



Argestes angolaensis* sp. nov. (Copepoda: Harpacticoida: Argestidae) from the Angola Basin (Southeast Atlantic), and the phylogenetic characterization of the taxon *Argestes* Sars, including the redescription of *A. mollis* Sars, 1910, and *A. reductus* (Itô, 1983)

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Abstract

Argestes angolaensis sp. nov. (Copepoda, Argestidae) is described from the Angola Basin. Detailed comparison with the other *Argestes* species, *A. mollis* Sars, 1910 and *A. reductus* (Itô, 1983), which are redescribed in the present contribution, reveals autapomorphies for the genus, finally enabling the characterization of *Argestes* as a monophylum: 1) body densely covered with fine small cuticular spinules, 2) sensilla of cephalothorax and free thoracic somites arising from long tubercles, 3) antennula with very strong seta terminally on 6th segment in female (9th–10th in male). This investigation, concentrating on the systematic status of *Argestes* and first remarks on its relationships to *Parargestes* Lang, is the first in a series dedicated to the phylogeny of Argestidae Por, 1986.

Key words: Systematics, Deep Sea, DIVA 1

Introduction

The DIVA 1 expedition of RV METEOR in the Angola Basin off Namibia in July 2000 provided a large number of specimens of *Argestes angolaensis* sp. nov. (Copepoda, Harpacticoida, Argestidae). Argestidae are considered as a typical and primarily deepwater inhabiting taxon (cf. overview in George 2004), and because of their frequent and abundant occurrence in deep-sea samples they form a quite interesting and informative taxon for chorological, faunistic, and biogeographical research. Nevertheless, the systematic status of Argestidae remains virtually uncertain (George 2004). When Por (1986) established the family in the process of splitting Cletodidae, he provided several “typical” argestid features, whose phylogenetic value has, however, still to be cleared up. As a consequence, subsequent allocations of new species and the establishment of higher argestid taxa were often done based on “intuition” rather than on real phylogenetic argumentation (cf. Huys & Conroy-Dalton 1997; George 2004), resulting in a relatively high number of species (and even genera) *incertae*.

As quantitative sampling demonstrates, the deep sea contains huge numbers of metazoan species, so a complete inventory of all deep-sea organisms has to be admitted as almost impossible. Of more importance is to clear up systematic relations of those deep-sea organisms, which may play important ecological roles in deepwater environments and can therefore be considered as representatives for more general statements. For deep-sea Harpacticoida, the Argestidae may be such a representative. The present contribution is the first one focussing on the phylogeny of Argestidae Por 1986.

Material and methods

Sampling was done during research cruise M 48/1 of RV METEOR (DIVA 1) in the Angola Basin in July/August 2000 (Balzer et al. 2006). Two stations were sampled repeatedly with a multiple corer (MUC): #325 in the southern Angola Basin, and #346 about 600 nautical miles north of #325 (Fig. 1). At #325, 7 replicates were obtained (#325/2 to #325/8), and eight replicates at #346 (#346/1 to #346/8), each replicate consisting of up to 12 parallel samples (= 12 MUC cores). For faunistic research, five cores out of 10 were chosen randomly. Rose et al. (2005) describe the material treatment in detail. For illustrating, the specimens were cleared with glycerol. The type material of *Argestes angolaensis* sp. nov. consists of 98 specimens. All individuals were sampled at northern station #346 that is therefore declared as the locus typicus. The specimens apart from the female holotype comprise of over 72 females and 25 males. The material at the author's disposal included 1 additional copepodid, but as copepodids had been picked out during former sorting with the object of separating the juvenile harpacticoids from adult stages, the single copepodid of *A. angolaensis* sp. nov. in the examined material is considered as an overlooked one that by no means reflects the relationship between adult and juvenile stages.

Description of *Argestes mollis* Sars, 1910 (female) is based on material collected by G.O. Sars (1910) at Bukken, south-west coast of Norway, kindly made available to the author by L. Bachmann and Å. Wilhelmsen, Zoological Museum of Oslo (Norway). As the specimen described by Sars (1910) is lost, the female here described is declared the lectotype. The male was described based on Lang's (1948) material from Bohuslän, Gullmaren, Sweden, kindly provided by K. Sindemark-Kronstedt, Swedish Museum of Natural History, Stockholm (Sweden).

Description of *Argestes reductus* (Itô, 1983) is based on the type material collected by Itô (1983) and kindly provided by S. Yamato, Kyoto University, Shirahama (Japan).

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

Abbreviations. Used in the text: cphth: cephalothorax, A1—antennule, A2—antenna, aes—aesthetasc, Md—mandible, Mxl—maxillule, Mx—maxilla, Mxp—maxilliped, enp—endopod, exp—exopod, exp/enp1—first segment of exp/enp, GF—Genital Field, FR—Furcal Ramus/Rami, P1 – P6—swimming legs 1—6, benp—base of endopod.

Taxonomy

Argestidae Por, 1986

***Argestes* Sars, 1910**

Generic diagnosis. Body long, slightly depressed, covered with small cuticular spinules. Cephalothorax less broad than following thoracic somite. Cephalothoracic integument posteriorly accompanied with rudimentary pleurotergite of fused first thoracic somite. FR of variable length, covered with spinules. Female genital double somite with suture, indicating former division. Telson more or less square, reaching at least length of preceding 2 abdominal somites. Anal operculum dentate. Body somites dorsally and laterally with long sensilla, arising from tubercles. Female A1 7-segmented, male A1 10–11-segmented, haplocer or subchirocer, penultimate or antepenultimate segment terminally with 1 very strong seta. A2 with allobasis and 1-segmented exp, bearing 1 seta and several long spinules. Gnathobase of md broad, with several teeth. Mandibular palp biramous. Syncoxa of mxp with 2 setae, enp produced into slender seta or claw, additionally with 1 long seta. All natatory legs with 3-segmented rami, covered with spinules. P5 benps fused, endopodal lobe completely reduced, being represented by 1–2 small setae. Exp distinct, elongate.

Type species. *A. mollis* Sars, 1910. Additional species: *A. reductus* (Itô, 1983), *Argestes angolaensis* sp. nov.

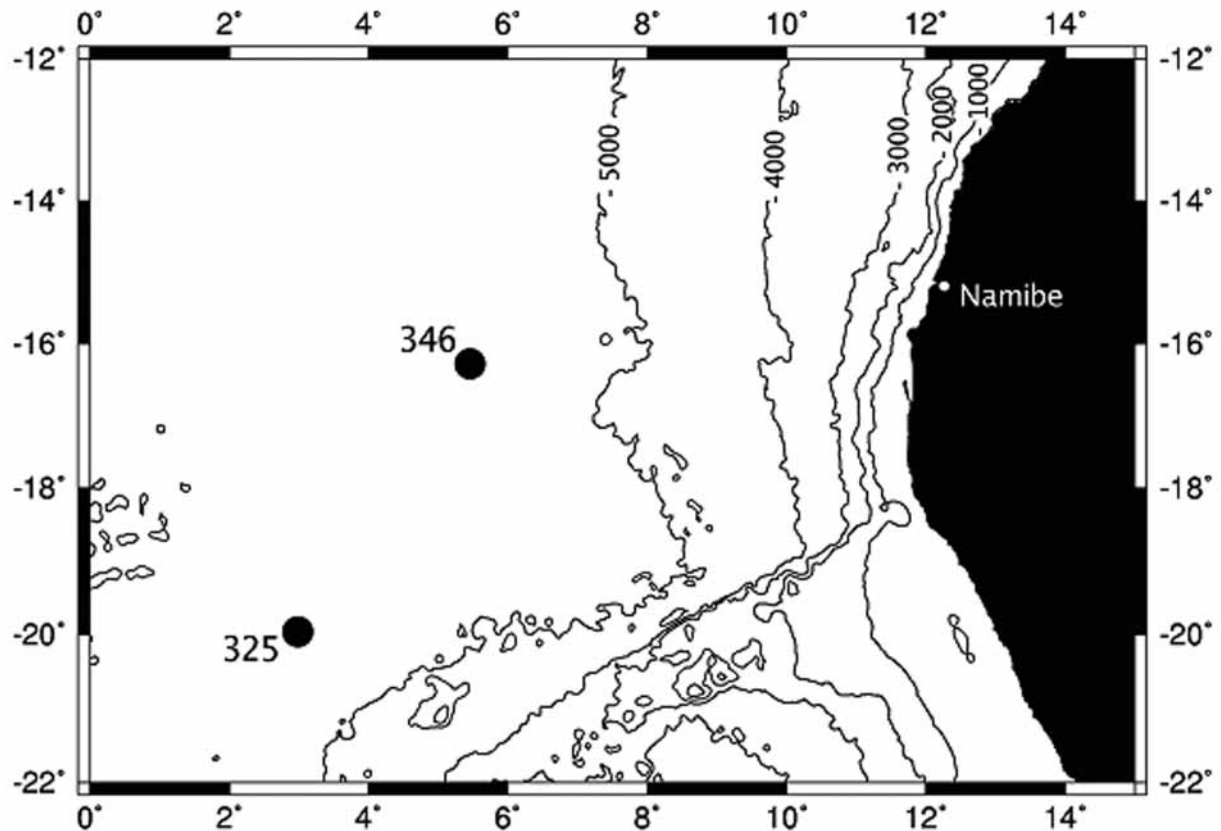


FIGURE 1: Map of the south-eastern Atlantic, indicating the geographical position of stations #325 and #346, sampled quantitatively with the Multicorer (from Rose et al., 2005)

***Argestes angolaensis* sp. nov.**

Figures 2–14

Locus typicus. Northern Angola Basin, #346 (16°17.0'S, 05°27.0'E, depth: 5389m). Holotype (#346/5-12) (i.e. station 346, replicate no. 5, MUC core no. 12): female, placed on 11 slides, coll. nos. SMF 32027/1-11. Seven paratypes (PT) were put on slides and used for species description: PT1 (#346/8-1): female, coll. no. SMF 32028, PT2 (#346/8-2): female, coll. no. SMF 32029, PT3 (#346/8-7): female, fixed on 10 slides, coll. nos. SMF 32030/1-10, PT 4 (#346/8-5): female, put on 10 slides, coll. nos. SMF 32031/1-10, PT5 (#346/8-1): female, coll. no. SMF 32032, PT6 (#346/6-1): male, placed on 3 slides, coll. nos. SMF 32033/1-3, PT7 (#346/7-10): male, fixed on 8 slides, coll. no. SMF 32034/1-8. The remaining 90 specimens are preserved in alcohol and distributed in eight vials with respect to the corresponding MUC cores, coll. nos. SMF 32035–SMF 32042.

Female.

Habitus (Fig. 2A, B) slender, body length including FR of approximately 545µm. Cphth less than 1/3 of total body length. Whole body densely covered with small spinules, except the P5-bearing thoracic somite, the second and the third abdominal somite, and the telson, which show fewer but bigger spinules. Body with several remarkably long sensilla arising from tubercles. In particular, the sensilla of the P5-bearing thoracic somite and abdominal somites are very long.

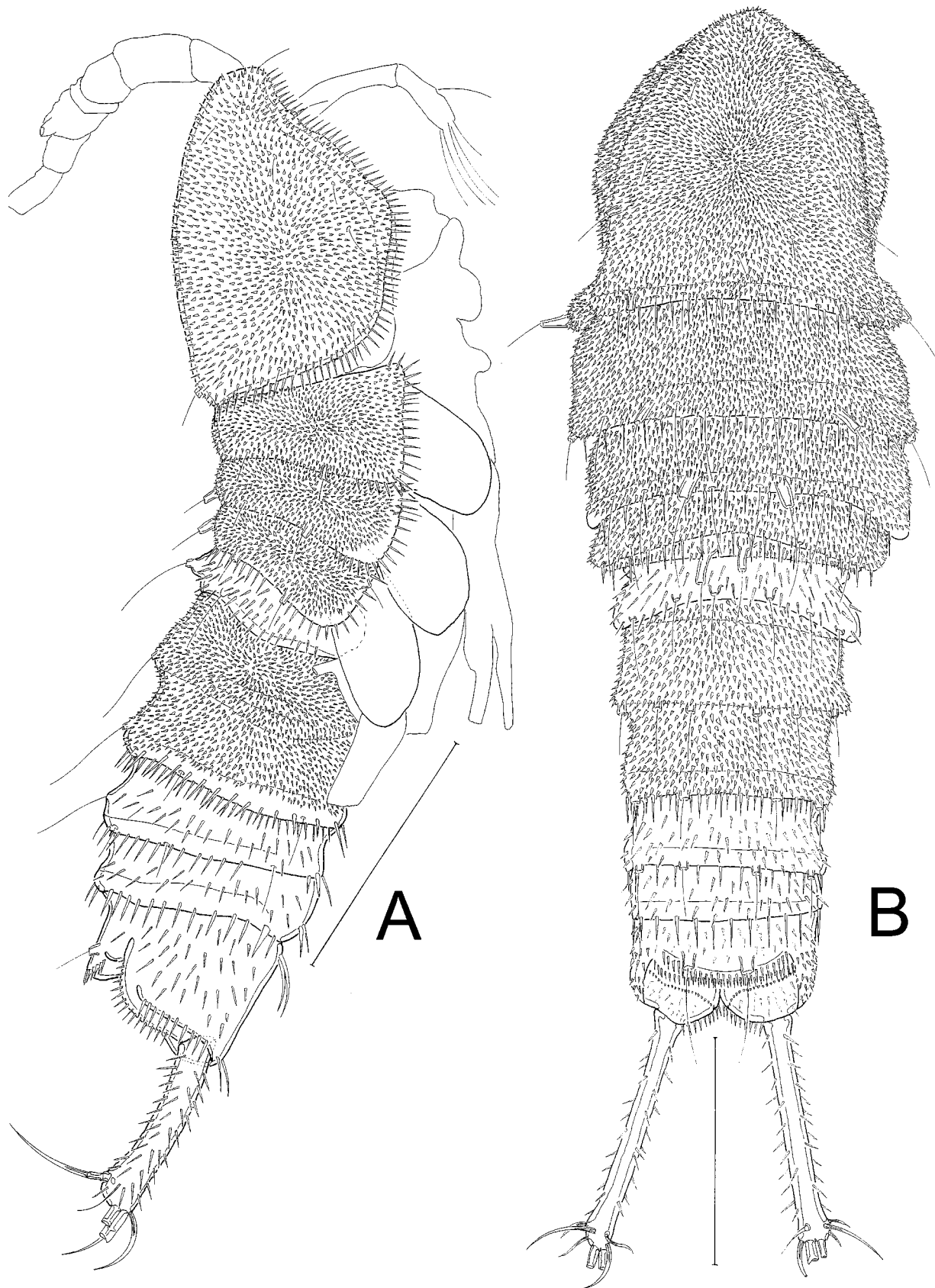


FIGURE 2: *Argestes angolaensis* sp. nov., female. A. Habitus, lateral view, B. Habitus, dorsal view. Scales: 100 μ m.

Telson (Fig. 3) as large as 2 preceding abdominal somites together, almost square from lateral view, but tapering slightly from dorsal/ventral view. Ventrally with a pair of small tube pores at inner margin close to

FR, and with some strong spinules near the proximal margin. Anal operculum small, with row of spinules at its distal margin and accompanied by 2 sensillate tubercles.

FR (Fig. 3) long and slender, varying remarkably in length (cf. Figs 2B, 3), and covered with many spinules of different sizes. All 7 setae concentrated at terminal part: I and II subterminally on outer margin, I smaller than II. III ventrally at terminal margin. IV and V largest setae, inserting terminally. VI as long as III, arising at the inner terminal margin. VII dorsally, arising from knob-like projection. Setae I–III and VI in many specimens of “rat-tail” appearance.



FIGURE 3: *Argestes angolaensis* sp. nov., female. Telson and FR, ventral view. Scale: 50µm.

