



## Systematics and phylogeny of Cristacoxidae (Copepoda, Harpacticoida): a review

RONY HUYS<sup>1,3</sup> & TERUE CRISTINA KIHARA<sup>2</sup>

<sup>1</sup>Department of Zoology, Natural History Museum, Cromwell Road, SW7 5BD, London, UK. E-mail: rjh@nhm.ac.uk

<sup>2</sup>Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, trav. 14, n° 321, 05508-900 São Paulo, Brazil. E-mail: tkihara@ib.usp.br

<sup>3</sup>Corresponding author

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## Abstract

Both sexes of a new species of *Noodtorthopsyllus* Lang, 1965 (Harpacticoida, Cristacoxidae) from a sandy beach in São Paulo State (Brazil) are described using light and scanning electron microscopy. *Noodtorthopsyllus tageae* **sp. nov.** displays a mosaic of characters drawn from both *Noodtorthopsyllus* and *Cristacoxa* Huys, 1990, blurring the boundaries between both genera. Consequently, *Cristacoxa*, the type genus of the nominal family-group taxon Cristacoxidae Huys, 1990, is relegated to a junior subjective synonym of *Noodtorthopsyllus*, and its type species is transferred to the latter as *N. petkovskii* (Huys, 1990) **comb. nov.** A new genus *Acuticoxa* is proposed to accommodate *A. ubatubaensis* **sp. nov.** (type species), collected on the northern continental shelf of São Paulo State, and *A. biarticulata* **sp. nov.**, previously identified as *Laophontisochra* sp., from the Northern Magellan Straits. Amended diagnoses are provided for *Noodtorthopsyllus* and *Laophontisochra*.

Autapomorphies supporting the monophyly of the Cristacoxidae are re-evaluated, including new data on P3 endopod sexual dimorphism and caudal ramus development. It is concluded that a recently published hypothesis of a deeply rooted split of the family into two highly divergent lineages cannot be supported. Consequently, both *Laophontisochra* and *Acuticoxa* **gen. nov.** are removed from the Cristacoxidae and tentatively assigned to the Nannopodidae (*ex* Huntetanniidae), forming a clade with three other genera displaying coxal modifications on leg 1 (*Rosacletodes* Wells, 1985; *Huntemannia* Poppe, 1884; and an as yet undescribed genus from Brazil). Based on the sexual dimorphism of the P4 endopod, we propose to transfer *Metahuntemannia* Smirnov, 1946 and *Pottekia* Huys, 2009 from the Nannopodidae to the Canthocamptidae (subfamily Hemimesochrinae) where they are probably most closely related to *Psammocamptus* Mielke, 1975; *Bathycamptus* Huys & Thistle, 1989; *Perucamptus* Huys & Thistle, 1989; and *Isthmiocaris* George & Schminke, 2003. An identification key to the genera of the Nannopodidae is presented.

**Key words:** *Acuticoxa* **gen. nov.**, *Noodtorthopsyllus tageae* **sp. nov.**, *Cristacoxa*, *Cubanocleta*, *Noodtorthopsyllus*, *Laophontisochra*, Nannopodidae, caudal ramus development, phylogeny

## Introduction

Huys (1990) established the harpacticoid family Cristacoxidae to accommodate three monotypic genera from primarily intertidal sandy habitats: *Noodtorthopsyllus* Lang, 1965, *Cubanocleta* Petkovski, 1977 and *Cristacoxa* Huys, 1990. The family was placed in the Laophontoidea T. Scott, 1905 on the basis of the presence of a posterior process on the second antennular segment, fusion of the antennary basis and proximal endopodal segment forming an allobasis, absence of an inner seta on P1 exp-2 and presence of only four elements on exp-3, 2-segmented P1 endopod with elongate enp-1 and only 2 elements on enp-2, at most 2-segmented condition of P2–P4 endopods, sexual dimorphism on P3 endopod (apophysis in male homologous to outer spine of female), and male sixth legs showing dimorphic asymmetry and bearing two elements each. According to Huys (1990) and Huys and Lee (1998/99) the Cristacoxidae shares a sistergroup relationship with the Laophontopsidae Huys & Willems, 1989 and the monophyly of the former is supported by an extensive suite of autapomorphies, including the extremely long and slender spermatophore with curled neck, presence of a posterior spinous process on the first antennular segment, absence of the antennary exopod and abexopodal seta, uniramous 2-segmented mandibular palp with asetose basis, presence of a modified basally fused spine on the proximal coxal endite of the maxilla, presence of outer cristae on the praecoxa and coxa of P1 and four geniculate setae on P1 exp-3, elongation of the apical exopodal spines of P2–P4, and pedomorphic origin of the fifth legs (*cf.* Huys 1990: 102–103), forming a common plate in both sexes.

The proposal of the genus *Laophontisochra* George, 2002 for the type species *L. maryamae* George, 2002 and a second unnamed species challenged the phylogenetic significance of the majority of Huys' (1990) cristacoxid autapomorphies, since this genus displayed distinctly more primitive character states (*e.g.* no spinous processes on antennule, antenna with vestigial exopod (and with abexopodal seta in *Laophontisochra* sp.), mandible with exopod and 2 setae on basis, biramous P5 in the type species) than any other cristacoxid (George 2002). In the absence of information on the male, George (2002) assigned *Laophontisochra* to the Cristacoxidae on the basis of limited supporting evidence, *i.e.* the presence of a crista on the coxa of P1, and a newly defined apomorphic state, the elongate maxillipeds. The former character state could, however, not be confirmed for *Laophontisochra* sp. and the evolutionary significance of morphometric characters at suprageneric level, such as maxillipedal size, has yet to be assessed in copepods. This is particularly the case

when the morphology of the limb concerned exhibits significant differences between the taxa under comparison. The maxilliped of *Laophontisochra* diverges from the typical cristacoxid condition in the presence of a geniculate claw and the absence of the syncoxal seta and most, if not all, elements accompanying the claw on the endopod. Although George (2002) did consider the option that *Laophontisochra* may not be a cristacoxid (consequently implying convergent evolution of the cristae on leg 1) he preferred to expand the Cristacoxidae to a more inclusive taxon, encompassing two divergent lineages. However, the morphological disparity between them is such that a dual origin of the protopodal cristae on leg 1 should be given more consideration as a plausible alternative.

The family Cristacoxidae has a primarily ampho-Atlantic distribution (Noodt 1955; Petkovski 1977; Huys 1990) with one recorded eastern Pacific outlier from the Galapagos (Huys 1990). Here we describe a new species of *Noodtorthopsyllus* from a sandy beach in São Sebastião, Brazil, and a new genus, closely related to *Laophontisochra*, from the inner continental shelf off Ubatuba, São Paulo State. The newly acquired Brazilian data is used to re-assess the generic distinction between *Noodtorthopsyllus* and *Cristacoxa* as initially defined by Huys (1990), and monophyly and family concept of the Cristacoxidae as proposed by George (2002).

## Material and methods

All material of *Noodtorthopsyllus tageae* **sp. nov.** was collected by Dr Guilherme Lotufo during an inventory of the interstitial fauna along the coast of São Paulo State as part of his PhD project “Psammic copepod crustaceans from the beaches of the State of São Paulo – Crustáceos Copépodes Psâmicos de Praias do Estado de São Paulo” at the Department of Zoology, Institute of Biosciences, University of São Paulo (IBUSP). Sandy beaches were sampled from Ubatuba to Cananéia between June 1990 and July 1991, using the modified Karaman-Chappuis sampling method as described by Pleša (1964).

The material described as a new genus was obtained during an ecological investigation of the meiofaunal diversity along the northern continental shelf and coastal areas of São Paulo State, as part of the project “Rational use of the coastal ecosystem from the Brazilian tropical region: São Paulo State” coordinated by the Departamento de Oceanografia Biológica, Instituto Oceanográfico da Universidade de São Paulo (IOUSP). Samples were collected at 12 stations along the inner continental shelf (15–53 m depth) between São Sebastião Island and Ubatumirim inlet (Ubatuba) during March and August 1989. Description of the sampling methodology and physical and chemical analysis is given by Corbisier (1993).

Before dissection, the habitus was drawn from whole specimens temporarily mounted in lactophenol. Adhesive plastic rings were used to support the coverslip in temporary mounts. Specimens were dissected in lactic acid and the dissected parts were mounted on slides in lactophenol mounting medium. Preparations were sealed with transparent nail varnish. All drawings were prepared using a camera lucida on a Zeiss Axioskop 2 Plus differential interference contrast microscope. Total body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. The descriptive terminology is adopted from Huys *et al.* (1996b). Abbreviations used in the text are: *ae*, aesthetasc; *P1–P6*, swimming legs 1–6; *exp*, *enp* and *benp*, exopod, endopod and baseoendopod, respectively; *exp (enp)-1* (-2, -3), proximal (middle, distal) segment of exopod (endopod). The term ‘acrothek’ denotes the trifid setal structure typically found on the apical margin of the distal antennular segment (Huys & Iliffe 1998). Type material is deposited in the collections of the Museu de Zoologia, Universidade de São Paulo (MZUSP) and the Natural History Museum, London (NHM).

Three females and three males of *Noodtorthopsyllus tageae* **sp. nov.** were prepared for scanning electron microscopy (SEM). Specimens were dehydrated through a series of graded acetone, critical-point dried, mounted on stubs, sputter-coated with palladium and observed using a Philips XL 30 field emission scanning electron microscope.

## Taxonomic account

### Order Harpacticoida Sars, 1903

#### Family Cristacoxidae Huys, 1990

**Diagnosis (amended).** Laophontoidea. Body cylindrical, no clear demarcation between prosome and urosome. First pedigerous somite fused to cephalosome. Pleurotergites of pedigerous somites slightly developed. Cephalic shield with pattern of cuticular pits. Rostrum large and broad, completely defined at base; with two sensilla and a ventral, subapical tube-pore. Genital and first abdominal somites completely fused in ♀, forming genital double-somite; original segmentation marked by almost continuous internal, transverse chitinous rib, and by surface ornamentation both laterally and dorsally. Anal operculum moderately developed; pseudoperculum absent. Caudal rami with 7 setae (seta V longest, sometimes bi-articulate); setae V and VI not forming a setal complex in copepodid I and seta V expressed as the principal seta during the entire copepodid development; with large spinous processes at inner distal corner and around posterior margin between setae III and IV, and smaller ones at the bases of setae I, III and VII. Sexual dimorphism in antennule, endopod P3 (distal inner and outer apical setae strongly reduced or absent in ♂; outer spine (*Cubanocleta*) or proximal inner seta (*Noodtorthopsyllus*) modified into an apophysis (ramus secondarily subdivided into 2 pseudosegments in *Noodtorthopsyllus*), P5, P6 and in genital segmentation; sometimes in P1 (length of inner seta on enp-1), P2 endopod, P4 (both rami), and caudal rami.

Antennule short, with posterior spinous process on segments I (prominent) and II (weakly developed); with numerous pinnate setae and spines; 4-segmented in female, with aesthetasc on segment III; 5-segmented and modified (segment IV extremely swollen, segments distal to geniculation fused) in male with geniculation between segments IV and V and with aesthetasc on segment IV and sometimes V (as part of apical acrothek). Antenna with allobasis; abexopodal seta and exopod absent; endopod with 2 spines and 1 vestigial seta medially, and 6 elements (2 pinnate spines, 3 geniculate setae, 1 vestigial seta) distally. Labrum undivided. Mandible with 2-segmented uniramous palp, comprising unarmed basis and 1-segmented endopod with 4 setae. Paragnaths well developed, strongly ornamented lobes. Maxillule with 1-segmented, bisetose exopod; endopod incorporated into basis, represented by 3 setae; basal endites well defined, proximal one with 2 setae, distal one with 1 geniculate claw and 2 setae. Maxillary syncoxa with 2 or 3 endites, praecoxal endite (when present) vestigial, with 1 seta; proximal coxal endite with modified, basally fused spine and 2 setae; distal coxal endite with 3 setae; endopod incorporated into basis, with 2–3 setae. Maxilliped with syncoxa bearing 1 seta; basis unarmed; endopod 1-segmented with 1 long claw and 2 accompanying setae.

P1 with well developed 3-segmented protopod; praecoxa (one) and coxa (two) with conspicuous serrate crests (cristae) around outer margin; basis with inner spine/seta located on anterior surface near the inner margin, without genuine pedestal for insertion of endopod; exopod 3-segmented, exp-3 with 4 geniculate setae; endopod prehensile, 2-segmented with elongated enp-1 (sometimes bearing inner seta) and short enp-2 with 1 short claw and 1 long, geniculate claw. P2–P4 outer margin of coxa with serrate crista (P2–P3) or sometimes lobate outgrowth (P4); exopods 3-segmented; endopods 1- (P3–P4; sometimes P2) or 2-segmented (sometimes P2); outer elements of exp-3 typically elongate and setiform. Spine and setal formula as follows (variation shown in brackets):

	Exopod	Endopod
P1	0.0.022	[0–1].020
P2	0.[0–1].122	1.120 or 220 (♀) [0–1].120 or 220 (♂)
P3	0.[0–1].222	22[0–1]
P4	0.0.222	[1–2]20

Fifth pair of legs not fused medially, defined at the base, remnant of intercoxal sclerite present, no distinction between exopod and baseoendopod; with 8 setae in both sexes.

Female gonopores not fused medially and each covered laterally by vestigial P6 bearing 2 tiny setae and sometimes very long seta; copulatory pore large, located in median depression; seminal receptacles paired, well defined. One egg-sac.

Male sixth pair of legs asymmetrical, with 2 setae each; either left or right P6 fused to ventral wall of genital somite, other member articulating and closing off single functional gonopore. Spermatophore extremely long, up to 1/3 of body length, with long curled neck. Male grasping terminal setae of caudal rami of female during precopulatory mate guarding.

Marine, interstitial, freeliving.

**Included genera:** *Noodtorthopsyllus* Lang, 1965 (type), *Cubanocleta* Petkovski, 1977.

## Genus *Noodtorthopsyllus* Lang, 1965

**Synonym.** *Cristacoxa* Huys, 1990 **syn. nov.**

**Diagnosis.** Sexual dimorphism in antennule, P1 endopod, P3 endopod, P5, P6 and in genital segmentation; occasionally in endopod of P2 and P4. Rostrum triangular, completely defined at base. Fusion of female genital double-somite demarcated by almost continuous internal transverse chitinous rib, and by surface ornamentation both laterally and dorsally. Caudal ramus seta V bi-articulated, consisting of styliform proximal part and flagelliform distal part.

Antennule with posterior spinous process on segment I and small or rudimentary process on segment II. Maxillary syncoxa with 2–3 endites; when present, praecoxal endite represented by 1 seta; endopod represented by 2–3 setae.

P1 with well developed serrate crests on praecoxa and coxa; enp-1 with or without inner seta (when present then sexually dimorphic in size). Coxa with crest around outer margin in P2–P3, and sometimes with lobate extension in P4. P2 with 2-segmented endopod; with inner seta on exp-2 in ♀, sometimes absent in ♂. P3 with inner seta on exp-2; endopod with or without outer spine in ♀; endopod subdivided in 2 pseudosegments in ♂, bearing long, sigmoid, inner apophysis on proximal pseudosegment (homologous with proximal inner seta of ♀) and one long pinnate apical seta and 1–2 vestigial elements on distal pseudosegment. Spine and setal formula as follows (variation shown in brackets):

	Exopod	Endopod
P1	0.0.022	[0–1].020
P2	0.1.122	1.120 (♀) [0–1].120 (♂)
P3	0.1.222	22[0–1]
P4	0.0.222	[1–2]20

P5 not bilobate, with 8 elements in both sexes. P6 ♀ with 1 pinnate seta.

**Type species:** *Orthopsyllus psammophilus* Noodt, 1955 [= *Noodtorthopsyllus psammophilus* (Noodt, 1955), by original designation].

**Other species:** *Cristacoxa petkovskii* Huys, 1990 [= *N. petkovskii* (Huys, 1990) **comb. nov.**; *N. tageae* **sp. nov.**]

### *Noodtorthopsyllus tageae* sp. nov.

(Figs 1–13)

**Type locality.** Brazil, São Paulo State, São Sebastião, São Francisco Beach (23°45'42.6" S, 45°24'27.7" W).

**Type material.** Holotype ♀ in ethanol (reg. no MZUSP 19623), collected September 1990. Undissected paratypes (in ethanol) deposited in MZUSP (reg. nos 19624–19625) are 2 ♀♀ and 2 ♂♂ (collected September 1990) and 2 ♀♀ and 2 ♂♂ (collected March 1991). Additional undissected paratypes (in ethanol) deposited in NHM are 2 ♀♀ [reg. nos 2009.8 (collected September 1990) and 2009.10 (collected March 1991)] and 2 ♂♂ [reg. nos 2009.9 (collected September 1990) and 2009.11 (collected March 1991)]. Dissected paratypes are retained in the collection of C.E.F. da Rocha (Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo): 1 ♀ and 1 ♂ (September 1990); 1 ♀ and 1 ♂ (collected March 1991). Registered naupliar and copepodid specimens used in the study of caudal ramus development deposited in NHM. All material collected from the type locality by G. Lotufo.

**Description.** FEMALE (Figs 1–6, 10–12). Total body length 494–575 µm ( $N = 8$ ; mean = 540 µm; holotype = 535 µm). Largest width measured at posterior margin of cephalic shield: 108–124 µm ( $N = 8$ ; mean = 117 µm). Body (Fig. 1A–B) cylindrical, without marked constrictions between somites. Urosome slightly narrower than prosome.

