



Description of two new species of *Dorsiceratus* Drzycimski, 1967 (Copepoda: Harpacticoida: Ancorabolidae) from Sedlo and Seine Seamounts (Northeastern Atlantic) and remarks on the phylogenetic status of the genus* §

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Abstract

Two new species of *Dorsiceratus* Drzycimski, 1967 (Copepoda, Harpacticoida, Ancorabolidae), *Dorsiceratus wilhelminae* sp. nov. and *D. dinah* sp. nov. are described from Sedlo and Seine Seamounts, respectively (both northeast Atlantic). These are the first records of *Dorsiceratus* species from seamount summits. Both new species resemble the described species *D. octocornis* Drzycimski, 1967, *D. triarticulatus* Coull, 1973, and *D. ursulae* George, 2006, with respect to most morphological features. On the other hand, *D. wilhelminae* sp. nov. has long spinules at the inner margin of the A2 enp, while *D. dinah* sp. nov. bears two, rather than one, tubepores dorsally on third abdominal somite, and a geniculate first outer seta on P1 exp2. These characters are considered as apomorphic relative to the described *Dorsiceratus* species. As discussed in the present paper, the maintenance of a genus *Dorsiceratus* appears to be problematic. Although specimens may be assigned without difficulty to a group “*Dorsiceratus*”, such assignments are based on diagnostic features only; no clear-cut apomorphies have been detected so far to characterize the monophyly of *Dorsiceratus*. Just two apomorphic characters appear to be synapomorphies for all of the described *Dorsiceratus* species: 1) P2 enp2 with one rather than two setae and 2) P4 exp sexually dimorphic. Unfortunately, these features are relatively widespread within the *Ceratonotus*-group sensu Conroy-Dalton (2001) and therefore of rather low value. The authors decided, however, to retain the genus *Dorsiceratus* until new insights provide more information to support or disprove that hypothesis.

Key words: Systematics, deep sea, seamounts, OASIS, Ancorabolinae, *Ceratonotus*-group, *Dorsiceratus wilhelminae* sp. nov., *Dorsiceratus dinah* sp. nov.

Introduction

As seamounts are of increasing interest for marine biologists (cf. Pitcher *et al.* 2007), the number of research cruises aiming to sample seamount summits increased remarkably in the past decade and are likely to continue increasing. For meiobenthologists, some important questions centre around chorological, phylogenetic, and biogeographical themes (e.g. Bartsch 2003; Gad & Schminke 2004; George 2004; George & Schminke 2002). We are interested in structure and composition particularly of the summit communities, asking e.g. (i) is there frequent (geographical and/or bathymetrical) species exchange?; (ii) are there isolated communities with high numbers of endemic species?; (iii) how did the meiofauna get there?; (iv) are the summit communities characterized by high or low species diversity (see Thistle 1998)? In the framework of biogeographical questions, it is important to establish where the species that inhabit a seamount’s summit

originate, and where their closest relatives live. This question is particularly interesting with respect to shallow-water species showing a wide geographical distribution, although usually these are unable to cross vast deep-sea areas (e.g. Bartsch 2003; George & Martínez 2005; George & Schminke 2002), or in the case that the summit of a seamount reaching shallow depths is dominated by deep-sea taxa rather than by shallow-water ones (George 2004).

The record of the genus *Dorsiceratus* Drzycimski, 1967 from seamounts' summits, in particular that of Seine Seamount, is noteworthy. The genus, belonging to the so-called *Ceratonotus*-group (Conroy-Dalton 2001) of Ancorabolinae Sars, 1909 (Copepoda, Harpacticoida, Ancorabolidae), is frequently found in deep water. It contains three described species: *D. octocornis* Drzycimski, 1967, collected at Korsfjorden, western Norway, at 680m depth (Drzycimski 1967); *D. triarticulatus* Coull, 1973, collected off North Carolina at 500m depth (Coull 1973); and *D. ursulae* George, 2006, collected at the Great Meteor Seamount (northeastern tropical Atlantic) at 2320–2722m depth (George 2006). Recent findings confirm the presence of *Dorsiceratus* also in Atlantic and Pacific deep-sea basins (~5000m depth; George unpublished, Mahatma pers. com.). The finding of *D. wilhelminae* sp. nov. at Sedlo Seamount agrees with formerly recorded depth ranges (the summit of Sedlo Seamount is at ~800m depth), supporting the hypothesis of *Dorsiceratus* being an exclusively deep-sea taxon. In contrast, *D. dinah* sp. nov. was collected from the summit of Seine Seamount, which lies in 179m depth, i.e. in shallow and even euphotic water. Future investigations will clarify whether the finding of *D. dinah* sp. nov. in such shallow water was a rare vagrant or whether *Dorsiceratus* really is an exclusive deep-sea taxon.

Material and methods

Samples were taken by KHG during the OASIS expedition M60/1 of RV "Meteor" at Sedlo and Seine Seamounts in November 2003 (<http://www1.uni-hamburg.de/OASIS/>). Two females of *Dorsiceratus* were collected from station 728 (Sedlo Seamount) and station 756 (Seine Seamount), respectively. Samples were fixed on board with 5% buffered formalin. For further analyses the samples were centrifugated using Levasil® to separate the organisms from the sediment (McIntyre & Warwick 1984; Pfannkuche & Thiel 1988).

For description, specimens were dissected in glycerol under a Leica stereomicroscope and subsequently mounted on several slides in glycerol (Higgins & Thiel 1988). The type material was deposited in the collection of the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt/Main (Germany).

Drawings were made with the aid of a camera lucida on a Leica-DMLB and on a Leica DMR compound microscope equipped with an interference contrast 100x objective.

General terminology is (mainly) adopted from Lang (1948) and Huys & Boxshall (1991). Terminology referring to phylogenetics follows Ax (1984). The terms "telson" and "furca" are used according to Schminke (1976).

Abbreviations used in the text: A1: antennule, A2: antenna, aes: aesthetasc, cphth: cephalothorax, md: mandible, mxl: maxillule, mx: maxilla, mxp: maxilliped, enp: endopod, exp: exopod, exp1: first segment of exp, GF: genital field, FR: furcal ramus/rami, P1–P6: swimming legs 1–6, benp: baseopod.

Terminology used for describing the tagmosis follows Ax (1999). Cphth: encloses the body starting from the A1 to (and including) P1. Thorax: body somites bearing natatory legs P2–P6: 5 somites. Abdomen: legless body somites located between last thoracic somite and telson: 3 somites.

Taxonomy

Harpacticoida Sars, 1903

Ancorabolidae Sars, 1909

Ancorabolinae Sars, 1909

Dorsiceratus Drzycimski, 1967

Type species: D. octocornis Drzycimski, 1967.

Additional species: D. triarticulatus Coull, 1973, *D. ursulae* George, 2006, *D. wilhelminae* sp. nov., *D. dinah* sp. nov. (both described here).

Generic diagnosis. Ancorabolinae Sars, 1909, *Ceratonotus*-group sensu Conroy-Dalton (2001). Body long, slender. Cphth frontally with peak, lacking lateral processes. Rostrum constricted, fused to cphth, square or rectangular in shape, with terminal pair of sensilla and single tubepore. Cphth and free thoracic somites with dorsal pair of spinulose cuticular processes at their distal margins, which bear single sensilla at their bases and tips. Thoracic somites bearing P2–P5 with dorsal single tubepores. Last thoracic somite and abdominal somites also with dorsal tubepores in differing numbers. Genital double somite present in female, with dorsal suture indicating former separation. Telson broader than long, trapezoid in shape. Anal operculum with row of spinules. FR of different length, with 7 setae, with terminal tubepore, furcal seta I minute. Female A1 4-segmented, male A1 5–6-segmented. A2 with allobasis bearing 2 abexopodal setae. Md with variable gnathobase and 1-segmented palpus bearing 4–5 setae. Mx1 with coxa and basis distinct or fused. Mx with 2 endites, each with 2–3 setae, syncoxa and basis distinct or fused. Mxp prehensile, syncoxa with 1 terminal seta, enp formed into a long claw with associated minute seta. Swimming legs 1–4 with transversely elongate bases and with exp and enp. P1 exp 2–3-segmented, in case of 2-segmented exp first outer spine of terminal segment may be translocated subterminally. Terminal segment with 4–5 geniculate setae. P1 enp not prehensile, 2-segmented, enp2 terminally with 1–2 setae. P2–P4 with 3-segmented exps and 2-segmented enps, enp1 much shorter than enp2. P5 enp completely reduced and represented by 1–2 setae that are accompanied by 1–2 tubepores. Outer basal seta arise from small setophore and are associated with a long tubepore. Exp distinct or fused to benp, with 5 setae, 1 long tubepore may be present subterminally.

***Dorsiceratus wilhelminae* sp. nov.**

Holotype: 1 female, dissected and mounted on 17 slides, deposited at the Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt, Germany), collection numbers SMF 31442/1–17.

Type locality: Atlantic Ocean, Sedlo Seamount, station #728 (27.11.2003, Giant Boxcorer, 40°18,5'N/26°42,0'W, 856m depth).

Etymology. The specific name of *Dorsiceratus wilhelminae* sp. nov. is given in grateful remembrance to the grandmother of CP, Mrs. Anna Wilhelmina Plum.

Description of female. Habitus (Fig. 1) long and slender (body length including FR 395µm). Cphth bearing a pair of cuticular processes with small apical sensilla and small spinules, each of which are accompanied by another sensillum at their bases. Cphth anteriorly drawn into a peak with 2 tubepores. Rostrum (Fig. 3B) constricted, fused to cphth, strongly prominent, about 2 times longer than broad, divided distally, with 2 sensilla and 1 long tubepore at its tip. Cphth with several sensilla, with anterolateral setular tufts. Body somites also with lateral setular tufts. Thoracic body somites bearing P2–P4 each with 1 pair of dorsal cuticular spiny processes bearing sensilla at their tips and bases. Each thoracic body somite with 1 dorsal, long tubepore. First abdominal somite ventrally fused with last thoracic body somite to form the genital double somite. First and second abdominal somite ventrally and dorsally with 2 tubepores, each with a sensillum; dorsal tubepores flanked by a row of dorsal spinules (Fig. 1 and 2A). Third abdominal somite with 1 dorsal tubepore. Abdominal somites (except telson) with posterior dorsal and ventral row of long hair-like spinules. In addition the third abdominal somite with dorsal and ventral strong and long spinules. Telson broader than long, without dorsal tubepore, but with 2 tubepores near the FR's base (Fig. 2A). Anal operculum with spinules.