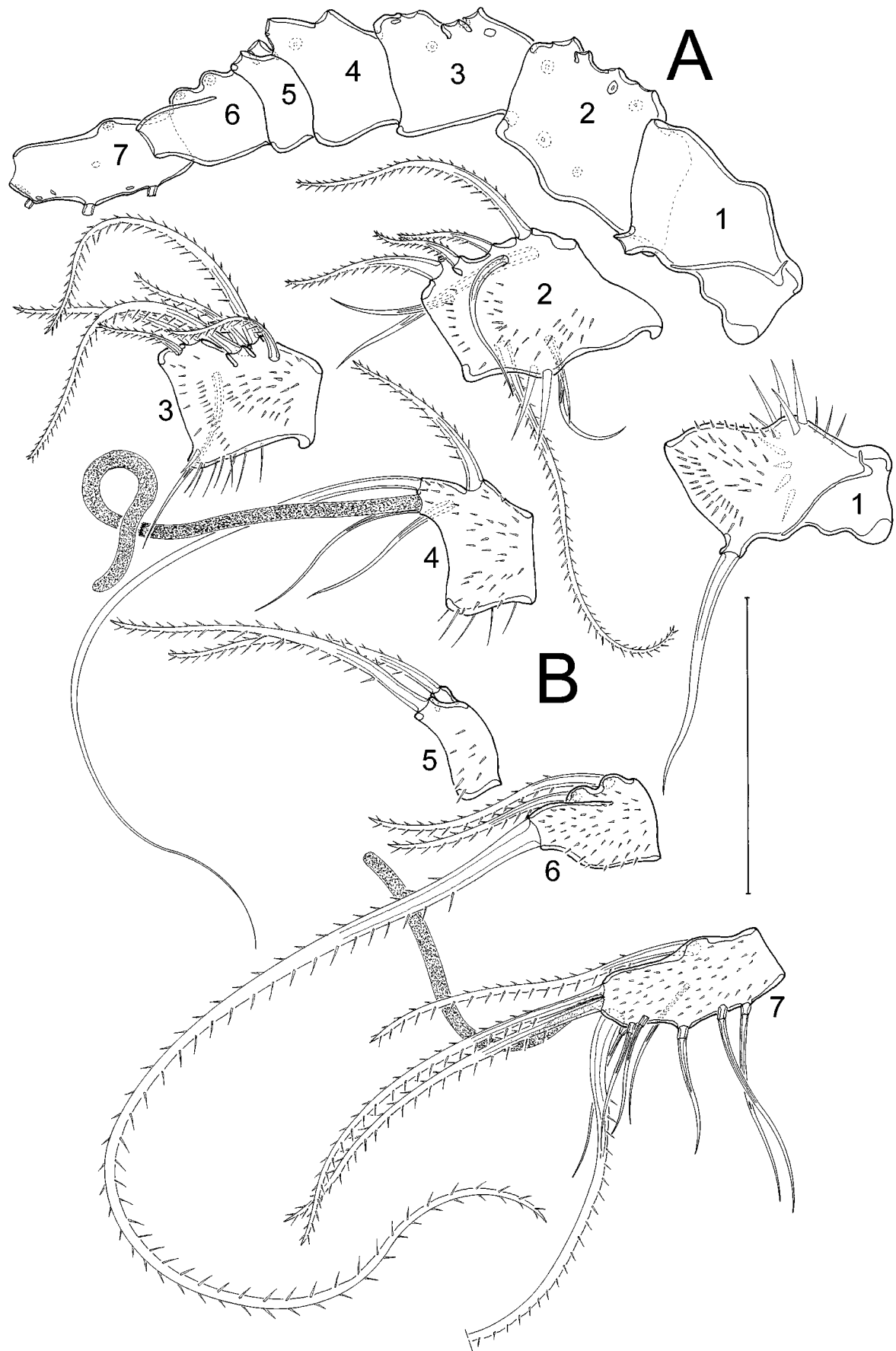


FIGURE 4: *Argestes angolaensis* sp. nov., female. A. A1, general shape, B. A1, setation of single segments. Scale: 50µm.

A1 (Fig. 4) 7-segmented, fifth segment smallest, all segments with several bare and bipinnate setae. Second segment at its posterior margin with few long spinules. Aes on fourth segment, arising together with 2 setae from protrusion. Sixth segment terminally with 1 very long bipinnate seta. Seventh segment terminally with small aes, and at posterior terminal margin with remarkable long seta. All segments covered with small spinules.

Setal formula: 1/1; 2/9; 3/7; 4/4 + aes; 5/2; 6/3; 7/11 + aes.

A2 (Figs 5A, A') with allobasis and 1-segmented exp bearing 1 bare seta and 3 long spinules. Enp and allobasis covered with small spinules. Enp laterally with 2 bipinnate setae, the second subterminal with tube pore. Terminally, enp carries 5 geniculate setae and 1 unipinnate seta. Subterminally with long tube pore, fused with longest seta.

Md (Fig. 6) with gnathobase (Fig. 6A, A') formed by several tooth-like projections. Subterminal seta not discernible. Md palp (Fig. 6B) strong, covered with spinules, basis with 2 bipinnate setae. Enp 1-segmented, with 1 outer bipinnate seta, additionally with 3 subterminal and 2 terminal bipinnate setae. Exp smaller than enp, with 1 outer and 2 terminal bipinnate setae.

Mxl (Fig. 5B, B') with distinct exp. Precoxal arthrite terminally with 6 spines, subterminally with another spine. At its proximal margin with 1 unipinnate seta, and on its surface with 2 bare setae. Coxa terminally with 3 setae. Basis terminally with 2 setae. Enp represented by 1 bare seta. Exp long and spinulose, terminally with 2 multipinnate setae.

Mx (Fig. 5C) unfortunately broken at its distal part that is therefore not described. Syncoxa with 2 endites, the proximal one bearing 1 bare seta. Distal endite with 3 setae, the biggest one fused to segment, bipinnate. Basis fused to syncoxa, with 3 setae. Enp distinct, with 2 bare setae.

Mxp (Fig. 5D) prehensile, syncoxa slightly shorter than basis, with many spinules of different sizes, distally with 2 long multipinnate setae. Basis covered with small spinules, additionally with 2 rows of long spinules. Enp produced into long unipinnate claw, with 1 bare seta at its base.

P1 (Fig. 7) with 3-segmented exp and enp. Coxa considerably bigger than basis, with several spinules and 1 row of setules at its outer margin. Intercoxal sclerite transversely long and bow-like. Basis with inner and outer spine, covered with small spinules and long setules at its inner margin. Both exp and enp covered with small spinules on anterior side. Exp1 without, exp2 with inner seta. Exp3 with 5 setae/spines, three of which are subterminal with tube pores. Enp1 and 2 with 1 inner seta each, enp3 with 2 terminal setae, the longer one subterminally with tube pore, and 1 outer spine. For setal formula see table 1.

P2–P4 (Figs. 8–10) with 3-segmented exps and enps. Coxae approximately 2.5 times bigger than bases, showing decreasing covering with small spinules from P2 to P4. Each coxa on outer side with 3 strong spinules. Bases much broader than long, exps and enps turned outwardly. Bases with outer spines, at inner margin with long setules, covered with small spinules as in coxae. Appendages covered with small spinules, in most specimens showing a decrease from P2 to P4 (but cf. Fig. 10B: female P4!). Setation of exp and enp as in table 1. Exp3 as long as exp1 and exp2 together. Enps showing increasing length of segments, enp1 being the shortest, and enp3 the longest segment. As shown in Fig. 10B, few females show a variability in the setation of P4 exp3 (as also in the covering with spinules). Instead of only 1, it bears 2 inner setae, the first being considerably smaller than the second.

TABLE 1: *Argestes angolaensis* sp. nov., female, setation of P1–P4 (no. outer spines in roman numbers).

Natatory leg	Exp1	Exp2	Exp3	Enp1	Enp2	Enp3
P1	I-0	I-1	III-2-0	0-1	0-1	I-2-0
P2	I-1	I-1	III-2-2	0-1	0-1	I-2-2
P3	I-1	I-1	III-2-3	0-1	0-1	I-2-2
P4	I-1	I-1	III-2-1(2)	0-1	0-1	I-2-2

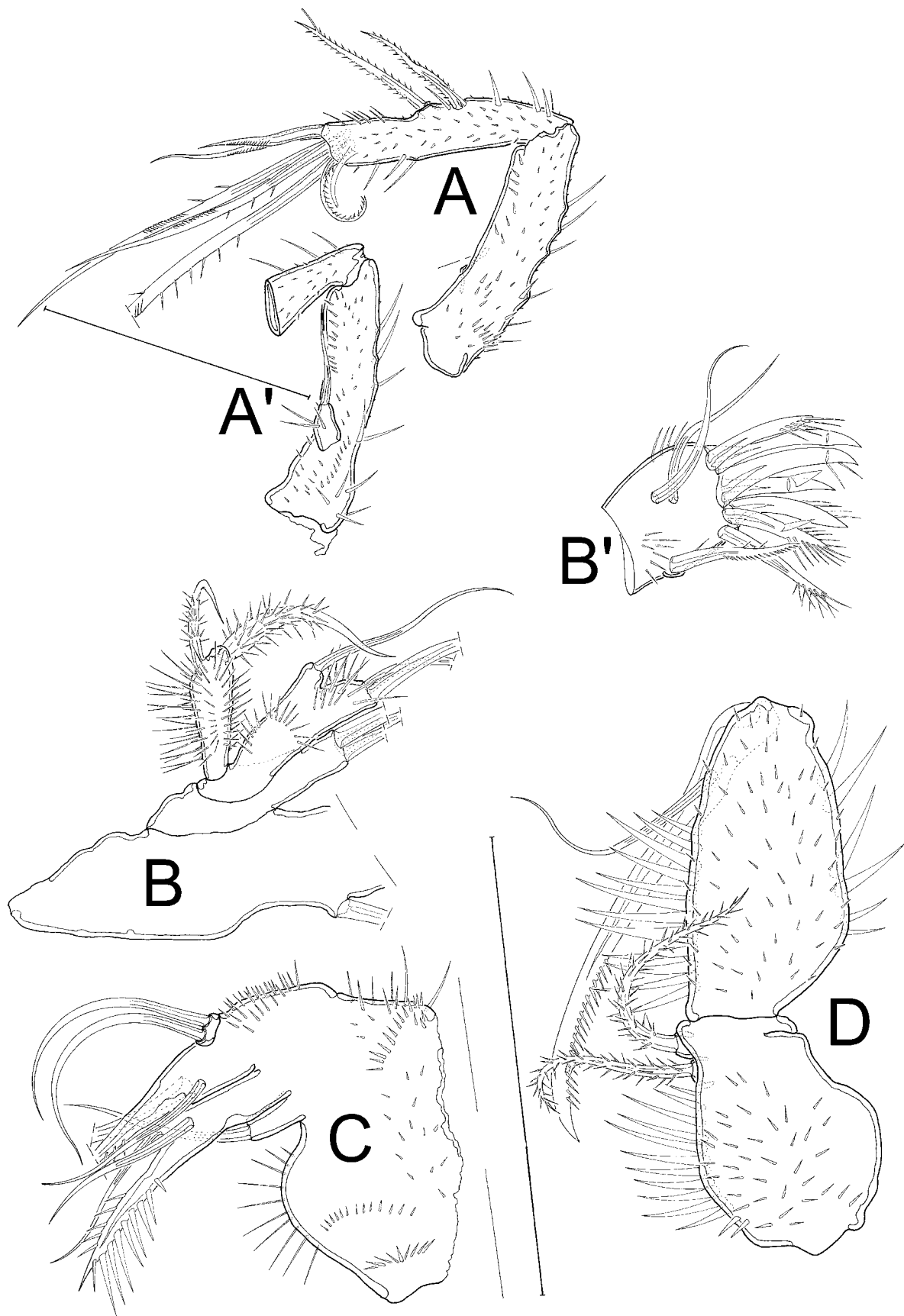


FIGURE 5: *Argestes angolaensis* sp. nov., female. A. A2, A'. A2 of counterpart, showing exp, B. MxI without praecoxal arthrite, B'. praecoxal arthrite, C. Mx, D. Mxp. Scales: 50µm.

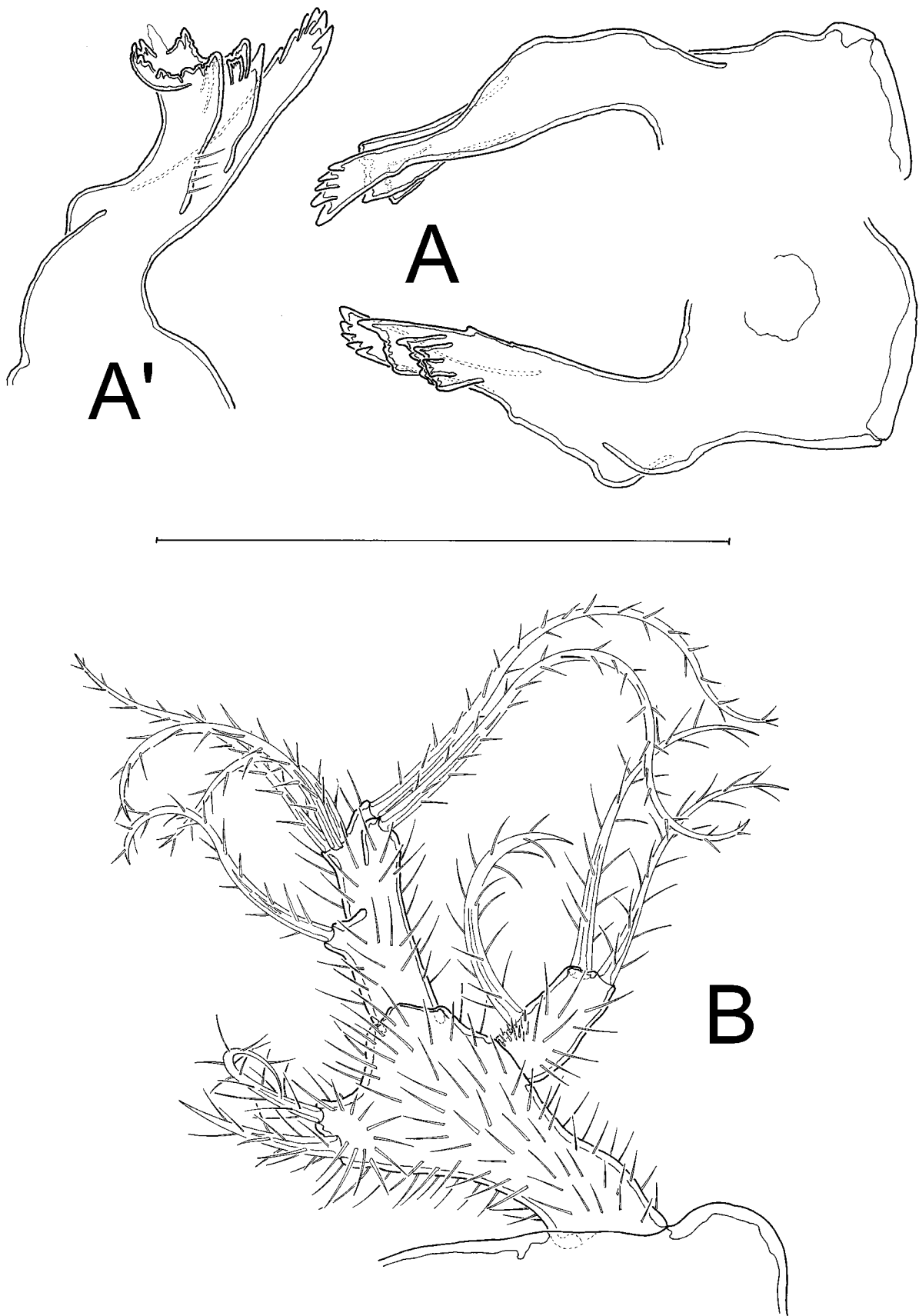


FIGURE 6: *Argestes angolaensis* sp. nov., female. A. Md gnathobase, shown from different positions, B. Md palpus. Scale: 50µm.

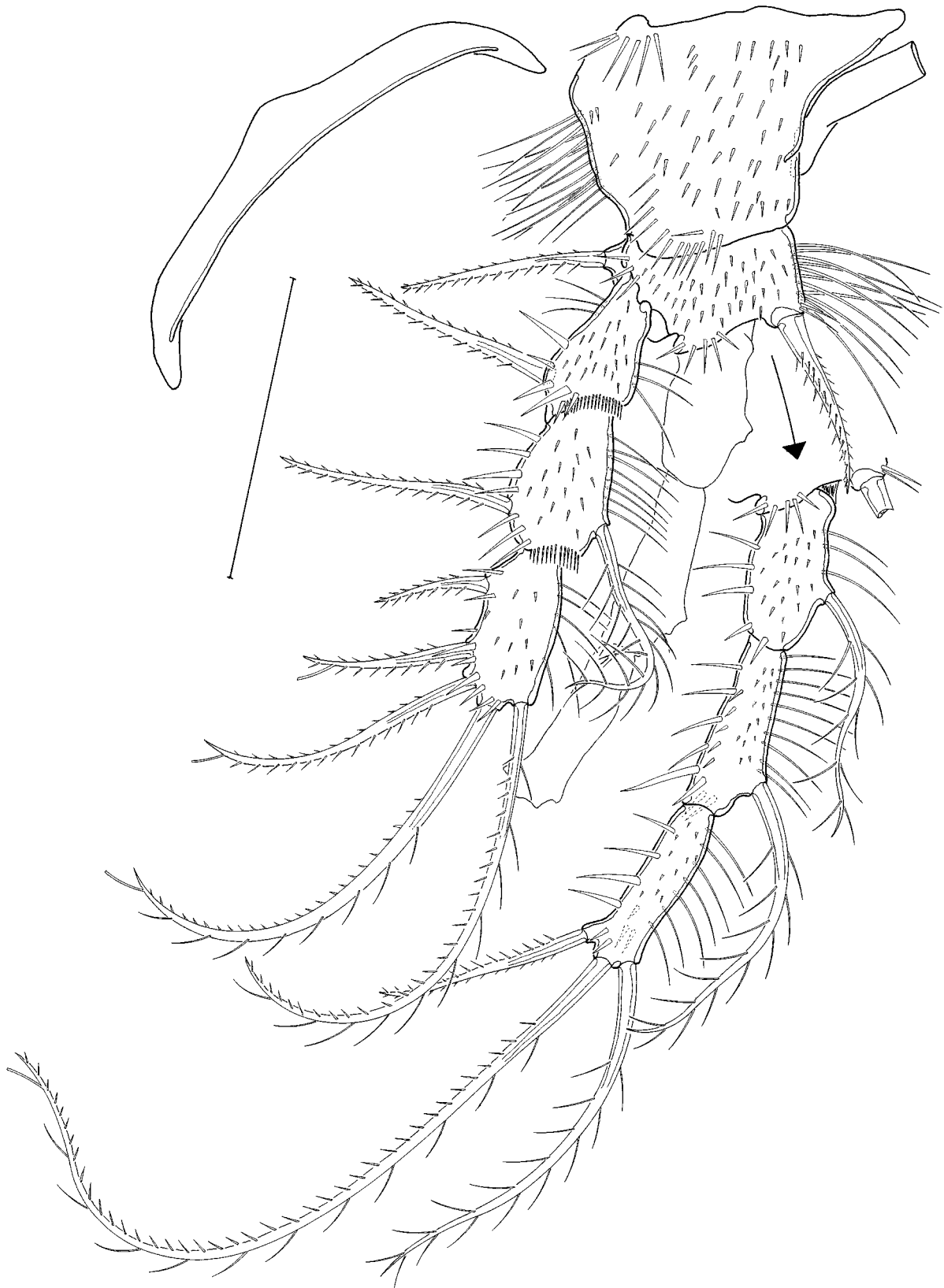


FIGURE 7: *Argestes angolaensis* sp. nov., female P1 with corresponding intercoxal sclerite. Scale: 50 μ m.