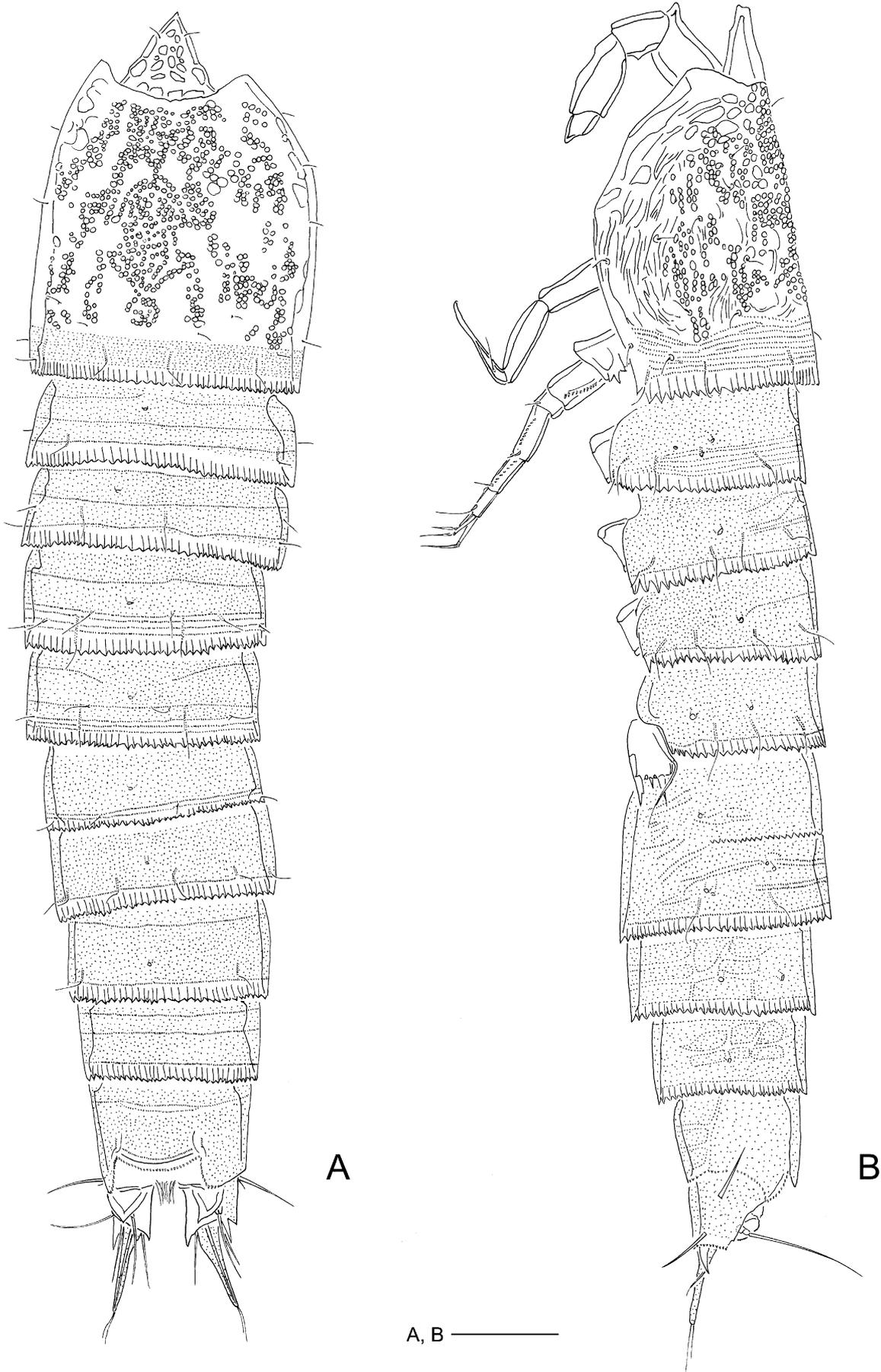
Rostrum (Fig. 2A) triangular, with broad base; completely defined at base; with pair of tiny sensillae subterminally and a midventral tube-pore near apex; dorsal surface with pattern of integumental depressions.

Cephalothorax (Fig. 1A–B) tapering towards rostrum; pleural areas moderately developed; integument with small, round depressions forming essentially symmetrical pattern; ornamentation consisting of sensillae and minute spinules as illustrated; posterior margin serrate. Pedigerous somites (Fig. 1A–B) covered with minute spinules and ornamentation consisting of sensillae and pores as illustrated; posterior margins serrate. Urosome (Figs 1A–B; 2B; 10A, C–E) 5-segmented, comprising P5-bearing somite, genital double-somite, 2 free abdominal somites and anal somite. Urosomites with surface ornamentation consisting of sensillae and minute spinules; ventral and ventrolateral spinules arranged in symmetrical pattern (Figs 2B; 10A, E); posterior margin serrate (Fig. 10C). Genital double-somite (Figs 1A–B; 2B; 10A, E) completely fused ventrally; original segmentation indicated by transverse, serrate surface ridge dorsally and dorsolaterally; surface ornamentation around genital field consisting of minute spinules and pores (Fig. 2C); large copulatory pore located in median depression (Figs 2C; 10A–B); gonopores fused medially forming single genital slit covered on both sides by opercula derived from sixth legs; P6 with small protuberance bearing 1 pinnate seta (Fig. 2A). Anal somite (Figs 1A–B; 2D) with moderately developed, rounded, serrate anal operculum flanked by row of multiserrate processes; anal opening (Fig. 2D) with fringe of fine setules; surface ornamentation consisting of a pair of sensillae and pores dorsally, and 2 pairs of pores ventrally; midventral posterior margin with serrate projections (Fig. 10D).

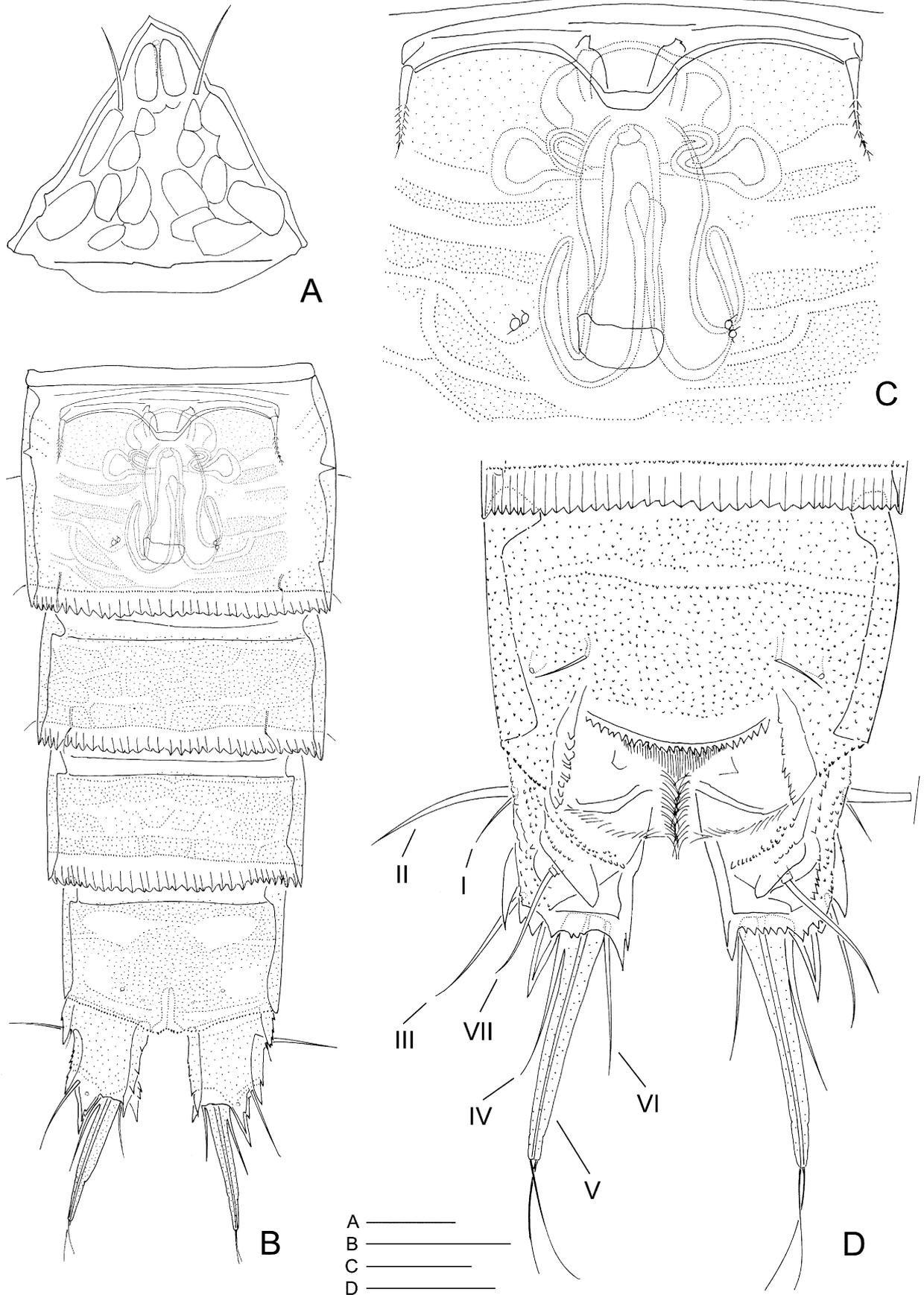
Caudal rami (Figs 2B, D; 3A–B; 11A) short, slightly longer than maximum width; tapering posteriorly. Each ramus with 1 ventral pore and 7 setae of which most are flanked by spinous processes: seta I naked, shortest and closely set to naked seta II; seta III naked and positioned ventrolaterally; setae IV and V fused basally; seta V consisting of styliform proximal part, sparsely covered with minute denticles, and very short bi-setular distal part (Figs 2D; 11B); seta VI naked; seta VII tri-articulate at base. Surface ornamentation of ramus consisting of minute spinules as shown in figures 2D, 3A–B and 11A.

Antennule (Fig. 3C) 4-segmented and with complex reticulate surface pattern as shown in figure 11D. Segment I with long posterior and short anterior spinous process, one setular array and one spinular patch; posterior margin of segment II without real process but with rudimentary, blunt protuberance; segment II with 2 modified setae bearing circular array of spinules (Fig. 11D); segment III longest with aesthetasc fused basally to seta and set on distinct pedestal; segment IV without aesthetasc. Armature formula: I-[1], II-[6+ 1 plumose + 2 modified], III-[8+ 1 pinnate + (1+ae)], IV-[8+ 1 pinnate + acrothek]. Acrothek reduced, consisting of 2 basally fused setae.

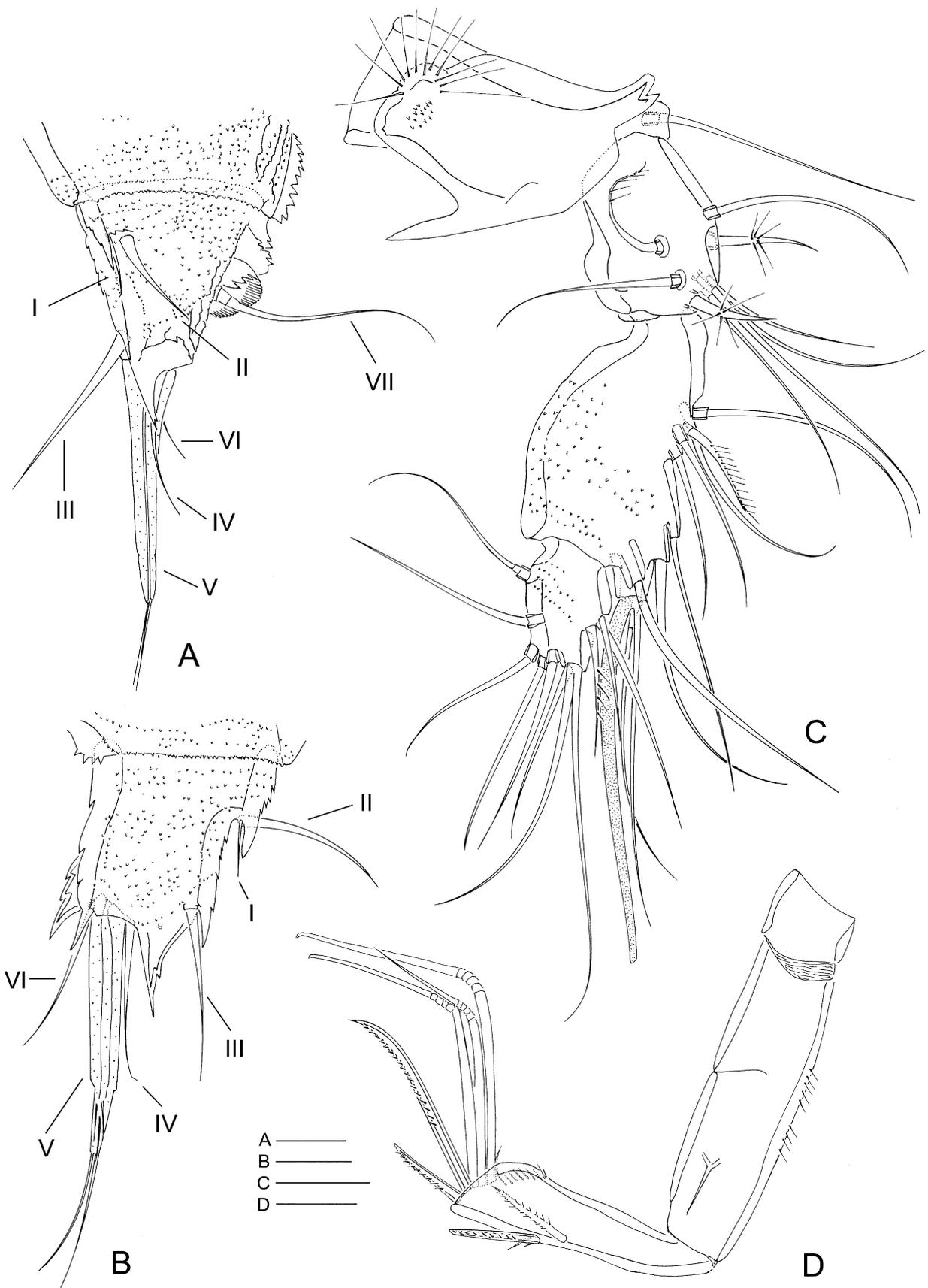
Antenna (Figs 3D; 11E–F) 3-segmented comprising coxa, allobasis and free 1-segmented endopod. Coxa small with no ornamentation. Basis and proximal endopod segment fused forming elongate allobasis, with minute spinules along abexopodal margin, abexopodal seta and exopod absent. Free endopod slightly shorter than allobasis; ornamented with row of spinules distally; medial armature consisting of 1 pinnate spine, 2 setae (1 small naked and 1 pinnate) and 1 short spinule (Fig. 11F); apical armature consisting of 2 pinnate spines and 3 geniculate setae, outermost one of which fused basally to short seta.



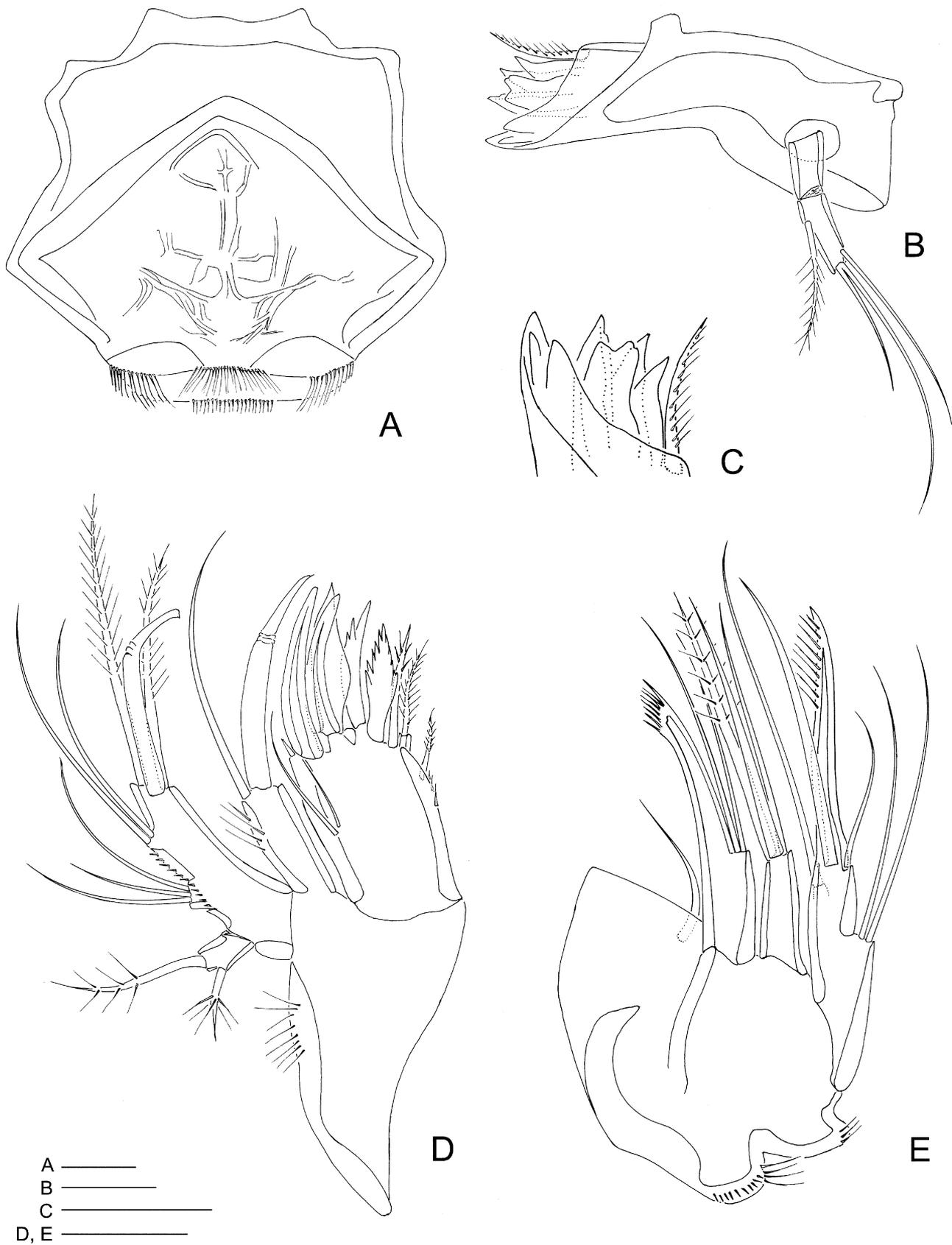
**FIGURE 1.** *Noodtorthopsyllus tageae* sp. nov. (♀): (A) habitus, dorsal; (B) habitus, lateral. Scale bars: 50 µm.