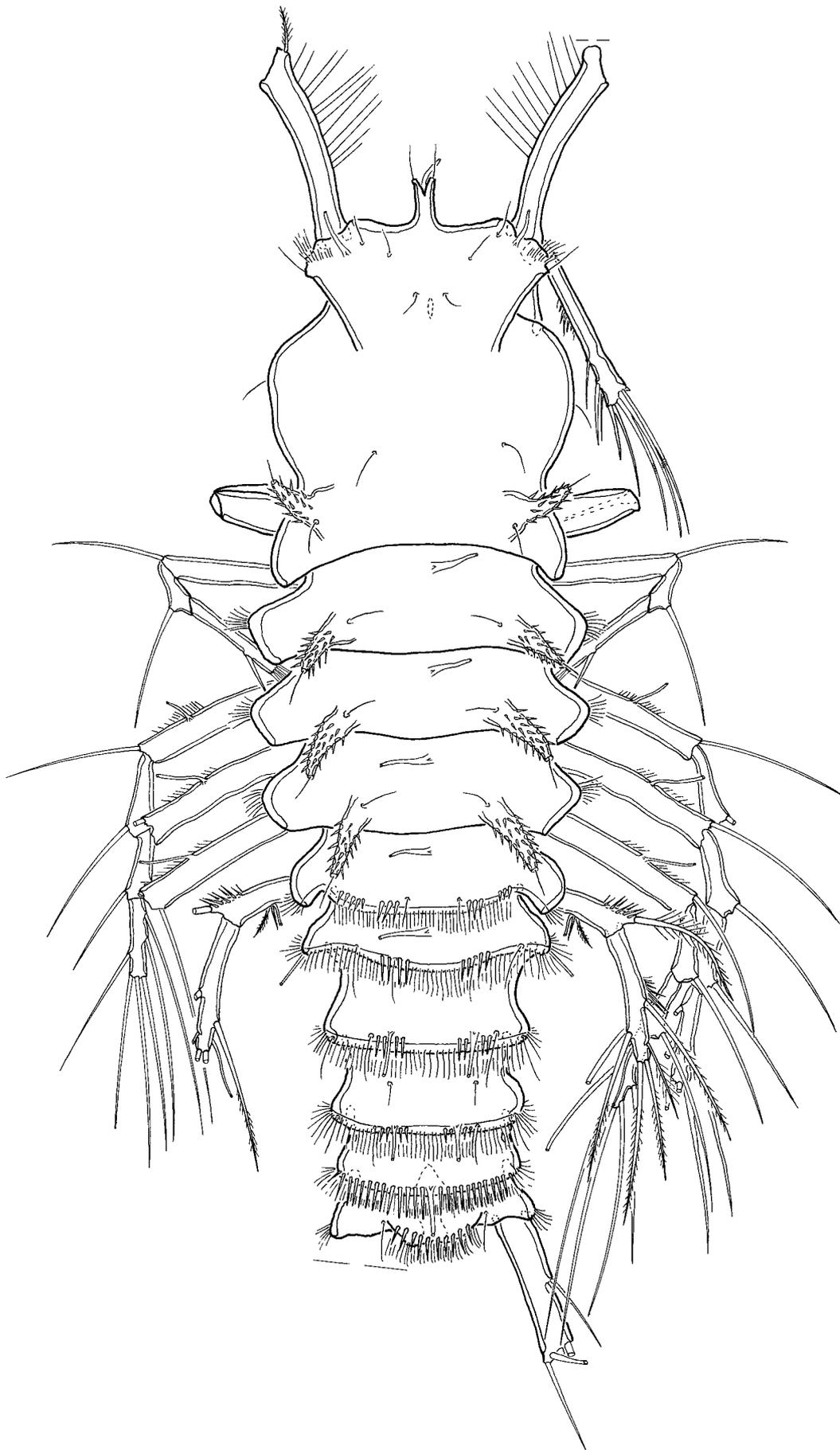


FIGURE 1. *Dorsiceratus wilhelminae* sp. nov., female holotype. Habitus, dorsal. Scale: 200 μ m.

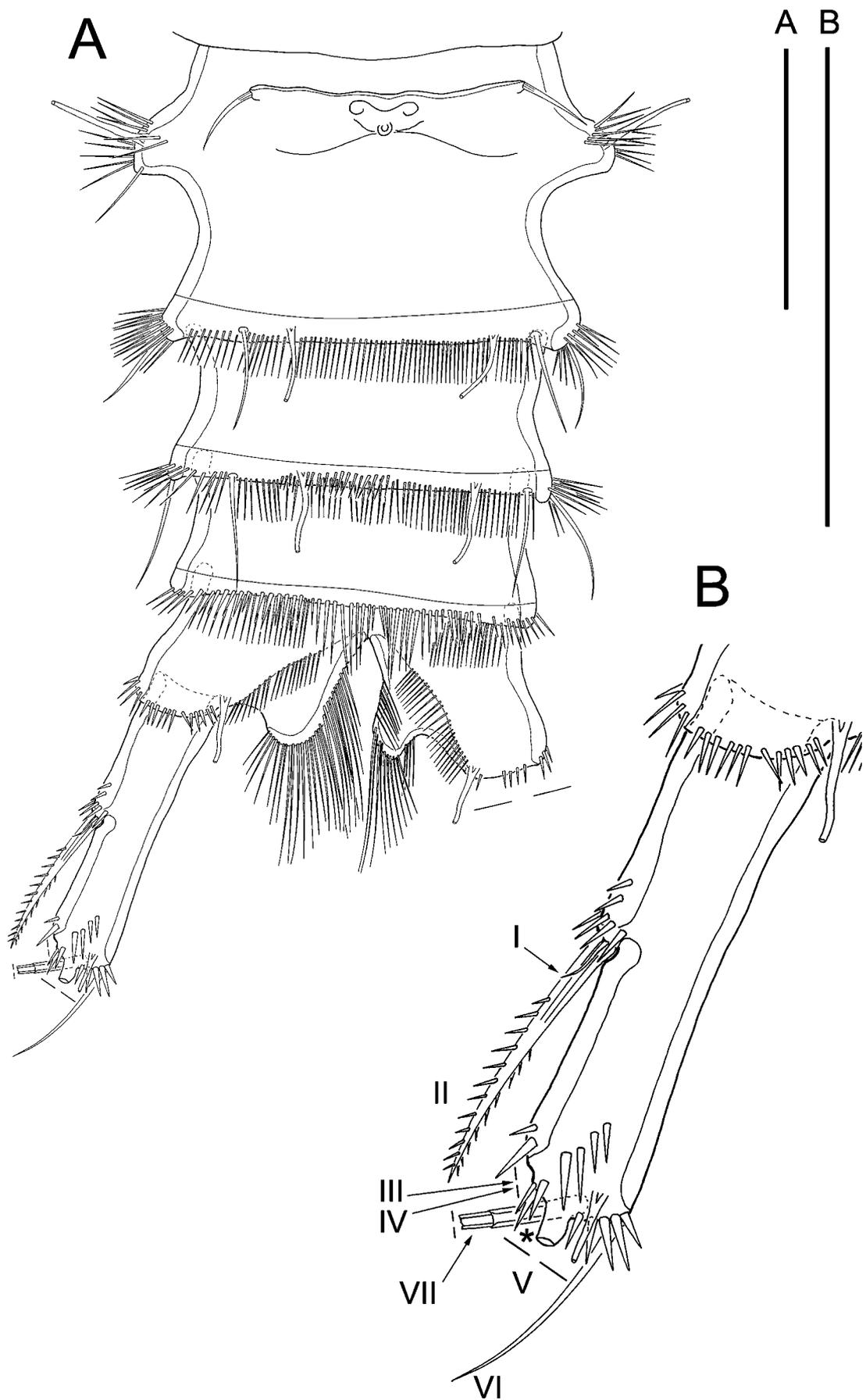


FIGURE 2. *Dorsiceratus wilhelminae* sp. nov., female holotype. A, Abdomen, ventral. B, Furcal ramus, ventral, asterisk indicating the broad but short tubepore. Scale: 50µm.

FR (Fig. 2B) slender, about 4 times longer than broad, bearing 7 setae and terminally ending in 1 short but broad, and 1 slender tubepore. Setae I and II inserting laterally, close together. Seta I very fine, small and bare. Seta II bipinnate, longer than I. Seta III (broken) inserting subterminally at outer margin, accompanied by a few spinules basally. Seta IV and V (both broken) inserting terminally. Seta VI bare, inserting terminally at inner margin and flanked by a few spinules. Seta VII arising dorsally from small knob.

A1 (Fig. 3A, B) 4-segmented. First segment (Fig. 3B) longest, second and third segment almost the same size, fourth segment smaller. First and second segments with a row of long spinules. First segment with 1 small, distal, bipinnate seta (Fig. 3B). Second segment with 7 setae. Third segment with 6 bare setae on its outer side, with strong subterminal aes, accompanied by a 7th seta. Fourth segment with 10 bare setae, one of which fused with 1 small aes. Armature formula: I-1; II-6; III-7 + aes, IV-10 + aes.

A2 (Fig. 4A) lacking exp. Allobasis with row of spinules and 2 abexpodal setae. Enp with lateral (several) long spinules, 2 well-developed bipinnate setae, and 1 small bare seta. Terminal end of A2 with 3 long, geniculate setae, one of which fused with small bare seta. In addition there are 2 unipinnate smaller setae. Subterminally with frill carrying spinules.

Md damaged, not illustrated.

Mxl (Fig. 4C) arthrite of praecoxa with 6 terminal spines and 1 bare seta. On surface with row of long spinules and 2 bare setae. 2 subapical bare and slender setae. Coxal endite with 1 bare and 1 unipinnate blunt seta. Basis, enp, and exp fused, forming a single lobe with 6 bare and 1 pinnate setae.

Mx (Fig. 4D) syncoxa and basis separate, syncoxa with 2 endites and several spinules. Proximal endite small, with 1 strong unipinnate seta, fused with the segment, and 1 smaller bare seta. Distal endite with 2 strong unipinnate setae. Basis with 1 unipinnate and 1 bare strong seta, both fused with segment. First seta drawn out into long claw-like spine. In addition it has 2 bare and slender setae. Enp fused with basis, represented by 2 bare setae.

Mxp (Fig. 4B) prehensile, syncoxa with row of short, but strong spinules and 1 unipinnate seta. Basis with row of long spinules. Enp drawn out into long bare claw, with 1 small seta at its base.

P1 (Fig. 5) with transversely elongate basis, bearing 1 bare inner and 1 bipinnate outer seta, and 1 row of long spinules on the dorsal margin. Enp broken. Exp 2-segmented, with exp2 much longer than exp1. Exp1 with 1 outer bipinnate seta; exp2 with row of long spinules along the inner margin, and with 1 outer unipinnate seta; with 4 terminal, bare, geniculate setae, the innermost translocated subterminally. Finally there is also a tubepore.

P2-P4 (Figs. 6-8) with transversely elongate bases, each carrying 1 bipinnate seta on the outer distal margin, a long tubepore and several long spinules on the dorsal margin. Enps broken. Exps 3-segmented, P2 exp1 and exp2 with row of long spinules along inner margin, exp3 with long subterminal tubepore. Outer setae of P2 exp1 and exp2, as well as terminal setae of exp3 slightly malformed. Exp3 of P2 also deformed at its inner margin, beneath the insertion of the inner seta. P3 exp2 with long spinules along inner margin. Setation of P2-P4 as listed in table 1.

P5 (Fig. 9) benp and exp separate. Benp with long anterior spinules. Endopodal lobe completely reduced, represented by 1 bare and 1 bipinnate seta that is accompanied by 2 long tubepores. Outer seta of benp arising from small setophore, accompanied by spinules and long tubepore. Exp with 1 bipinnate outer seta, with 1 subterminal small bipinnate seta; with terminal triplumose (1) and bipinnate (1) setae, and with 1 bipinnate inner seta, accompanied by long tubepore and bearing 1 small tubepore at its tip.

GF (Fig. 2A) gonopores and copulatory pore free, not covered by P6, which are fused and form a cuticular fold, with 2 small setae.

Male unknown.