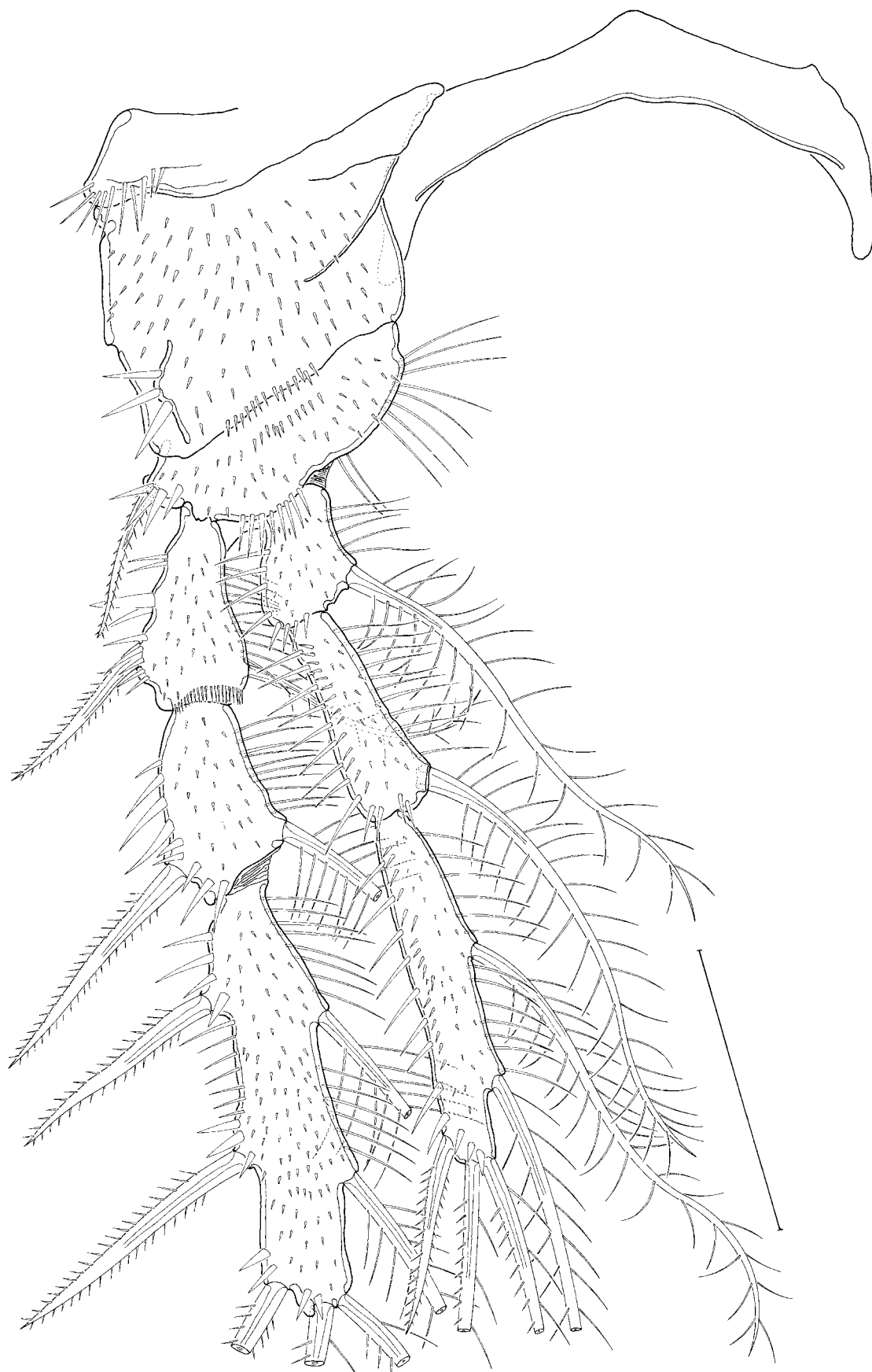


FIGURE 8: *Argestes angolaensis* sp. nov., female P2 with intercoxal sclerite. Scale: 50µm.

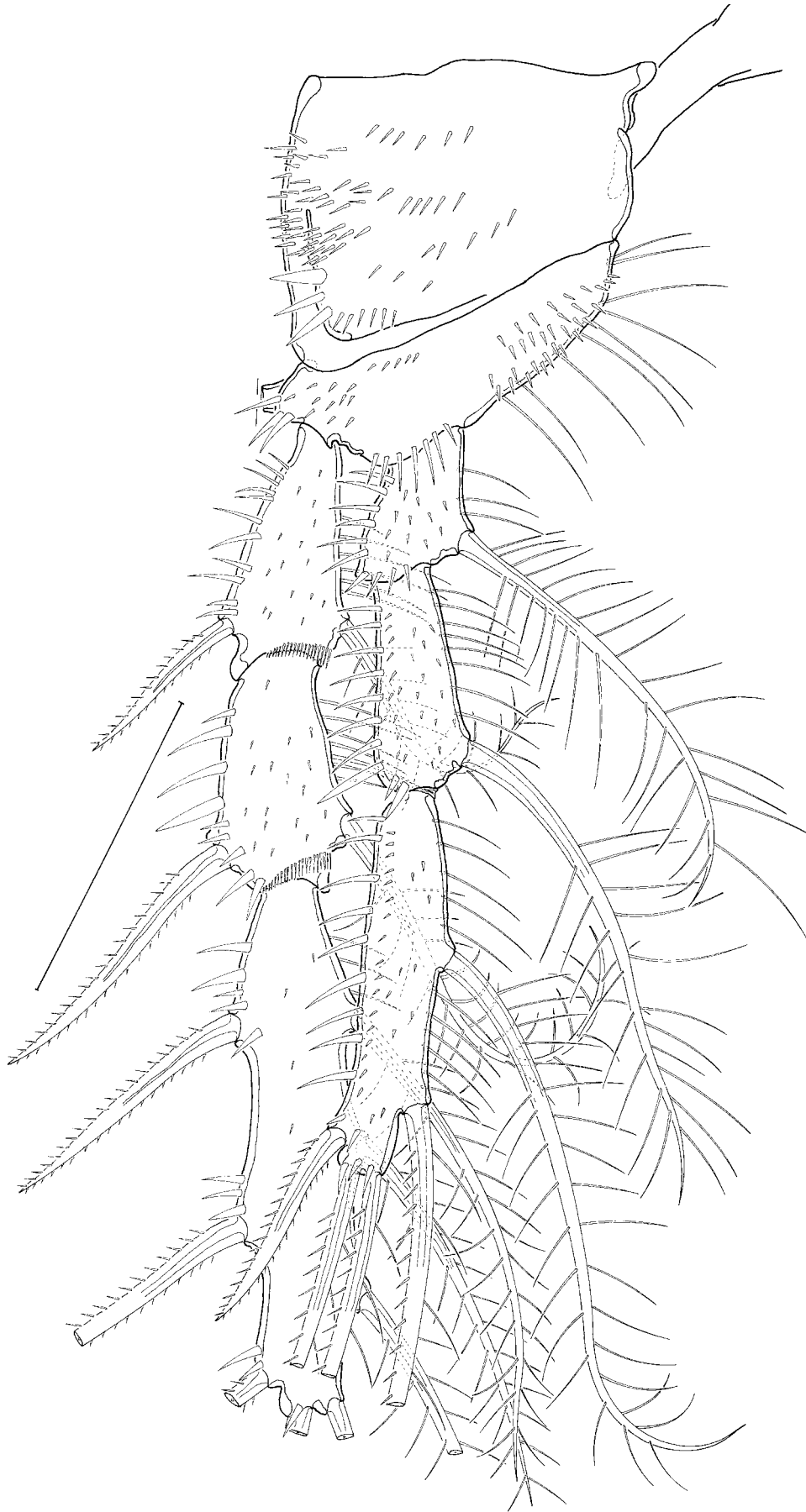


FIGURE 9: *Argestes angolaensis* sp. nov., female P3. Scale: 50 μ m.

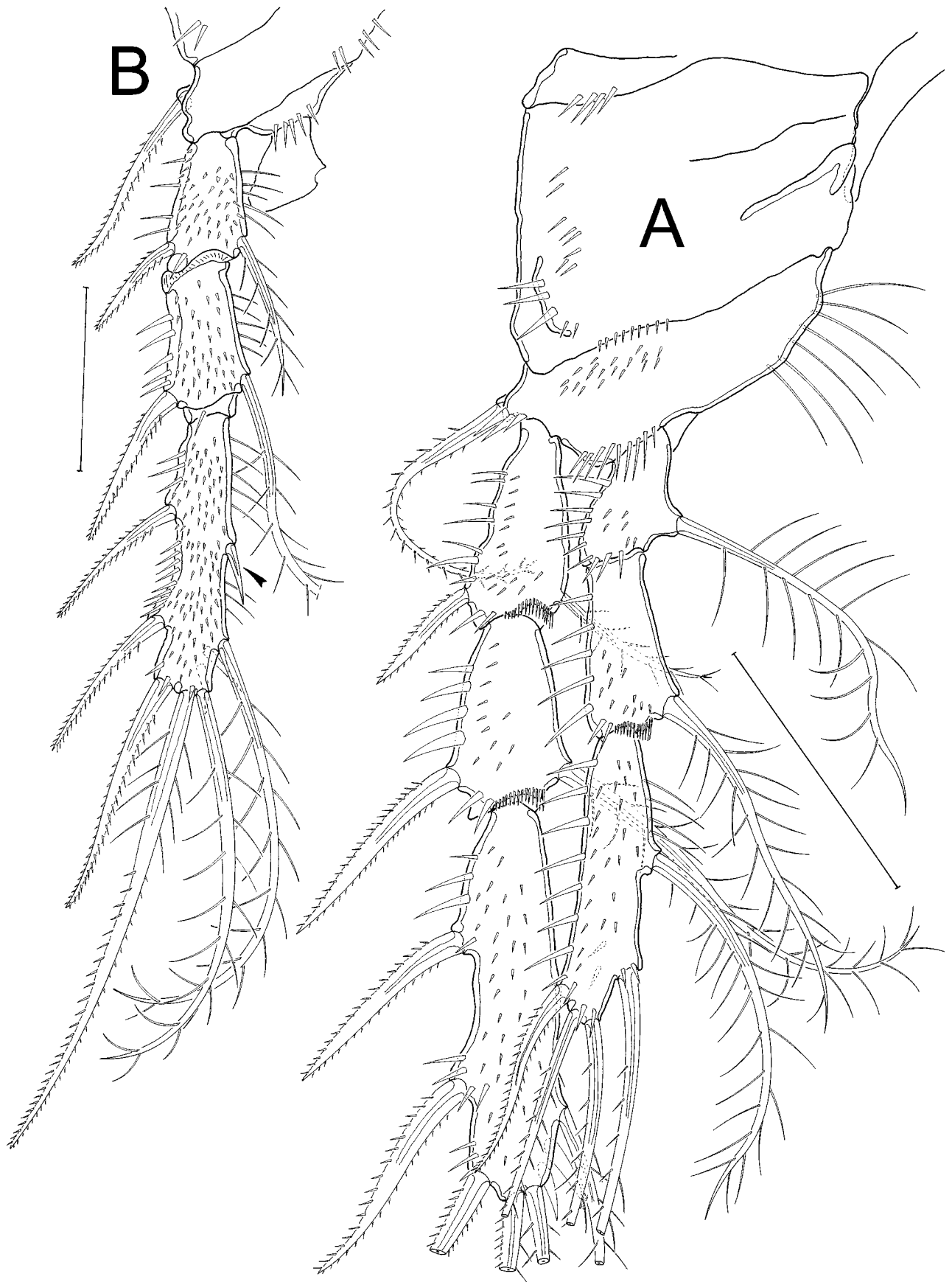


FIGURE 10: *Argestes angolaensis* sp. nov., A. female P4, note exp3 with only 1 inner seta, B. P4 exp of another female, showing small first inner seta (triangular arrow). Scales: 50 μ m.

P5 (Fig. 11A) benps fused together, forming a single plate. Outer basal seta arising from moderately produced setophore. Endopodal lobe strongly reduced, represented by 1 longer biplumose and 1 shorter bare seta. Exp distinct, long and slender, with 2 outer, 2 terminal, and 1 inner seta. Additionally, outer distal margin with extremely long tube pore.

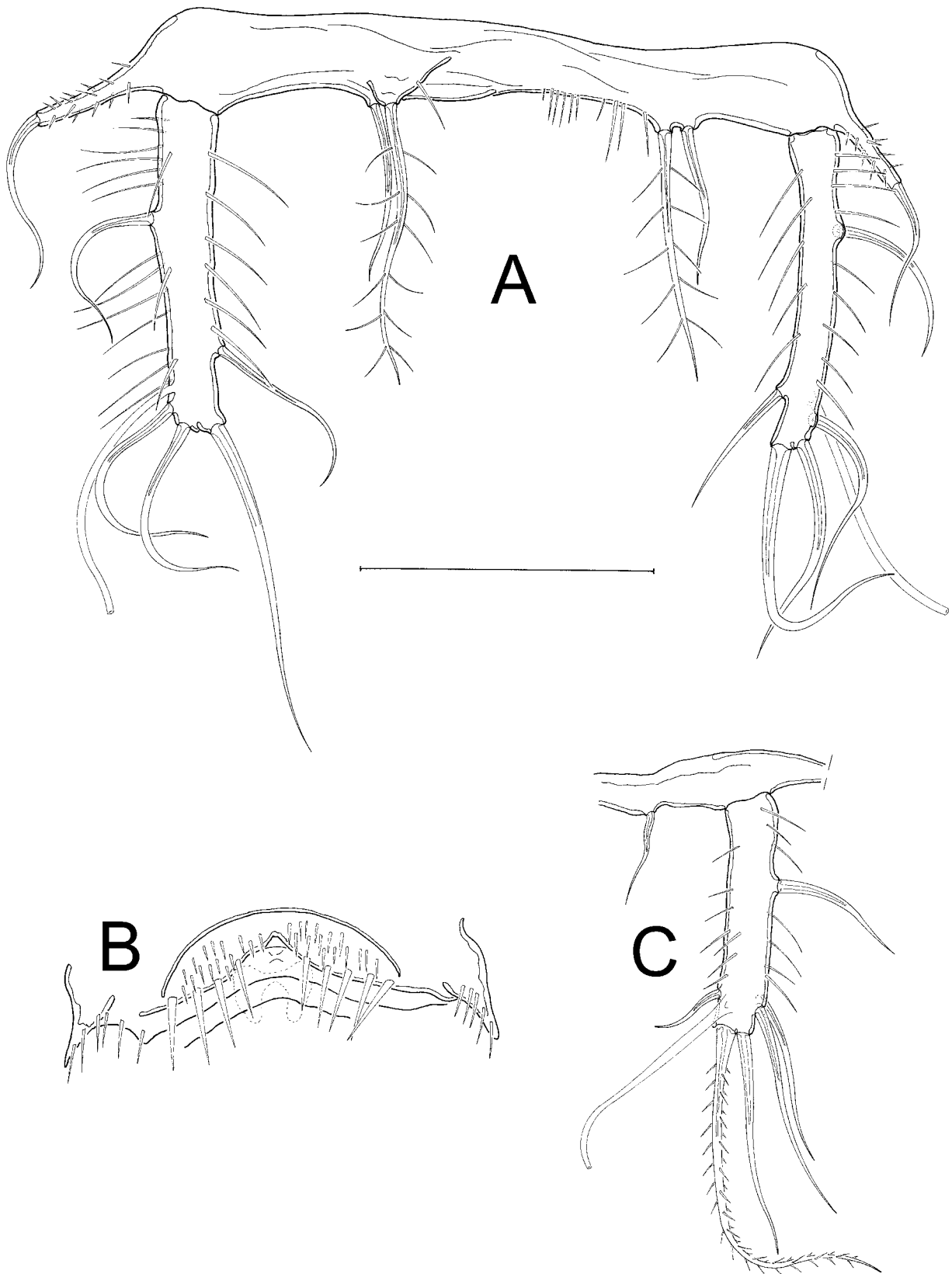


FIGURE 11: *Argestes angolaensis* sp. nov., A. female P5, B. female genital field, C. male P5. Scale: 50 μ m.