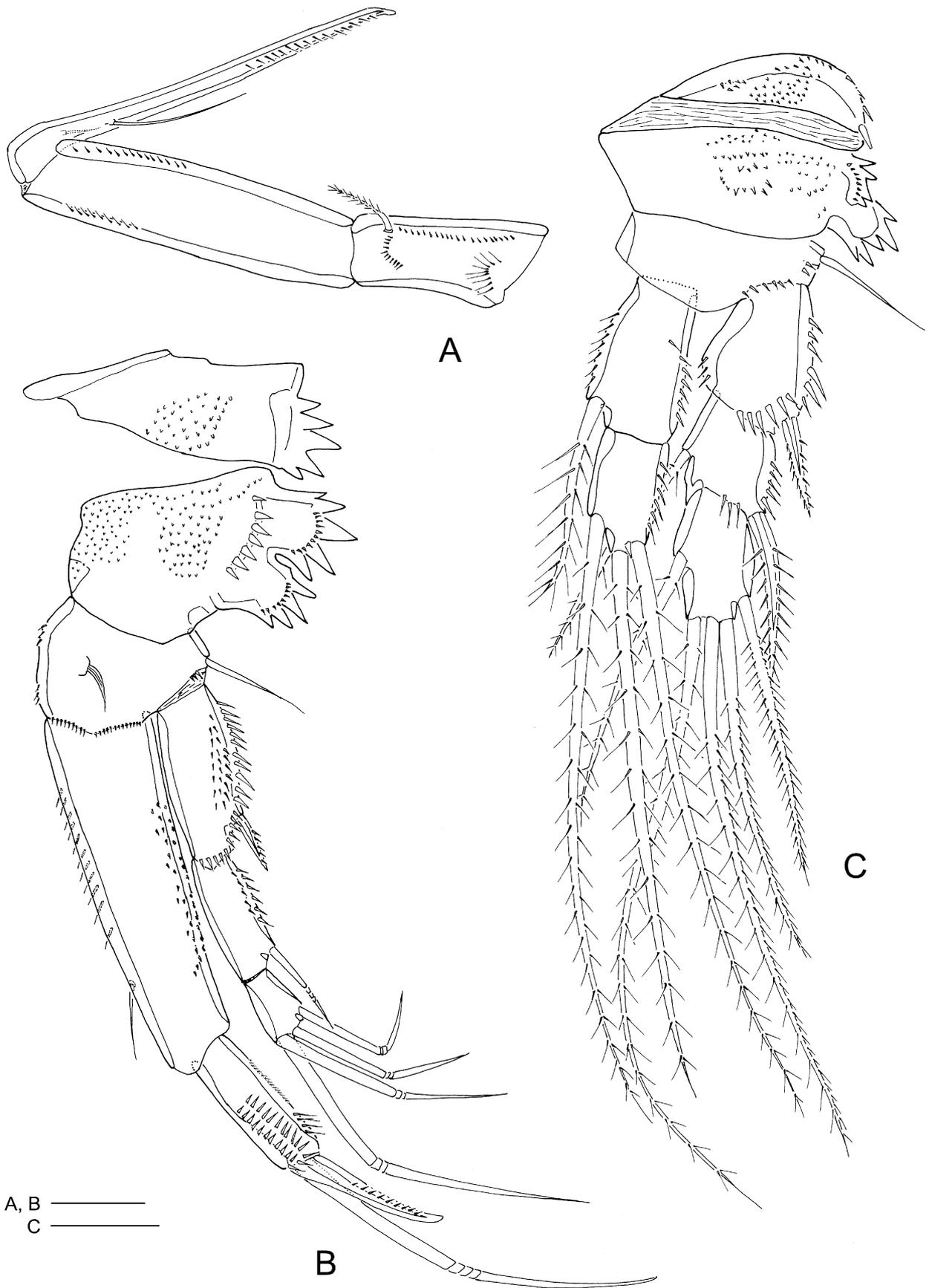
**FIGURE 2.** *Noodtorthopsyllus tageae* sp. nov. (♀): (A) rostrum, dorsal; (B) urosome, ventral [segment bearing P5 omitted]; (C) genital field; (D) anal somite and caudal rami, dorsal. Scale bars: 25  $\mu$ m.



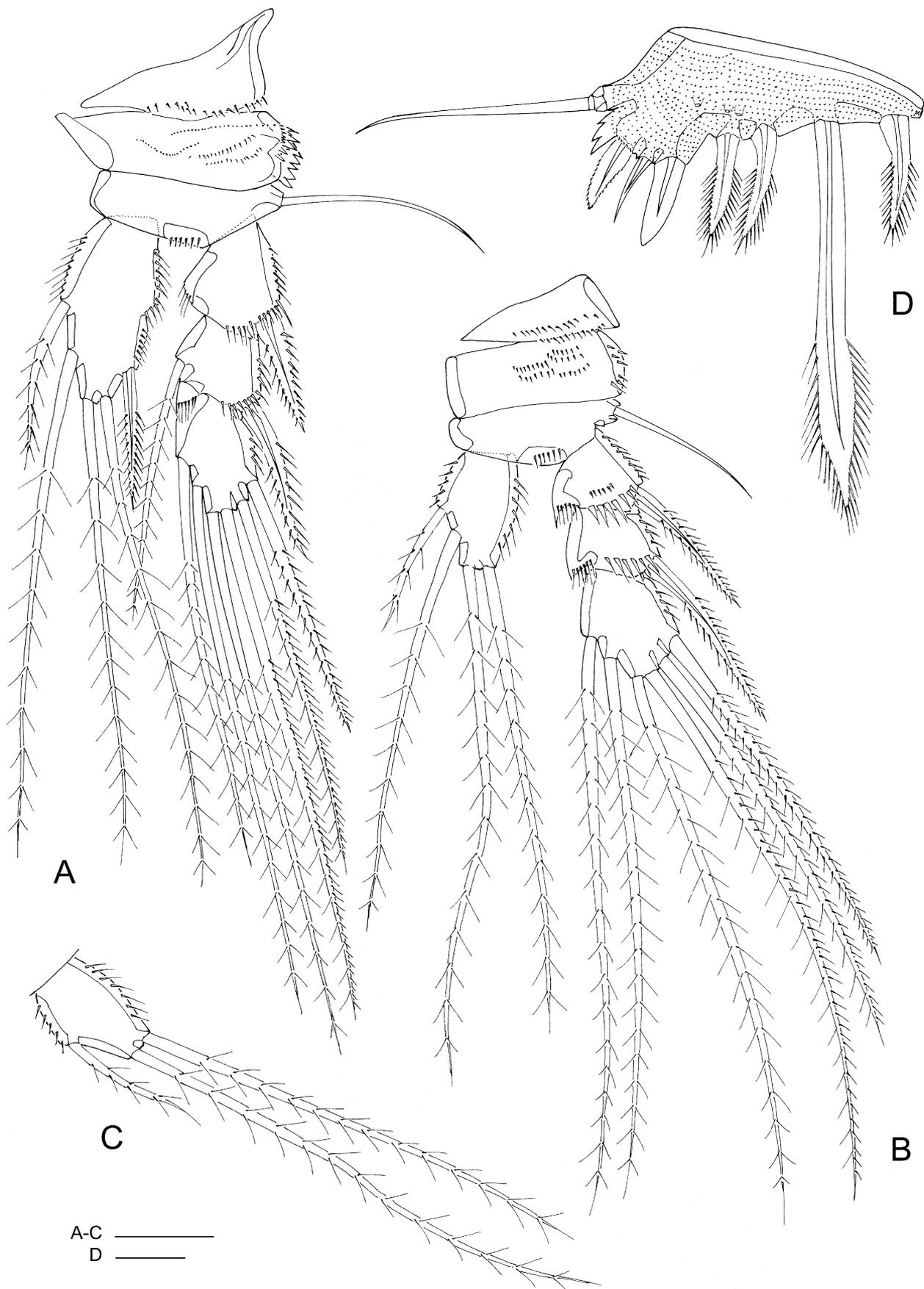
**FIGURE 3.** *Noodtorthopsyllus tageae* sp. nov. (♀): (A) caudal ramus, lateral; (B) caudal ramus, ventral; (C) antennule, dorsal; (D) antenna. Scale bars: 12.5  $\mu$ m.



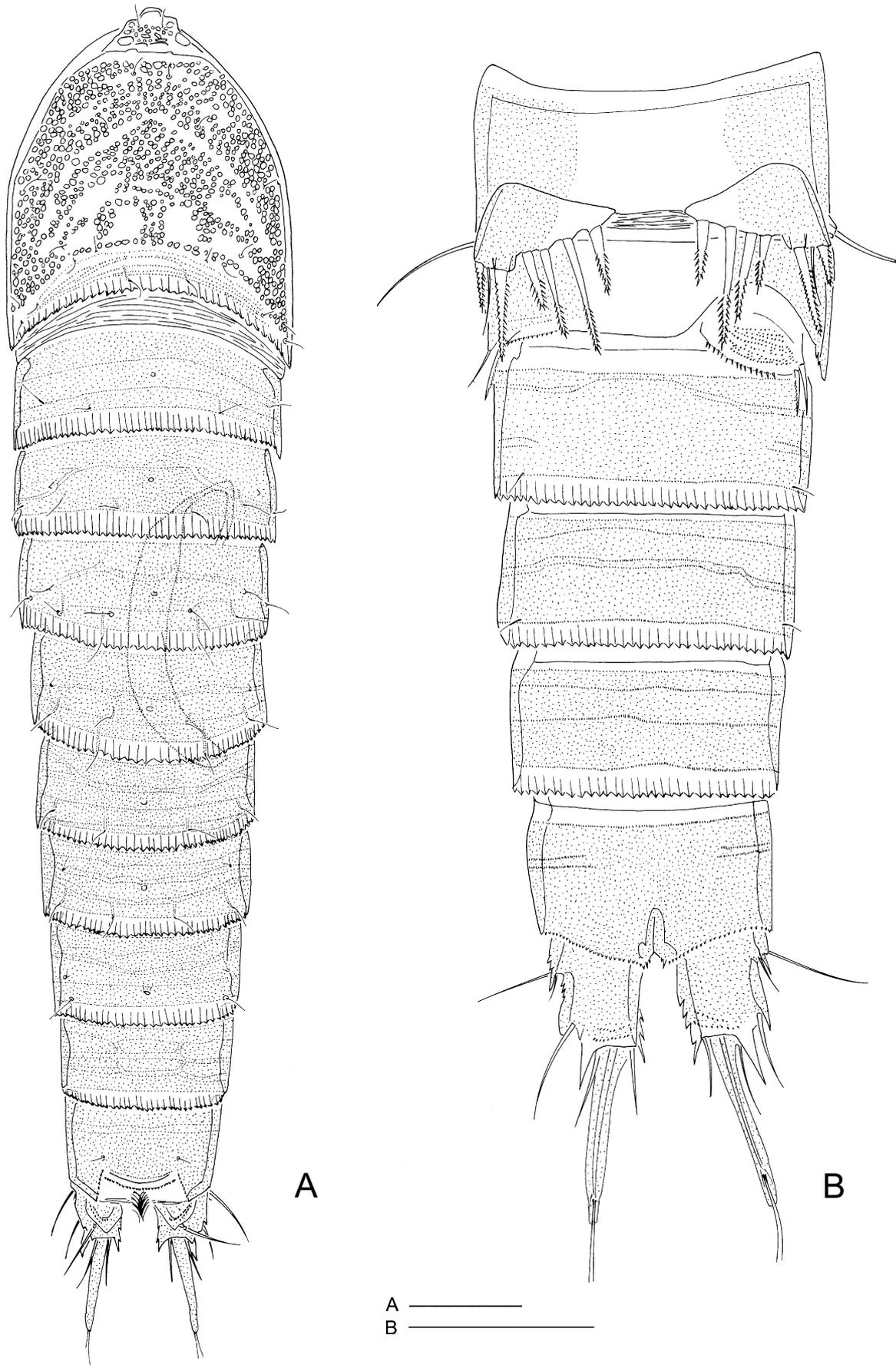
**FIGURE 4.** *Noodtorthopsyllus tageae* sp. nov. (♀): (A) labrum, anterior; (B) mandible; (C) mandibular gnathobase; (D) maxillule; (E) maxilla. Scale bars: 12.5 µm.



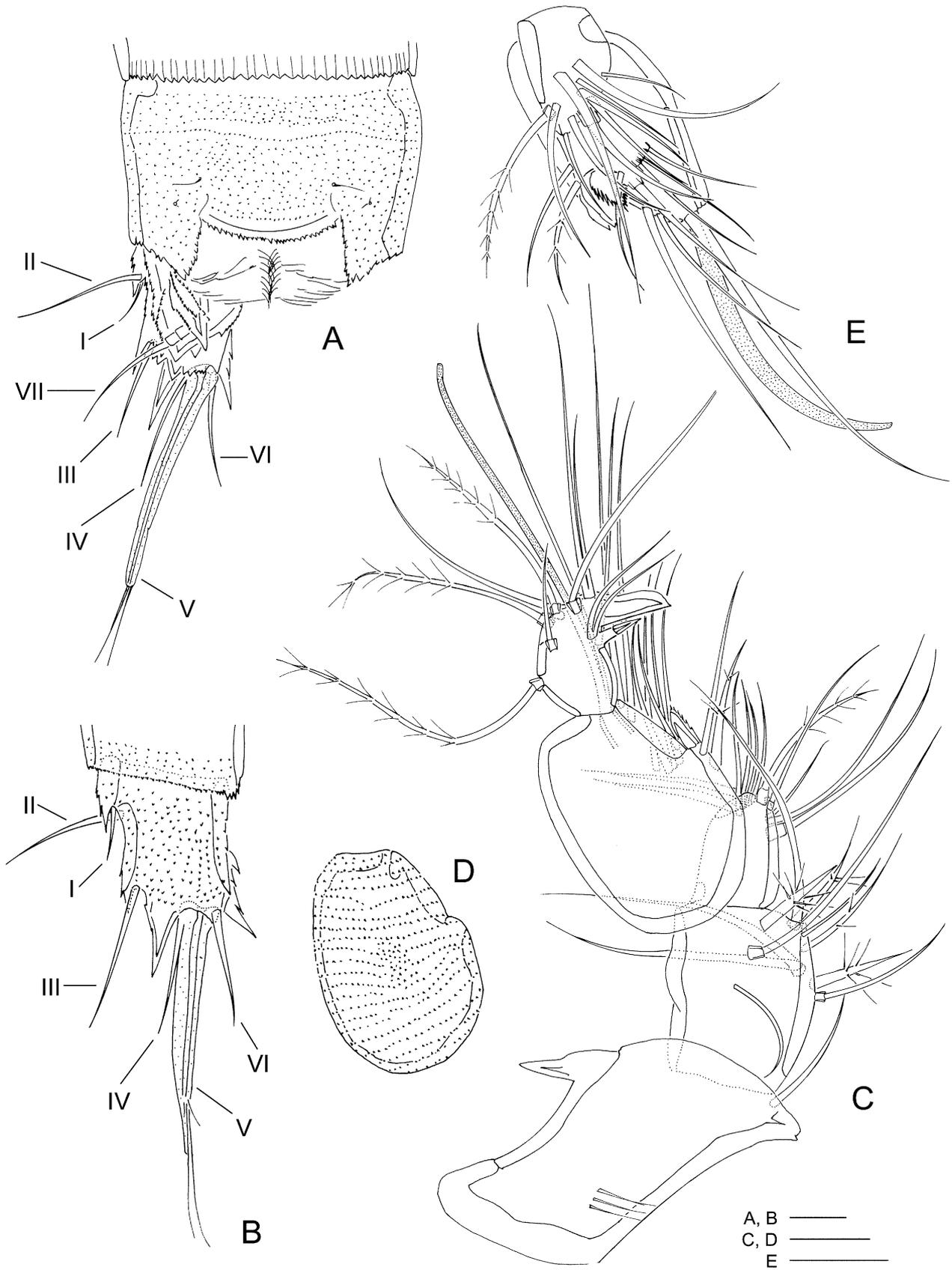
**FIGURE 5.** *Noodtorthopsyllus tageae* sp. nov. (♀): (A) maxilliped; (B) P1, anterior; (C) P2, anterior. Scale bars: 12.5  $\mu\text{m}$ .