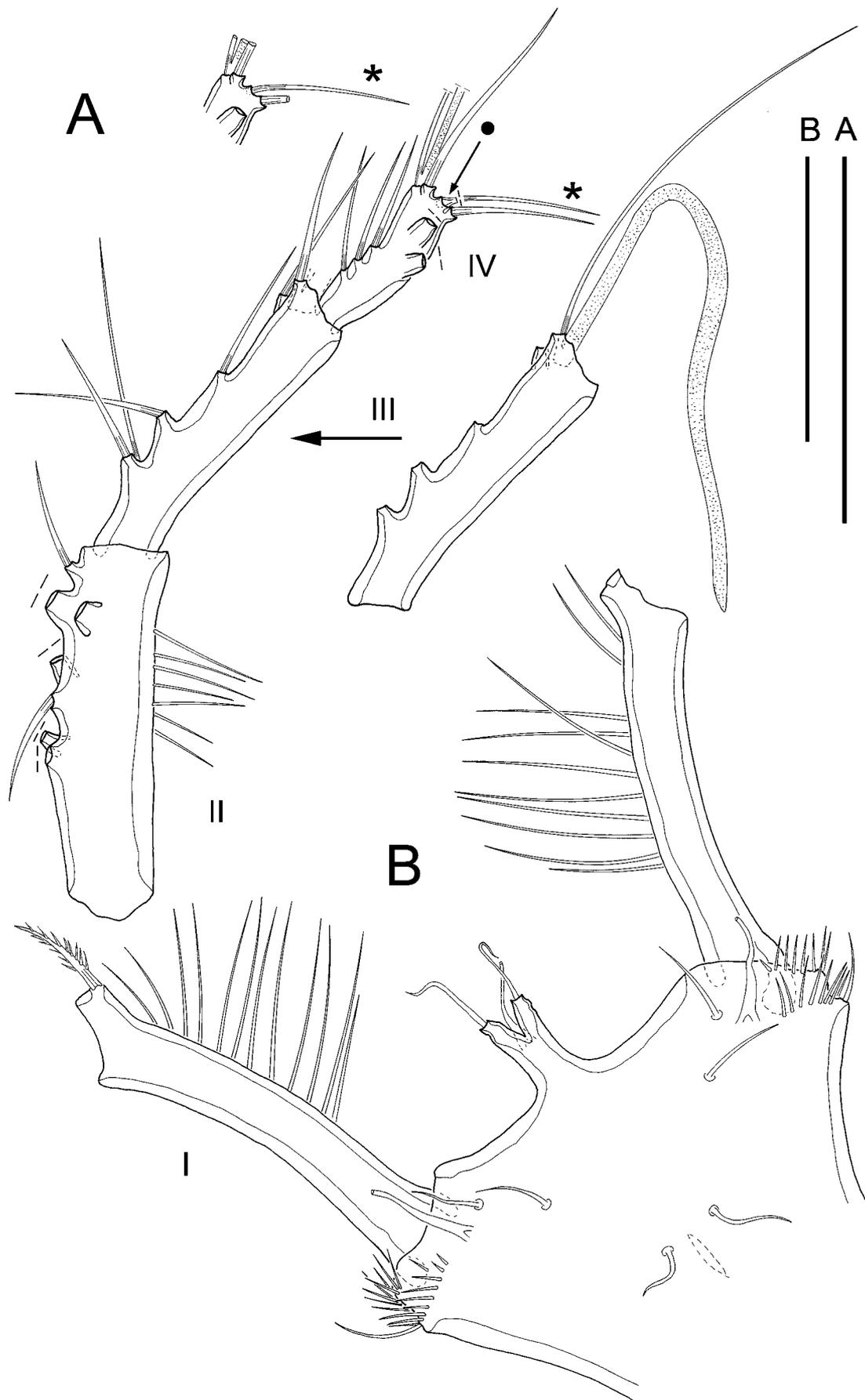


FIGURE 3. *Dorsiceratus wilhelminae* sp. nov., female holotype. A, A1, black point indicating the front seta (broken), asterisk indicating the seta behind; B, Rostrum, dorsal. Scales: 50µm.

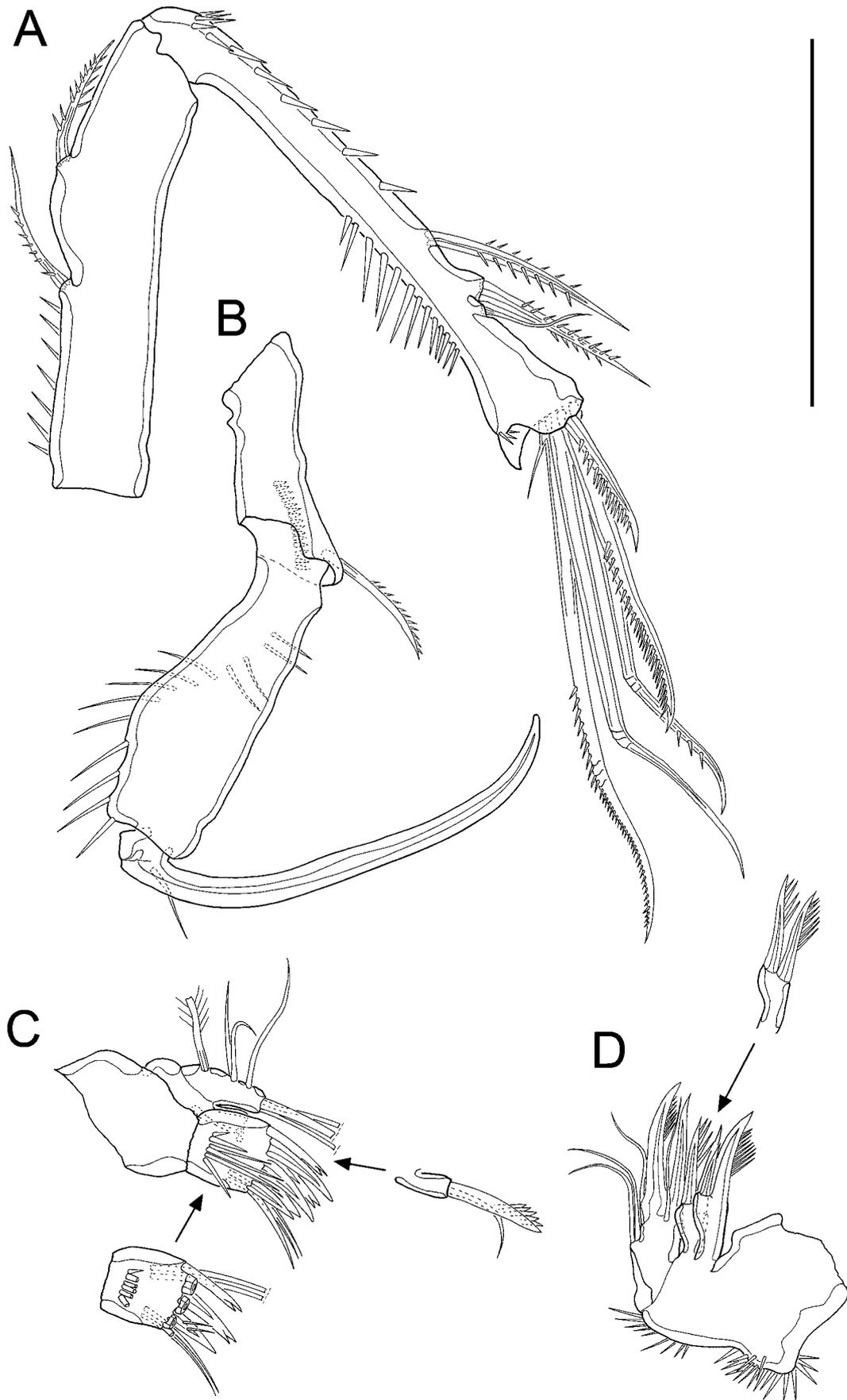


FIGURE 4. *Dorsiceratus wilhelminae* sp. nov., female holotype. A, A2; B, Mxp; C, Mx; D, Mxl. Scale: 50µm.

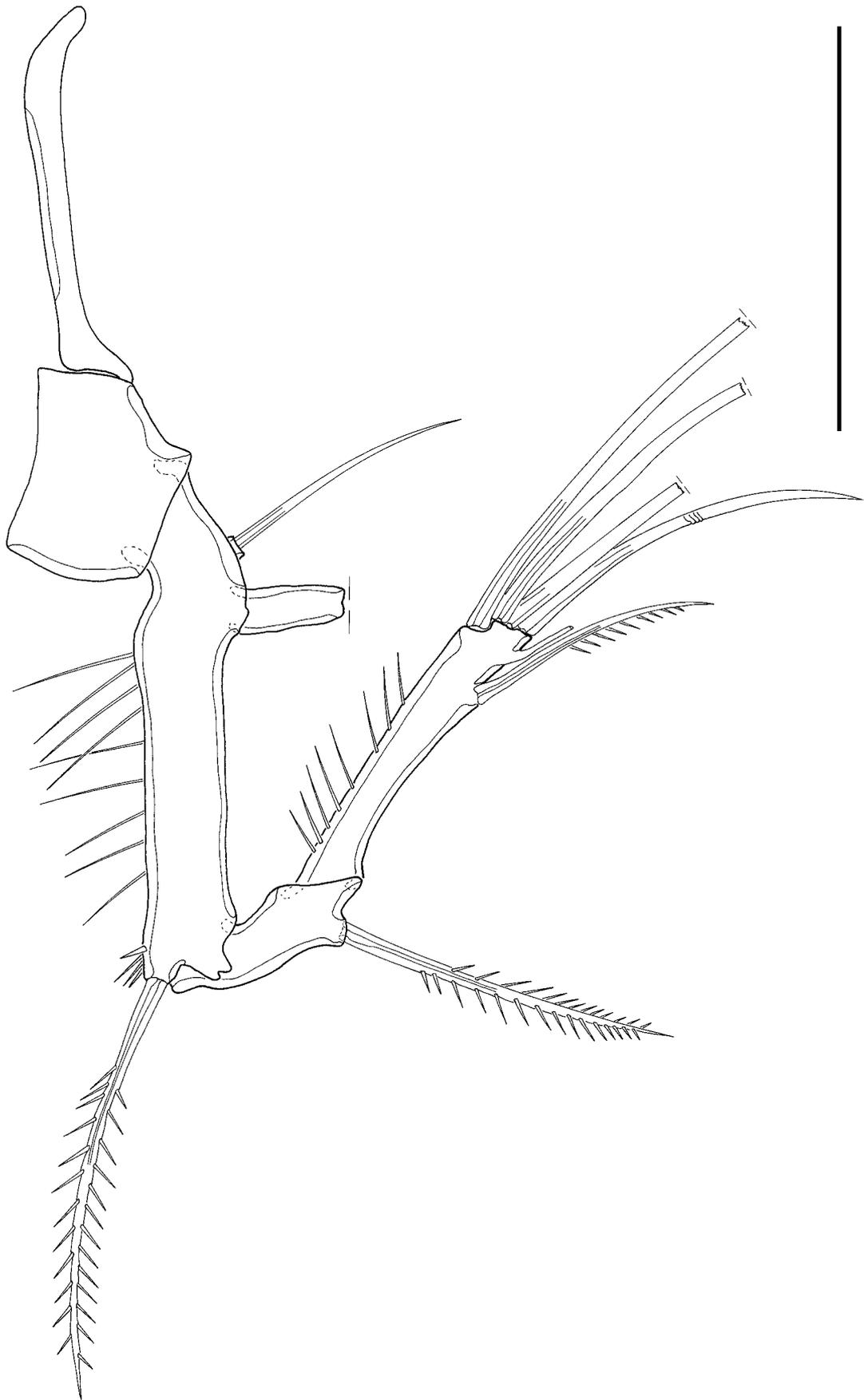


FIGURE 5. *Dorsiceratus wilhelminae* sp. nov., female holotype. P1. Scale: 50 μ m.



FIGURE 6. *Dorsiceratus wilhelminae* sp. nov., female holotype. P2. Scale: 50 μ m.



FIGURE 7. *Dorsiceratus wilhelminae* sp. nov., female holotype. P3. Scale: 50 μ m.