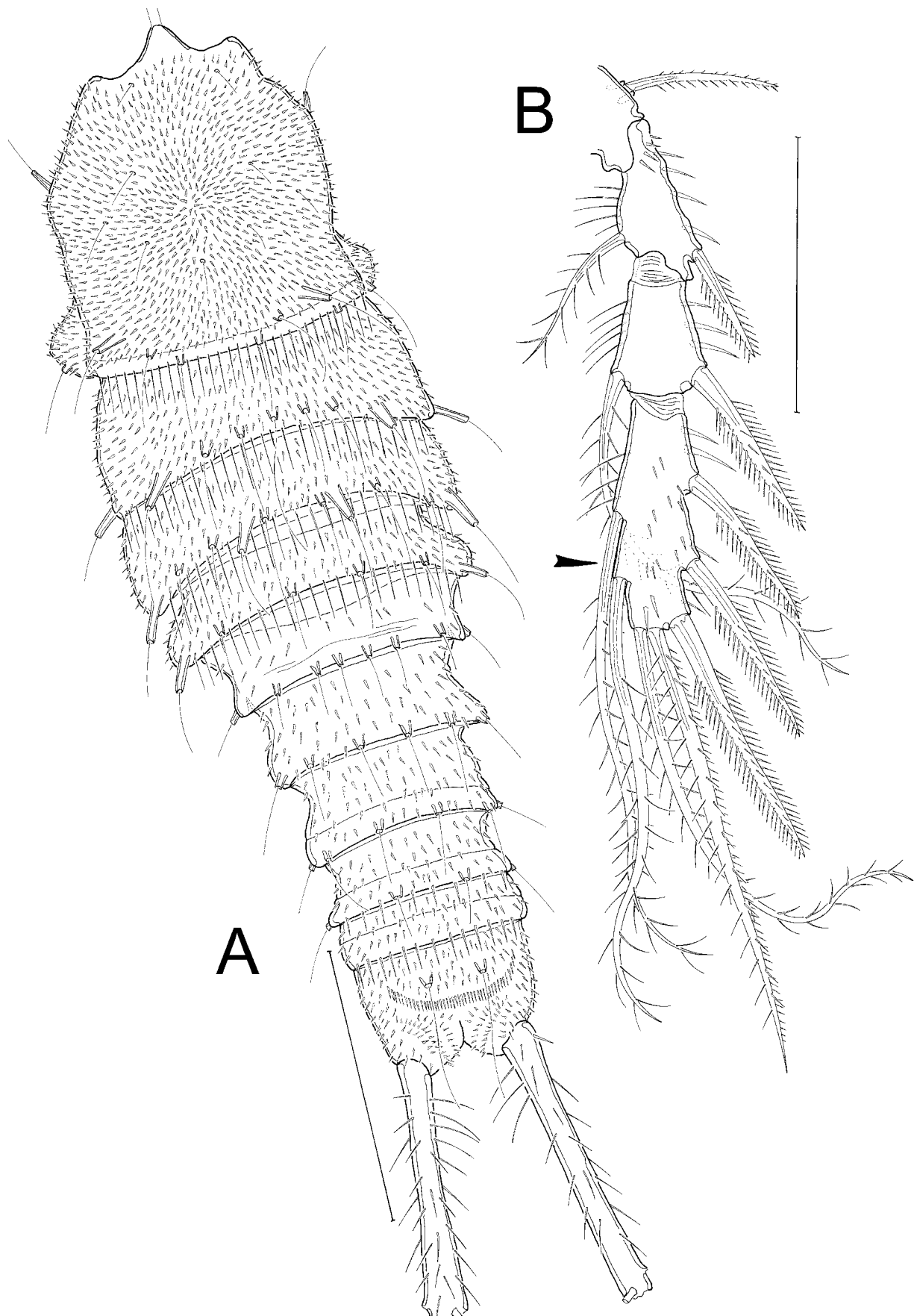


FIGURE 12: *Argestes angolaensis* sp. nov., male. A. Habitus, dorsal view, B. P4 exp, triangular arrow pointing to normally developed first inner seta. Scales: A. 100 μ m, B. 50 μ m.

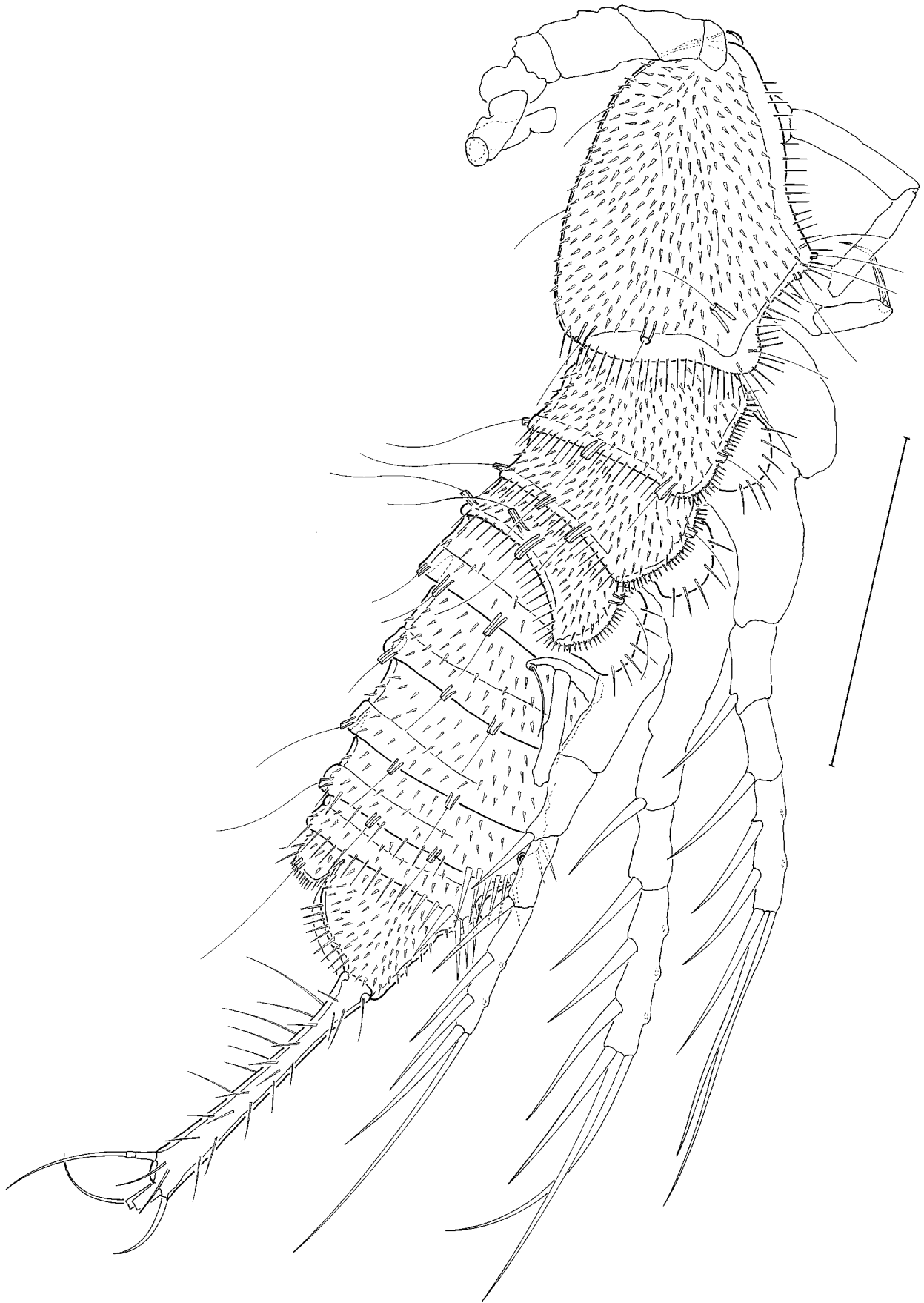


FIGURE 13: *Argestes angolaensis* sp. nov., male. Habitus, lateral view. Scale: 100 μ m.

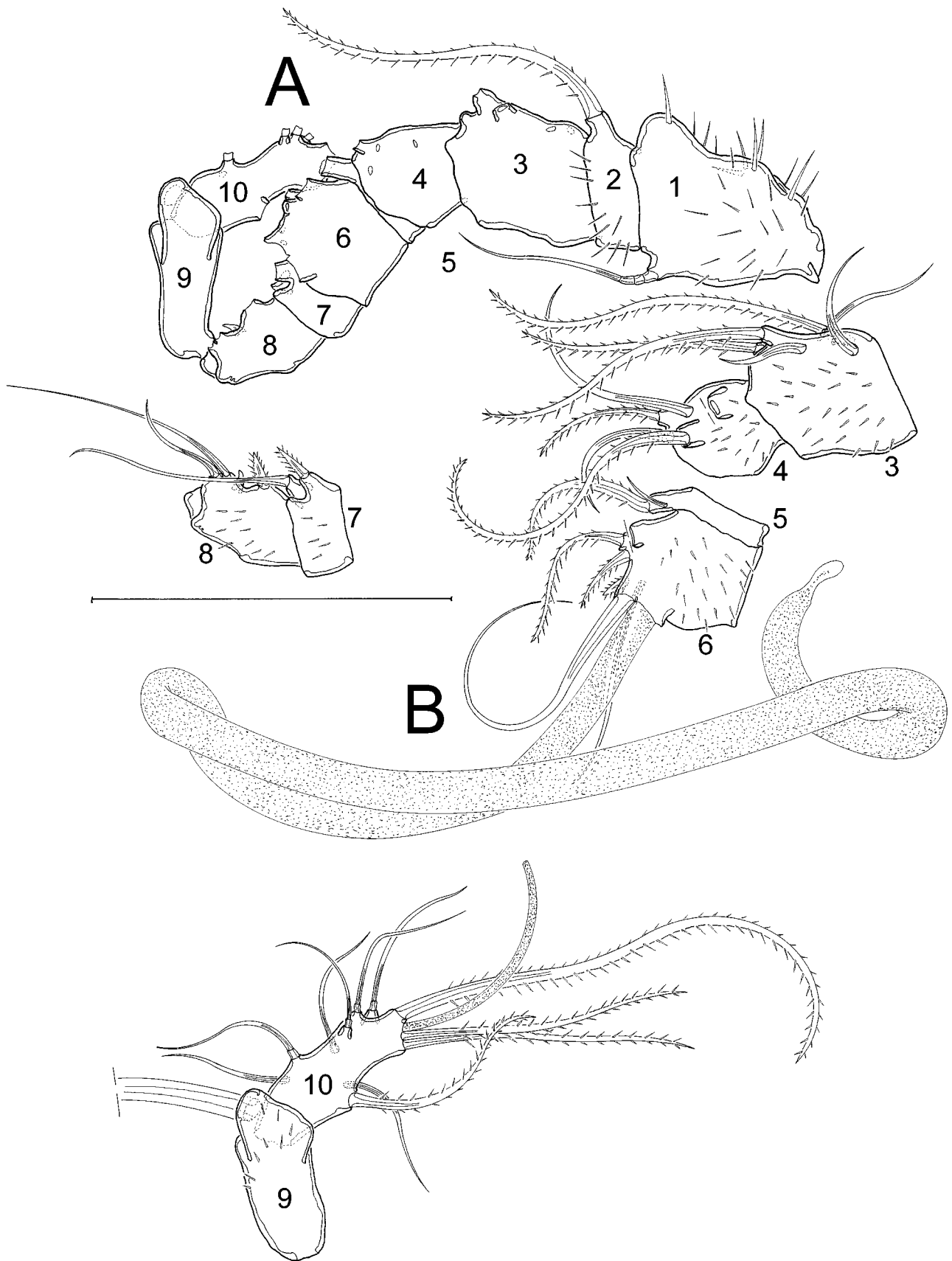


FIGURE 14: *Argestes angolaensis* sp. nov., male A1. A. general shape, B. Setation of single segments. One seta broken at both segments 4 and 6. Scale: 50 μ m.

GF (Fig. 11B) strongly cuticularized, with several small and long spinules surrounding the gonoporus. P6 reduced, detectable as paired small processes without setae, flanking the GF.

Male.

Habitus (Fig. 12A, 13) smaller than female, body length including FR approximately 480µm. Coverage of body with small cuticular spinules not reaching density as in female. Tubercles bearing sensilla longer than in female.

A1 (Fig. 14A, B) haplocer, 10-segmented. All segments except fifth and tenth with small spinules. Sixth segment with strong aes. Eighth segment additionally with tooth-like spinule. Ninth segment terminally with strong seta (broken in Fig. 14B).

Setal formula: 1/1; 2/1; 3/6; 4/5; 5/2; 6/6+aes; 7/2; 8/3; 9/1; 10/11+aes.

P4 (Fig. 12B) sexually dimorphic. General shape as in female, but exp3 always bears 2 well-developed inner setae.

P5 (Fig. 11C) exp distinct, shorter than in female, with 6 setae and 1 long tube pore. Benps fused, with 1 small seta.

Remarks. With 98 adult individuals, *Argestes angolaensis* sp. nov. was by far the most abundant argestid taxon collected in the Angola Basin during DIVA 1 expedition in 2000. The high number of collected specimens, usually a highly uncommon occurrence for deep-sea sampling, provides a good insight into the intraspecific morphological variability, which certainly exists, but whose study is not the object of the present contribution. However, comparison of the specimens revealed remarkable variability in body and furcal length (male bodies varying between 380 and 480µm length), in body ornamentation (density and size of spinules covering body and appendages), and even in setation (cf. P4 exp, Fig. 10B). Nevertheless, an assignment of the corresponding specimens to different new species seems rather implausible, because the mentioned variability shows a quite heterogeneous distribution over the individuals, preventing the recognition of any morphological pattern. Moreover, all specimens share a series of apomorphic characteristics (cf. discussion), justifying their allocation into one single species. Taking into account similar conditions in other taxa e.g. Ancorabolidae (George 2006; George, personal observation), it has to be stated, that intraspecific variability in deep-sea Harpacticoida is greatly underestimated.

Redescription of *Argestes mollis* Sars, 1910

Figs. 15–20

Material. Collected by G.O. Sars (1910) at Bukken, eastern Norway. The material comprises of 10 individuals, 9 of which resulting as *A. mollis* females, the 10th corresponds to another harpacticoid family. One female was dissected and placed on 13 slides, labelled as “Zool. Mus. Oslo, F. 20352 b-n, Mp. 435g”. It is designated as lectotype, as no holotype exists. During dissection it was noted that the specimen showed minor damage, i.e. to the mouthparts and P5. A second female was selected for completion of illustrations (lateral habitus, telson/FR) without dissection, and returned into alcohol.

The male was described based on material from the Langian Collection of the Swedish Museum of Natural History, Department of Invertebrate Zoology, coll. no. SMNH – 54818. K. Lang collected the material on July 21st, 1937 in Bohuslän, Gullmaren, Sweden, at 80m depth. It includes 28 representatives of *A. mollis* (and additionally 5 specimens of other harpacticoid species) One male and one (badly damaged) female were dissected and placed on 7 and 5 slides, respectively.

Female.

Habitus (Figs. 15A, B) dorsolaterally slightly depressed. Total body length including FR approximately 980µm. Similar to *A. angolaensis* sp. nov., cphth reaches approximately 1/3 of whole body length. Urosoma smaller than prosoma, markings varied within the examined specimens. All body somites including telson covered with small spinules, which decrease in density in the genital double somite, the dorsal parts of cphth

and second and third thoracic somite. Cphth dorsally with tube pores, and at its posterior margin with a row of larger spinules. Whole body with sensilla, mainly at the posterior margin of the somites, with several arising from tubercles.

Telson (Figs. 15A, B, 17A) almost square in shape, reaching length of preceding 2 abdominal somites together, dorsally with small anal operculum bearing a row of spinules at distal margin, ventrally with proximal row of larger spinules.

FR (Fig. 17A) small, square, and covered with small spinules. 7 setae: I, II, and III of almost same length, all inserting in distal half of FR. IV and V longest setae, inserting terminally. VI longer than I–III, inserting terminally on inner margin. VII arising from small knob-like projection on dorsal side, subterminal. Setae I–III, and VI of rat-tail shape.

A1 (Figs. 16A, A') 7-segmented, first and second segment covered with small spinules, forming rows in second segment. Second segment at its outer margin with few long spinules. All segments with bipinnate setae, seventh segment additionally with bare setae. Fourth segment with aes, sixth segment terminally with 1 very long and tripinnate seta. Seventh segment terminally with small aes and 1 strong but short seta.

Setal formula: 1/1; 2/8; 3/5; 4/3 + aes; 5/2; 6/3; 7/11 + aes.

A2 (Fig. 15C) with allobasis and 1-segmented exp bearing 1 bare seta, accompanied by 4 spinules. Allobasis covered with small spinules, anterior margin with some longer spinules. Enp as long as basis, bearing several spinules and anteriorly 2 bipinnate setae. Terminally with 6 setae, 1 of which is fused with tube pore at its base.