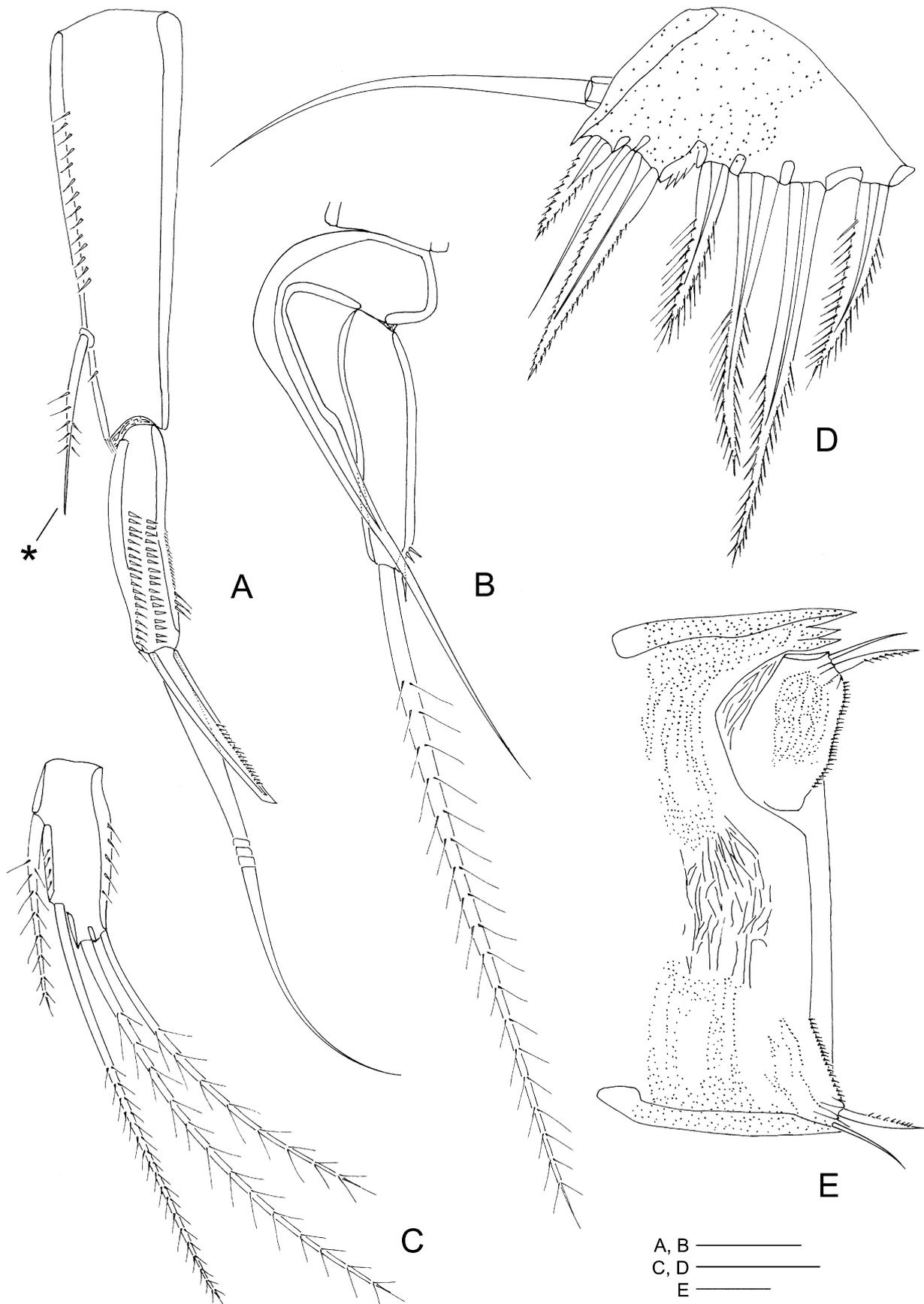
**FIGURE 6.** *Noodtorthopsyllus tageae* sp. nov. (♀): (A) P3, anterior; (B) P4, anterior; (C) P4 endopod with aberrant armature pattern; (D) P5, anterior. Scale bars: 12.5  $\mu$ m.



**FIGURE 7.** *Noodtorthopsyllus tageae* sp. nov. (♂): (A) habitus, dorsal; (B) urosome, ventral. Scale bars: 50  $\mu$ m.



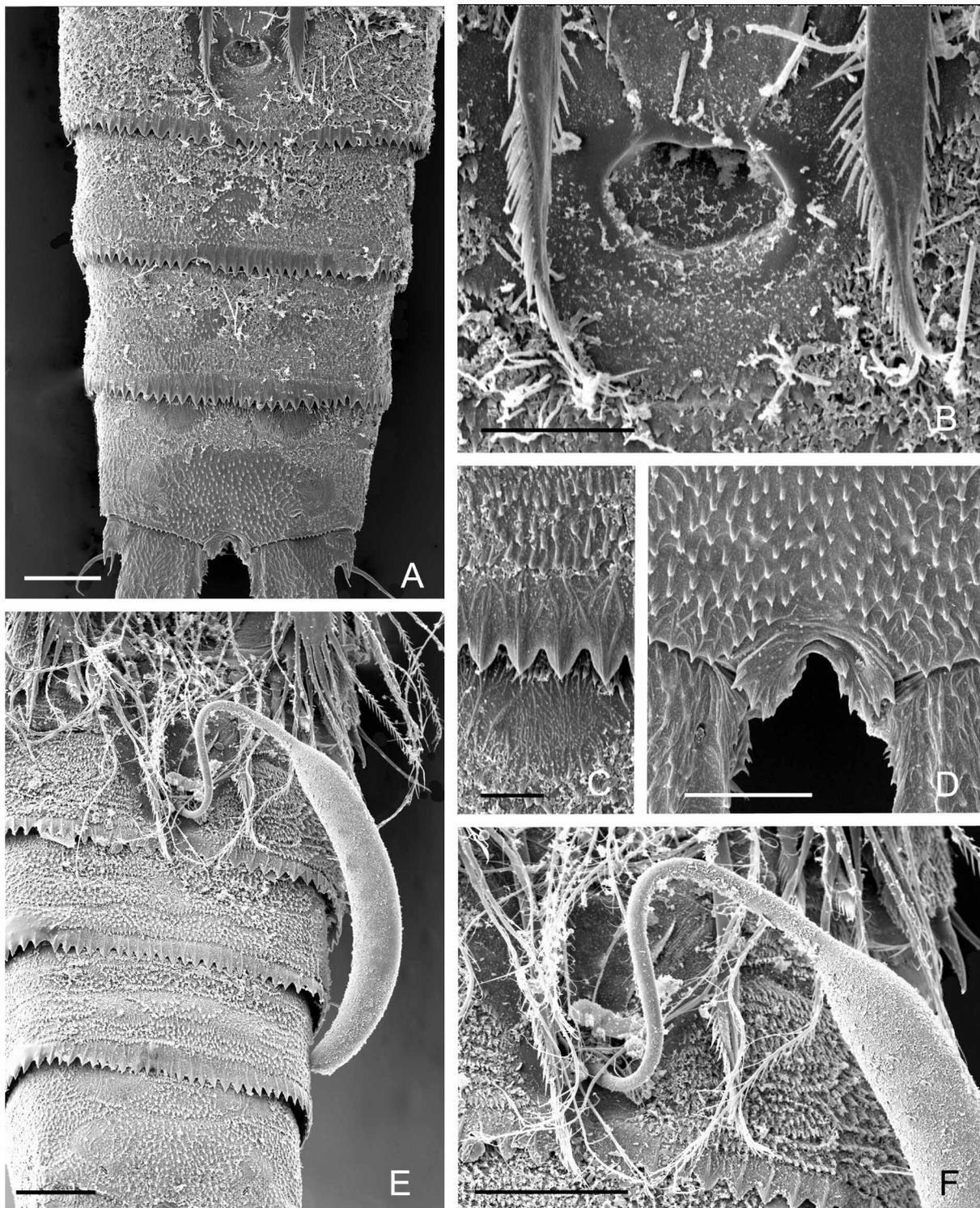
**FIGURE 8.** *Noodtorthopsyllus tageae* sp. nov. (♂): (A) anal somite and caudal ramus, dorsal; (B) caudal ramus, ventral; (C) antennule, dorsal; (D) fourth antennulatory segment [armature omitted]; (E) antennulatory segments 4–5, anterior. Scale bars: 12.5  $\mu$ m.



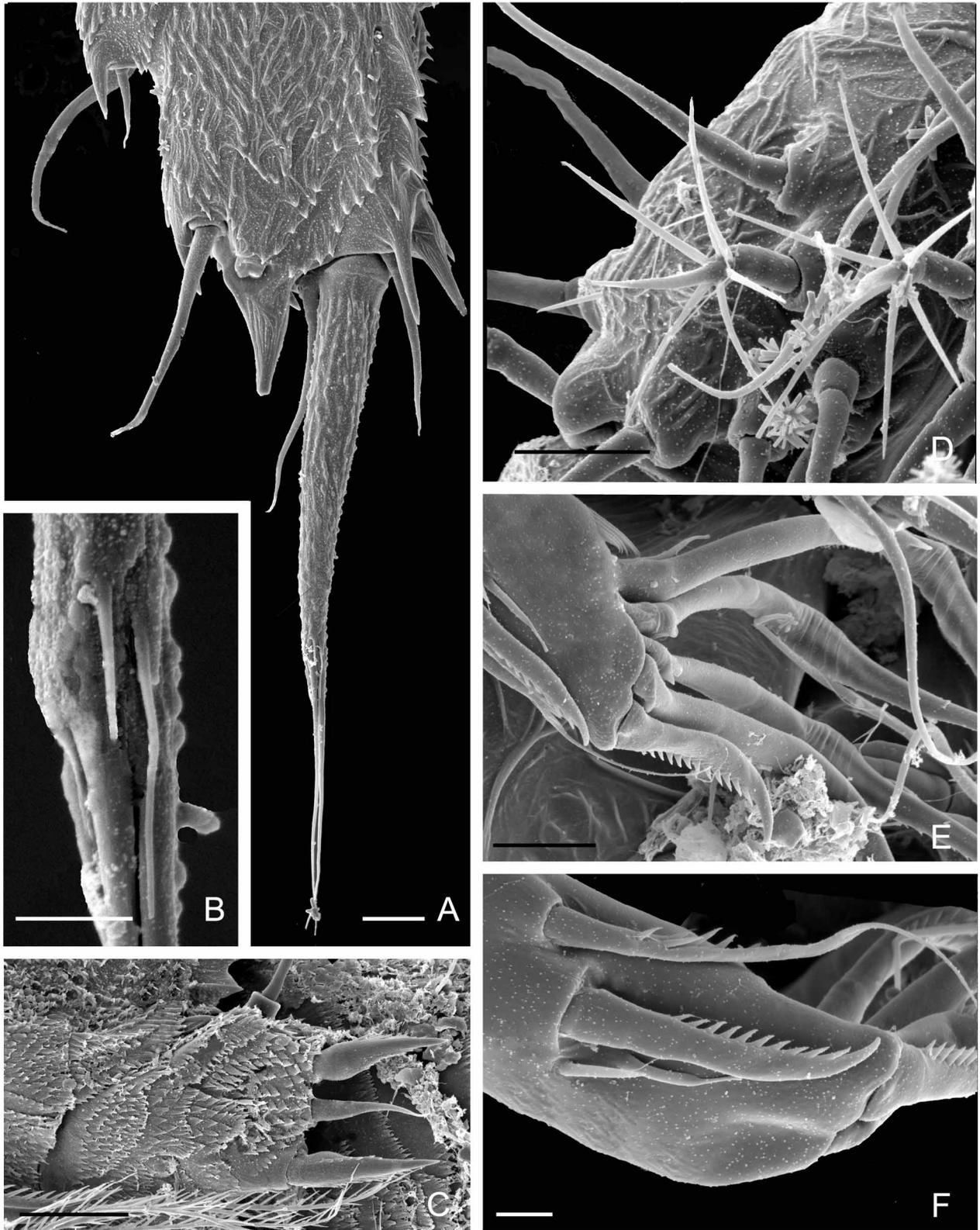
**FIGURE 9.** *Noodtorthopsyllus tageae* sp. nov. (♂): (A) P1 endopod, anterior [asterisk indicating sexually dimorphic inner seta]; (B) P3 endopod, anterior; (C) P4 endopod, anterior; (D) P5, anterior; (E) sixth pair of legs, anterior. Scale bars: 12.5  $\mu$ m.

Labrum (Fig. 4A) well developed, with spinular ornamentation along distal margin; no pores discernible.

Mandible (Fig. 4B–C). Coxa with well developed gnathobase bearing several multicuspitate teeth and 1 pinnate seta around distal margin (Fig. 4C). Palp small and uniramous; basis asetose; exopod absent; endopod with 1 plumose seta medially, 1 subapical naked seta and 2 apical naked setae fused at base (Fig. 12B).



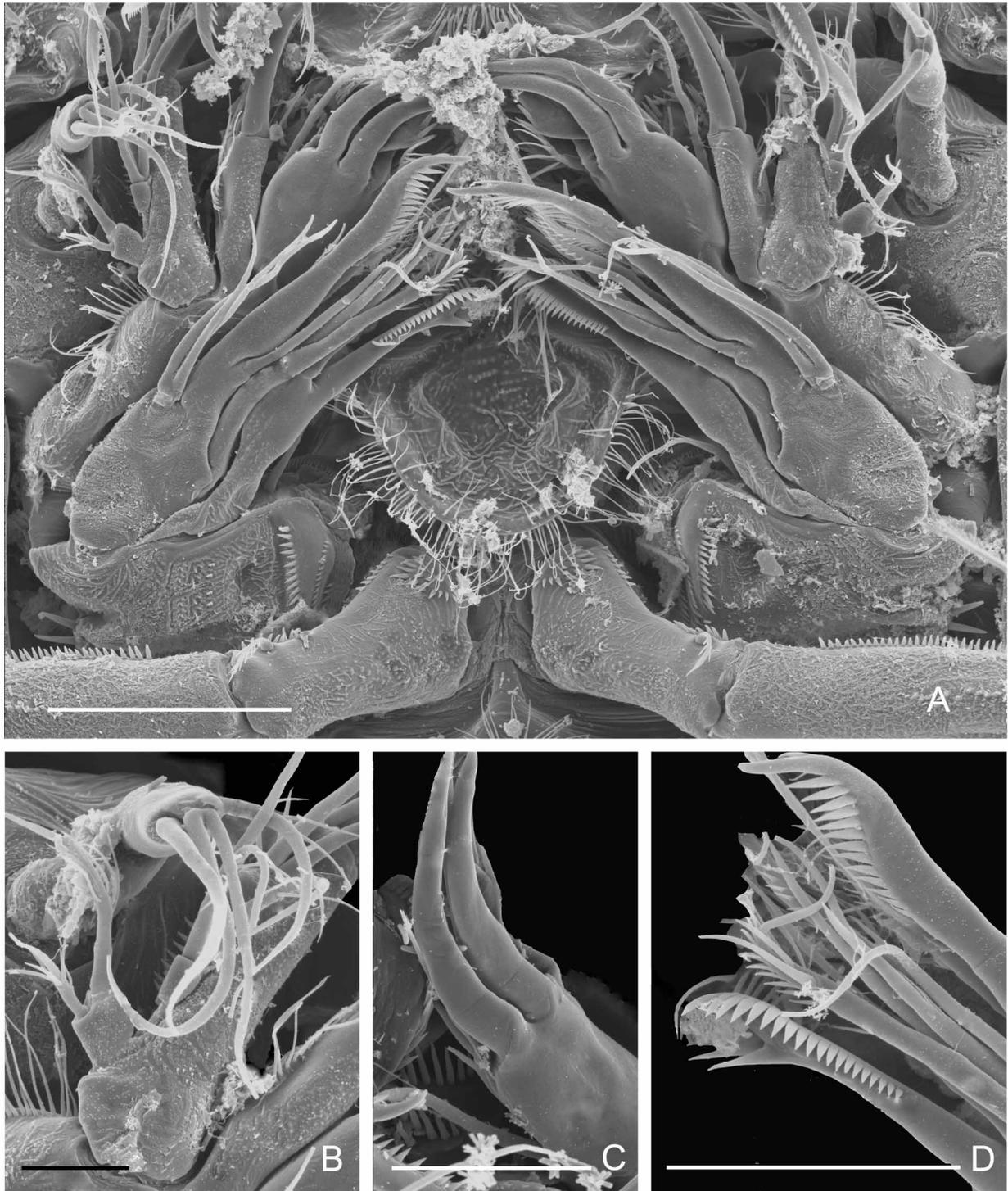
**FIGURE 10.** *Noodtorthopsyllus tageae* sp. nov. (♀), scanning electron micrographs: (A) urosome, ventral [segment bearing P5 omitted]; (B) copulatory pore; (C) detail of surface ornamentation and serrate posterior margin of urosomites, ventral; (D) detail of surface ornamentation and posterior margin of anal somite, ventral; (E) genital double-somite with spermatophore inserted in copulatory pore; (F) close-up of spermatophore neck inserted in copulatory pore. Scale bars: 5  $\mu$ m (C), 10  $\mu$ m (B, D), 20  $\mu$ m (A, E, F).



