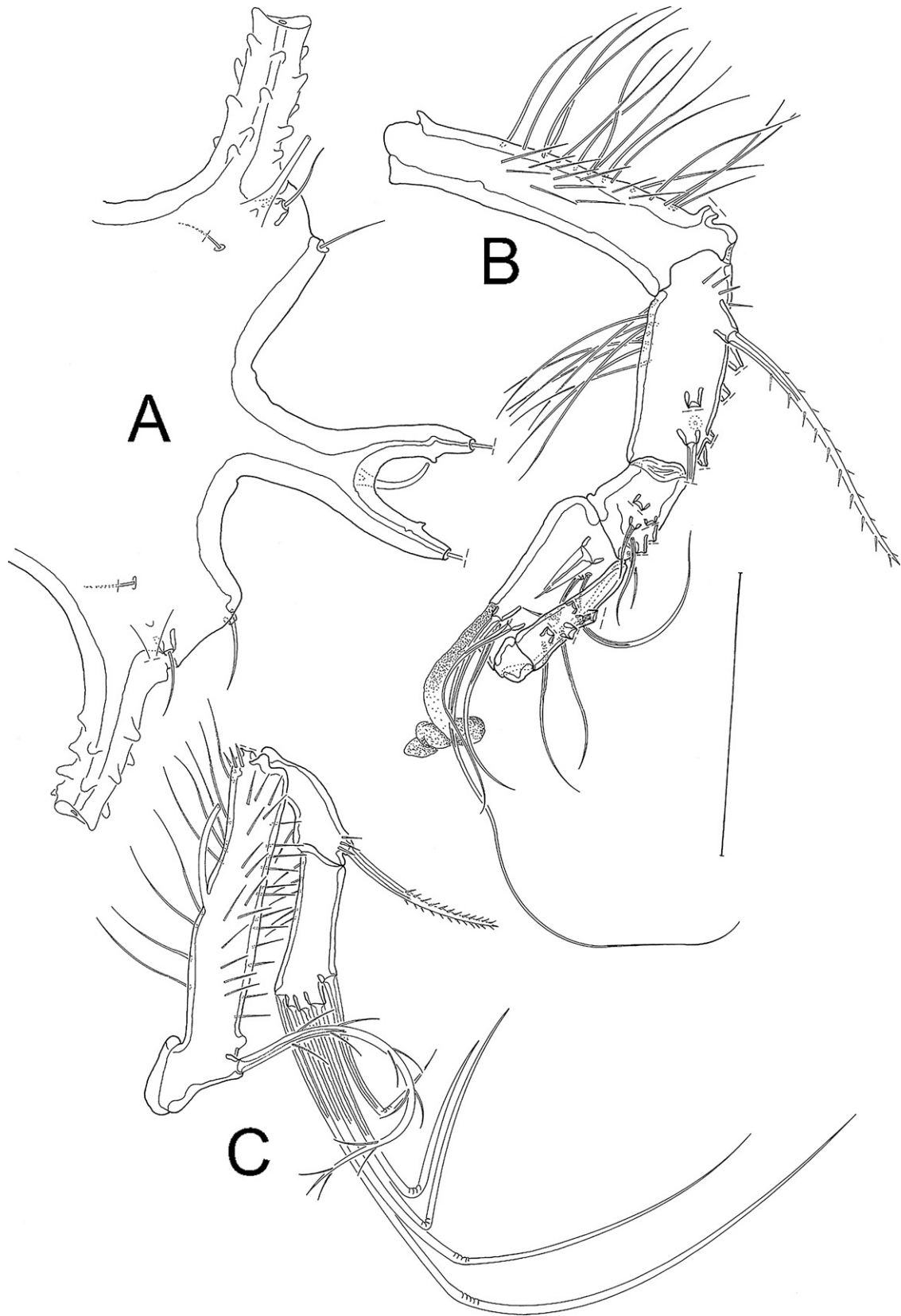
2. P2 lacking enp; female P3 enp 2-segmented, enp-2 with 2 apical setae; female P4 enp 2-segmented . . . *P. martinezi* George, 1998

– P2 enp 1-segmented, with 1 seta; P3 enp 1-segmented, with 1 apical seta; P4 enp 1-segmented . . . *P. gorbunovi* (Smirnov, 1946)





**Fig. 7.** *Polyascophorus monoceratus* sp. nov., male. (A) Habitus, dorsal view, (B) P3 enp, (C) P4 enp and (D) P5 benp (exp broken). Scales: A: 100  $\mu$ m, B–D: 50  $\mu$ m.