Md (Fig. 16B, B') palpus missing, not drawn. Gnathobase massive and broad, with several strongly cuticularized teeth. In male, 1 small subterminal seta discernable (triangular arrow in Fig. 16B'), but not in female (Fig. 16B).

Mxl (Fig. 17B) with several spinulose fields and massive precoxal arthrite, showing terminally 6 big spines, subterminally 1 bipinnate seta, and on its surface 2 long and slender bare setae. Coxa terminally with 2 bare and 1 bipinnate seta. Basis distinct, incorporating enp and exp, and bearing in total 5 setae, one of which is unipinnate.

Mx (Fig. 17C, C') syncoxa with 2 endites (Fig. C), the proximal one with 1 bipinnate seta (Fig. 17C'), the distal one with 3 setae. Basis distinct, fused with 1 terminal seta, additionally with 3 setae. Enp distinct, with 2 bare and 1 bipinnate setae.

Mxp (Fig. 15D) syncoxa small, terminally with 2 bipinnate setae. Basis approximately 3 times longer than syncoxa, with several small spinules. Enp produced into long and slender claw accompanied by 1 bare seta.

P1 (Fig. 18A) with 3-segmented exp and enp. Coxa and basis of almost same size, coxa with some long spinules at outer margin. Intercoxal sclerite (Fig. 18A') elongate. All exopodal segments of same size, exp2 with inner seta, exp3 with 5 setae/spines. Endopodal segments also of nearly same size, enp3 with 1 outer spine and 2 terminal setae. For setal formula see table 2.

P2–P4 (Figs. 18B, 19A, B) with 3-segmented exps and enps. Intercoxal sclerites (Figs. 18B', 19B) bow-like. Coxae about 2 times bigger than bases, with few spinules. Bases broader than long, appendages turned outward. At inner margin, bases with a few long setules. Exps bigger and longer than enps, setation as shown in table 2. P3 exp and enp as well as P4 exp2 covered with small spinules.

TABLE 2: *Argestes mollis* Sars, 1910, female, setation of P1–P4 (no. outer spines in roman numbers).

Natatory leg	Exp1	Exp2	Exp3	Enp1	Enp2	Enp3
P1	I-0	I-1	III-2-0	0-1	0-1	I-2-0
P2	I-1	I-1	III-2-2	0-1	0-1	I-2-2
P3	I-1	I-1	III-2-3	0-1	0-1	I-2-2
P4	I-1	I-1	III-2-2	0-1	0-1	I-2-2

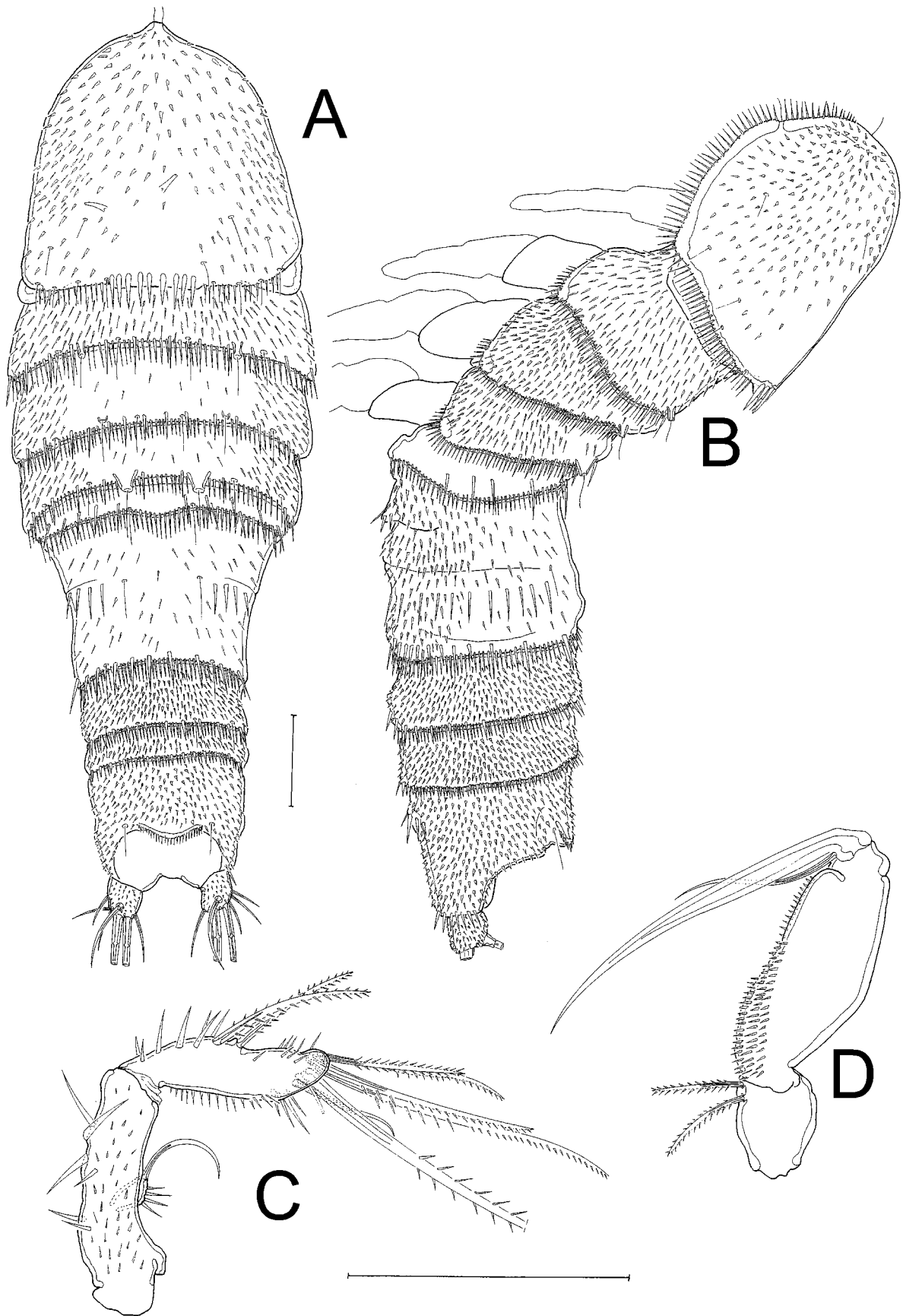


FIGURE 15: *Argestes mollis*, female. A. Habitus, dorsal view, B. Habitus, lateral view, C. A2, D. Mxp. Scales: A, B. 100µm, C, D. 50µm.

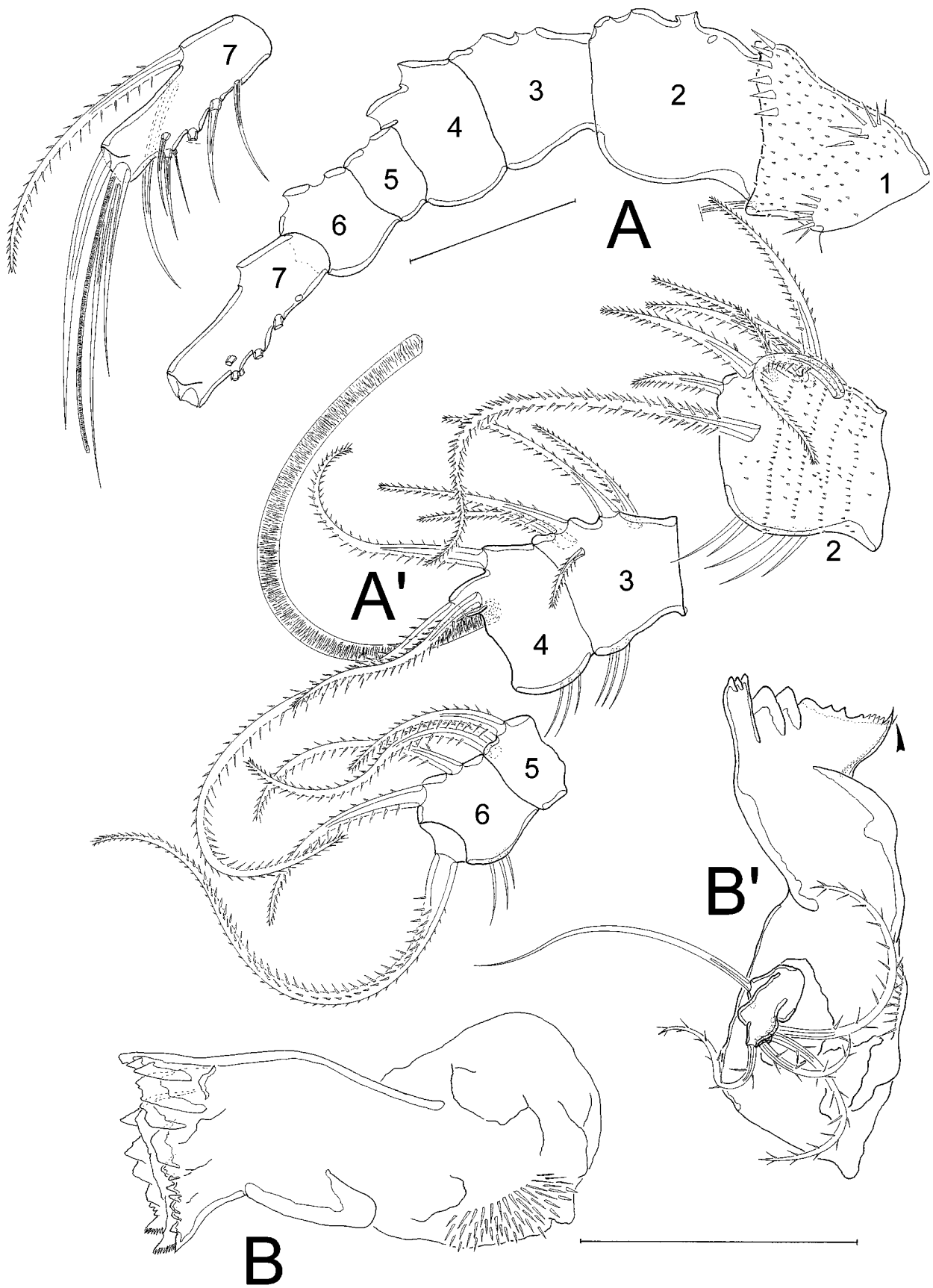


FIGURE 16: *Argestes mollis*. A. A1 female, general shape, A'. A1 female, setation of single segments, B. Md gnathobase, palpus not drawn, B'. male Md gnathobase, triangular arrow pointing to small subterminal seta. Scales: 50µm.

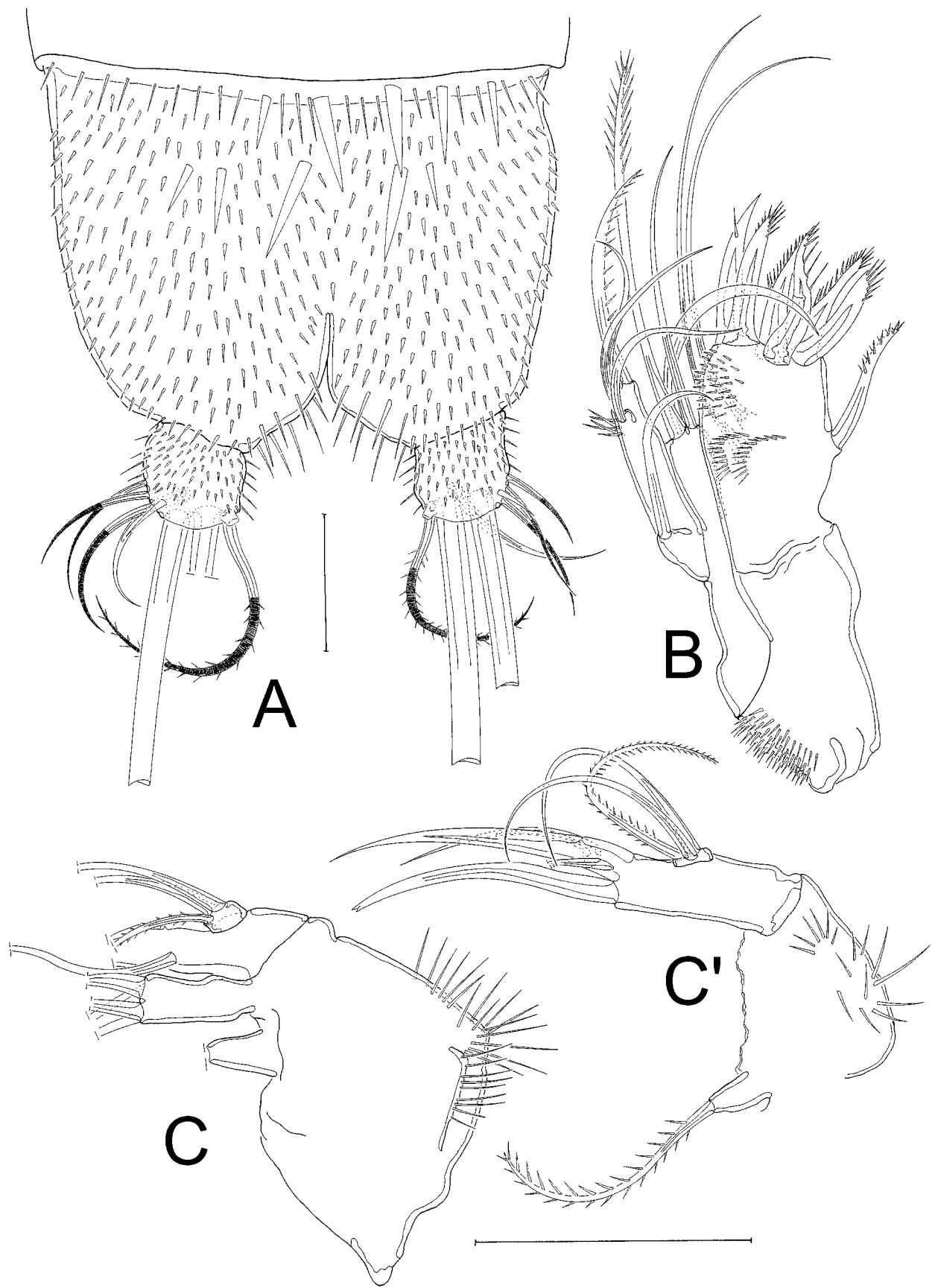


FIGURE 17: *Argestes mollis*, female. A. Telson and FR, ventral view, B. MxI, C. Mx, C'. Mx of counterpart. Scales: A. 100µm, B-C, C'. 50µm.

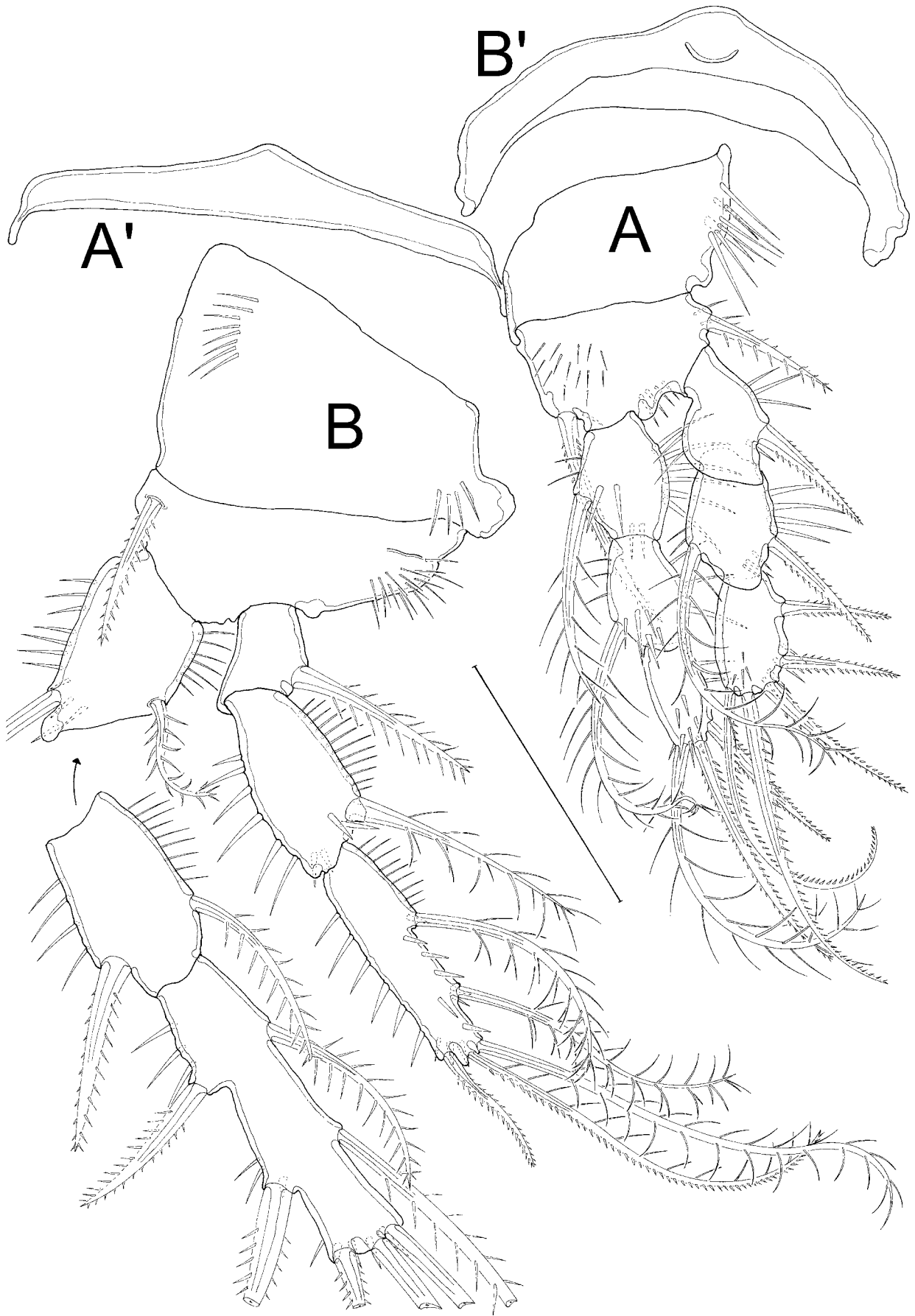


FIGURE 18: *Argestes mollis*, female. A, P1, A'. P1 intercoxal sclerite, B, P2, B'. P2 intercoxal sclerite. Scale: 50 μ m.