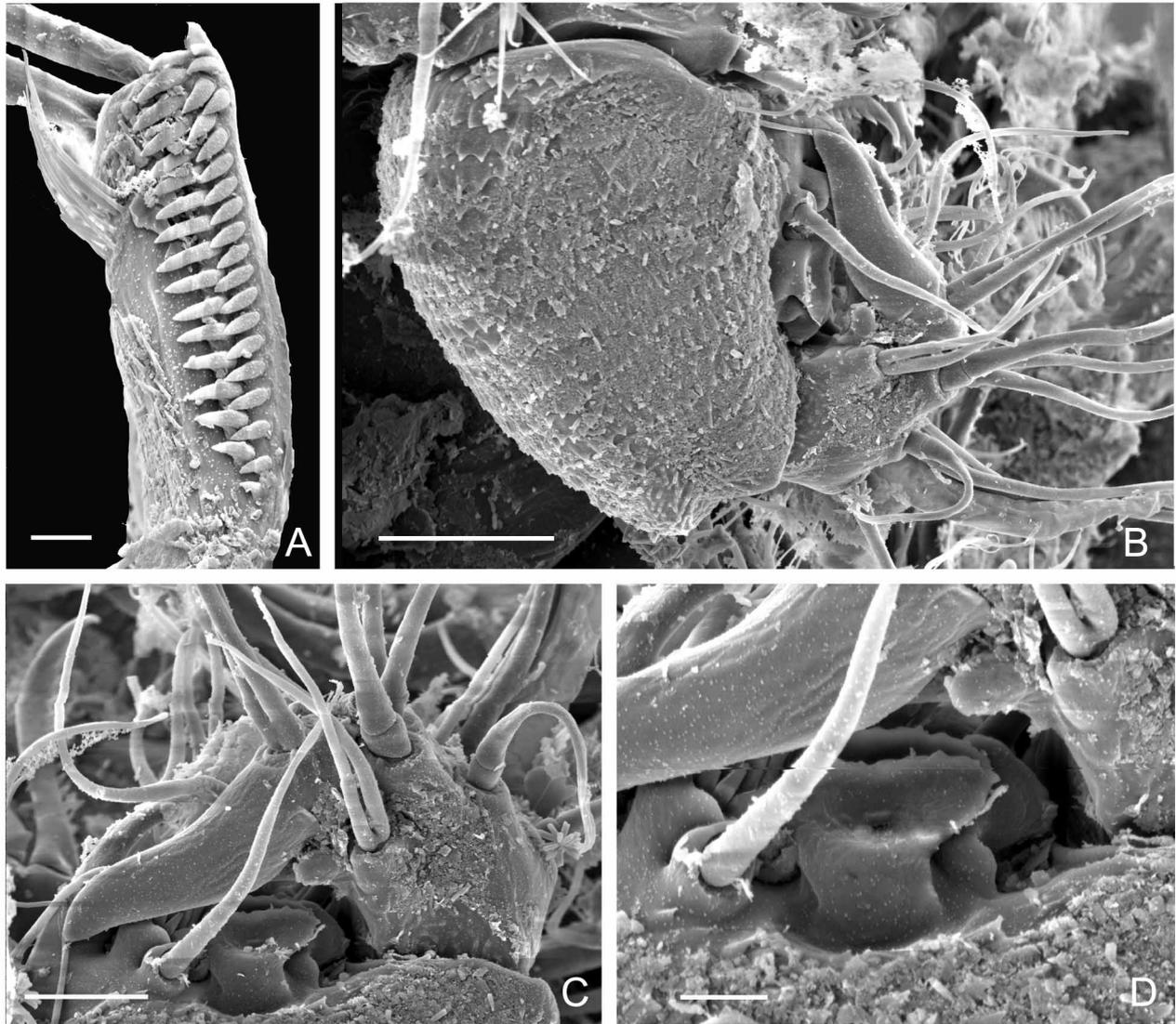
**FIGURE 11.** *Noodtorthopsyllus tageae* sp. nov. (♀), scanning electron micrographs: (A) caudal ramus, ventral; (B) detail of setular section of seta V; (C) P5, anterior; (D) second antennular segment, dorsal; (E) distal armature (note geniculate setae) of antennary endopod; (F) lateral armature of antennary endopod. Scale bars: 2  $\mu$ m (F), 2.5  $\mu$ m (B), 5  $\mu$ m (A, D, E), 10  $\mu$ m (C).

Maxillule (Figs 4D; 12A). Praecoxa with a row of spinules along distal outer margin; arthrite well developed, with 7 spines/setae and a small spinule around distal margin (Fig. 12C), 1 pinnate seta and a row of

spinules along inner margin and 2 naked setae on anterior surface. Coxa with cylindrical endite bearing 1 geniculate spine and 1 naked seta distally, and a row of setules along outer margin. Basis with 2 endites and spinular row around outer margin; proximal endite with 2 naked setae; distal endite with 1 geniculate spine and 2 pinnate setae. Endopod incorporated into basis, represented by 3 naked setae. Exopod 1-segmented, with 2 pinnate setae (Fig. 12B).



**FIGURE 12.** *Noodtorthopsyllus tageae* sp. nov. (♀), scanning electron micrographs: (A) oral region, showing mandibular palps, maxillules, maxillae and syncoxae of maxillipeds [note large semi-circular setulose raised area between maxillae]; (B) detail of mandibular endopod and maxillary rami; (C) detail of maxillary arthrite; (D) detail of maxilla, showing serrate spoon-shaped spine on proximal coxal endite and pinnate claw on allobasis. Scale bars: 5  $\mu$ m (B, D), 10  $\mu$ m (C), 20  $\mu$ m (A).



**FIGURE 13.** *Noodtorthopsyllus tageae* sp. nov. (♂), scanning electron micrographs: (A) detail of P1 enp-2, anterior surface; (B) fourth antennular segment; (C) antennule, segments distal to geniculation; (D) modified elements on anterior surface of fourth antennular segment. Scale bars: 2 μm (A, D), 5 μm (C), 10 μm (B).

Maxilla (Figs 4E; 12A). Syncoxa with bilobate outer margin, each lobe bearing spinules or setules as figured; medial margin with 3 endites; praecoxal endite vestigial, represented by a single 1 seta; proximal coxal endite with 2 naked setae and 1 spine which is fused to the endite, spoon-shaped and irregularly serrate at the apex (serrations only discernible in SEM micrographs; Fig. 12D); distal coxal endite with 1 pinnate and 2 naked setae. Allobasis drawn out into strong, pinnate claw (Fig. 12D); accompanying armature consisting of 3 naked setae. Endopod incorporated into basis and represented by 2 naked setae.

Maxilliped (Figs 5A; 12A) with 1 pinnate seta and 2 rows of spinules on syncoxa. Basis with row of spinules along distal area of palmar (= inner) and outer margins. Endopod drawn out into long, distally pinnate claw; accompanying armature consisting of 1 long and 1 vestigial naked setae.

P1 (Fig. 5B) with well developed praecoxa, with patch of minute spinules on anterior surface and serrate crest at outer margin. Coxa with patches of minute spinules and a row of stronger spinules on anterior surface; outer margin with 2 serrate crests, each ornamented with anterior row of minute spinules. Basis with short spine on anterior surface and naked seta at outer distal corner; ornamentation consisting of rows of minute spinules along inner and distal margins. Exopod 3-segmented; exp-1 with spinules along outer and distal margins, and 1 pinnate spine near outer distal corner; exp-2 with row of spinules along outer margin and 1

geniculate seta at outer distal corner; exp-3 with 4 geniculate setae of different lengths. Endopod 2-segmented, 1.4 times as long as exopod; enp-1 at least twice longer than enp-2, with spinules along inner and outer margins, and 1 small inner seta. Enp-2 with row of spinules along outer margin, 2 rows of stout spinules on anterior surface and 1 denticulate claw and 1 long geniculate seta apically.

P2–P4 (Figs 5C; 6A–C). Praecoxa without crest but with spinular pattern on anterior surface as figured. Coxae of P2–P3 with rows of minutes spinules on anterior surface and with outer serrate crest accompanied by smaller crest proximally; P4 without coxal crests. Basis with row of tiny spinules along distal margin; with naked outer seta. Exopod 3-segmented with spinular rows as figured. Endopods 1- (P3–P4) or 2-segmented (P2); P4 endopod smaller than P3 endopod; segment(s) with rows of spinules along inner and outer margins as figured. Spine and setal formula as follows:

	Exopod	Endopod
P1	0.0.022	1.020
P2	0.1.122	1.120
P3	0.1.222	221
P4	0.0.222	220

P5 (Figs 6D; 11C) not fused to supporting somite; baseoendopod and exopod fused forming triangular plate; anterior surface with 3 secretory pores and dense irregular pattern of minute spinules; armature consisting of 4 pinnate spines (3 small and 1 very long), 1 smooth spine, 1 weakly serrate spine, and 2 naked setae (one of which being the outer basal one); 2 innermost elements of endopodal origin; margin between outer basal seta and outer spine produced into serrate outgrowth.

MALE (Figs 7–9, 13). Body length 436–535  $\mu\text{m}$  ( $N = 8$ ; mean = 491  $\mu\text{m}$ ). Largest width measured at posterior margin of cephalic shield: 105–128  $\mu\text{m}$  ( $N = 8$ ; mean = 116  $\mu\text{m}$ ). Prosome (Fig. 7A) 4-segmented, comprising cephalothorax and 3 free pedigerous somites. Urosome (Fig. 7A–B) 6-segmented, comprising P5-bearing somite, genital somite, 3 abdominal somites and anal somite. Ornamentation of cephalothorax and body somites comparable to that of the female. Caudal rami (Fig. 8A–B) similar to the female.

Antennule (Figs 8C–E; 13B–D) 5-segmented, chirocer with geniculation between segments IV and V. Segment I with long posterior and short anterior spinous process; dorsal surface with few long setules; posterior margin of segment II without real process but with rudimentary, blunt protuberance; segment II with 2 modified setae bearing circular array of spinules; segment IV swollen, with pattern of minute denticles (Figs 8D; 13B), modified elements along anterior margin (Fig. 13D) and aesthetasc fused basally to seta and set on distinct pedestal; segment V produced into anteriorly directed, recurved spinous apex (Figs 8C; 13B–C), without aesthetasc. Armature formula: I-[1], II-[7 + 2 pinnate + 2 modified], III-[10 + 1 pinnate], IV-[8 + 1 pinnate + 3 modified elements + (1 + ae)], V-[8 + 3 pinnate + 1 spine]. Acrothek reduced, consisting of 2 basally fused setae.

P1 endopod (Fig. 9A) 2-segmented; enp-1 with inner seta well developed and pinnate (marked with asterisk in Fig. 9A); enp-2 proportionately longer than in ♀; with row of spinules along outer margin and 2 rows of stout spinules on anterior surface (Fig. 13A).

P3 endopod (Fig. 9B) with constriction subdividing segment in two pseudosegments; swollen proximal pseudosegment with long sigmoid apophysis, arising from the inner margin and 1.7 times as long as entire endopod; distal pseudosegment 3.3 times length of proximal one, bearing 1 long pinnate seta apically, 1 minute spinous outer process (representing vestigial seta) and few small spinules near outer distal corner.

P4 endopod (Fig. 9C) 1-segmented and slightly more slender than in ♀.

P5 (Fig. 9D) not fused to supporting somite; baseoendopod and exopod fused, forming triangular plate; anterior surface covered with minute spinules; armature consisting of 4 distinctly pinnate setae/spines, 2 minutely pinnate spines and 2 naked setae (outer one of which representing outer basal seta); 2 innermost elements endopodal in origin.

Sixth pair of legs (Figs 7B; 9E) asymmetrical; represented on both sides by a small plate, one side fused to ventral wall of genital somite, other side articulating at base with genital somite and covering single functional

gonopore; ornamentation consisting of minute spinules on anterior surface and row of spinules along distal margin; outer distal corner with naked outer and pinnate inner seta. Spermatophore very large (about 1/4 of body length) and slender, with long, curved neck (Figs 7A; 10E–F).

**Variability.** P4 enp-1 presumably bears 2 inner and 2 distal setae in the normal condition (formula [220]; 7 ♀♀ and 8 ♂♂ examined), however, in 10 females only one inner seta was present (formula [120]), and in 4 females P4 enp-1 displayed [220] on one side and [120] on the other side. A similar left/right asymmetry was observed in the holotype of *Cristacoxa petkovskii* Huys, 1990 (*cf.* Huys 1990: Figs 4B–C). No setal variability was observed in the males examined.

**Etymology.** The new species is named in honour of Prof. Tagea Kristina Simon Björnberg (Centro de Biologia Marinha – Universidade de São Paulo) in recognition of her significant contributions to the taxonomy of Copepoda.

## Family Nannopodidae Brady, 1880

**Synonym.** Huntemanniidae Por, 1986a

**Diagnosis.** Same as in Por (1986a: 421)

## Genus *Acuticoxa* gen. nov.

**Diagnosis.** Nannopodidae. Body cylindrical; slightly depressed dorsoventrally; somites with finely incised hyaline frills and dense setular surface ornamentation; genital double-somite ♀ completely fused. Rostrum prominent, triangular. Anal operculum moderately developed, spinulose. Caudal ramus long and rectangular; with 7 setae; seta V longest, typically composed of swollen proximal and setular distal part.

Antennule without spinous processes; 4-segmented in female; segment I elongate, segments III–IV oriented posteriorly and with aesthetasc. Antenna with abexopodal seta on allobasis; exopod absent or represented by minute unisetose segment; endopod with 6 distal (3 geniculate and 3 simple) and 2 medial elements. Mandible biramous with unisetose exopod fused to basis and 1-segmented trisetose endopod; basis with 2 setae. Maxillule with 2 elements on coxal endite; basal endites represented by 2 and 3 setae, respectively; endopod incorporated into basis and represented by 2 setae; exopod absent. Maxillary syncoxa with 2 endites bearing 2 and 3 elements, respectively; allobasis with claw and 1 accompanying seta; endopod represented by 2 setae. Maxillipedal syncoxa and basis unarmed; endopod 1-segmented with long geniculate claw and typically 1 accompanying seta.

P1 with strong unguiform outer spinous process on coxa; basis with inner and outer seta; exopod 2-segmented, exp-1 with or without outer seta, exp-2 with 5 setae; endopod prehensile, enp-1 without inner seta, enp-2 with 1 claw and 1 basally reinforced seta. P2–P4 with outer spinous projection on coxa; P2–P3 exopods 1- (*A. ubatubaensis*) or 2-segmented (*A. biarticulata*); P4 exopod 1-segmented; P2–P4 endopods 1-segmented with single apical element. Spine and setal formula as follows:

	Exopod	Endopod
P1	0.023	0.020
P2	0.022 or 023	010
P3	0.022 or 023	010
P4	023	010

P5 exopod and baseoendopod fused in ♀, forming single plate with 8 setae/spines; intercoxal sclerite discernible. Genital field ♀ with large median copulatory pore; P6 represented by 2 short setae.

**Type species:** *Acuticoxa ubatubaensis* gen. et sp. nov.

**Other species:** *Laophontisochra* sp. *sensu* George (2002) [= *Acuticoxa biarticulata* sp. nov.]

**Etymology.** The generic name is derived from the Latin adjective *acutus*, meaning pointed, sharp, and the Latin noun *coxa*, meaning hip, and refers to the pointed projection found on the coxae of at least legs 2–4. Gender feminine.

***Acuticoxa ubatubaensis* sp. nov.**

**Type locality.** Brazil, São Paulo State, Ubatuba (23°31.2' S, 44°51.0' W); 44 m depth, medium coarse sand.

**Type material.** Holotype ♀ dissected on 8 slides (reg. no MZUSP 19626). Collected in March 1989 by T. Corbisier.

**Description.** FEMALE (Figs 14–17). Total body length 568 µm. Largest width measured at posterior margin of P2-bearing somite (102 µm). Body (Fig. 14A) cylindrical and elongate, slightly flattened dorsoventrally, without deep constrictions between somites. Urosome slightly narrower than prosome.

Rostrum (Figs 14A; 15C) well developed, triangular, with acuminate tip; completely defined at base; with pair of dorsal sensillae at about halfway its length; dorsal surface covered by small setules/spinules.