**Fig. 8.** *Polyascophorus monoceratus* sp. nov., male. (A) Cephalic peak with rostrum, (B) A1 and (C) P1. Scale: 50  $\mu$ m.

#### 4. Discussion

##### 4.1. Systematics and a phylogenetic re-evaluation of *Polyascopephorus*

The genus *Polyascopephorus* was established by George (1998) to allocate new taxa collected from the Arctic (*P. martinezi* George, 1998) and the Antarctic (*P. schminkei* George, 1998), and to transfer the former *Ceratonotus gorbunovi* (Smirnov, 1946) into this genus. Subsequently, Conroy-Dalton (2001) erected the genus *Touphapleura* Conroy-Dalton, 2001, transferring *P. schminkei* into this taxon as *Touphapleura schminkei* (George, 1998).

George (1998) listed five characters as apomorphies for *Polyascopephorus*:

- a. Bulb-like hyaline appendages on the small rostrum;
- b. The size of FR;
- c. Position of furcal seta III;
- d. Presence of tube pores on cpth and body somites;
- e. Presence of tube pores on exp-3 of P2 and P3, and on P5 benp.

However, as George (1998) did not provide a detailed phylogenetic justification, these features remain without a defined basis. Moreover, some of them have subsequently been detected in other Ancorabolidae (e.g. character [a] in *Arthricornua anendopodia* Conroy-Dalton, 2001 and in *Dorsiceratus ursulae* George 2006; characters [d; e] in several different ancoraboline species (e.g. Conroy-Dalton and Huys, 2000; Conroy-Dalton, 2001; George, 2001, 2006a,b,c; George and Plum, 2009; Wandenness et al., 2009; Gheerardyn and George, 2010) and therefore lost their autapomorphic character for *Polyascopephorus*.

Later, Conroy-Dalton (2001) provided and discussed four apomorphies to justify the monophyly of *Polyascopephorus*:

- I. Bifurcated lateral cephalothoracic processes originated from the dorsal conical ones present in all the then remaining members of the *Ceratonotus*-group, except *Touphapleura*;
- II. Transformation of the distal outer spine of the P1 exp distal segment into a geniculate seta;
- III. Significant reduction in size of the P1 enp;
- IV. Reduction of 1 seta/spine on the distal segment of the P1 enp.

The record of *Polyascopephorus monoceratus* sp. nov. enables us to better define the phylogenetic status of this genus, re-examining Conroy-Dalton's (2001) set of apomorphies I–IV:

*Apomorphy I: the bifurcated lateral processes on the cpth originate from the dorsal conical ones:*

The hypothesis of migration and origin of the lateral bifurcated processes from the conical ones present in the laterodorsal position cannot be maintained any longer. As shown in Figs. 2A and 7A, *Polyascopephorus monoceratus* sp. nov. has both dorsal conical and lateral bifurcated processes on the cpth, hence proving their different origins. The morphological similarity of the dorsal processes in *P. monoceratus* sp. nov. to those of the following thoracic somites confirms Conroy-Dalton's (2001) assumption of their thoracic origin, being derived from the former P1-bearing thoracic somite that later became fused with the cephalosome, forming the cpth. In contrast, the position of the bifurcated lateral processes in *Polyascopephorus* may point to a homology with corresponding processes present in *Echinopsyllus* Sars, 1909 and *Pseudechinopsyllus* (George, 2006b). Thus, the autapomorphy of *Polyascopephorus* regarding these lateral processes becomes their shape, namely the bifurcation, which is developed neither in *Echinopsyllus* nor in *Pseudechinopsyllus*.

*Apomorphy II: transformation of the distal outer spine of the P1 exp distal segment into a geniculate seta*

It is true that all *Polyascopephorus* species show this derived condition. Nonetheless, this character must be regarded as rather weak, as it is present in several other ancoraboline taxa. Within the *Ceratonotus*-group, most species (13 of 22) show this derived condition, with the exception of the 7 *Ceratonotus* species (cf. Conroy-Dalton, 2003a; George, 2006c) plus *Echinopsyllus normani* Sars, 1909 and *E. nogueirae* Wandenness, George and Santos, 2009 (cf. Conroy-Dalton, 2003b; Wandenness et al., 2009). This incongruence, which has been already noted by Conroy-Dalton (2001), points to a convergent development of the geniculate seta; it may, however, be regarded as a synapomorphy of all *Polyascopephorus* species, in combination with additional apomorphies. A similar consideration applies to another feature, namely the subapical displacement of the proximal outer spine of the P1 exp-2. Future investigation may prove the phylogenetic relevance of this character.