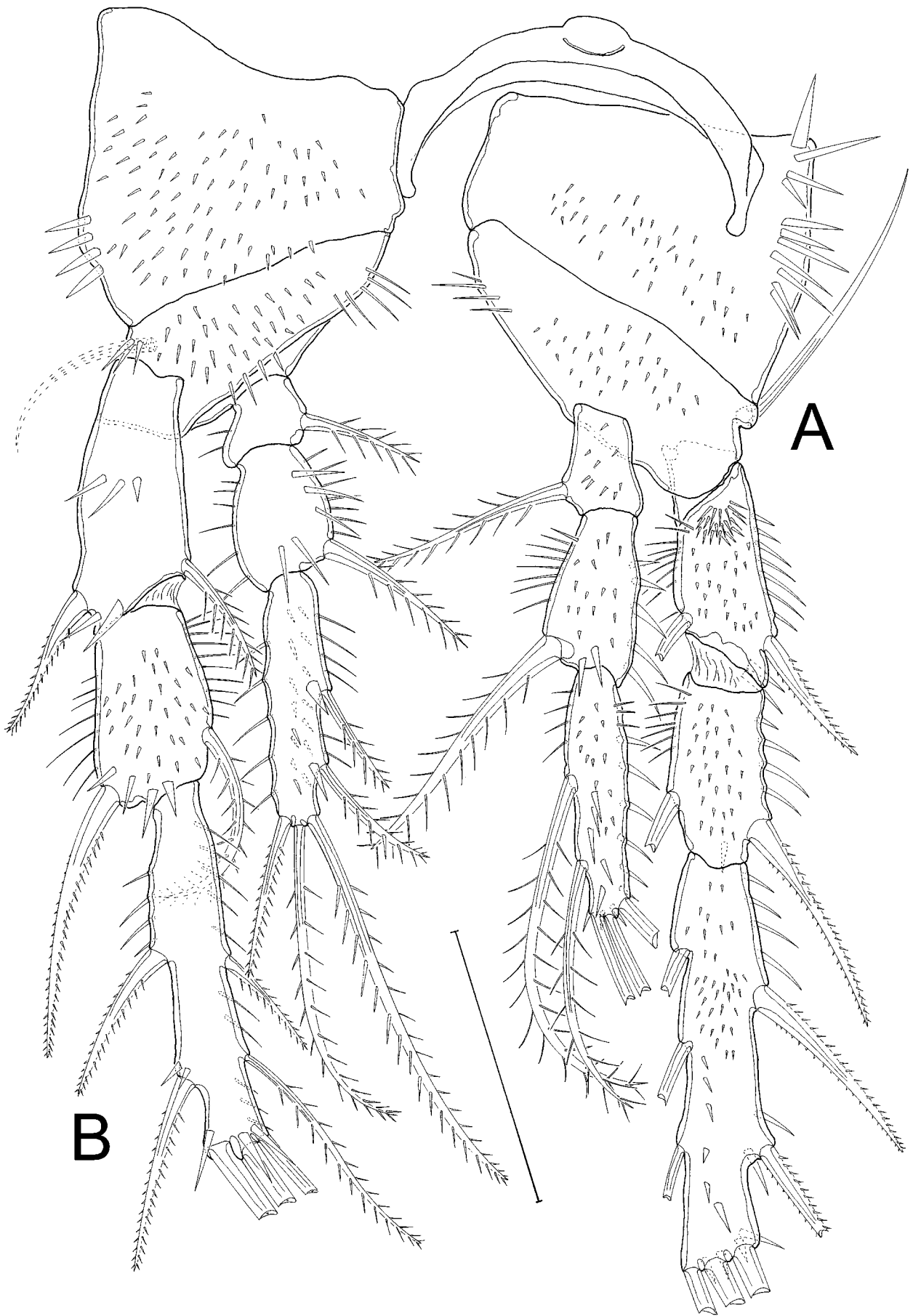


FIGURE 19: *Argestes mollis*, female. A. P3, B. P4. Scale: 50 μ m.

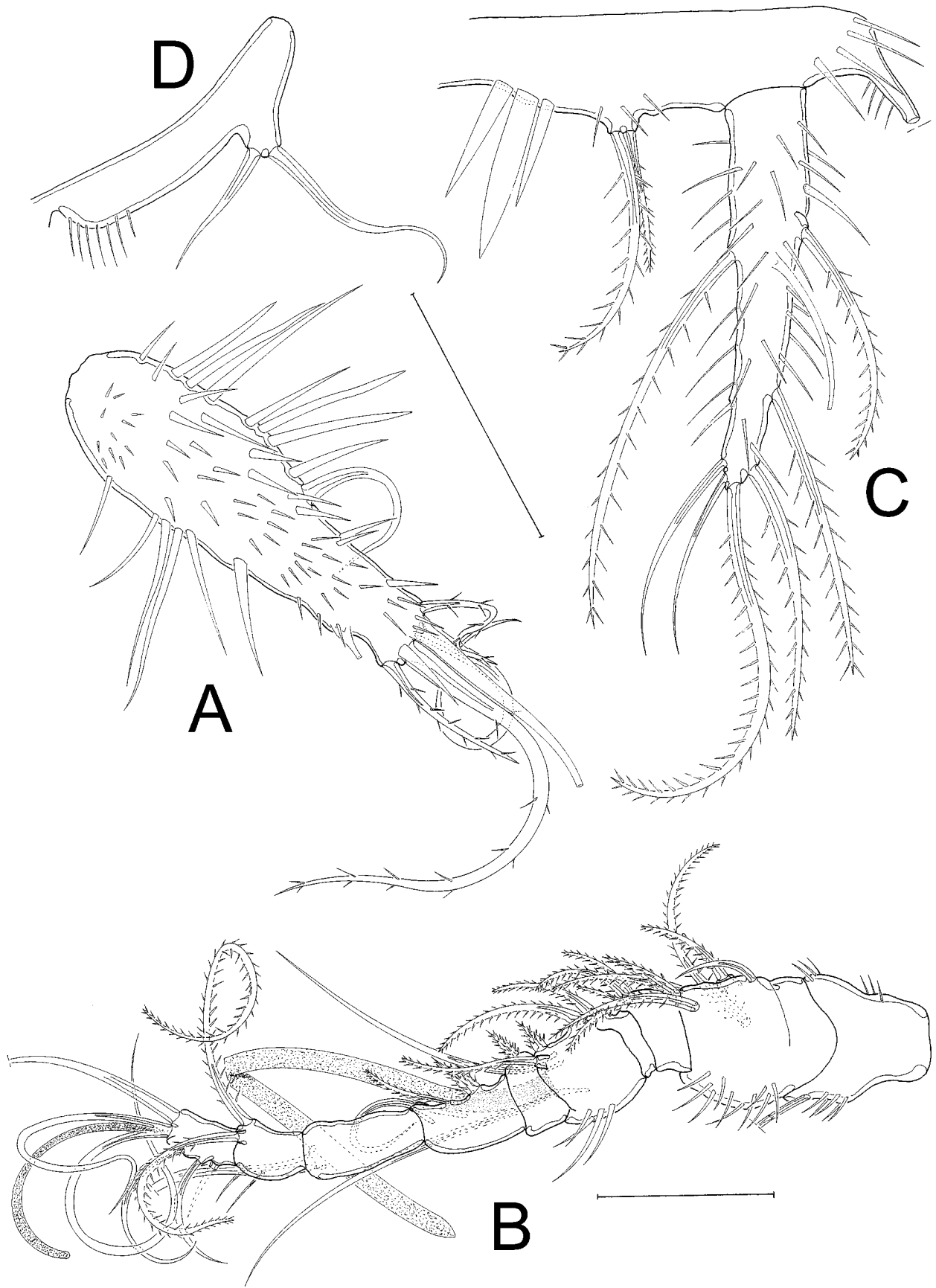


FIGURE 20: *Argestes mollis*. A. Female P5 exp, enp not drawn, B. Male A1, C. Male P5, D. Male P6. Scales: 50 μ m.

P5 (Fig. 20A) benp lost, not drawn. Exp approximately 3 times longer than broad, covered with spinules of different sizes, some reaching size of setae. Terminally with 4 setae and 1 long tube pore. Laterally on outer margin with 1 bare seta. Subterminally on inner margin with small tube pore.

Male:

Habitus and most characteristics as in female, but differing in the following features:

A1 (Fig. 20B) 10-segmented, haplocer, aes on fifth segment. First segment with 1 seta, fifth, sixth, and seventh segments each with 1 additional short and thick multipinnate seta. Eighth segment with just 1 big seta. Setal formula: 1/1; 2/6; 3/3; 4/1; 5/5 + aes; 6/1; 7/3; 8/1; 9/4; 10/6 + aes.

P5 (Fig. 20C) benp fused, endopodal lobe virtually absent, represented by 1 long and 1 smaller bipinnate seta. Exp approximately 4 times longer than broad, with 7 setae, outer margin with long tube pore. (Sub-)Terminally no tube pore discernible.

P6 (Fig. 20D) small, with 2 bare setae and row of spinules at proximal margin.

Redescription of *Argestes reductus* (Itô, 1983)

Figs. 21–25

The description is based on the type material collected by Itô (1983). It consists of 3 male specimens, all of which are dissected and mounted on slides: Holotype on six slides, labelled 6-II-1979, KH-79-1, St. 5, A-1/1-6, paratype 1 on six slides, labelled 6-II-1979, KH-79-1, St. 5, A-2/1-6, paratype 3 on six slides, labelled 6-II-1979, KH-79-1, St. 5, A-3/1-6. Due to the bad conditions of the embedded urosomes, no telson and FR of *A. reductus* could be illustrated.

Male.

Habitus not drawn, as well as telson and FR, the latter due to the bad conditions of the slide material.

A1 (Fig. 21A) 11-segmented, all segments covered with small spinules. Ninth segment terminally with 1 very strong seta.

Setal formula: 1/1; 2/1; 3/6; 4/6; 5/1; 6/8 + aes; 7/1; 8/2; 9/1; 10/3; 11/6 + aes.

A2 (Fig. 21B) with allobasis, covered in small spinules and bearing 1-segmented exp with 1 seta, additionally with long hair-like spinules. Enp at its anterior margin laterally with 2 bipinnate setae. Terminally with 6 setae, 5 of which are “rat-tail”-like, and 1 small tube pore which is fused to longest seta basally (triangular arrow in Fig. 21B).

Md (Fig. 22A) with strong palp but weak, reduced gnathobase. Palpus with enp and exp. Basis with a few spinules and 2 bipinnate setae. Enp also with some spinules, laterally with 1 bipinnate seta, terminally with 4 bipinnate and 2 bare setae. Exp smaller than enp, each laterally and terminally with 2 bipinnate setae.

Mxl (Fig. 22B) atrophied, poorly sclerotized. Precoxal arthrite laterally with 1 bare seta, terminally with 7 setae. Coxa(?) terminally with 3 bare setae, no more structures discernible.

Mx not drawn, due to inability to determine it clearly.

Mxp (Fig. 22C) weak, basis longer than syncoxa, the latter covered with spinules and bearing 2 setae (1 of which is broken). Basis laterally with row of spinules. Enp produced into long and slender seta, which is accompanied by a second seta.

P1 (Fig. 23A) with 3-segmented rami. Coxa bigger than basis, intercoxal sclerite boomerang-like in shape. Basis with inner and outer seta, and with long spinules at inner margin. All segments covered with small spinules. Exp2 with inner seta. Outer setae of exps 1–3 subterminally with tube pores. Terminal setae “rat tail”-like at their distal half. Enps 1 and 2 with 1 bipinnate inner seta, whose spinules are remarkably long. Enp3 terminally with 2 long setae, showing “rat-tail” shape in their distal half, and with 1 shorter outer seta with a tube pore subterminally.

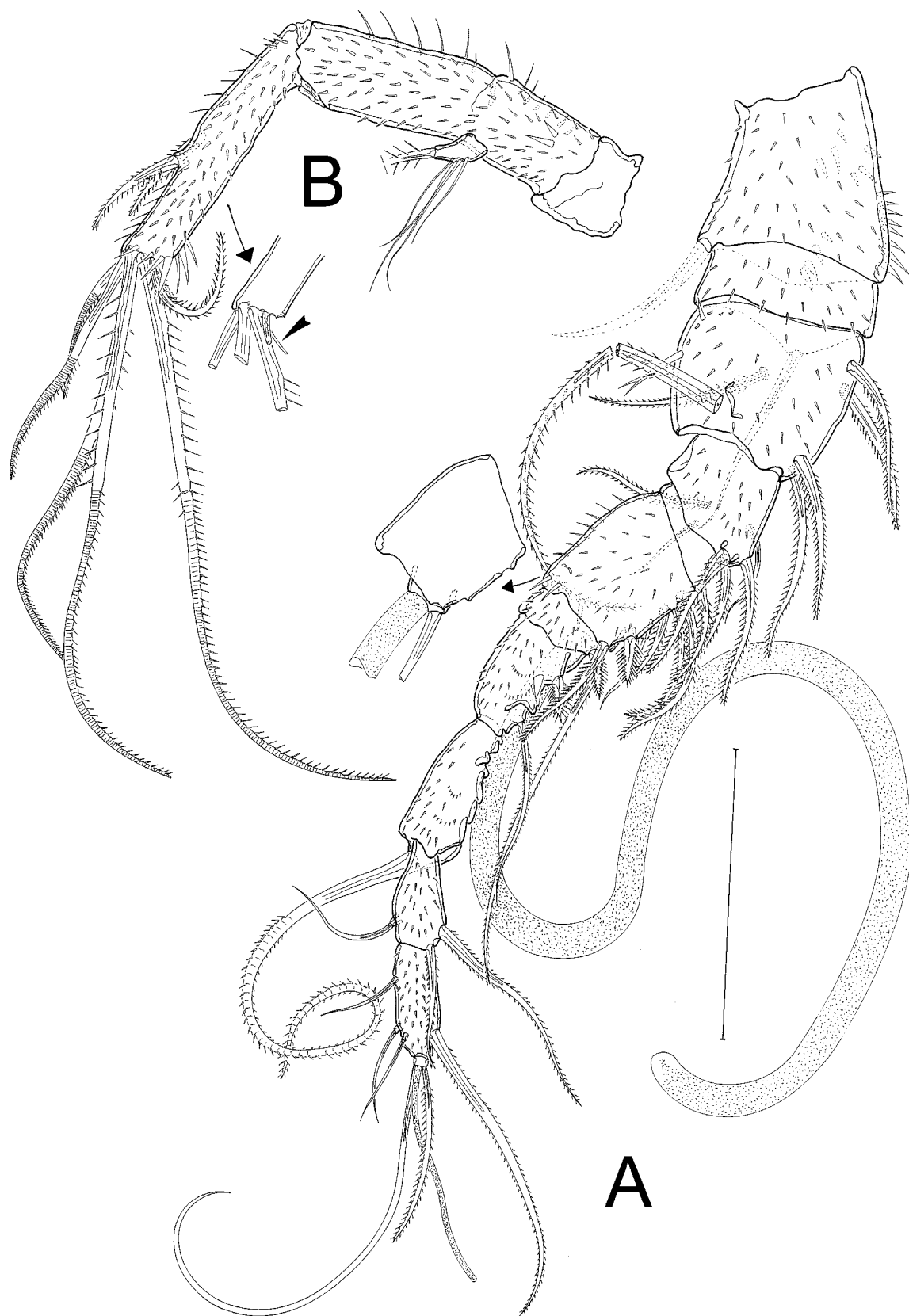


FIGURE 21: *Argestes reductus*, male. A. A1, arrow indicates single sixth segment showing position of aes and accompanying seta, B. A2, arrow indicates distal part of enp, showing tube pore (triangular arrow). Scale: 100µm.