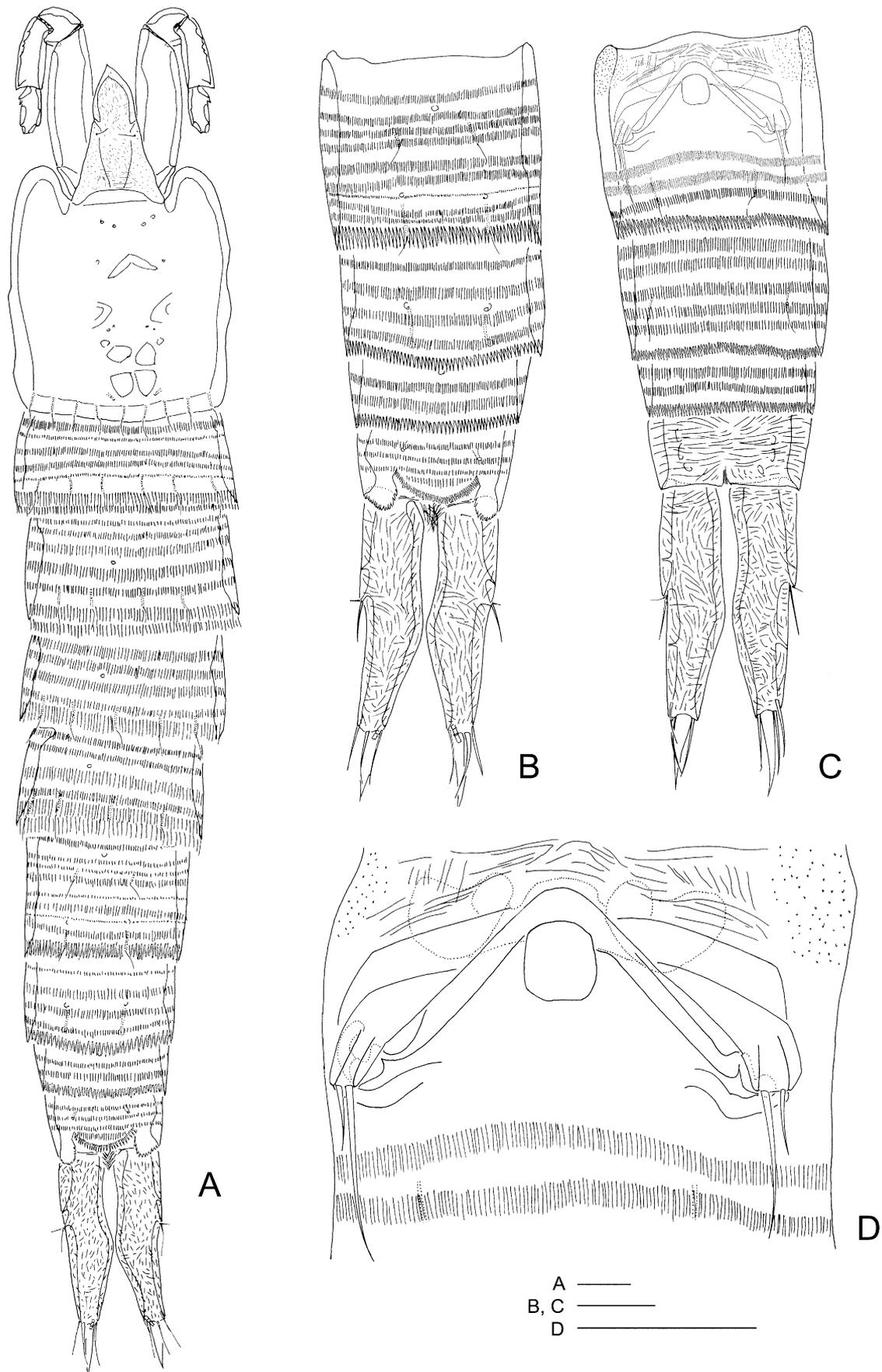
Cephalothorax rectangular, anterior margin with rounded, lobate extensions either side of rostrum; moderately produced ventrally; ornamentation consisting of sensillae and pores as illustrated in figure 14A; posterior margin smooth. Pedigerous somites (Fig. 14A) densely covered with rows of setules and with sensillae and pores as illustrated; posterior margin finely spinulose. Urosome (Fig. 14A–C) 5-segmented, comprising P5-bearing somite, genital double-somite, 2 free abdominal somites and anal somite. Urosomites with surface ornamentation consisting of rows of setules, sensillae and minute spinules (Fig. 14A–C); posterior margin of P5-bearing somite finely spinulose, genital double somite to penultimate somite with incised subulate hyaline frill (Fig. 14B–C). Genital double-somite (Fig. 14B–C) completely fused dorsally and ventrally; ventrally with minute spinules anterior to genital field and with transverse setular rows in posterior half (Fig. 14C–D); large copulatory pore located in midventral depression (Fig. 14C–D); gonopores fused medially, forming single genital slit covered on both sides by opercula derived from sixth legs. P6 with small protuberance bearing 2 naked setae, innermost longest. Anal somite (Figs 14B–C; 15A) with moderately developed, rounded, spinulose anal operculum; surface ornamentation consisting of setules and a pair of pores dorsally; anal opening with fringe of fine setules; posterior margin of somite serrate dorsally (Fig. 15A) and smooth ventrally (Fig. 14C).

Caudal rami (Fig. 15A–B) elongate, 3.6 times as long as maximum width; with inner bulge halfway the ramus length and tapering posteriorly. Each ramus with 2 lateral tube-pores near outer margin, surface ornamentation consisting of irregular pattern of striations, and 7 setae: seta I naked, vestigial and closely set to naked seta II; seta III naked and displaced to ventrolateral position; seta IV naked; seta V short and stubby, less than one third the length of the ramus (but setular distal part probably broken off; cf. condition in *A. biarticulata*); setae IV and V not fused basally; seta VI naked; seta VII incomplete on both sides but tri-articulate at base.

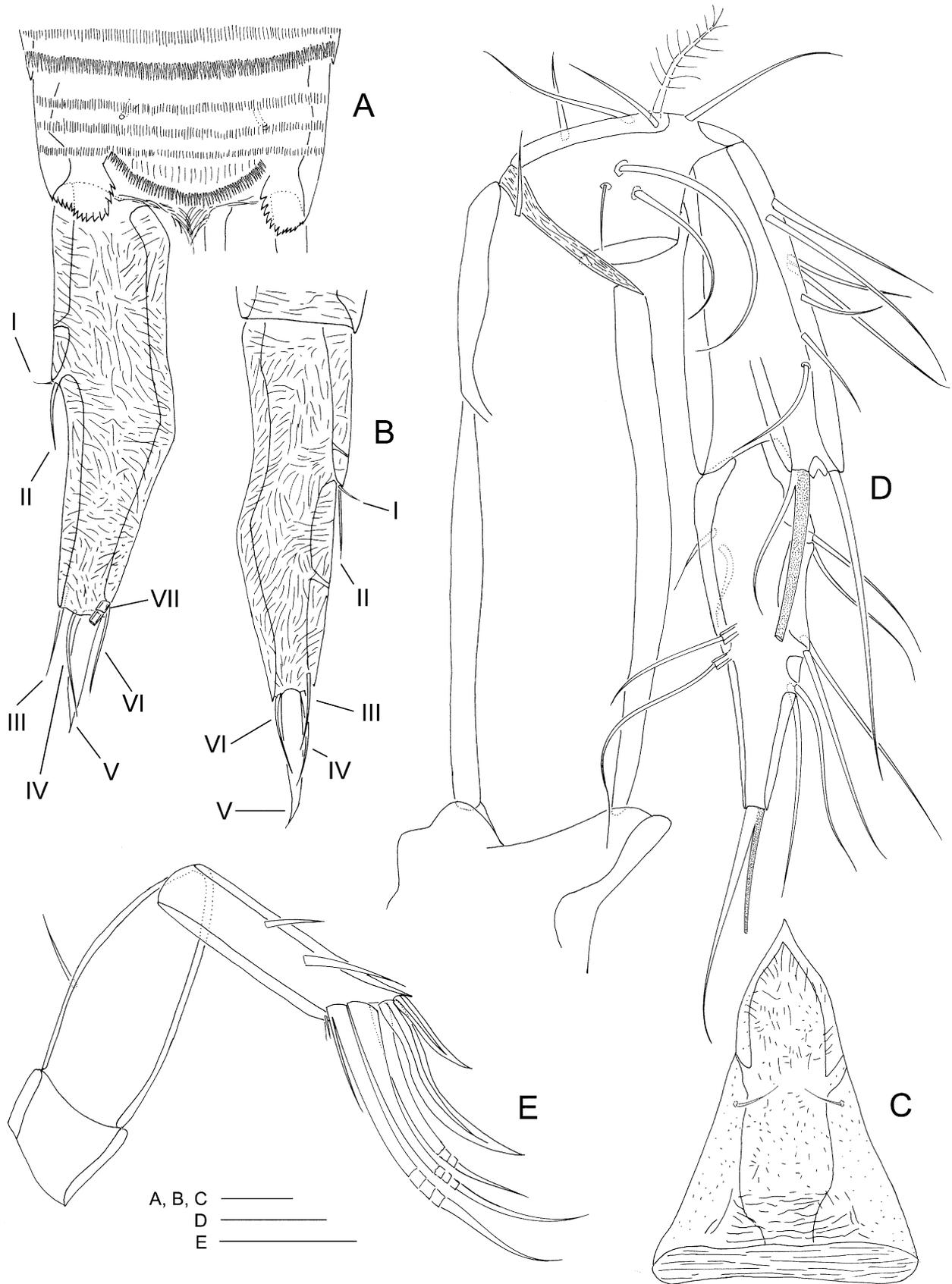
Antennule (Fig. 15D) 4-segmented, arising from subcylindrical pedestal, with segments III–IV oriented posteriorly. Segment I very long, with 1 small naked seta; segment III with aesthetasc fused basally to seta and arising from distinct setophore; segment IV tapering distally. Armature formula: I-[1], II-[7 + 1 pinnate], III-[8 + (1 + ae)], IV-[10 + acrothek]. Acrothek reduced, consisting of fused seta and aesthetasc.

Antenna (Fig. 15E) 3-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small, with no ornamentation. Basis and proximal endopod segment fused, forming elongate allobasis; with small naked abexopodal seta. Exopod completely absent. Free endopod slightly shorter than allobasis; medial armature consisting of 2 widely separated spines; apical armature consisting of 2 spines and 3 geniculate setae, outermost one of which fused basally to short seta and surrounded at base by few short spinules.

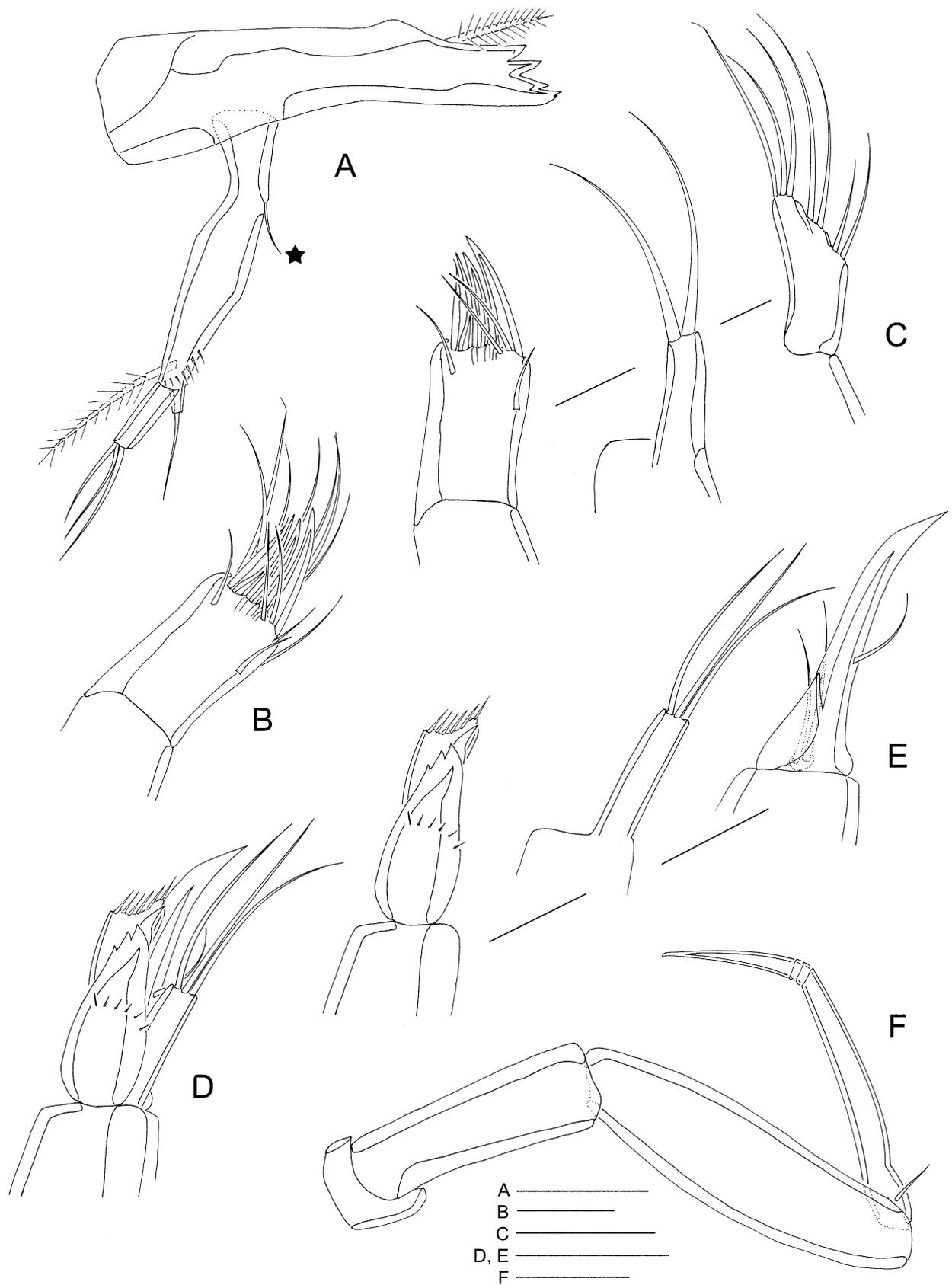
Mandible (Fig. 16A) with well-developed, elongate gnathobase bearing several multicuspidate teeth and 1 pinnate seta along distal margin. Palp biramous with incorporated exopod and discrete endopod; basis with 2 setae near distal margin (1 naked seta set on a conical protuberance and 1 long pinnate seta); exopod represented by a naked seta arising from proximal half of basis (indicated by asterisk in Fig. 16A); endopod short, about ¼ the length of basis, with about 3 apical setae.



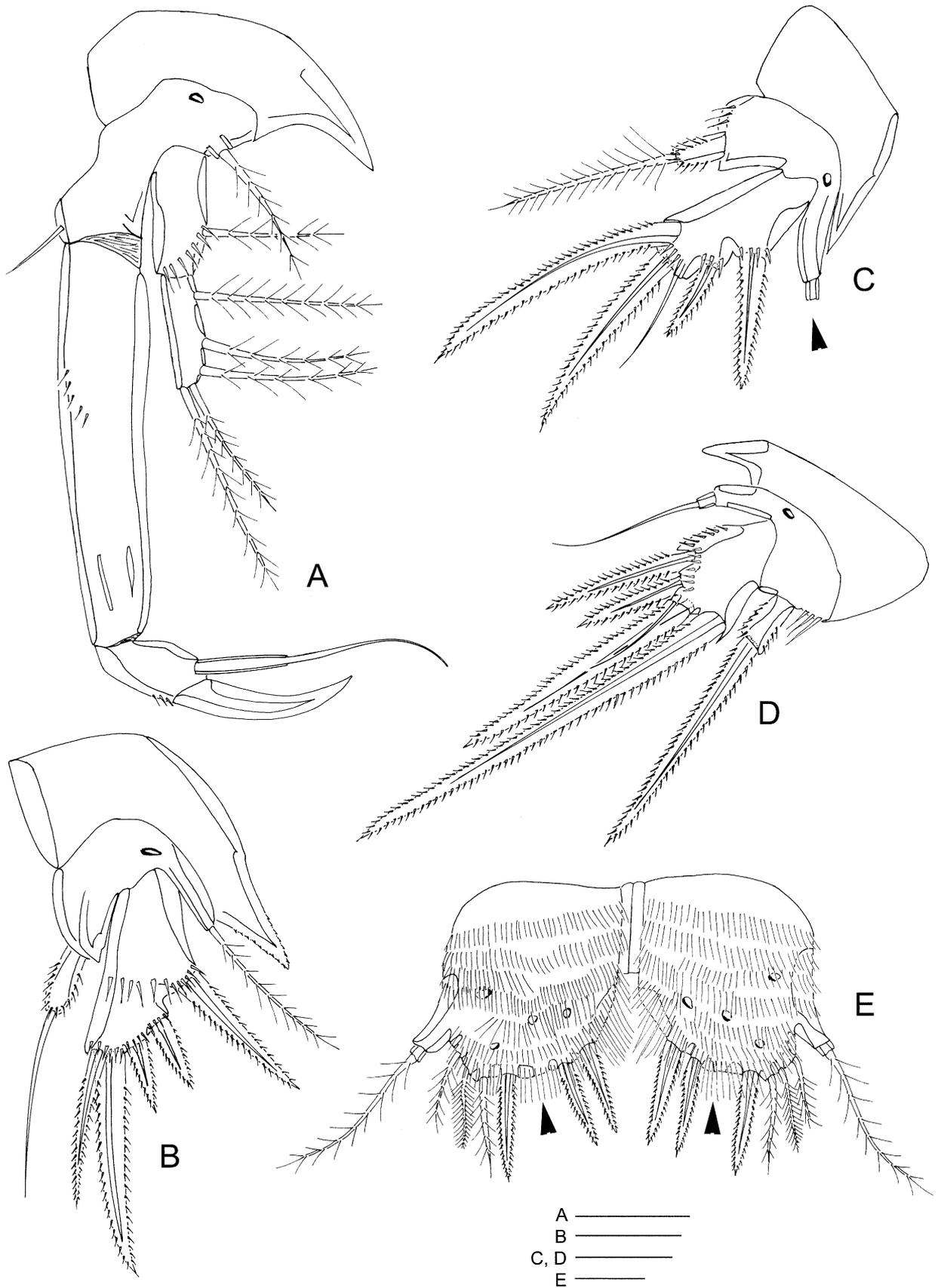
**FIGURE 14.** *Acuticoxa ubatubaensis* gen. et sp. nov. (♀): (A) habitus, dorsal; (B) urosome, dorsal [segment bearing P5 omitted]; (C) urosome, ventral [segment bearing P5 omitted]; (D) genital field. Scale bars: 25 μm.