*Apomorphy III. significant reduction in size of the P1 enp*

Comparison of the length ratio between the P1 enp and exp within the *Ceratonotus*-group confirms Conroy-Dalton's (2001) observation of a clear decrease of endopodal length in *Polyascopephorus*. The taxa *Ceratonotus* Sars, 1909, *Dendropsyllus* Conroy-Dalton, 2001, *Dorsiceratus Drzycimski*, 1967, and *Touphapleura* have P1 enps that are at least half as long as the exp, whereas *Arthricornua* Conroy-Dalton, 2001, *Echinopsyllus*, and *Pseudechinopsyllus* lost their P1 enps. Thus, *Polyascopephorus* seems to occupy an intermediate position between these extremes: if a P1 enp is present, it is clearly reduced in size, reaching at most 1/3 of the exp. In agreement with Conroy-Dalton (2001), this condition is interpreted as apomorphic for *Polyascopephorus* compared with those taxa bearing a longer P1 enp, and within the *Ceratonotus*-group it may point to a trend starting with a cletodid-like P1 enp in *Polyascopephorus*, *Ceratonotus*, *Dendropsyllus*, *Dorsiceratus*, and *Touphapleura*, and continuing towards its complete loss in *Arthricornua*, *Echinopsyllus*, and *Pseudechinopsyllus*. In this context, the complete loss of the P1 enp in the male of *Polyascopephorus monoceratus* sp. nov. is notable. Although such a pronounced sexual dimorphism in the first swimming leg is not reported for any other ancoraboline taxon, the presence of characteristic features such as the single cuticular apical process on the P2 exp-3 in both the female and male here described, justify its interpretation as a sexual dimorphism rather than a distinction between two species, and hence their combination of male and female in the same taxon.

*Apomorphy IV: reduction of 1 seta/spine on the distal segment of the P1 enp*

Similarly to *Polyascopephorus martinezi* and *Dendropsyllus*, the female of *P. monoceratus* sp. nov. bears only 1 seta instead of the primary 2 on the P1 enp-2. Conroy-Dalton (2001) interpreted this reduction as a convergent apomorphy for *Polyascopephorus* and some other species (later united as *Dendropsyllus* by Conroy-Dalton (2003a,b)), although she noted that in each genus a different element is reduced: *Dendropsyllus* presumably lost the inner geniculate one, whereas *Polyascopephorus* lost the outer spiniform seta. Thus, "apomorphy IV" as used by Conroy-Dalton (2001; character 21 in her phylogenetic analysis) cannot be maintained as valid character, as it actually mixes two different features. However, as the corresponding seta is broken in the female of *P. monoceratus* sp. nov. (cf. Fig. 5A) and not clearly discernible in Smirnov's (1946) description of *P. gorbunovi*, the supposed reduction of the outer

spiniform seta in P1 enp-2 cannot yet be verified as an apomorphy for *Polyascopephorus*, as it is confirmed for *P. martinezi* only.

Concluding, the re-examination of the apomorphies listed by Conroy-Dalton (2001) revealed that one apomorphy can be retained (III), one needs further investigation and is ignored in the meantime (IV), and two characters must be discarded (I, II). In combination with a detailed comparison of *Polyascopephorus* with the remaining members of the *Ceratonotus*-group, the following four apomorphies of a monophylum *Polyascopephorus* are recognized [in the following, plesiomorphies in square brackets]:

1. Lateral posterior cephalothoracic processes bifurcate [processes conical];
2. P1 enp reduced in size, reaching at most 1/3 of exp [P1 enp reaching at least 1/2 of exp];
3. Furcal rami rounded on outer apical margin [furcal rami not rounded];
4. Furcal apical setae IV, V, VI displaced to inner apical edge of ramus [apical setae occupying entire apical front of ramus];

*Character 1: lateral posterior cephalothoracic processes bifurcate*

The phylogenetic status of this character has been discussed above (cf. Apomorphy I). It is considered as an apomorphy for *Polyascopephorus*.