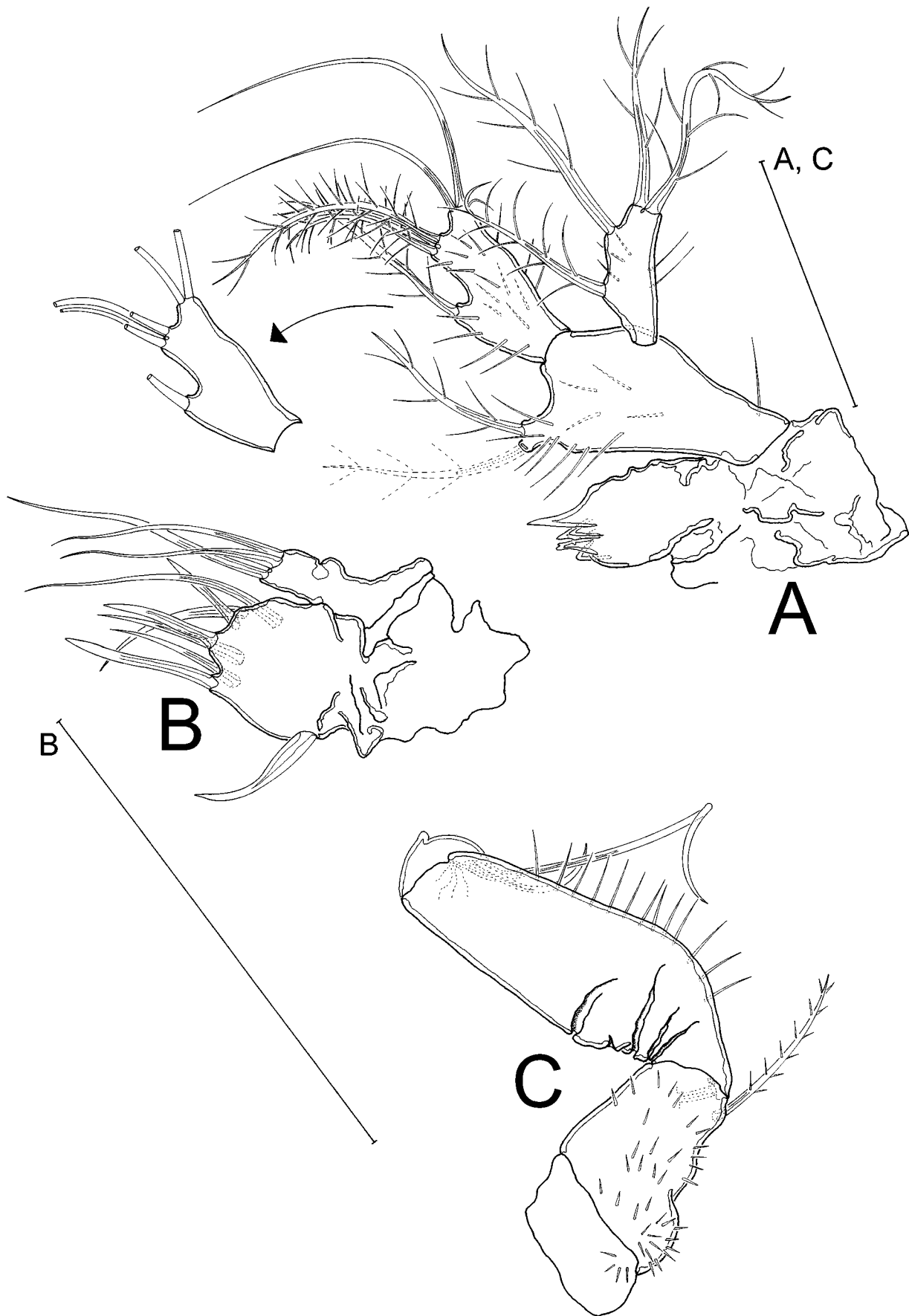


FIGURE 22: *Argestes reductus*, male. A. Md, arrow indicates single enp showing setation, B. Mxl, C. Mxp. Scales: 50 μ m.

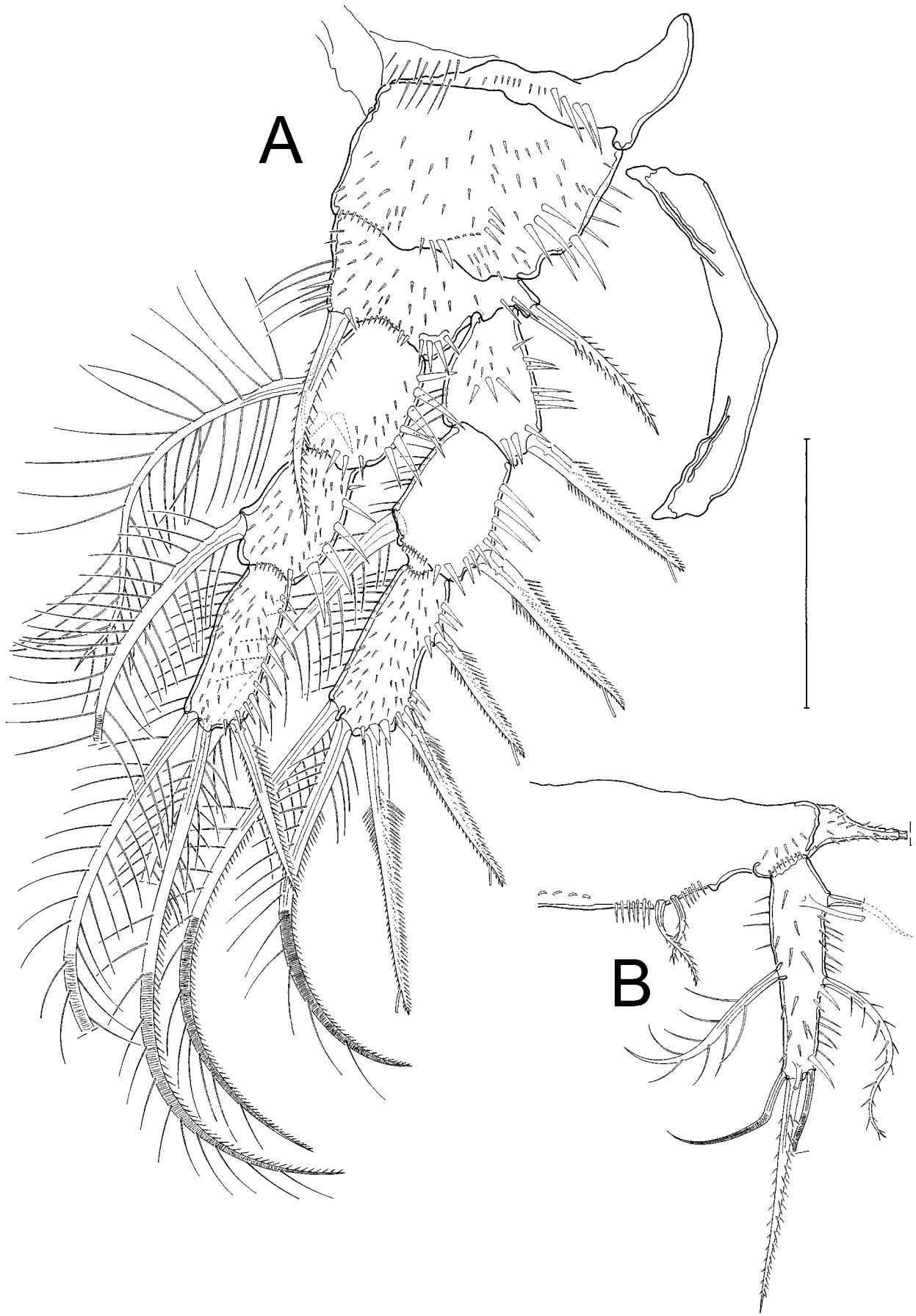


FIGURE 23: *Argestes reductus*, male. A. P1 with corresponding intercoxal sclerite, B. P5. Scale: 50 μ m.



FIGURE 24: *Argestes reductus*, male P2 with corresponding intercoxal sclerite. Scale: 50 μ m.

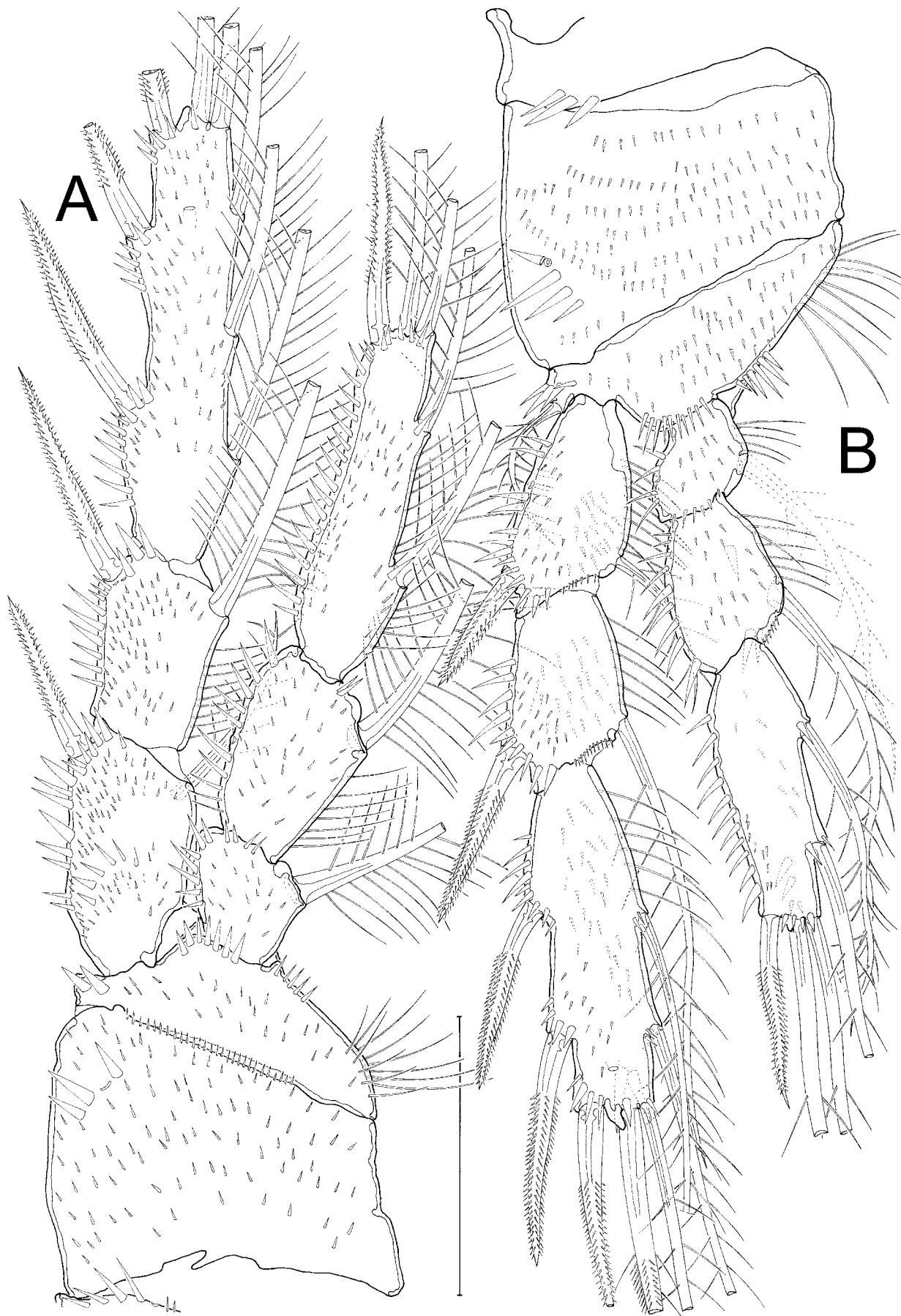


FIGURE 25: *Argestes reductus*, male. A. P3, B. P4. Scale: 50µm.

P2–P4 (Figs. 24, 25A, B) with 3-segmented rami and bow-like intercoxal sclerites (cf. Fig. 24). All segments covered with small spinules. Coxa much bigger than basis, the latter with 1 outer seta and long spinules on the inner margin. Last exopodal and endopodal segments approximately as long as preceding segments together. Outer setae of P2 tripinnate and at P3 and P4 tetrapinnate. Setation as shown in table 3.

TABLE 3: *Argestes reductus* (Itô, 1983), male, setation of P1-P4 (no. outer spines in roman numbers).

Natatory leg	Exp1	Exp2	Exp3	Enp1	Enp2	Enp3
P1	I-0	I-1	III-2-0	0-1	0-1	I-2-0
P2	I-1	I-1	III-2-2	0-1	0-1	I-2-2
P3	I-1	I-1	III-2-3	0-1	0-1	I-2-2
P4	I-1	I-1	III-2-2	0-1	0-1	I-2-2

P5 (Fig. 23B) benps fused, endopodal lobe reduced, represented by 2 small, bipinnate setae. Exp distinct, approximately 4 times longer than broad, covered with spinules and bearing 6 setae, 2 of which are “rat tail”-like. Each with 1 tube pore proximally and terminally.

Female unknown.

Discussion

Historical background

When erecting the genus *Argestes*, Sars (1910) placed it together with *Fultonia* T. Scott, 1902 into Tachidiidae Sars, 1909. He noted, however, a remarkable similarity with Cletodidae T. Scott, 1904 “...in general appearance and in the structure of most of the appendages” (Sars 1910, p. 341), in particular because of the supposed high affinity to the at that time cletodid taxon *Eurycletodes* Sars, 1909. Gurney (1932; cited after Lang 1936a) transferred *Argestes* and *Fultonia* into Cletodidae, where they remained until Por (1986) undertook a splitting of Cletodidae into several new taxa. One of them is Argestidae Por, 1986, then including 14 genera: *Argestes*, *Argestigenes* Willey, 1935, *Corallicletodes* Soyer, 1966, *Dizahavia* Por, 1979, *Eurycletodes*, *Fultonia*, *Hemicletodes* Lang, 1936, *Hypalocletodes* Por, 1967, *Leptocletodes* Sars, 1920, *Megistocletodes* Por, 1986, *Mesocletodes* Sars, 1909, *Neoargestes* Drzycimski, 1967, *Odiliacletodes* Soyer, 1964, *Parargestes* Lang, 1944. Although Por’s (1986) family diagnosis of Argestidae allows a differentiation from other harpacticoid taxa (cf. Boxshall & Halsey 2004, for recent family diagnosis), the justification of Argestidae as a monophylum is still pending, due to missing autapomorphies (George 2004). As a consequence, several new species have subsequently been placed into the family only as *species incertae* in the past years (cf. Bodin 1997; George 2004): *Actinocletodes woutersi* Fiers, *Argestoides prehensilis* Huys & Conroy-Dalton, *Austrocletodes tricomatosum* Pallares (cf. Fiers 1987), *Bodinia meteorensis* George, *B. peterrummi* George, *Pontocletodes ponticus* Apostolov, and *Rosacletodes kuehnemanni* (Pallares) (cf. Wells 1985). Moreover, Wells (1965) described an unknown “Cletodidae gen. et sp. nov.?”, which according to Bodin (1997) is but a juvenile and therefore not taken into account in further analyses. Lacking of unequivocal phylogenetic characterization of Argestidae leads to uncertainties regarding the affiliation of genera like *Argestigenes* (cf. Huys et al. 1996) and *Abyssameira* Itô, 1983. Huys et al. (1996) placed the latter into Argestidae and later, Bodin (1997) synonymised it with *Argestes*. Both assertions were made without any phylogenetic argumentation, and the present study tries to provide a phylogenetic basis for the transference. Summarising, it is stated that up to now, Argestidae comprise 20 genera (with 86 species), 7 of which (including 10 species) are *genera incertae* (Table 4).

TABLE 4: List of known Argestidae (*species *incertae sedis*).