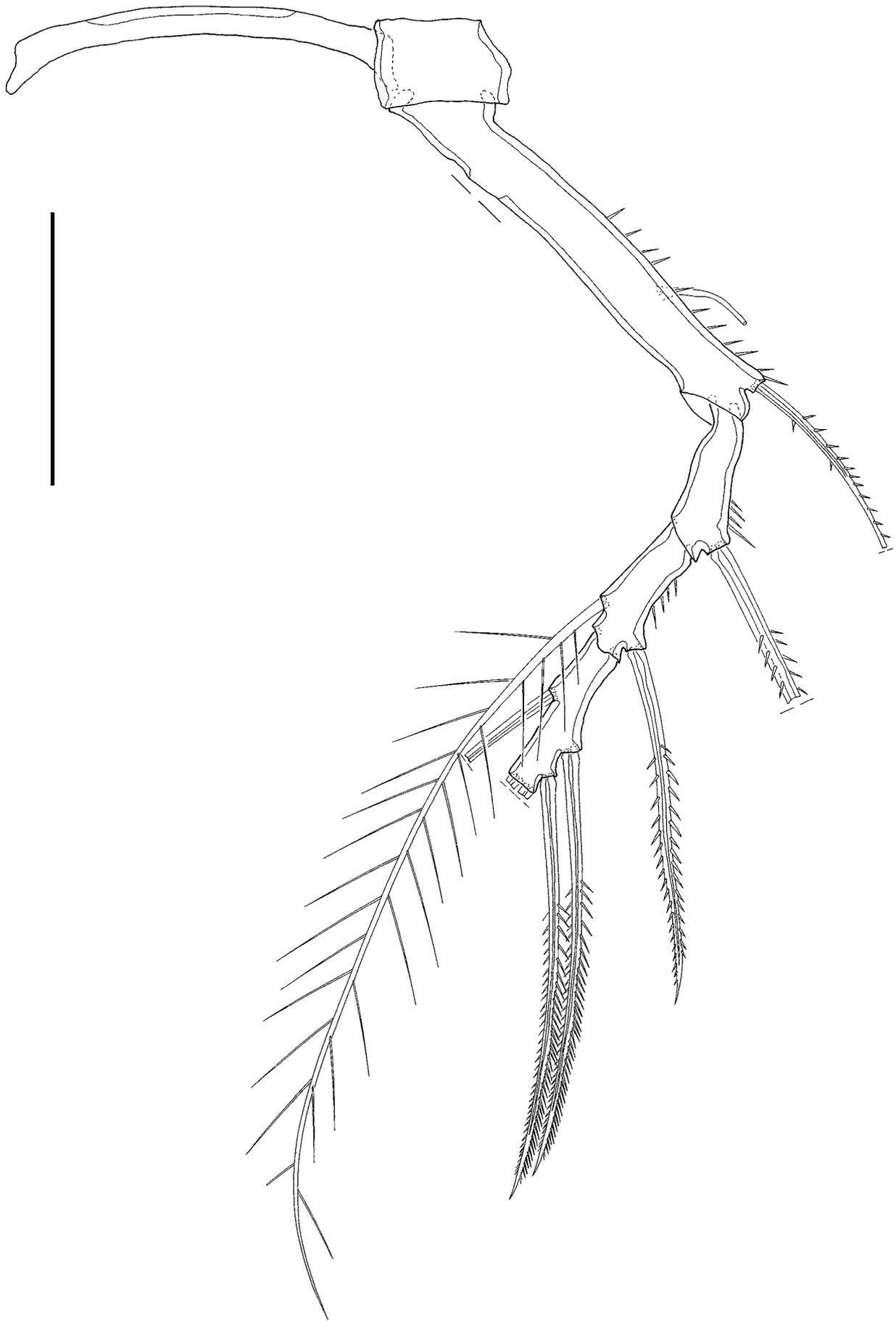


FIGURE 8. *Dorsiceratus wilhelminae* sp. nov., female holotype. P4. Scale: 50 μ m.

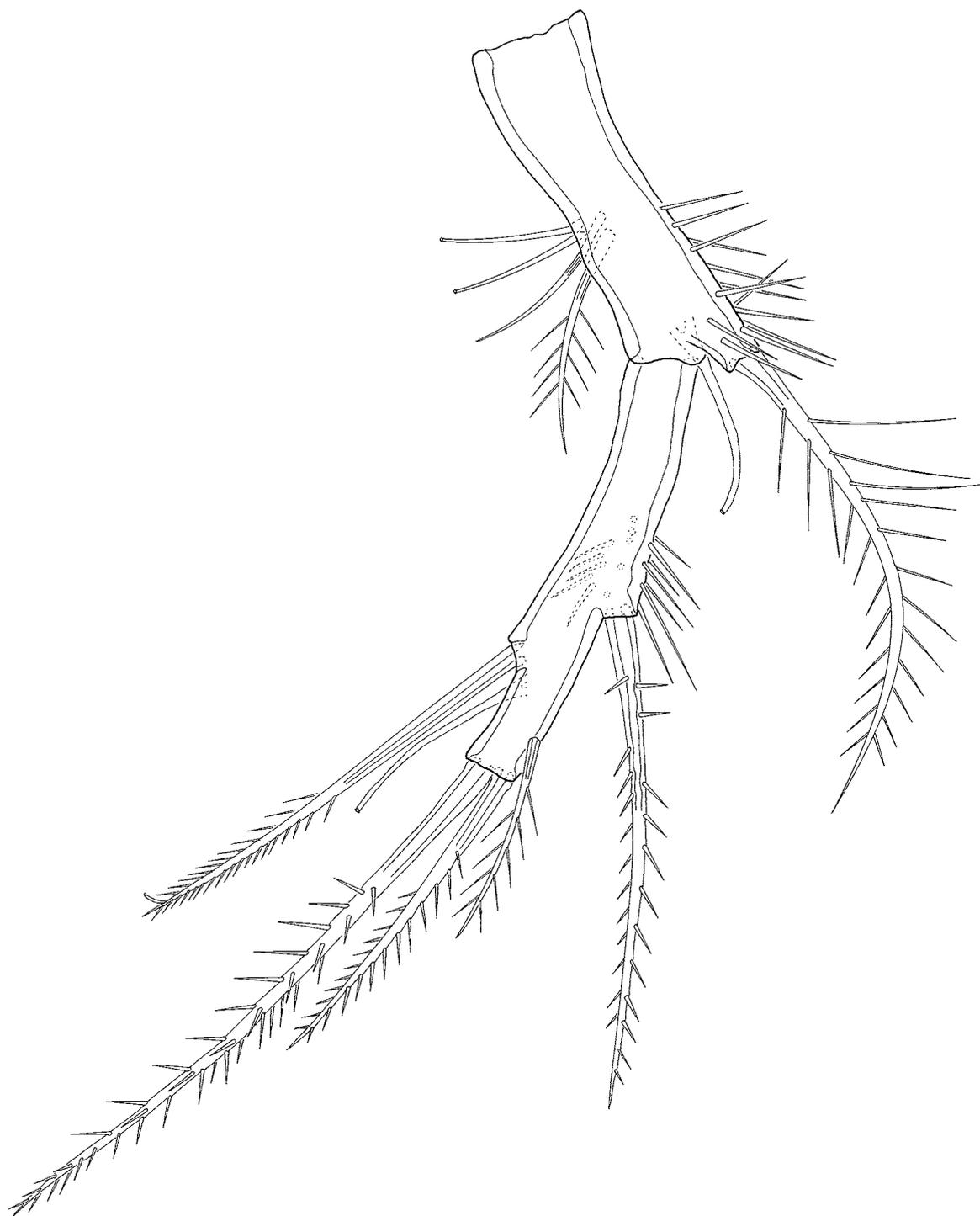


FIGURE 9. *Dorsiceratus wilhelminae* sp. nov., female holotype. P5. Scale: 50µm.

TABLE 1. Setation of P1–P4 *Dorsiceratus wilhelminae* sp. nov.

	<i>coxa</i>	<i>basis</i>	<i>exopod</i>	<i>endopod</i>
P1	0–0	I–0	I–0; I–3–1	?(missing)
P2	0–0	I–0	I–0; I–1; II–2–2	?(missing)
P3	0–0	I–0	I–0; I–1; II–2–2	?(missing)
P4	0–0	I–0	I–0; I–1; II–2–1	?(missing)

***Dorsiceratus dinah* sp. nov.**

Holotype: 1 female, dissected and mounted on 15 slides, deposited at the Forschungsinstitut und Naturmuseum Senckenberg (Frankfurt, Germany), collection numbers SMF 31443/1–15.

Type locality: Atlantic Ocean, Seine Seamount, Station #756, (04.12.2003, MUC, 33°46,0'N/14°21,9'W, 179m depth).

Etymology. The specific name of *Dorsiceratus dinah* sp.nov. is fondly dedicated to KHG's twin sister, Mrs. Dinah George.

Description of female. Habitus (Fig. 10) long and slender (body length including FR 380µm). Cphth with pronounced frontal peak and dorsally with 1 pair of long spinulose cuticular processes at its distal margin, bearing small sensilla at their tips and bases. Peak with 2 tubepores near the A1 base, and with 3 pairs of sensilla; with lateral setular tufts and 1 sensillum at each side. Rostrum (Fig. 12B) constricted, fused to cphth, remarkably prominent and divided distally, with 2 sensilla and 1 long tubepore at its tip. Cphth with several sensilla. Thoracic somites bearing P2–P4 each with a pair of long cuticular spiny processes at their dorsal distal margin, with sensilla at their tips and bases; with lateral setular tufts. Thoracic somites bearing P2–P5 dorsally with 1 long dorsal tubepore. Last thoracic, P6-bearing somite incompletely fused with first abdominal somite, forming a genital double somite, whose former separation is indicated by a dorsal cuticular suture; ventrally and laterally with 2 tubepores and 2 sensilla (Fig. 11A). Genital double somite with 2 pairs of dorsal tubepores, second abdominal somite with 1 pair of dorsal tubepores. All abdominal somites with 2 lateral tubepores, genital double somite and second abdominal somite with additional tubepores at their ventral side. P5-bearing somite, genital double somite, and all abdominal somites each with dorsal row of long hair-like spinules at their distal margins. Third abdominal somite also with ventrally hair-like spinules and row of well-developed long spinules. All abdominal somites with dorsal pair of tubepores at distal margin. Telson without dorsal tubepore, but with 2 tubepores near the FR base (Fig. 11A). Telson broader than long, trapezoid in shape; its distal margin broader than its proximal one. Anal operculum with spinules.

FR (Fig. 11) about 5 times longer than broad, bearing 2 terminal tubepores and 7 setae (I–VII). I and II insert laterally, close together. I very fine, small and bare. II unipinnate, longer than I. III bipinnate, inserts subterminally at outer margin, accompanied by a few spinules at its base. Setae IV, V, and VI insert terminally, IV and VI small and bare, V bipinnate and longest of all setae. Seta VI inserts terminally at inner margin, flanked by a few spinules. VII at dorsal side arises from small knob.

A1 (Fig. 12A, B) four-segmented. First segment longest, second and third segment almost the same size, and fourth segment smallest. First and second segment with lateral row of long spinules. First segment with 1 distal seta at inner margin. Second segment with 6 setae on its outer margin and 1 seta on anterior surface. Third segment with 6 bare setae on its outer side, with strong subterminal aes, accompanied by a 7th seta. Fourth segment with 11 bare setae and 1 small aes. Armature formula: I–1; II–7; III–7 + aes; IV–11 + aes.

A2 (Fig. 13A) lacks exp. Allobasis with row of spinules and 2 abexpodal setae. Enp 1-segmented, with several long lateral spinules, 2 well-developed bipinnate setae and 1 small bare seta. There are 5 terminal setae, 3 of which geniculate. One geniculate seta bipinnate and basally fused with additional 6th small bare seta. There are also subterminal frill carrying spinules.

Md (Fig. 13B, C) Gnathobase elongate with 3 teeth, lacking seta at inner margin. Basis, enp, and exp fused, forming a long mandibular palp with 3 bipinnate and 2 unipinnate setae, with several additional spinules.

Mxl (Fig. 13D) Arthrite of praecoxa with 6 terminal spines, subapically with 2 bare, slender setae. Surface with 2 bare setae. Coxa, basis, enp, and exp fused, forming a single lobe that bears 9 setae.

Mx (Fig. 13E) Syncoxa and basis separate, carrying the syncoxa 2 endites. Proximal endite small, with 1 bipinnate and 1 bare seta, both well developed and equal in size. Distal endite with 1 unipinnate and 1 bare seta. Basis with 1 claw-like unipinnate seta and 1 smaller bare seta, both fused with the segment. There are 2 additional bare and slender setae. Enp distinct but very small, with 2 bare setae.



FIGURE 10. *Dorsiceratus dinah* sp. nov., female holotype. Habitus, dorsal. Scale: 200 μ m.