It is noteworthy that within Ancorabolinae, also *Ancorabolina* (George, 2006a) encloses species that bear a pair of lateral cephalic processes that are bifurcated. In *A. anaximenesi* Gheerardyn and George, 2010, the corresponding processes show a beginning bifurcation that is, however, only weakly developed (Gheerardyn and George, 2010). Nonetheless, *A. cavernicola* George and Tiltack, 2009 has well-bifurcated lateral cephalic processes in which the anterior branches are almost the same length as the posterior ones (George and Tiltack, 2009). Comparison of these processes with those of *Polyascopephorus* reveals, however, that they differ remarkably in structure: those in the named *Ancorabolina* species are strongly sclerotized and inflexible, with sporadically placed sensilla and/or setules on their anterior margin; whereas the processes in *Polyascopephorus* are elastic, pimped, and bear sensilla at their tips, therefore resembling in their general appearance the frontal cephalic processes of *Ceratonotus*. These morphological differences, in combination with the fact that both *Ancorabolina* and *Polyascopephorus* are each characterized by additional, distinct autapomorphies, suggest a convergent development of the superficially similar processes.

*Character 2: P1 enp reduced in size, reaching at most 1/3 of exp*

This character, which corresponds to apomorphy III discussed above, is regarded as an apomorphy for *Polyascopephorus*.

*Characters 3 and 4: furcal rami rounded on outer apical margin; apical setae IV–VI displaced to inner apical edge of ramus*

*Polyascopephorus* is the only taxon within Ancorabolinae that shows a convex curvature of the outer distal margin of the furcal rami (cf. Fig. 1A–C). This curvature may be due to an elongation of the furcal area between setae III and IV that consequently leads to a simultaneous displacement of the apical furcal setae IV–VI towards the inner apical edge of the furcal rami, giving the furcal rami a characteristic shape. Because such a FR is found exclusively in *Polyascopephorus*, it is interpreted as a phylogenetic deviation and therefore regarded as an apomorphy for the genus.

*4.2. Systematic characterization of Polyascopephorus monoceratus sp. nov.*

Apart from the generic apomorphies, *Polyascopephorus monoceratus* sp. nov. has a set of 5 autapomorphies that justify its establishment as a distinct species:

5. First abdominal somite (GDS in female) with single cuticular process dorsally on posterior margin [no process developed];
6. Anterior branch of female lateral bifurcate cephalic processes elongate [anterior branch distinctly shorter than posterior one];
7. Furcal seta VII plumose on distal half [furcal seta VII bare];
8. Male P1 lacking enp [enp present];
9. P2 exp-3 apical setae bare, geniculate [setae bipinnate, not geniculate];

*Character 5: first abdominal somite (GDS in female) with single cuticular process dorsally on posterior margin*

The presence of a single, centrally located cuticular process posteriorly on the first abdominal somite (corresponding to the distal half of the female GDS) is unique within not only the *Ceratonotus*-group but in all Ancorabolidae. Therefore, it can doubtlessly be interpreted as an apomorphic character for *P. monoceratus* sp. nov.

*Character 6: anterior branch of female lateral bifurcate cephalic processes elongate*

In both *Polyascopephorus gorbunovi* and *P. martinezi*, the anterior branches of the female lateral bifurcate cephalic processes are clearly shorter than the posterior ones (Smirnov, 1946; George, 1998; Conroy-Dalton, 2001), while in *P. monoceratus* sp. nov. they are elongate, reaching almost the length of the posterior branches in the female (cf. Fig. 1A). Based on the assumption that the bifurcation of the lateral processes began from a former conical lateral process, as present in, e.g., *Echinopsyllus* and *Pseudechinopsyllus*, the interpretation of the elongate anterior branches as derived, i.e., an apomorphic character, appears more plausible than the alternative of its secondary reduction in both *P. gorbunovi* and *P. martinezi*. Elongation of the anterior branches is therefore considered as apomorphic for *P. monoceratus* sp. nov.

*Character 7: furcal seta VII plumose on distal half*

It is somewhat difficult to determine if a bare or a pinnate (plumose) seta constitutes the derived character. However, regarding the furcal seta VII, interpretation is relatively easy: in Harpacticoida, this seta is typically bare, so the plumosity on its distal half is regarded as a derived condition for *P. monoceratus* sp. nov.

*Character 8: male P1 lacking enp*

Within *Polyascopephorus*, a trend towards the loss of the (male?) P1 enp is observable. While it is 2-segmented in *P. martinezi* and 1-segmented in *P. gorbunovi*, *P. monoceratus* sp. nov. shows a 2-segmented P1 enp in the female, but an absent P1 enp in the male. This constitutes a sexually dimorphic condition, which is observed for the first time for the P1 in Ancorabolinae, and it is regarded as an apomorphy for *P. monoceratus* sp. nov.