**FIGURE 15.** *Acuticoxa ubatubaensis* gen. et sp. nov. (♀): (A) anal somite and left caudal ramus, dorsal ; (B) left caudal ramus, ventral; (C) rostrum, dorsal; (D) antennule, ventral; (E) antenna. Scale bars: 12.5  $\mu$ m.



**FIGURE 16.** *Acuticoxa ubatubaensis* gen. et sp. nov. (♀): (A) mandible [asterisk indicating exopodal seta]; (B) maxillule; (C) maxillule, disarticulated; (D) maxilla; (E) maxilla, disarticulated; (F) maxilliped. Scale bars: 12.5  $\mu$ m.



**FIGURE 17.** *Acuticoxa ubatubaensis* gen. et sp. nov. (♀): (A) P1, anterior; (B) P2, anterior; (C) P3, anterior [arrow showing insertion site of dislodged outer seta]; (D) P4, anterior; (E) P5, anterior [arrows showing insertion sites of missing seta]. Scale bars: 12.5  $\mu$ m.

Maxillule (Fig. 16B–C). Arthrite well developed, with 6 spines/setae around distal margin (Fig. 16C) and 1 naked seta subapically on both anterior and posterior surface. Coxa with cylindrical endite bearing 2 naked setae. Basis with 2 endites; proximal one with 2 naked setae; distal one with 3 naked setae. Endopod incorporated into basis, represented by 2 naked setae. Exopod absent.

Maxilla (Fig. 16D–E) with 2 endites on syncoxa. Praecoxal endite absent. Proximal coxal endite with 1 pinnate spine and 1 spine with swollen spinulose tip (Fig. 16E). Distal coxal endite with 3 naked setae. Allobasis drawn out into strong claw showing pore along outer margin and accompanying naked seta along inner margin. Endopod incorporated into basis and represented by 2 naked setae.

Maxilliped (Fig. 16F) elongate, arising from short pedestal. Syncoxa and basis unarmed. Endopod drawn out into long and geniculate claw; accompanying armature consisting of 1 naked seta.

P1 (Fig. 17A) prehensile. Coxa with outer margin forming large unguiform projection. Basis with 1 pore on anterior surface, 1 pinnate seta on outer distal corner and 1 small naked seta along inner margin. Exopod 2-segmented; exp-1 with row of spinules along distal margin and 1 pinnate outer seta; exp-2 with 3 lateral and 2 apical pinnate setae. Pinnules on outer basal seta and exopodal setae long and fine. Endopod 2-segmented, twice longer than exopod; enp-1 at least 4.3 times longer than enp-2, with few spinules along inner margin and cuticular reinforcement near distal margin; enp-2 with few spinules near inner distal corner, 1 claw and 1 long seta with reinforced basal part and setular distal part.

P2–P4 (Fig. 17B–D) small with reduced segmentation. Coxae with outer margin forming a pointed projection, smooth in P2–P3, fringed with small spinules in P4. Bases with outer corner produced into long setophore bearing pinnate (P2) or naked (P4) seta (lost in P3); with 1 large pore on anterior surface and row of spinules at inner corner (in P3–P4 only). Exopods 1-segmented, with spinules along outer and distal margins (except P4); original segmentation of P2 exopod indicated by transverse row of long spinules; all elements bipinnate and spiniform except for distal outer element on P3–P4 being naked and setiform. Endopods 1-segmented, small; with rows of spinules along inner and outer margins; with 1 naked (P2), plumose (P3) or pinnate (P4) seta apically. Armature formula as follows:

	Exopod	Endopod
P1	0.023	0.020
P2	023	010
P3	023	010
P4	023	010

P5 (Fig. 17E) with baseoendopod and exopod fused, forming single plate; not fused to supporting somite; narrow intercoxal plate discernible; anterior surface with 4 secretory pores and densely covered with minute setules; with 8 elements, including 3 pinnate spines, 4 plumose setae and one of unconfirmed shape and size (missing on both sides in holotype; insertion site arrowed in Fig. 17E).

MALE. Unknown.

**Etymology.** The new species is named after the Ubatuba municipality where the type locality is situated.

## Discussion

### Generic distinction between *Noodtorthopsyllus* and *Cristacoxa*

Noodt (1955) described both sexes of *Orthopsyllus psammophilus* Noodt, 1955 from a sandy beach in Tenerife and remarked on its isolated position in the genus. Lang (1965) subsequently fixed the species as the type of a new genus *Noodtorthopsyllus* within the family Canthocamptidae Brady, 1880. Huys (1990) removed the latter genus and *Cubanocleta* (previously claimed to form a link between the Ancorabolidae and Normanellidae; cf. Petkovski 1977) to a new family Cristacoxidae and proposed the genus *Cristacoxa* to accommodate a new species *C. petkovskii* Huys, 1990 based on a single male from Bonaire. According to Huys (1990) the close relationship between *Noodtorthopsyllus* and *Cristacoxa* is demonstrated by the shared

presence of the composite caudal ramus seta V, segmentation and ornamentation of P2–P4, same type of sexual dimorphism on the P3 endopod, and general morphology of P5. Conversely, both genera were distinguished primarily on the basis of the presence/absence of the inner seta on P1 enp-1, praecoxal endite on the maxilla, and sexual dimorphism on P2 enp-1. The documented sexual dimorphism in *Cubanocleta* in conjunction with the left/right asymmetry noted in the male holotype of *C. petkovskii* made Huys (1990) postulate that female *Cristacoxa* also exhibits two inner setae on the P4 endopod (instead of one in the male). Although such sexual dimorphism was initially regarded as another potential character differentiating the latter genus from *Noodtorthopsyllus*, it has now transpired that the endopod of P4 is an unstable ramus (see variability above) and that the observed setal differences between females and males carry less weight as generic discriminants. Huys (1990) also listed additional differences between *Cristacoxa* and *Noodtorthopsyllus* such as the length of the apophysis of the P3 endopod in the male, the shape of the coxal crests on P1 and the number of endopodal setae on the maxilla.

The new species *N. tageae* is similar to *N. psammophilus* in the structure of the antennular acrothek (2 setae), presence of an inner seta on P1 enp-1, and distal inner seta of the P4 endopod being well developed and pinnate, however, shares with *C. petkovskii* the pointed outer process on segment I of the male antennule, vestigial praecoxal endite on the maxillary syncoxa, presence of only two setae on the maxillary endopod and, potentially, the absence of sexual dimorphism on P2. Given this mosaic of characters drawn from both genera, it is clear that the discovery of *N. tageae* has made the distinction between *Cristacoxa* and *Noodtorthopsyllus* no longer tenable. Consequently, *Cristacoxa* Huys, 1990, the type genus of the nominal family-group taxon Cristacoxidae Huys, 1990, is here relegated to a junior subjective synonym of *Noodtorthopsyllus* Lang, 1965. According to ICZN Art. 40.1 this course of action does not affect the validity of the family name (see Huys *et al.* (2005) for a similar case in the Latiremididae Božić, 1969). The three species currently included in *Noodtorthopsyllus* can be differentiated by the characters compiled in Table 1.

Huys (1990) noted that the outer apophysis on the male P3 endopod in *Cubanocleta* is not homologous with the inner apophysis displayed by *Noodtorthopsyllus* (and at that time *Cristacoxa*). The former is the homologue of the outer spine expressed in the female and is a characteristic of the laophontoidean groundpattern (as defined by Huys, 1990). The latter is a novel structure that is derived from the proximal inner seta and has – prior to this study – been found only in cristacoxids that lack the outer spine in the female (Fig. 18). The discovery of *N. tageae*, displaying the full complement of elements on the female P3 endopod (Fig. 6A), shows that the expression of the inner apophysis in male *Noodtorthopsyllus* is not correlated with the presence or absence of the outer spine in the female.

Being the homologue of the proximal inner seta (number 1 in Fig. 18) in the female (which primitively originates from enp-3 in harpacticoids displaying a 3-segmented endopod), the position of the inner apophysis on the proximal “segment” in male *Noodtorthopsyllus* (Fig. 18) unequivocally demonstrates that the subdivisions are not genuine segments and should therefore be called “pseudosegments”.

### Autapomorphies of Cristacoxidae

Previous phylogenetic analyses (Huys 1990; Huys & Lee 1998/99) of the relationships of the families within the Laophontoidea suggested a sistergroup relationship between the Cristacoxidae and the Laophontopsidae. An extensive suite of autapomorphies in support of the monophyly of the Cristacoxidae was recognized by Huys (1990) including:

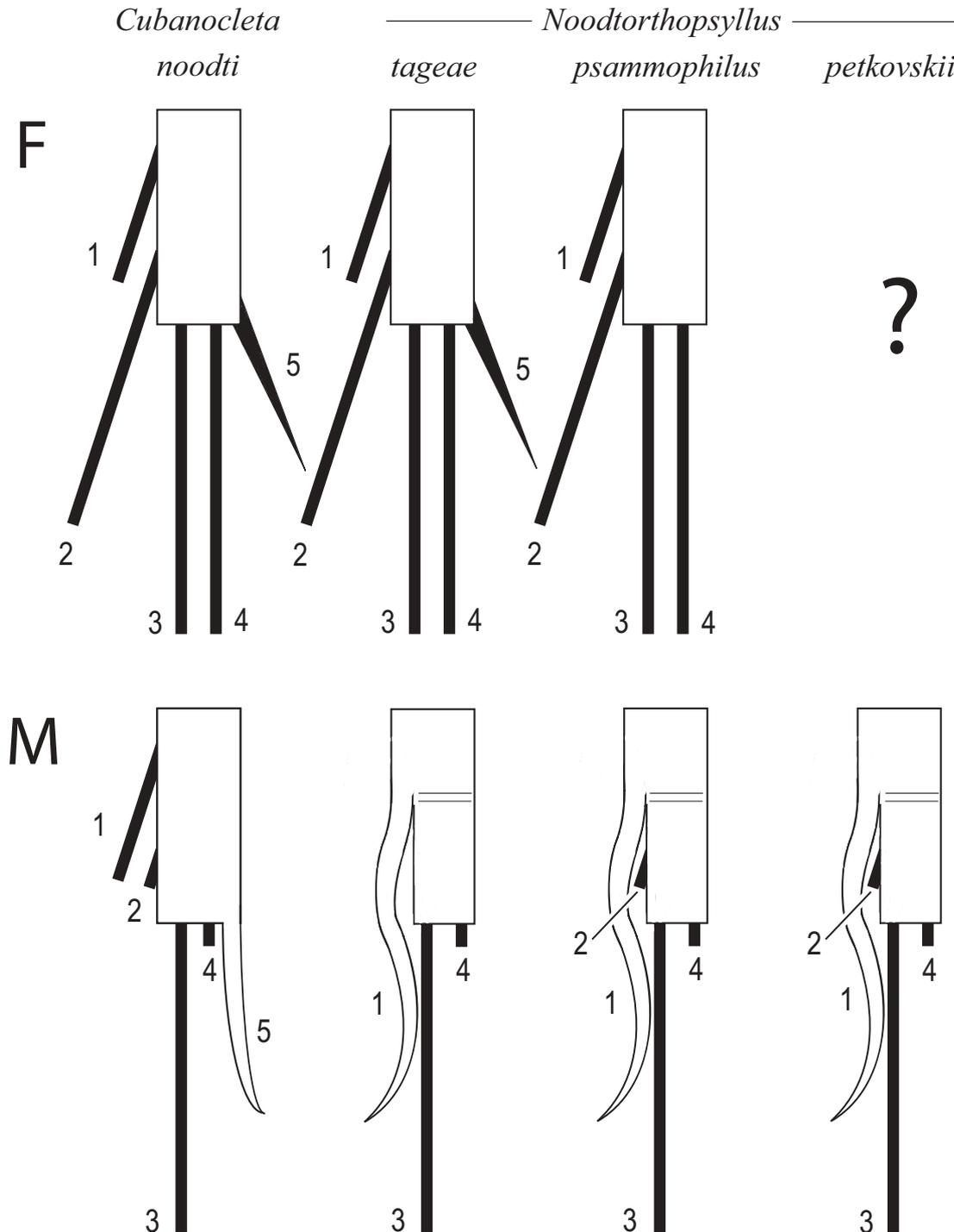
(1) spermatophore extremely long and slender with curled neck, comprising up to one third of the body length (when observed *in situ*);

(2) first antennular segment with a posterior spinous process in both sexes;

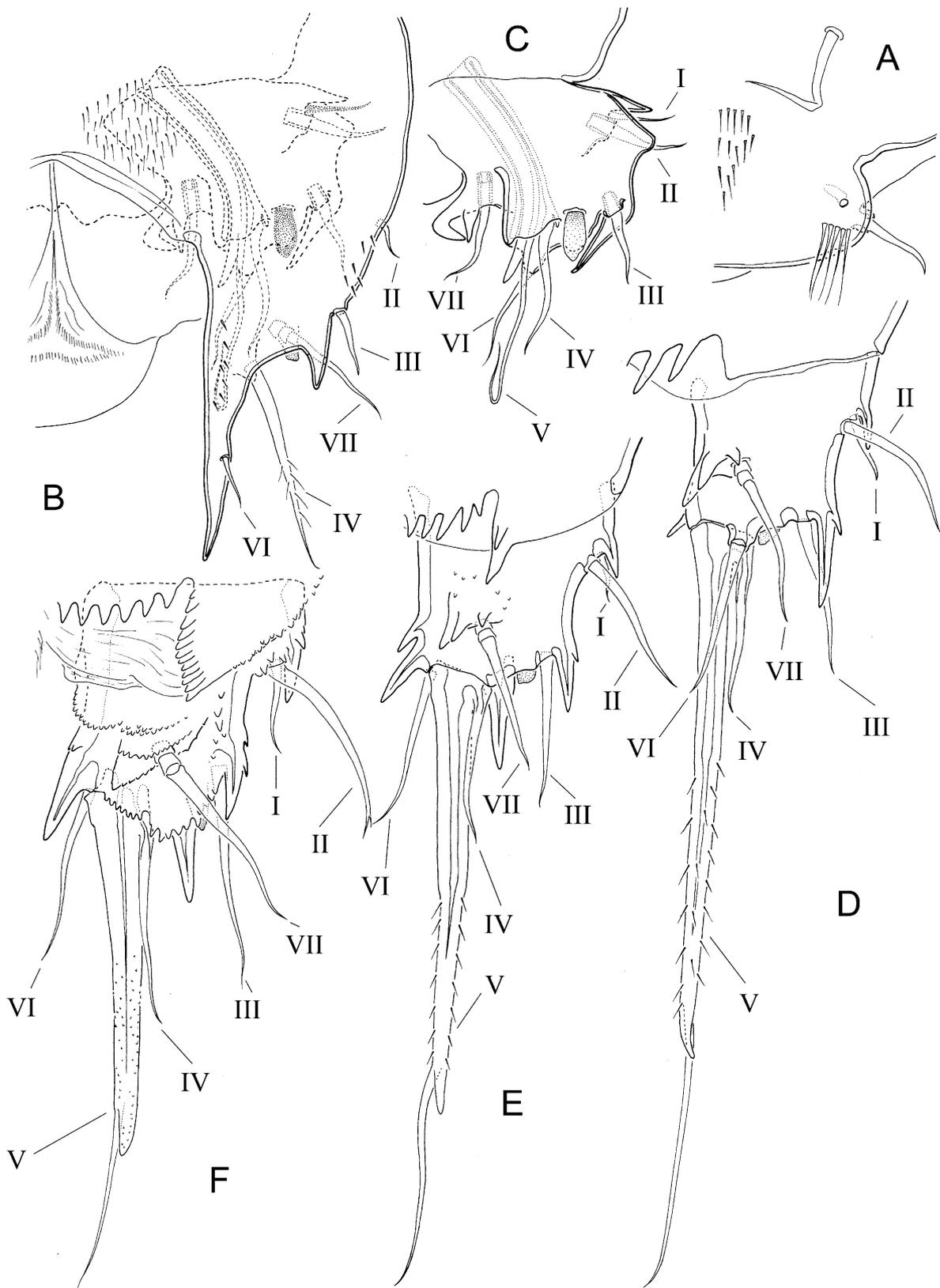
(3) antennary exopod and abexopodal seta on allobasis absent. According to Ferrari (1992; based on unpublished data from F. Fiers) the antenna in *Noodtorthopsyllus* (presumably *psammophilus*) bears a small sclerotized segment with one seta at the position of the exopod in copepodid I. He further claimed that in all later copepodids (including the adult) this segment is absent but the seta is retained. The latter part of this statement is erroneous since no exopodal seta is expressed in any of the known adult cristacoxids (or in any of

the later copepodids of *N. tagueae* examined in this study). Ferrari (1992) suggested that the absence of an antennary exopod in copepodids II–VI resulted from gene repression rather than gene loss because it is still expressed in the naupliar stages;

(4) mandibular palp uniramous and 2-segmented, comprising an asetose basis and quadrisetose endopod (Fig. 12B);



**FIGURE 18.** Schematic depicting sexual dimorphism in P3 endopod (F = female; M = male). Note secondary subdivision of endopod into two pseudosegments in *Noodtorthopsyllus* and reduction of distal inner and outer distal setae in males.