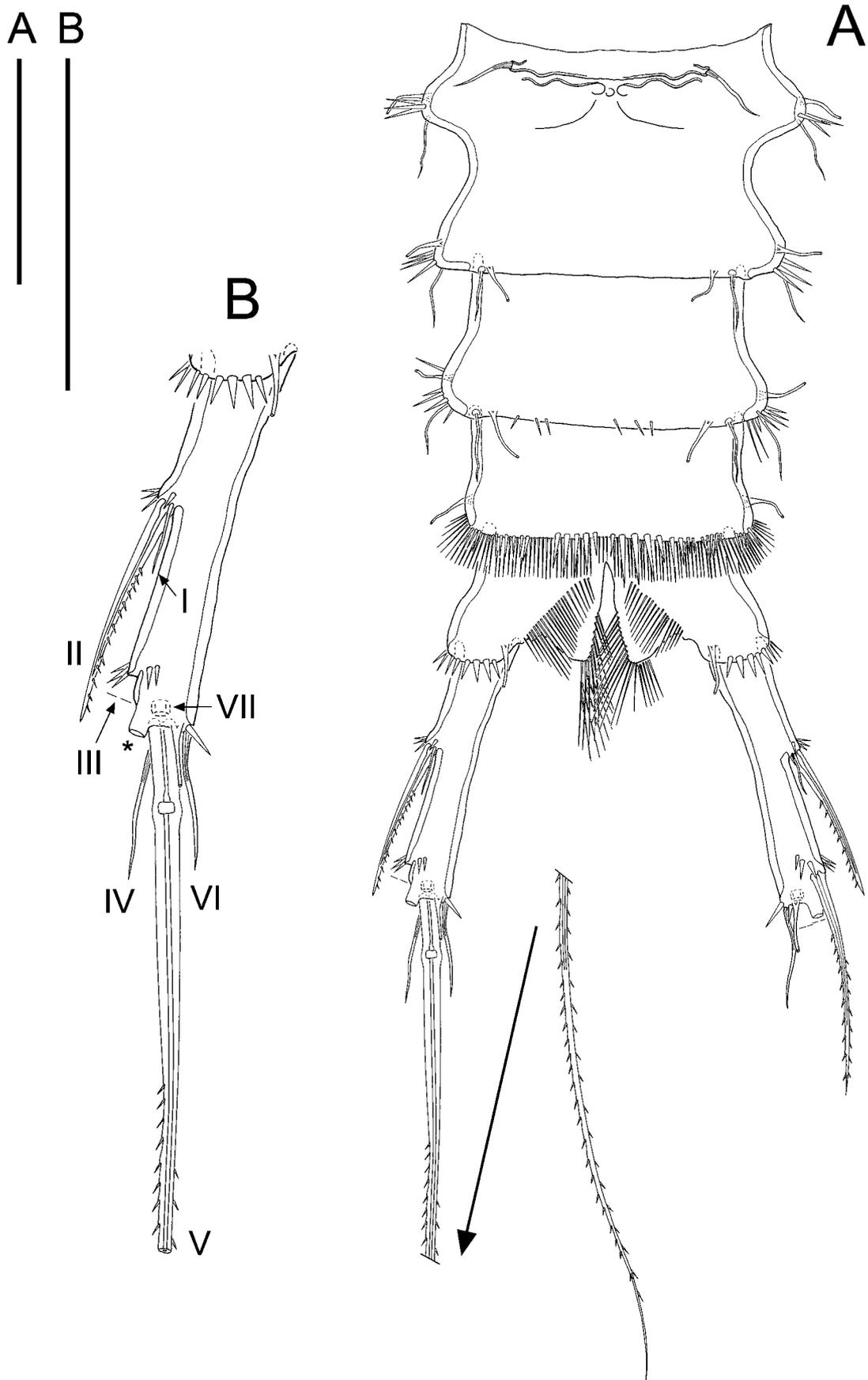


FIGURE 11. *Dorsiceratus dinah* sp. nov., female holotype. A, Abdomen, ventral; B, Furcal ramus, ventral, asterisk indicating the broad but short tubepore. Scales: 50 μ m.

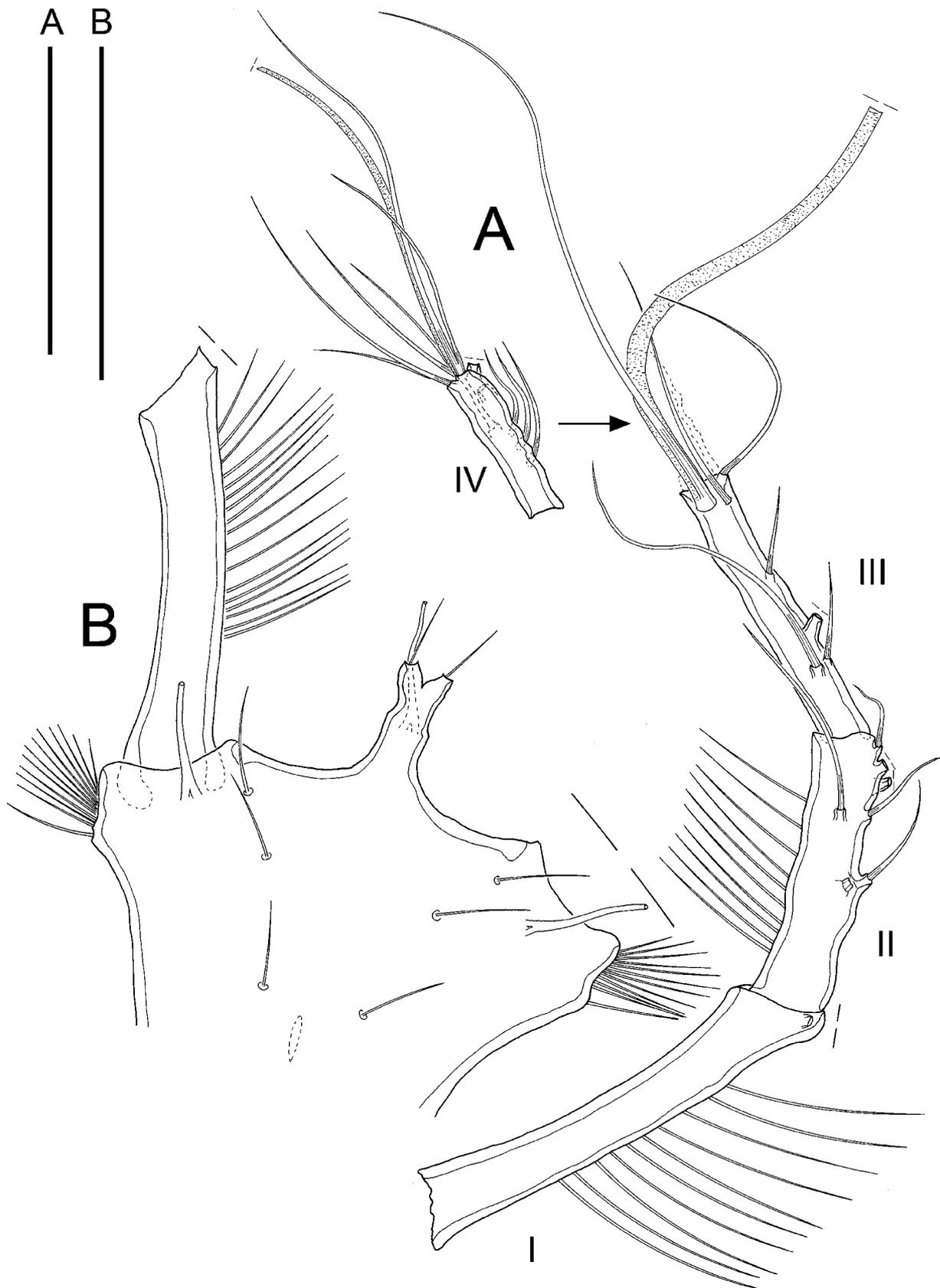


FIGURE 12. *Dorsiceratus dinah* sp. nov., female holotype. A, A1; B, Rostrum, dorsal. Scales: 50 μ m.

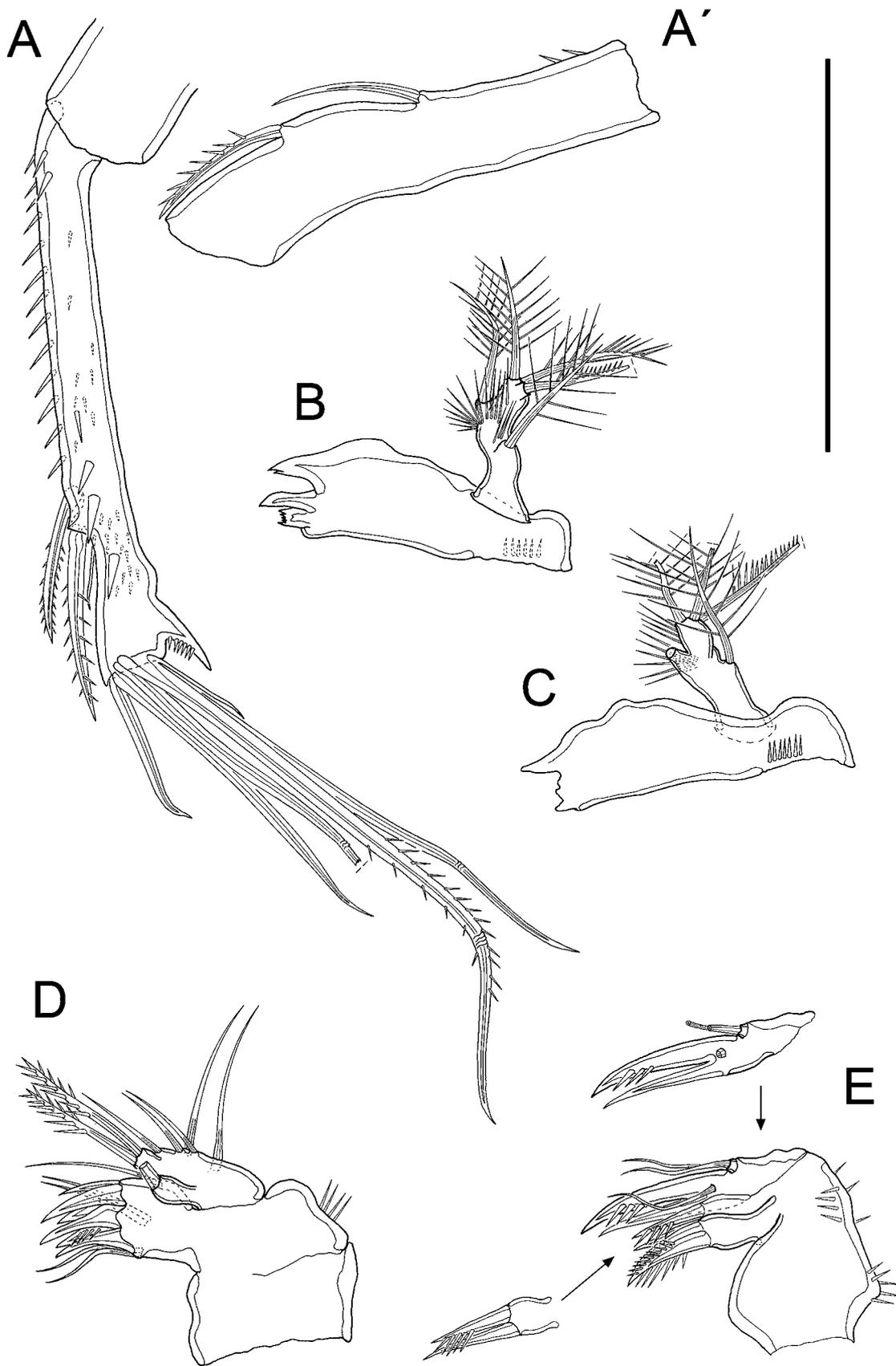


FIGURE 13. *Dorsiceratus dinah* sp. nov., female holotype. A, A2, A', A2 allobasis from counterpart; B, Md; C, Md from counterpart; D, Mxl; E, Mx. Scale: 50µm.