*Character 9: P2 exp-3 apical setae bare, geniculate*

Usually, the apical setae of P2–P4 exp-3, at least within Ancorabolidae, are bipinnate but non-geniculate. Thus, the transformation of the apical setae of the P2 exp-3 into bare geniculate

setae must be considered as an apomorphy for *P. monoceratus* sp. nov.

#### 4.3. Systematic characterization of *Polyascophorus gorbunovi*

*Polyascophorus gorbunovi* may be characterized by means of the following autapomorphies (only the female is considered, as the male is unknown):

10. P1 enp 1-segmented [enp 2-segmented];
11. P3 enp 1-segmented [enp 2-segmented];
12. P4 enp 1-segmented [enp 2-segmented];

*Characters 10–12: enps of P1, P3, and P4 1-segmented*

As oligomerisation is assumed to be the derived condition within Harpacticoida (Huys and Boxshall, 1991), the “reduction” of segments (pragmatically speaking) in females of *P. gorbunovi* constitutes an apomorphic state compared with *P. martinezi* and *P. monoceratus* sp. nov. (keeping in mind, however, the unsatisfying quality of Smirnov’s (1946) description), as both of these species retain 2 segments in the corresponding female appendages.

#### 4.4. Systematic characterization of *Polyascophorus martinezi*

Finally, *P. martinezi* shows the following autapomorphies:

13. Female: P3 enp-2 outer apical seta shortened, at most twice as long as inner apical seta [outer apical seta about 3.5 times longer than inner apical seta];
14. Male P3 enp with elongate apophysis, at least twice as long as enp-3 [apophysis at most 1.5 times longer than enp-3];
15. Male P4 enp-2 inner apical seta lost [enp-2 with inner apical seta].

*Character 13: P3 enp-2 apical outer seta shortened*

In most Harpacticoida, the apical setae of P2–P4 enps bear long bipinnate or biplumose elements. In the P3 enp of *P. monoceratus* sp. nov. the outer element shows such primary condition (Fig. 6A). In contrast, the corresponding seta in *P. martinezi* is significantly shorter, presumably due to reduction. This is regarded as an apomorphy for this species.

*Character 14: elongation of apophysis in male P3 enp-2*

The male apophysis on P3 enp-2 is a striking feature, constituting a distinctive sexual dimorphism. In *P. martinezi* it is more pronounced than in *P. monoceratus* sp. nov. (not yet confirmed for *P. gorbunovi*). This is considered as an apomorphy for *P. martinezi*.

*Character 15: loss of inner apical seta on male P4 enp-2*

As shown in Fig. 7C, the male of *Polyascophorus monoceratus* sp. nov. shows a small bare inner apical seta. In contrast, the male of *P. martinezi* has lost this inner seta, which is interpreted as apomorphic for this species.

As observable from characters 13 and 14, the phylogenetic characterization of *P. martinezi* appears to be relatively uncertain. Except for character 15, no unambiguous, high-quality apomorphic feature can be listed, but only morphometric ones that may be reassessed in future revisions. This is due to several circumstances: (i) *Polyascophorus martinezi* and *P. monoceratus* sp. nov. resemble each other in most morphological features, and the differences detected show the derived condition in *P. monoceratus* sp. nov. rather than in *P. martinezi*; (ii) derived characters observed in

*P. martinezi* are not unique for this species but are shared with *P. gorbunovi* (i.e., the reduced rostrum armoured with long setules) or with *P. monoceratus* sp. nov. (i.e., the loss of the P2 enp); (iii) the phylogenetic status of certain characters remains unclear, for instance whether (a) the absence of posterior dorsal cephalothoracic processes in *P. martinezi* (and in *P. gorbunovi*), (b) the elongate rostrum in *P. monoceratus* sp. nov., and (c) the row of spinules on the posterior margin of the second abdominal somite in the female of *P. monoceratus* sp. nov. are the derived or the original conditions. Other features, such as the reduction of 1 spine on the maxillar distal endite in *P. monoceratus* sp. nov. (compared to *P. martinezi*) indicate the need for urgent redescription of *P. gorbunovi* before the use of these detailed characteristics in a more elaborate phylogenetic comparison.

Elucidation of those pending questions is the object of an ongoing extensive phylogenetic analysis of Ancorabolinae, and will be published elsewhere.

The finding of *Polyascophorus monoceratus* sp. nov. off Brazil extends the distributional range of this genus from the northern polar region to the tropical southern Atlantic.

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