No.	Species	Author
I	<i>Actinocletodes</i>*	
1	<i>Actinocletodes woutersi</i> *	Fiers
II	<i>Argestes</i>	
2	<i>Argestes mollis</i>	Sars
3	<i>Argestes reductus</i>	Itô (as <i>Abyssameira reducta</i>)
4	<i>Argestes angolaensis</i>	This contribution
III	<i>Argestigens</i>*	
5	<i>Argestigens uniremis</i> *	Willey
6	<i>Argestigens glacialis</i> *	Lang
7	<i>Argestigens abyssalis</i> *	Becker, Noodt & Schriever
IV	<i>Argestoides</i>*	
8	<i>Argestoides prehensilis</i> *	Huys & Conroy-Dalton
V	<i>Austrocletodes</i>*	
9	<i>Austrocletodes tricomasum</i> *	Pallares
VI	<i>Bodinia</i>*	
10	<i>Bodinia meteorensis</i> *	George
11	<i>Bodinia peterrummi</i> *	George
VII	<i>Corallicletodes</i>	
12	<i>Corallicletodes boutieri</i>	Soyer
VIII	<i>Dizahavia</i>	
13	<i>Dizahavia halophila</i>	Por
IX	<i>Eurycletodes</i>	
14	<i>Eurycletodes (Oligocletodes) abyssi</i>	Lang
15	<i>Eurycletodes (Oligocletodes) aculeatus</i>	Sars
16	<i>Eurycletodes (Oligocletodes) arcticus</i>	Lang
17	<i>Eurycletodes (Oligocletodes) denticulatus</i>	Por
18	<i>Eurycletodes (Oligocletodes) echinatus</i>	Lang
19	<i>Eurycletodes (Oligocletodes) ephippiger</i>	Por
20	<i>Eurycletodes (Oligocletodes) hoplurus</i>	Smirnov
21	<i>Eurycletodes (Oligocletodes) irelandica</i>	Roe
22	<i>Eurycletodes (Oligocletodes) latus</i>	T. Scott
23	<i>Eurycletodes (Oligocletodes) major</i>	Sars
24	<i>Eurycletodes (Oligocletodes) minutus</i>	Sars

..... continued

TABLE 4 (continued)

No.	Species	Author
25	<i>Eurycletodes (Oligocletodes) monardi</i>	Smirnov
26	<i>Eurycletodes (Oligocletodes) oblongus</i>	Sars
27	<i>Eurycletodes (Oligocletodes) parasimilis</i>	Por
28	<i>Eurycletodes (Oligocletodes) peruanus</i>	Becker, Noodt & Schriever
29	<i>Eurycletodes (Oligocletodes) petiti</i>	Soyer
30	<i>Eurycletodes (Oligocletodes) profundus</i>	Becker, Noodt & Schriever
31	<i>Eurycletodes (Oligocletodes) quadrispinosa</i>	Schriever
32	<i>Eurycletodes (Oligocletodes) similis</i>	T. Scott (as <i>Cletodes similis</i>)
33	<i>Eurycletodes (Oligocletodes) uniarticulatus</i>	Smirnov
34	<i>Eurycletodes (Oligocletodes) verisimilis</i>	Willey
35	<i>Eurycletodes (Eurycletodes) gorbunovi</i>	Smirnov
36	<i>Eurycletodes (Eurycletodes) laticauda</i>	Boeck (as <i>Cletodes laticauda</i>)
37	<i>Eurycletodes (Eurycletodes) rectangulatus</i>	Lang
38	<i>Eurycletodes (Eurycletodes) serratus</i>	Sars
X	<i>Fultonia</i>	
39	<i>Fultonia bougisi</i>	Soyer
40	<i>Fultonia gascognensis</i>	Bodin
41	<i>Fultonia hirsuta</i>	T. Scott
42	<i>Fultonia sarsi</i>	Smirnov
XI	<i>Hemicletodes</i>	
43	<i>Hemicletodes typicus</i>	Lang
XII	<i>Hypalocletodes</i>	
44	<i>Hypalocletodes aberrans</i>	Marinov
45	<i>Hypalocletodes salomonis</i>	Por
XIII	<i>Leptocletodes</i>	
46	<i>Leptocletodes chaetophorus</i>	Smirnov
47	<i>Leptocletodes debilis</i>	Sars
XIV	<i>Megistocletodes</i>	
48	<i>Megistocletodes translucens</i>	Por
XV	<i>Mesocletodes</i>	
49	<i>Mesocletodes abyssicola</i>	T. & A. Scott
50	<i>Mesocletodes ameliae</i>	Soyer
51	<i>Mesocletodes arenicola</i>	Noodt
52	<i>Mesocletodes bathybia</i>	Por

..... continued

TABLE 4 (continued)

No.	Species	Author
53	<i>Mesocletodes bodini</i>	Soyer
54	<i>Mesocletodes brevifurca</i>	Lang
55	<i>Mesocletodes carpinei</i>	Soyer
56	<i>Mesocletodes commixtus</i>	Coull
57	<i>Mesocletodes dolichurus</i>	Smirnov
58	<i>Mesocletodes duosetosus</i>	Schriever
59	<i>Mesocletodes farauni</i>	Por
60	<i>Mesocletodes faroerensis</i>	Schriever
61	<i>Mesocletodes fladensis</i>	Wells
62	<i>Mesocletodes glaber</i>	Por
63	<i>Mesocletodes guillei</i>	Soyer
64	<i>Mesocletodes inermis</i>	Sars
65	<i>Mesocletodes irrasus</i>	T. & A. Scott (as <i>Cletodes irrasa</i>)
66	<i>Mesocletodes katharinae</i>	Soyer
67	<i>Mesocletodes kunzi</i>	Schriever
68	<i>Mesocletodes langi</i>	Smirnov
69	<i>Mesocletodes makarovi</i>	Smirnov
70	<i>Mesocletodes monensis</i>	I.C. Thompson (as <i>Cletodes monensis</i>)
71	<i>Mesocletodes opotheros</i>	Por
72	<i>Mesocletodes parabodini</i>	Schriever
73	<i>Mesocletodes parirrasus</i>	Becker, Noodt & Schriever
74	<i>Mesocletodes quadrispinosa</i>	Schriever
75	<i>Mesocletodes robustus</i>	Por
76	<i>Mesocletodes sarsi</i>	Becker, Noodt & Schriever
77	<i>Mesocletodes soyeri</i>	Bodin
78	<i>Mesocletodes thieli</i>	Schriever
79	<i>Mesocletodes trisetosa</i>	Schriever
80	<i>Mesocletodes variabilis</i>	Schriever
XVI	<i>Neoargestes</i>	
81	<i>Neoargestes incertus</i>	Becker, Noodt & Schriever
82	<i>Neoargestes variabilis</i>	Drzycimski
XVII	<i>Odiliaclatodes</i>	
83	<i>Odiliaclatodes gracilis</i>	Soyer
XVIII	<i>Parargestes</i>	
84	<i>Parargestes tenuis</i>	Sars (as <i>Argestes tenuis</i>)

..... continued

TABLE 4 (continued)

No.	Species	Author
XIV	<i>Pontocletodes</i> *	
85	<i>Pontocletodes ponticus</i> *	Apostolov
XX	<i>Rosacletodes</i> *	
86	<i>Rosacletodes kuehnemanni</i> *	Pallares (as <i>Echinocletodes kuehnemanni</i>)

Relation of Argestes angolaensis sp. nov. with Argestidae

Argestes angolaensis sp. nov. fulfils most of the morphological features of Argestidae, as listed by Por (1986) and George (2004): (1) integument poorly chitinized, (2) telson nearly square, (3) anal operculum shifted posteriorly, (4) FR set wide apart at corners of telson, (5) A2 exp 1-segmented, (6) natatory legs remarkably elongate, (7) P2–P4 rami displaced to the outer margin of basis, (8) bases broader than long. Furthermore, like in almost all Argestidae, the coxae of P1–P4 are much bigger than the corresponding bases. As stated before, the above listed features are only diagnostic ones so far, as their phylogenetic relevance has still to be proved, which would, however, surpass the scope of the present contribution. Moreover, it is of less importance in the present context, which deals particularly with a possible monophyly of the taxon *Argestes*. Ongoing phylogenetic studies on Argestidae shall elucidate whether *Argestes* shows any closer phylogenetic relationships with remaining Argestidae.

Phylogenetic relationships within Argestes

The allocation of *Argestes angolaensis* sp. nov. into the taxon *Argestes* was not indisputable, because like Argestidae itself, *Argestes* also still lacks a characterization as a monophylum. However, when comparing *A. angolaensis* sp. nov. with other Argestidae, its high similarity with the species of *Argestes/Parargestes* was noted. Moreover, the redescription of both *A. mollis* and *A. reductus* and their comparison with *A. angolaensis* sp. nov. provide at least 3 synapomorphies for the three species. One additional character (4) may also be considered as autapomorphic for *Argestes*, but its confirmation for *A. reductus* is still pending [plesiomorphic states in squared brackets]:

1. Body densely covered with small cuticular spinules [no spinule coverage]
2. A1 with very strong seta terminally on 6th segment in female, penultimate/last but two segment in male [no strong seta developed]
3. FR setae I, II, III, and VI of “rat-tail” shape [setae of normal shape]
4. Sensilla of free thoracic somites arising from cylindrical tubercles [tubercles absent]

Character 1: Body and appendages densely covered with small cuticular spinules:

All three (re)described *Argestes* species are characterized by the presence of small cuticular spinules covering almost all body somites dorsally and laterally (Figs. 2, 12, 13, Itô 1983). Such coverage is absent in most other Harpacticoida and is therefore considered here as derived, i.e. an autapomorphic character for *Argestes*.

Character 2: A1 with very strong seta terminally on 6th segment in female, penultimate/antepenultimate segment in male:

Argestes angolaensis sp. nov. and *A. mollis* females bear a remarkably long and strong seta on their 6th antennular segment. No other argestid species shows that character, with exception of *Fultonina hirsuta* (personal observation). Therefore, the character may be regarded as apomorphic at least for *Argestes* (as done

here), but it may perhaps even be synapomorphic for *Argestes* and *Fultonia*. Also the males of the three (re)described species bear such remarkable seta, which may be homologous with that of the females. Ongoing investigation that includes additional taxa (*Dizahavia*, *Fultonia*, *Parargestes*) may clear up the phylogenetic status of that character.

Character 3: FR setae I, II, III, and VI of “rat-tail” shape:

Willen (1996) first detected what she called “rat-tail setae” in Pseudomesochrinae T. Scott, 1902, describing them with “distal half throughout geniculate, trimmed with hairs and flexible” (Willen 1996, p. 82). Figs. 3 and 17A show furcal setae I, II, III, and VI of *Argestes angolaensis* sp. nov. and *A. mollis* being of “rat-tail” shape, with exception of the presence of hairs in most setae. In Argestidae, no other taxon shows such a shape of (furcal) seta, which doubtlessly can be considered as derived. Unfortunately, the urosoma of all three *A. reductus* specimens is in relatively bad conditions (furcal setae broken, embedding medium turned opaque), inhibiting the illustration of urosoma, telson, and FR. However, furcal seta III of both the holotype and PT 3 are not broken and show the “rat-tail” aspect (personal observation). Thus, for *A. reductus* the possession of “rat tail” setae is also supposed. Consequently, their presence in all *Argestes* species is considered as an autapomorphic character for that taxon.

Character 4: Sensilla of free thoracic somites arising from cylindrical tubercles:

In Harpacticoida, the body somites bear dorsal and lateral sensilla that (1) mainly project through the cuticula (Huys et al. 1996). Sometimes, (2) the sensilla arise from small knobs, or (3) their bases are produced into small cuticular projections of different shape (e.g. in many Cletodidae). The extreme is observable in Ancorabolidae, where (4) the sensilla are displaced to the tip of long and bizarre cuticular processes. Argestidae present conditions (1–3), but only the presently described *Argestes angolaensis* sp. nov. and *A. mollis* show (5) the development of more or less long cylindrical tubercles (cf. Figs. 2, 12, 13). These are considered as derived character and constitute therefore a synapomorphy for both species. It has to be remarked, however, that the verification of such tubercles is still pending for *A. reductus*, as Itô (1983) did not mention them, his illustrations of the habitus do not allow their recognition, and no complete individuals of *A. reductus* are available. Thus, until the verification of the presence of the tubercles also for *A. reductus*, character 4 is not useful for characterization of *Argestes* itself.

In addition to the listed apomorphies, 3 diagnostic characters can be added: (i) cphth with rudimentary pleurotergite of fused first thoracic somite, (ii) A2 exp with long spinules, and (iii) P1 enp 3-segmented. None of the remaining Argestidae presents these conditions. Future investigation will have to clear up the phylogenetic value of any of these characters.

Based on the above listed 3(-4) synapomorphies of *Argestes angolaensis* sp. nov., *A. mollis*, and *A. reductus*, the phylogenetic uniting of the three species into one monophylum *Argestes* with its type species *A. mollis* appears to be sufficiently justified. On the other hand, each species is characterized by several autapomorphic characters, confirming their specific status in comparison with each other [relatively plesiomorphic states as observable in the remaining *Argestes* species in squared brackets]:

Argestes mollis:

5. Cphth dorsally with row of remarkably strong spinules at distal margin [no row of strong spinules]

Argestes reductus:

6. Spinules on A2 exp transformed into very long setules [spinules short]
7. 5 of 6 terminal setae on A2 enp “rat-tail”-shaped [setae of normal shape]
8. Male mouthparts including mxp atrophied [male mouthparts of normal shape]
9. P1 with several “rat-tail” setae [setae of normal shape]

Argestes angolaensis sp. nov.:

10. FR showing elongation at their proximal half, being therefore all setae displaced distally [FR small, squared]
11. Seta III of FR translocated ventrally [inserting terminally at outer margin]
12. Male benp P5 with only 1 small seta [with 2 small setae]

First preliminary comparison with *Parargestes*

Although an extensive phylogenetic analysis, which will include detailed (re-)descriptions of *Fultonia* and *Parargestes* species, is in preparation and will be published elsewhere, first conclusions on the relation between *Argestes* and *Parargestes* are presented, because apart from the above mentioned synapomorphies with *A. mollis* and *A. reductus*, *Argestes angolaensis* sp. nov. presents one particular feature attributed to *Parargestes* (cf. Lang 1944, 1948). According to Lang (1944, 1948), *Argestes* shows close affinity to the taxon *Parargestes*. In fact, after describing *A. mollis*, Sars (1921) added a second species he named *Argestes tenuis* Sars, 1921, due to the high similarity of the appendages, particularly the swimming legs, with that of *A. mollis* (Sars, 1921). Two decades later, Lang (1944) noted differences between *A. mollis* and *A. tenuis*, as listed in table 5:

TABLE 5: Differences between *Argestes mollis* and *A. tenuis*, according to Lang (1944).

	<i>Character</i>	<i>Argestes mollis</i>	<i>Argestes tenuis</i>
a)	Body form	Urosoma narrower than prosoma	Urosoma as broad as prosoma
b)	A2	With basis	With allobasis, suture still present
c)	Md	With exp well developed, distinct	Exp represented by 1 seta only
d)	P1	Exp1 with inner seta	Exp1 without inner seta
e)	Shape/size of FR	Very small, squared	4–5 times longer than broad

As a consequence, Lang (1944) established the taxon *Parargestes* to place *A. tenuis* into that genus, making both genera monotypic, until Bodin's (1997) transference of the former *Abyssameira reducta* Itô, 1983 into *Argestes* (see above). *Parargestes* still encloses the only *P. tenuis* so far, which comprises a second form, *P. tenuis* var. *arcticus* (Lang).

Reviewing Lang's (1944, 1948) supposed differences between *Argestes* and *Parargestes* (Table 5), most of them can no longer be maintained.

Character a), body shape:

Although *A. mollis* indeed presents the urosoma clearly narrower than the prosoma, this is not that strongly expressed in *A. reductus* nor in *A. angolaensis* sp. nov. On the other hand, specimens of *P. tenuis* also show a certain narrowing of the urosoma compared with the prosoma. Therefore, and as *Parargestes* is represented by *P. tenuis* only, the body shape is regarded here as a specific but not a generic difference.

Character b), A2 with basis/allobasis:

Redescription reveals (in *A. mollis*) and confirms (in *A. reductus*) that neither the first nor the second species show a basis but like *A. angolaensis* sp. nov. an allobasis. Thus, that character is not valid anymore.

Character c), Md palp with/without exp:

Redescription of the mandibular palp for *A. mollis* was unfortunately impossible, due to the damaged mouthparts in the female and an unsatisfactory condition of the male's md palp (cf. Fig. 16B'). However,

Sars' (1910, p. 343) description clearly mentions a palp "... with both rami well developed and setiferous", which is the same in both *A. reductus* (Fig. 22A) and *A. angolaensis* sp. nov. (Fig. 6B). The condition in *P. tenuis* (Md palp without exp) supports the specific distinctness. The maintenance of a genus *Parargestes* would, however, not remain that well justified if based only on this single character, mainly because its (so far) monotypic status. It means that the character could also represent simply a specific one.

Character d), P1 exp1 with inner seta:

None of the (re-)described species presents an inner seta at P1 exp1, contradicting Sars' (1910) description of *A. mollis*. This is remarkably, because apart from becoming useless for distinguishing between *Argestes* and *Parargestes*, the absence of an inner seta on P1 exp1 confirms that *Argestes* indeed belongs to Syngnathartha, as stated for all Argestidae by Seifried (2003).

Character e), shape/size of FR:

It has to be admitted that *A. angolaensis* sp. nov. indeed bears long furcal rami, similar to that of Lang's *Parargestes* rather than of *Argestes*. But here the same as in character c) applies: it remains questionable whether the elongation of the FR as the one and only character should be used as phylogenetic justification for the maintenance of the taxon *Parargestes*, particularly because this single character has to face the above listed synapomorphies 1-3(4) of *A. angolaensis* sp. nov., *A. mollis*, and *A. reductus*.

Concluding, the following is stated: The three species *Argestes angolaensis* sp. nov., *A. mollis*, and *A. reductus* are united in the monophylum *Argestes*, which is justified by 3 (to 4) synapomorphies. Comparison of *A. angolaensis* sp. nov. with *Parargestes tenuis* reveals just one derived character both species share, the elongate FR. While *P. tenuis* presents a reduced exp on the Md palp, considered here as second apomorphy for that taxon, *A. angolaensis* sp. nov. shares as a primitive condition a 1-segmented exp with the remaining *Argestes* species. Therefore, it seems more plausible to allocate the new species into *Argestes* due to (at least) 3 synapomorphic characters than to assign it to *Parargestes* because of 1 synapomorphy. Moreover, the reduced Md exp in *P. tenuis* is regarded here as specific instead of generic character. Therefore, it is suggested that *Parargestes tenuis* should be re-allocated into *Argestes* as *Argestes tenuis* Sars, 1921. Ongoing investigation on basal Argestidae (*Argestes*, *Dizahavia*, and *Fultonina*) will prove whether more characters supporting this hypothesis arise.

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