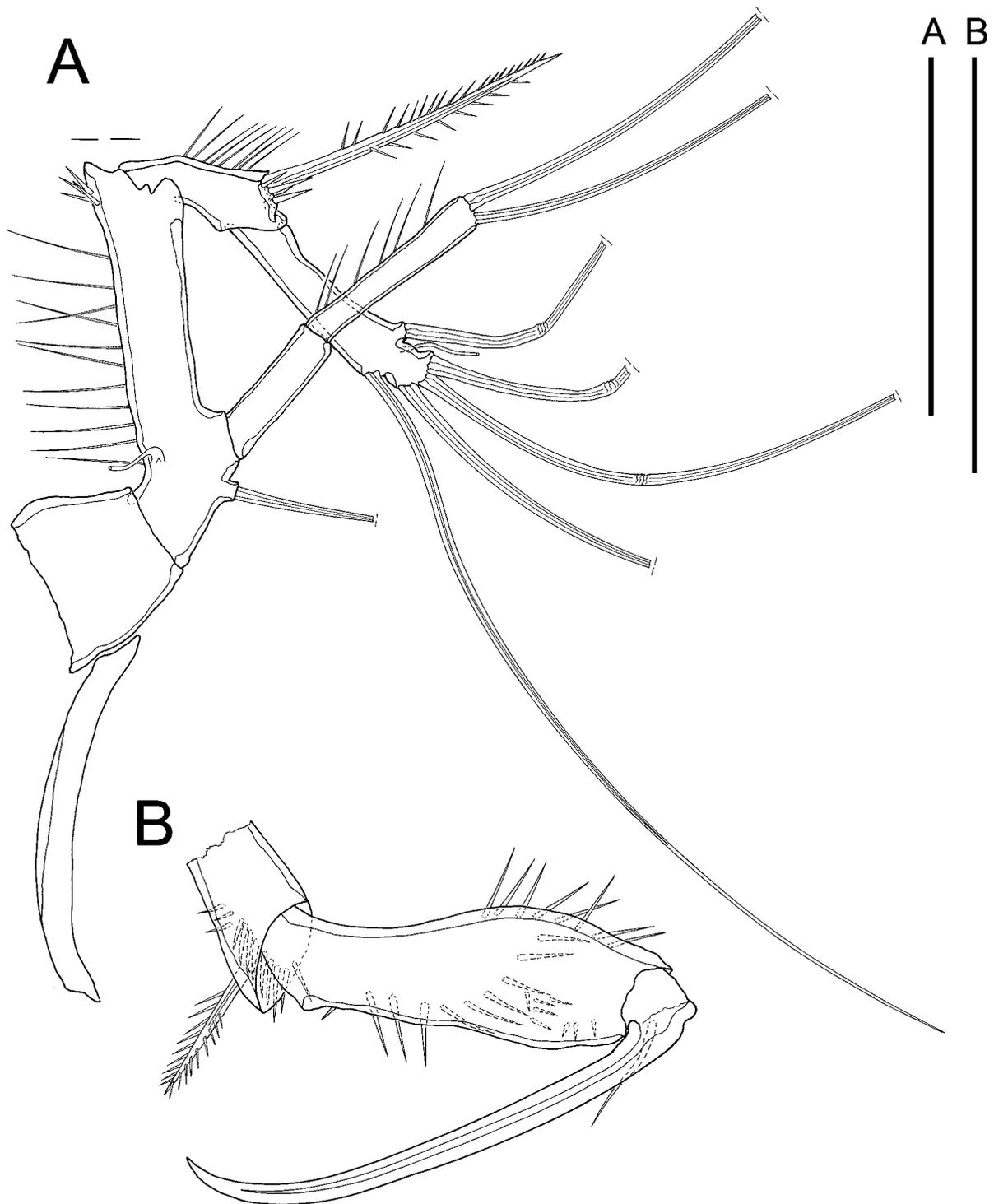


FIGURE 14. *Dorsiceratus dinah* sp. nov., female holotype. A, P1; B, Mxp, syncoxa broken. Scales: 50µm.

Mxp (Fig. 14B) prehensile, syncoxa with a row of long lateral spinules, with subterminal row of strong spinules and 1 bipinnate seta. Basis with a transverse row of long spinules. Enp drawn out into a long bare claw, accompanied by 1 small seta at its base.

P1 (Fig. 14A) with transversely elongate basis, bearing 1 bare inner and 1 outer seta (broken in Fig. 14A), and 1 row of long spinules on the dorsal margin. With 1 additional tubepore. Enp 2-segmented, second segment with row of long spinules at outer margin and 2 bare terminal setae. Exp 2-segmented, with exp2

longer than exp1. Exp1 with a row of long spinules along the outer margin and 1 outer bipinnate seta; exp2 with 1 outer geniculate bare seta, with 3 terminal bare, geniculate setae and with 1 subterminal long, bare seta. Also with 1 subterminal tubepore.



FIGURE 15. *Dorsiceratus dinah* sp. nov., female holotype. P2. Scale: 50 μ m.

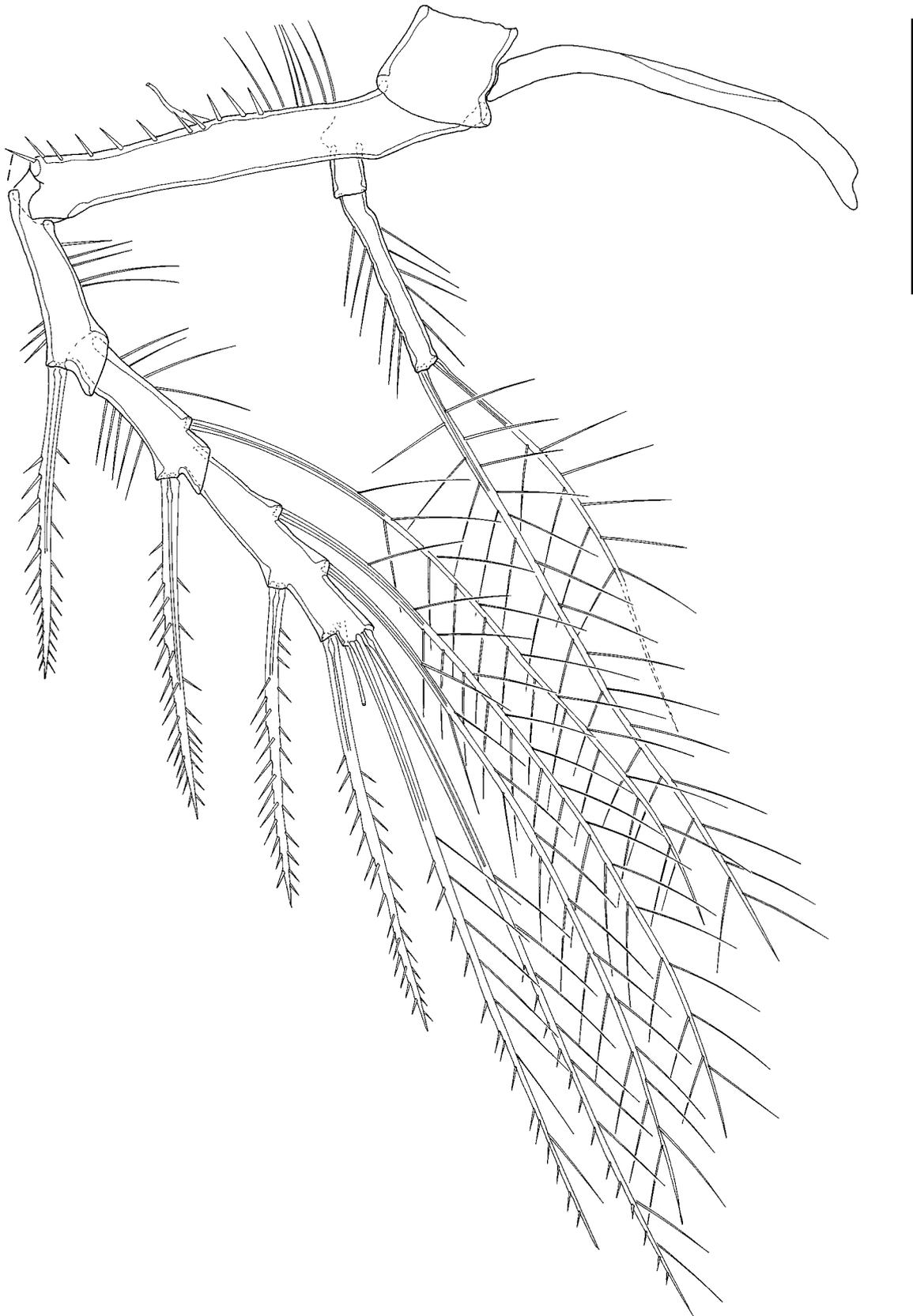


FIGURE 16. *Dorsiceratus dinah* sp. nov., female holotype. P3. Scale: 50 μ m.

P2–P4 (Figs. 15–17) with transversely elongate bases, carrying 1 bipinnate seta on the outer distal margin, a long tubepore and several long spinules on the dorsal margin. Enps 2-segmented, first segment bare and much shorter than second; second segment with 1 bipinnate seta in P2 and 2 setae in P3 and P4 (1 seta broken

in Fig. 17). Enp2 with additional row of spinules at inner (P2, P3), and outer margin (P3), while bare in P4. Exps 3-segmented, with row of long spinules along the inner and outer margin of exp1 and exp2. Exp1 and exp2 equal in length, but exp3 longer than exp2. Exp3 of P2 and P3 with 1 subterminal long tubepore. Setation of P2–P4 as listed in table 2.

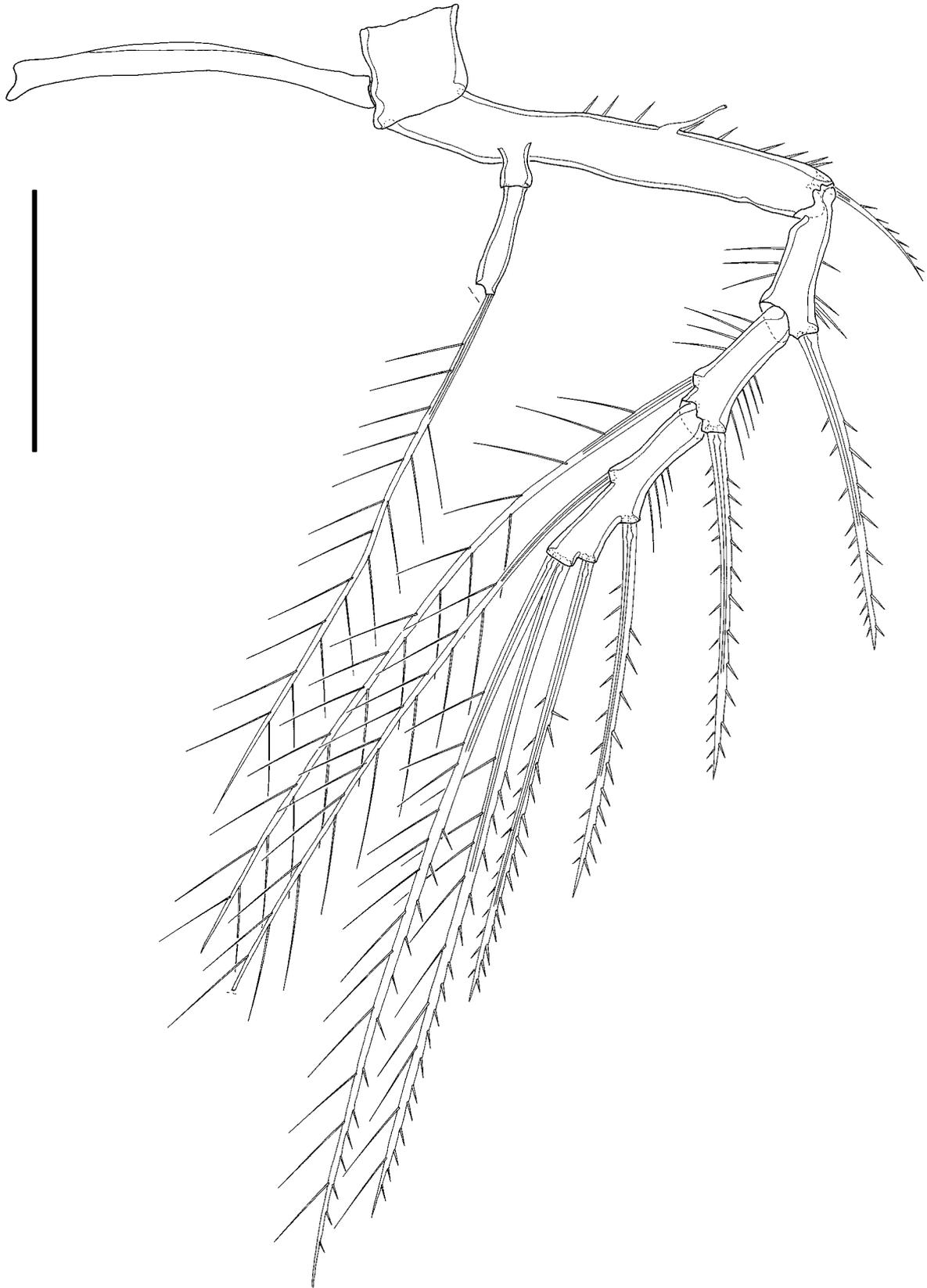


FIGURE 17. *Dorsiceratus dinah* sp. nov., female holotype. P4. Scale: 50 μ m.

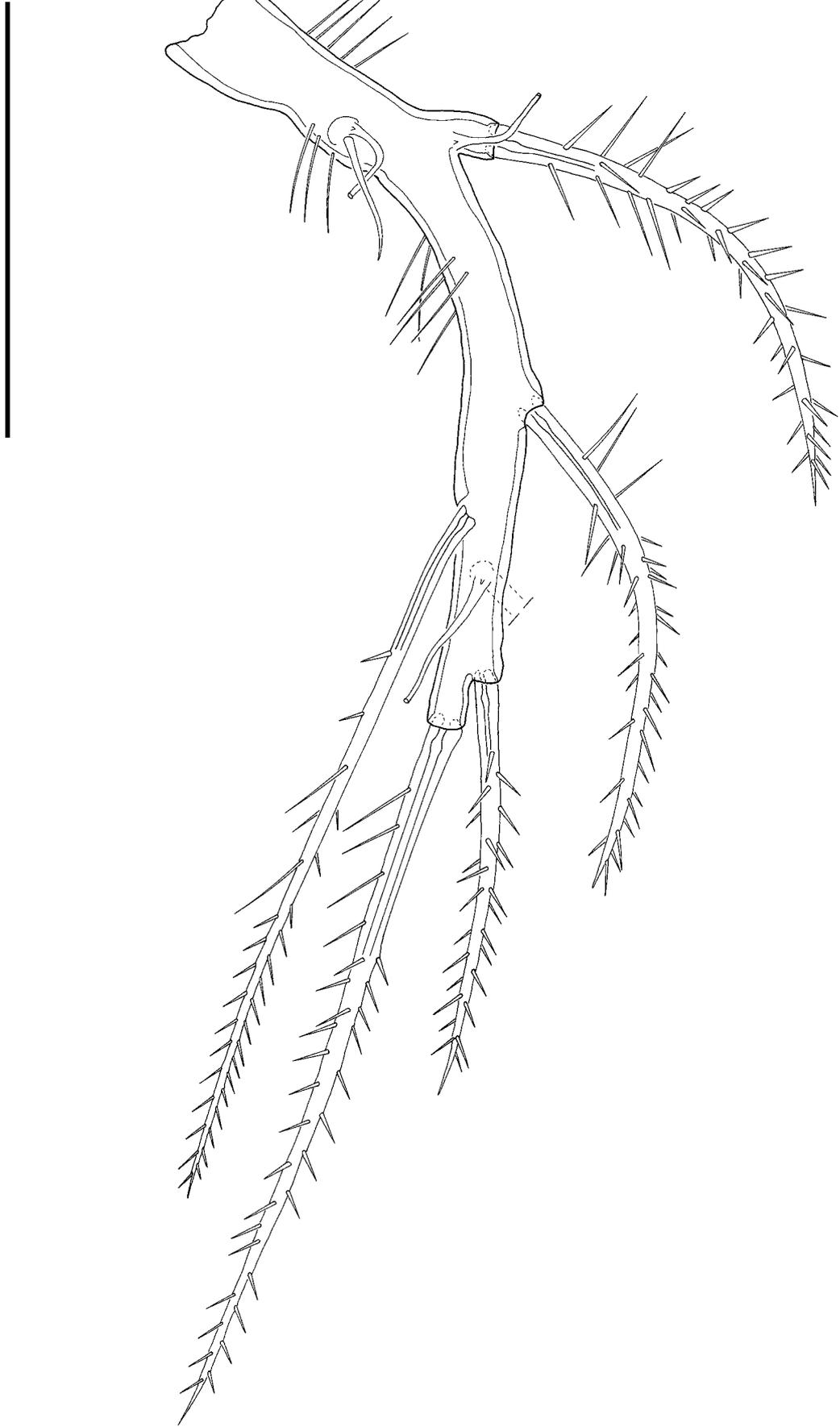


FIGURE 18. *Dorsiceratus dinah* sp. nov., female holotype. P5. Scale: 50µm.

P5 (Fig. 18) Benp and exp fused. Anterior part of baseoendopod with long spinules and 1 bare seta in the middle, representing the enp, accompanied by 1 long tubepore. Outer basal seta arises from a small setophore, accompanied by 1 long tubepore. Exp with 2 multipinnate outer setae (1 seta broken), 1 tripinnate subterminal and 1 tripinnate terminal seta, and 1 bipinnate inner seta. There is also 1 long tubepore.

GF (Fig. 11A) copulatory pore free, not covered by fused unisetose P6, which form a cuticular fold.

Male unknown.

TABLE 2. Setation of P1–P4 *Dorsiceratus dinah* sp. nov.

	<i>coxa</i>	<i>basis</i>	<i>exopod</i>	<i>endopod</i>
P1	0–0	I–1	I–0; I–3–1	0–0; 0–2–0
P2	0–0	I–0	I–0; I–1; II–2–1	0–0; 0–1–0
P3	0–0	I–0	I–0; I–1; II–2–2	0–0; 0–2–0
P4	0–0	I–0	I–0; I–1; II–2–1	0–0; 0–2–0

Discussion

General remarks

The decision to describe *D. wilhelminae* and *D. dinah* spp. nov. was not made easily, because the description of new (harpacticoid) species based on single specimens is certainly somewhat questionable because no information on character variability within the species can be provided (cf. George 2006a). This problem applies in particular to the genus *Dorsiceratus*. Recent discovery of many individuals apparently belonging to this genus has caused taxonomic confusion and has not elucidated phylogenetic relationships, mainly because of (i) high similarity of most characters, and (ii) a quite heterogenous distribution of particular, distinct characters over different specimens that prohibits their unequivocal assignment to a definite species (George, personal observation). Against that background, one may ask why then describe two new *Dorsiceratus* species that are represented by single specimens only. The answer we would give is that representatives of that genus (and of almost all deep-sea Ancorabolinae) are commonly collected in very low individual numbers only (cf. George 2006b). The descriptions of *Dorsiceratus octocornis*, *D. triarticulatus*, and *D. ursulae* are based on very few (3–4) specimens, and several ancorabolid species have been described based on single specimens, e.g. *Breviconia australis* (George, 1998), *Ceratonotus thistlei* Conroy-Dalton, 2003, *Dendropsyllus antarcticus* (George & Schminke, 1998), and *D. thomasi* Conroy-Dalton, 2003. The alternative would simply be not to describe new ancorabolid species, when only single specimens are available. However, as any species description is but the erection of a hypothesis, in certain cases (e.g. rare species) we prefer to provide new taxonomic information describing new species even if based on single individuals, instead of ignoring new findings of ancorabolid representatives. This takes the risk that future investigation will reject our hypotheses. Intraspecific variability within the Ancorabolidae, and in particular in *Dorsiceratus*, has been discussed briefly before (George 2006a, b) and is the object of an ongoing investigation that will be published elsewhere. The difficulty of finding congruent characters for characterizing (i) distinct *Dorsiceratus* species and (ii) even a monophylum *Dorsiceratus* itself, can be seen in the following character discussion.

The taxon Dorsiceratus Drzycimski, 1967

According to George (2006a), only two weak apomorphies have been detected to support the hypothesis of *Dorsiceratus* being monophyletic [in the following, plesiomorphies are set in square brackets]:

- 1) P2 enp2 with 1 seta (also in *Polyascopephorus* George, 1998, *Dendropsyllus* Conroy-Dalton, 2003) [with 2 setae];

- 2) P4 enp2 sexually dimorphic, females lack the outer seta (also in *Ancorabolina* George, 2006, *Arthuricornua* Conroy-Dalton, 2001, *Ceratonotus* (part.), *Polyascophorus*) [no sexual dimorphism; female P4 enp2 with outer seta].

As argued by that author, the weakness of both apomorphies is because of their (convergent?) presence in other ancorabolid taxa. The problem with *Dorsiceratus* is that it cannot yet be characterized by any clear autapomorphy, while most remaining ancorabolid genera can. Newly collected specimens can easily be allocated into *Dorsiceratus* because of clear-cut diagnostic features, e.g. the general body shape, the presence of long cuticular processes on cphth and thoracic somites only, and a small but prominent rostrum (cf. George 2006a). But these features (except the “general body shape”) are, although disjunct, widespread in Ancorabolinae. On the other hand, assignment of *Dorsiceratus* to any other ancorabolin genus is currently impossible, because *Dorsiceratus* species fit no apomorphy of any other ancorabolin genus. Therefore, one faces what we would call a “taxonomical mess.” Although we can assign certain specimens clearly to a group “*Dorsiceratus*” based on diagnostic features, we are still in search of autapomorphies for the characterization of a monophylum *Dorsiceratus*, with exception of the above listed characters 1 and 2. However, in the meantime, we prefer to retain the group “*Dorsiceratus*” tentatively as a valid (= monophyletic) genus, until new information is provided that supports or disproves its monophyletic status.

Characterization of the Dorsiceratus species known to date:

The difficulty of finding congruent characters also applies for the species within the genus *Dorsiceratus*. Although derived characters can be recognized, these show a heterogenous distribution over the individuals available for detailed comparison (see below). As a consequence, we feel unable to provide a detailed phylogenetic analysis. For that purpose, more material will have to be examined very carefully, which is the object of an ongoing investigation. However, as both *Dorsiceratus wilhelminae* and *D. dinah* species novae fit the generic diagnosis, and based on the above argument, their allocation to *Dorsiceratus* is plausible. Moreover, at least *D. dinah* sp. nov. shares the supposed apomorphies 1 and 2, which cannot yet be verified for *D. wilhelminae* sp. nov., because of the broken endopods of its swimming legs.

For comparison within the genus, 22 characters were scored (Tab. 3). Their comparison may provide insights into phylogenetic relationships within *Dorsiceratus*.

As stated before, all species may be united because of characters 1 and 2 (Tab. 4) (still uncertain for *D. wilhelminae* sp. nov.).

Inside *Dorsiceratus*, both new species resemble *D. octocornis* and *D. ursulae*, particularly because they have a 2-segmented P1 exp (character 3) (Tabs. 3, 4). As reduced segmentation (“reduced” from a phylogenetical, not from an ontogenetical point of view) is generally considered as derived, that feature is regarded as synapomorphy of all four species, compared with the remaining *D. triarticulatus*.

Character (4) implies closer relation between *D. octocornis* and the new species. The translocation of the seta originally corresponding to the outer one of P1 exp2 (*D. triarticulatus*) to an outer subterminal position, we regarded as derived and therefore an apomorphic condition. It can be observed in *D. octocornis* and the new species (cf. Figs. 5, 14), while it is retained in its original position in *D. ursulae* (cf. George 2006a).

Contrary to character 4, the following characters 5–7 point to a closer relationship of *D. dinah* sp. nov., *D. wilhelminae* sp. nov., and *D. ursulae*. Geniculation of setae, i.e. development of a flexure point is considered as derived from an ancestral state that consisted of a simple flexible structure without any specialisation (cf. Huys *et al.* 1996). Thus, the development of a third geniculate seta in A2 enp of the new species and *D. ursulae* (character 5) is considered as synapomorphy for the three species.

Evolution of tubepores occurs frequently in Ancorabolinae but not in the remaining Harpacticoida. Therefore, tubepore development as well as an increase in tubepore number is regarded here as a derived condition. *Dorsiceratus octocornis* shows only 1 tubepore on the first and second abdominal somites (unknown for *D. triarticulatus*), while *D. dinah* sp. nov., *D. wilhelminae* sp. nov., and *D. ursulae* bear 2 tubepores (character 6), which is considered as apomorphic for these species.

TABLE 3. List of characters used for phylogenetic comparison of *Dorsiceratus triarticulatus*, *D. octocornis*, *D. ursulae*, *D. wilhelminae* sp. nov., and *D. dinah* sp. nov. Plesiomorphies in square brackets. Characters present in other, non-related taxa in parentheses. Parentheses in character 7 indicating its restricted phylogenetic value.

Character no.	Character
1	P2 enp2 with 1 seta (also in <i>Polyascophorus</i> , <i>Dendropsyllus</i> Conroy-Dalton, 2003) [with 2 setae];
2	P4 enp2 sexually dimorphic, females lack the outer seta (also in <i>Ancorabolina</i> George, 2006, <i>Arthuricornua</i> Conroy-Dalton, 2001, <i>Ceratonotus</i> (part.), <i>Polyascophorus</i>) [no sexual dimorphism; female P4 enp2 with outer seta];
3	P1 exp 2-segmented [3-segmented in <i>D. triarticulatus</i>];
4	P1 exp2 with subterminally translocated outer seta [seta located in original position in <i>D. ursulae</i>];
5	Presence of 3 geniculate terminal setae on A2 enp [2 geniculate setae]
6	Presence of 2 tubepores dorsally on first and second abdominal somite [1 tubepore];
(7)	(Presence of row of hair-like spinules on distal margin of abdominal somites);
8	P1 inner basal seta strongly reduced [seta of normal length];
9	P1 enp2 with 1 seta [with 2 setae (not yet confirmed for <i>D. wilhelminae</i> sp. nov.)];
10	Hair-like spinules at the distal margins of cphth and thoracic somites [no hair-like spinules];
11	FR clearly elongate (at least 5.5 times longer than basal width) [of moderate length (3.6–4.6 times longer than basal width)];
12	Second female antennular segment with 6 setae [with 7 setae];
13	Second female antennular segment covered with spinules [segment bare];
14	Third antennular segment with 9 setae [with at least 10 setae];
15	Presence of 2 tubepores dorsally on penultimate body somite [1 tubepore in remaining <i>Dorsiceratus</i> species];
16	P1 exp2 with first outer seta geniculate [seta non-geniculate in remaining <i>Dorsiceratus</i> species];
17	A2 enp with row of long spinules at inner margin [no spinules, margin bare];
18	Mx enp fused with basis (also in <i>Dorsiceratus triarticulatus</i>) [distinct in <i>D. ursulae</i> and <i>D. dinah</i> sp. nov., unknown in <i>D. octocornis</i>];
19	Female P5 benp and exp fused (also in <i>D. octocornis</i>) [benp and exp distinct];
20	P5 benp with 1 seta (also in <i>D. octocornis</i>) [benp with 2 setae];
21	Rostrum remarkably elongate and strongly bifurcated [rostrum small, barely bifurcated];
22	P1 exp2 subterminally with tubepore [tubepore not developed].

Character 7 refers to the development of very fine and hair-like structures on the abdominal segments. *D. octocornis* and *D. triarticulatus* lack such ornamentation. Examining the remaining members of the *Ceratonotus*-group, only *Arthuricornua* seems to share such structures with *Dorsiceratus* [cf. Figs. 1 and 2 in Conroy-Dalton (2001), but they are not explicitly mentioned in the text by that author], while *Ceratonotus*, *Dendropsyllus*, *Echinopsyllus*, *Polyascophorus*, *Pseudechinopsyllus*, and *Touphapleura* lack them. There exist two possible explanations:

- 1) A common ancestor possessed such structures, which are retained in *Arthuricornua* and most *Dorsiceratus* species but reduced in the remaining members of the *Ceratonotus*-group. That would mean that their loss also in *D. octocornis* has to be considered as apomorphic (and convergent, compared to the other members of the *Ceratonotus*-group).
- 2) A common ancestor lacked such fine hair-like spinules, which developed convergently in both *Arthuricornua* and a group inside *Dorsiceratus* (excluding *D. octocornis*).

Comparison with members of the supposed sister taxon of the *Ceratonotus*-group, the *Ancorabolus*-group sensu Conroy-Dalton & Huys (2000), reveals that similar fine and hair-like structures appear in the females of most species (e.g. *Arthropsoyllus serratus* Sars, 1909, *Ancorabolus confusus* Conroy-Dalton & Huys, 2000, *A. inermis* Conroy-Dalton & Huys, 2000, *Juxtaramia polaris* Conroy-Dalton & Huys, 2000, and *Uptionyx verenae* Conroy-Dalton & Huys, 2000). These structures might constitute therefore sexual dimorphism. If the structures were homologous in all corresponding species, one could conclude their plesiomorphic condition for the respective *Dorsiceratus* species, as they are also present inside the *Ancorabolus*-group. Their absence in the above-mentioned taxa should then be regarded as secondary loss, which would support explanation 1. However, as we feel unable to decide if character 7 is an apomorphic or a plesiomorphic one, it has to be treated merely as diagnostic (character set in parentheses in Tabs. 3 and 4).

TABLE 4. Distribution of plesiomorphic (0) and apomorphic (1) states of characters 1–22 over the known *Dorsiceratus* species. “?”: state unknown. Grey fields indicate (syn-)apomorphic conditions. Parentheses in character 7 pointing to its restricted phylogenetic value. Detailed explanations in the text.

Character	<i>D. triarticulatus</i>	<i>D. ursulae</i>	<i>D. dinah</i>	<i>D. wilhelminae</i>	<i>D. octocornis</i>
1	1	1	1	1	1
2	1	1	1	1	1
3	0	1	1	1	1
4	0	0	1	1	1
5	0	1	1	1	0
6	0	1	1	1	0
(7)	(0)	(1)	(1)	(1)	(0)
8	1	0	0	0	0
9	1	0	0	0	0
10	0	1	0	0	0
11	0	1	0	0	0
12	0	1	0	0	0
13	0	1	0	0	0
14	0	1	0	0	0
15	0	0	1	0	0
16	0	0	1	0	0
17	0	1	0	1	0
18	1	0	0	1	?
19	0	0	1	0	1
20	0	0	1	0	1
21	0	1	1	1	0
22	0	0	1	1	0

Three *Dorsiceratus* species may be characterized by unambiguous apomorphies (Tabs 3, 4): *Dorsiceratus triarticulatus* because of characters 8–9: the inner basal seta of P1 presents a moderate length in all remaining representatives of the *Ceratonotus*-group, including all *Dorsiceratus* species except *D. triarticulatus* that shows a seta strongly reduced in size (character 8) (Coull 1973). It is therefore regarded as an apomorphy for that species. The same applies for the number of setae present in P1 enp2 (character 9). Like e.g. *Ceratonotus*, all *Dorsiceratus* species bear two setae, except *D. triarticulatus*, which has only 1 seta (but yet to be confirmed for *D. wilhelminae* sp. nov.).

Dorsiceratus ursulae seems to be well characterized by apomorphies 10–14; only that species bears several thin and quite flexible, hair-like setules at the distal half of cphth, and thoracic somites (character 10).

As such covering of setules is not found in any other taxon of Ancorabolinae, it is considered as apomorphic. Elongation of FR (character 11) is generally considered as apomorphic in Harpacticoida, so this should also apply to *Dorsiceratus*. Although occurring frequently in Harpacticoida, reduction of one seta in the second (character 12) and fourth (character 14) antennular segment, respectively, is a clear apomorphic state. Whereas all members of the *Ceratonotus*-group develop long spinules on the first antennular segment, in most species the following antennular segments lack such long spinules. Within *Dorsiceratus*, only *D. ursulae* shows a second antennular segment completely covered with spinules (character 13) (George 2006a). This character state is regarded as apomorphy, because the alternative – the synapomorphic loss of such spinules in all remaining *Dorsiceratus* species – would lead to an increasing incongruence with respect to the remaining characters (cf. Tab. 3).

Dorsiceratus dinah sp. nov. shows characters 15–16 as autapomorphic ones. It is the only species bearing two tubepores on the third abdominal somite (character 15). For character 16, the geniculate seta on P1 exp2, applies the same as stated for character 5 (see above): the first seta of P1 exp2 being geniculate shows a derived condition, compared with all remaining *Dorsiceratus* species that bear an unmodified bipinnate seta. For the remaining two species, *Dorsiceratus wilhelminae* sp. nov. and *D. octocornis*, no clear autapomorphies have been found. Although both species do have derived features (Tab. 4), these features occur on other *Dorsiceratus* species too, hindering complete phylogenetic resolution within the genus. For instance, *D. wilhelminae* sp. nov. shows derived conditions in characters 17 and 18 (cf. Tabs. 3, 4). However, it shares the (derived) possession of a row of long spinules on A2 enp (character 17) with *D. ursulae*, and the maxillar enp fused to the basis (character 18) with *D. triarticulatus*. Similarly, *D. octocornis* also shows two apomorphic characters: Fusion of benp and exp in female P5 (character 19), and loss of 1 seta in female benp (character 20). Both apomorphies are, however, also detectable in *D. dinah* sp. nov., so they are useless to characterize the species *D. octocornis*. However, they may at least indicate a close relationship between *D. dinah* sp. nov. and *D. octocornis*. Nevertheless, there is a second species constellation formed by the new species that may be supported by stronger apomorphies.

Both, *D. dinah* and *D. wilhelminae* spp. nov. deviate from all remaining *Dorsiceratus* species by apomorphic conditions of characters 21 and 22. In particular character 21, regarding the rostral shape and size, may be of high phylogenetic relevance. As stated by George (2006a: 151), a "...small bifurcated rostrum is quite characteristic for the genus". Nevertheless, as listed in character 21 (cf. Tab. 3), both, *D. wilhelminae* and *D. dinah* spp. nov. bear a clearly elongate and bifurcated rostrum. While George (2006a) felt unable to interpret the rostral development in Ancorabolinae, we believe that the ancestor of the *Ceratonotus*-group had a small and constricted one, as seen in several ancorabolin genera. Our assumption is based on the observation that the *Ceratonotus*-group encloses highly derived taxa that have a rostrum which is either virtually absent (*Ceratonotus*, *Dendropsyllus*) or remarkably elongate (*Echinopsyllus*, *Pseudechinopsyllus*), while those species considered as more primitive (*Arthuricornua*, *Dorsiceratus*, *Polyascophorus*, *Touphapleura*) have a smaller one. It is that small rostrum that probably represents the groundpattern ("Grundmuster" sensu Ax 1984) of the last common ancestor of all members of the *Ceratonotus*-group. It was small, constricted, and square in shape. The discovery of *D. wilhelminae* and *D. dinah* spp. nov. enables us to polarise the rostral evolution in the *Ceratonotus*-group. In our opinion the rostral evolution did not occur convergently several times inside that group. As its rather primitive representatives (cf. above) show a small, constricted, and square rostrum, we deduce that both its total loss, as well as its elongation evolved from the originally small rostrum. This seems to be supported by the fact, that all apparent differences may easily be based on that small type (e.g. increasing elongation always restricted to the proximal half; rostral tip blunt; increasing bifurcation of rostral tip). As a consequence, within the *Ceratonotus*-group two lineages arose:

- A) A *Ceratonotus/Dendropsyllus*-lineage, where the rostrum became reduced more and more until its virtual absence;
- B) An *Echinopsyllus/Pseudechinopsyllus*-lineage, where the small and constricted rostrum grew in length in its proximal half.

In our opinion, the rostral evolution did not occur convergently several times within Ancorabolinae. If this

is correct, then the apomorphic character 21 would become of strong weight and therefore support a close relation between the new species. Such relation may furthermore be supported by character 22; only *D. wilhelminae* and *D. dinah* spp. nov. bear a tubepore at the outer margin of P1 exp2, which according to the statement made for character 6 is considered as synapomorphic for both new species.

Conclusions

In contrast with the general presumption that the discovery of new species may lead to elucidation of formerly confusing phylogenetic relationships, the description of *D. wilhelminae* and *D. dinah* spp. nov. was not that helpful to clear up the phylogenetic status of the genus itself nor of phylogenetic relations inside *Dorsiceratus*. As already noted by George (2006a), the new species are remarkably similar to the known species in most morphological features. Character discussion reveals that *Dorsiceratus* species show quite conservative conditions in most characters, while some other, derived characters appear to be distributed quite heterogeneously in the species, inhibiting the recognition of clear-cut morphological patterns that would allow the assignment of individuals to distinct species. Differentiation between species may depend on very fine morphological differences. To recognize whether such fine differences are specific ones or simply reflecting intraspecific variability, as it has been found in recent studies of deep-sea Harpacticoida (e.g. George 2006a; Seifried & Martínez Arbizu 2008) much more material will have to be examined. Furthermore, to resolve the “*Dorsiceratus* case”, genetic analyses may be of considerable importance.

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