**FIGURE 19.** Caudal ramus development in *Noodtorthopsyllus tageae* sp. nov.: (A) left part of caudal area of nauplius II, ventral; (B) left caudal ramus of nauplius VI intermoult stage showing developing copepodid I inside, ventral; (C) caudal ramus of copepodid I shown in (B), ventral; (D) right caudal ramus of fully developed copepodid I, dorsal; (E) right caudal ramus of copepodid II, dorsal; (F) right caudal ramus of adult, dorsal. Roman numerals refer to caudal ramus setae as coded by Huys (1988) and Huys and Boxshall (1991).

**TABLE 1.** Differentiating characters and known distribution of *Noodtorthopsyllus* species (ps-1, -2 = proximal and distal pseudosegment, respectively).

	<i>N. psammophilus</i>	<i>N. petkovskii</i>	<i>N. tagueae</i> sp. nov.
Body size ♀ (µm)	520–570	unknown	494–575
♂ (µm)	510–530	480	436–535
Antennule segment I posterior process ♀	medium size, pointed	unknown	large, pointed
Antennule segment I posterior process ♂	medium size, blunt	medium size, pointed	medium size, pointed
Antennule segment II posterior process ♀	small, pointed	unknown	rudimentary, blunt
Antennule segment II posterior process ♂	small, blunt	small, blunt	rudimentary, blunt
Antennulary acrothek	2 setae	1 seta + ae	2 setae
Maxillary endopod	3 setae	2 setae	2 setae
Maxillary praecoxal endite	absent	present	present
P1 enp-1 inner seta	present	absent	present
P1 enp-2:enp-1	2.7	3.0	2.5
P2 enp-1 armature sexual dimorphism	present	probably absent	absent
P3 endopod outer spine	absent	unknown	present
P3 endopod ♂	ps-1 < ps-2	ps-1 = ps-2	ps-1 << ps-2
P3 apophysis ♂	1.3	2.25	1.70
- ratio to endopod length	inner distal corner	inner distal corner	inner margin
- origin	well developed, pinnate	small, naked	well developed, pinnate
P4 endopod ♂ distal inner seta	5 short + 2 long	unknown	6 short + 1 long
P5 ♀ armature (excl. outer basal seta)	long	unknown	short
P6 ♀ pinnate seta	elongate, setular	elongate, setular	reduced, bi-setular
Caudal ramus seta V distal part			
Distribution	Tenerife, El Hierro	Bonaire	São Paulo State (Brazil)

(5) proximal coxal endite of the maxilla with a modified basally fused spine; Huys (1990) described the spine as having "... a specialized, swollen tip consisting of fine spinules arranged in a U-shaped excavation..." but SEM observations revealed that the distal part of the spine is spoon-shaped with asymmetrically arranged serrations (Fig. 12A, D);

(6) praecoxa (one) and coxa (two) of P1 with serrate cristae around the outer margin; serially homologous crests are also present on the coxae of P2 and P3, and a lobate outgrowth is sometimes discernible on the coxa of P4;

(7) inner basal spine/seta of P1 displaced onto anterior surface of basis;

(8) P1 exp-3 with four geniculate setae;

(9) P2–P4 exp-2 without inner seta;

(10) P2–P4 exp-3 with two outer elements instead of three; these elements are typically elongate and setiform instead of short and spiniform;

(11) P3–P4 endopods 1-segmented (ancestral enp- 1 and enp-2 failed to separate); and

(12) fifth legs pedomorphic (neotenic) forming a common plate in both sexes, bearing two endopodal and five exopodal elements in addition to the outer basal seta.

During the course of this study two additional autapomorphies were identified, *i.e.*

(13) sexual dimorphism of P3 endopod. Despite the documented variation observed in the origin of the apophysis and the secondary subdivision of the P3 endopod into two pseudosegments, all known members of the Cristacoxidae consistently display the strong reduction (and sometimes complete loss, *cf. N. tageae*) of the distal inner seta and the outer distal seta in the male (Fig. 18); and

(14) the caudal ramus provides a double apomorphy. In all cristacoxids the caudal setae have spinous processes at their bases, the largest ones typically located at the inner distal corner and around the posterior margin between setae III and IV, the smaller ones at the bases of setae I, III and VII. Secondly, examination of developmental stages of *N. tageae* revealed that the ontogenetic trajectories of the caudal setae IV–VI deviate from the generalized podoplean model for caudal ramus development proposed by Huys *et al.* (2007). In this model, setae are gradually added in a regular pattern during the naupliar phase, commencing with the expression of setae IV and VII in nauplius I (Fig. 19A) and resulting in a total of five setae (II, III, IV, VI, VII) in nauplius VI (Fig. 19B). The moult from nauplius VI to copepodid I (*cf.* intermoult stage shown in Fig. 19C) is marked by the addition of two setae, the anterolateral seta (I) and the inner terminal seta (V), completing the full array of caudal setae (Fig. 19D). The timing and expression of individual setae in *N. tageae* follows the podoplean model during the naupliar phase but the subsequent modification of setae IV–V does not. In generalized podopleans seta V appears as a short element, which is fused at the base to the long terminal accessory seta VI, forming a bifid setal complex. At the moult to copepodid II the setal complex separates completely at the base, seta VI reduces dramatically in size and seta V becomes the principal seta. This pattern persists in all subsequent copepodid stages, including the adult. In *N. tageae* (and conceivably all other cristacoxids) a [V–VI] setal complex is never formed (Fig. 19D–F) and seta V is the principal seta from copepodid I onwards when it is first expressed as a composite element. The latter forms a different bifid setal complex with seta IV which, unlike in typical podopleans, does not alter its length during the copepodid phase.

### **Relationships between *Laophontisochra* George, 2002 and *Acuticoxa* gen. nov.**

George (2002) proposed the genus *Laophontisochra* for two deepwater species from the Magellan region which shared a cylindrical, slightly dorsoventrally depressed body shape, a large maxilliped, a spinous outgrowth on the coxa of leg 1, a prehensile P1 endopod, reduced P2–P4 and long caudal rami. Despite these similarities, the type species *L. maryamae* and the unnamed *Laophontisochra* sp. also display many important differences. George (2002) suggested that the discrepancies in body ornamentation, caudal seta V, antennule, antenna and P1–P5 were indicative of the presence of two distinct species. The discovery of our new species from the northern continental shelf off São Paulo State suggests, however, that the observed morphological variation between both *Laophontisochra* species is such that two distantly related lineages can be recognized. *Laophontisochra* sp. shows a close relationship with *Acuticoxa ubatubaensis* **sp. nov.** based on the following

synapomorphies: (1) the presence of dense setular surface ornamentation on the body somites; (2) distal margin of antennary endopod with three geniculate and three non-geniculate setae; (3) P2–P4 with outer spinous projection on coxa; (4) P4 exopod 1-segmented; and (5) P5 exopod and baseopod fused in ♀, forming a single plate with 8 setae/spines. The plesiomorphic states of these characters are expressed in *L. maryamae*: body somites virtually smooth (except for spinular tufts on pleural areas of pedigerous somites), antennary endopod with four geniculate and two non-geniculate setae around apex, P2–P4 without coxal processes, P4 exopod 2-segmented, and P5 biramous in ♀. Autapomorphies for *L. maryamae* include (1) the dense setular ornamentation on the first antennary segment; (2) loss of the abexopodal seta on the antennary allobasis; (3) loss of P2–P3 endopods; (4) the reduced armature on ♀ P5, comprising 1 endopodal and 4 exopodal setae (the precise homology of these elements with respect to the 7 non-basal elements expressed in *Laophontisochra* sp. and *A. ubatubaensis* are difficult to assess but it is conceivable that 2 endopodal elements were lost in *L. maryamae*); and (5) P6 ♀ set on raised protuberance.

Given its close resemblance to *A. ubatubaensis*, *Laophontisochra* sp. (also based on a single female specimen) is here formally assigned to the genus *Acuticoxa*. The characters compiled in Table 2 show that both females cannot be conspecific and hence the specimen figured by George (2002: Figs 5–7) is here designated as the holotype of a new species, *A. biarticulata* **sp. nov.** (the specific name refers to the 2-segmented condition of the exopods of P2–P3), which can be differentiated from the type species by the diagnostic characters given in Table 2. The holotype (dissected on 8 slides) was deposited in the collections of the AG Zoosystematik und Morphologie of the Carl von Ossietzky-Universität in Oldenburg (Germany) (reg. nos UNIOIOL-1999.016/1–8). *Acuticoxa biarticulata* is known only from its type locality (53°59.7'S, 70°33.0'W) at 79 m depth in the Northern Magellan Straits.

**TABLE 2.** Morphological differences between females of *Acuticoxa* species (P5 setal numbering starting from outer basal seta = seta 1).

	<i>A. ubatubaensis</i> <b>sp. nov.</b>	<i>A. biarticulata</i> <b>sp. nov.</b>
Antennule segment I	without ornamentation	with dense setules
Antennule segment II setae	7 naked + 1 pinnate	9 naked
Antennary exopod	absent	minute unisetose segment
Maxillipedal seta accompanying endopodal claw	present	absent
P1 exp-1 outer seta	present	absent
P1 exp-2 setae	with long pinnules	naked
P3–P4 outer coxal projections	short and broad, not reaching beyond basal setophore	long and narrow, reaching well beyond basal setophore
P2–P3 exopods	1-segmented	2-segmented
P3–P4 distal outer element exp	setiform, naked	spiniform, bipinnate
P5 seta 4	subequal to seta 3	twice as long as seta 3
P5 element 5	spiniform	setiform

As a result of the removal of *Laophontisochra* sp. to *Acuticoxa* an updated generic diagnosis of *Laophontisochra* is presented below:

**Diagnosis (amended).** Nannopodidae. Body cylindrical; slightly depressed dorsoventrally; somites with finely incised hyaline frills but no setular ornamentation dorsally; pleural areas of pedigerous somites with spinular tufts; original segmentation of genital double-somite ♀ marked by lateral constrictions and transverse ribs. Rostrum prominent, bell-shaped. Anal operculum unknown. Caudal ramus long and rectangular; with 7 setae; seta V longest, spiniform, not composite.

Antennule without spinous processes; 4-segmented in female; segment I elongate, segments III–IV with aesthetasc and posteriorly directed. Antenna without abexopodal seta on allobasis; exopod represented by seta; endopod with 6 distal setae (4 geniculate and 2 simple) and 2 lateral spines. Mandible biramous with

incorporated unisetose exopod and 1-segmented trisetose endopod; basis with 2 setae. Maxillule with 2 elements on coxal endite; basal endites represented by 3 and 2 setae, respectively; endopod incorporated into basis and represented by 2 setae; exopod absent. Maxillary syncoxa with 2 endites, each bearing 2 elements; allobasis with claw and 1 accompanying seta; endopod represented by 2 setae. Maxillipedal syncoxa and basis unarmed; endopod 1-segmented with long geniculate claw and 1 accompanying seta.

P1 with conical, distally pinnate protuberance on outer margin of coxa; basis with inner (arising from anterior surface) and outer seta; exopod 2-segmented, exp-1 with outer seta, exp-2 with 5 setae; endopod prehensile, enp-1 without inner seta, enp-2 with 1 claw and 1 long seta. P2–P3 (and almost certainly also P4) without spinous projections or protuberances on coxa; P2–P4 exopods 2-segmented; P2–P3 endopods absent, P4 endopod 1-segmented with single apical element. Spine and setal formula as follows:

	Exopod	Endopod
P1	0.023	0.020
P2	0.022	absent
P3	0.022	absent
P4	0.022	010

P5 exopod and baseoendopod distinct in ♀; exopod small, with 4 elements; baseoendopod with weakly developed endopodal lobe bearing 1 spine. Genital field ♀ with P6 represented by paired raised protuberances bearing 2 short setae; copulatory pore unconfirmed.

**Type and only species:** *Laophontisochra maryamae* George, 2002 (by original designation)

#### Monophyly of Cristacoxidae *sensu* George (2002)

Although George's (2002) assessment of the position of *Laophontisochra* was hampered by the absence of males, the evidence supporting his assignment of the genus to the Cristacoxidae was nevertheless weak. Both *Laophontisochra* and *Acuticoxa* have a radically divergent morphology, exhibiting only four (7, 9, 10, 11) of the 12 female cristacoxid autapomorphies listed above. At least for some of these the question arises whether the apomorphic state observed is homologous to the typical cristacoxid condition: the inner basal spine/seta of P1 is displaced onto the anterior surface of the basis (character 7), P2–P4 exp-2 has lost the inner seta (character 9; however, the homologue of exp-2 is not expressed as a discrete segment, but its outer spine is), P2–P4 exp-3 has only two outer elements instead of three (character 10; however, these elements are not typically elongate and setiform as in *Noodtorthopsyllus* and *Cubanocleta*), and P3–P4 endopods 1-segmented (character 11: the validity of this character is difficult to assess since the endopods are either lost (P3 in *Laophontisochra*) or represented by a small unisetose segment).

George (2002) advocated a basal split of the Cristacoxidae into two lineages, *i.e.* a clade uniting the “more derived” traditional cristacoxid genera (*Cristacoxa*, *Noodtorthopsyllus*, *Cubanocleta*) and a “more plesiomorphic” clade comprising *Laophontisochra* (and by inference, *Acuticoxa*). The sistergroup relationship (and therefore the monophyly of the family) was based on three character states, *i.e.* (1) the presence of cristae on the coxa of P1, (2) large maxillipeds, and (3) “atrophy of antennary exopod and abexopodal seta”. Each of these character states leave room for interpretation. *Noodtorthopsyllus* and *Cubanocleta* have paired serrate crests on the coxa and a single one on the praecoxa of leg 1, in addition to serially homologous crests on the coxae of P2 and P3 and occasionally a lobate outgrowth on the coxa of P4. In *Acuticoxa* and *Laophontisochra* a single non-serrate, lobate or spinous outgrowth (not a genuine crest!) is present on the coxa of P1 but no such structure is discernible on the praecoxa. Serially homologous spinous projections are also present on the coxae of P2–P4 of *Acuticoxa* but not in *Laophontisochra*. The single pointed projection on the P1 coxa in *Acuticoxa* clearly does not resemble the paired serrate cristae exhibited by *Noodtorthopsyllus* and *Cubanocleta* and is probably the result of convergent evolution. Secondly, the maxillipeds are fundamentally different between *Laophontisochra-Acuticoxa* (L-A) and *Noodtorthopsyllus-Cubanocleta* (N-C). In the former two genera the syncoxa is unarmed and the endopod is represented by a geniculate claw bearing a minute accompanying seta along its outer margin (secondarily lost in *A.*

*biarticulata*); in the latter the syncoxa has a pinnate seta and the endopodal claw is not geniculate, bearing a short accompanying seta along the outer margin and, more distally, a distinct long seta along the inner margin. Given these morphological differences, using maxillipedal size as evidence in support of a sistergroup relationship between *L-A* and *N-C* appears a weak argument. Finally, adult cristacoxids consistently lack the antennary exopod (its former position in copepodid I is indicated by a membranous insert in the adult) and the abexopodal seta on the allobasis. Such consistency is not observed in *Laophontisochra* or *Acuticoxa* where the “atrophied” condition prevails, with the antennary exopod being absent (*A. ubatubaensis*) or represented by a seta (*L. maryamae*) or a minute unisetose segment (*A. biarticulata*), and the abexopodal seta being lost only in *L. maryamae*. George (2002) pointed out that including *Laophontisochra* in the Cristacoxidae would draw the family to a much more basal position in the Laophontoidea because of certain primitive characters displayed by *L. maryamae* such as the presence of two basal setae on the mandibular palp, a character thus far only reported from some primitive Laophontidae (subfamily Esolinae; cf. Huys & Lee 2000) and effectively excluding both *Acuticoxa* and *Laophontisochra* from the clade [Adenopleurellidae + Orthopsyllidae + Laophontopsidae + Cristacoxidae]. Two of the cristacoxid autapomorphies mentioned above (characters 1 and 13) cannot be verified in either *Laophontisochra* or *Acuticoxa* since they are based on male character states. However, the recent discovery of a closely related genus from Paranaguá Bay (Brazil), represented by both sexes (named hereafter “Genus X”), showed that neither the spermatophore nor the P3 sexual dimorphism are of the cristacoxid type (P.H.C. Corgosinho & M. Büntzow, pers. commn), and that the male sixth legs bear 3 setae (except for the basal Normanellidae all other laophontoidean families have 2 setae; cf. Huys & Lee 1998/99). Neither *Acuticoxa* nor *Laophontisochra* have setiform outer elements on the distal exopod segment of P2–P4. The absence of this character would place these genera outside the clade [Laophontopsidae + Cristacoxidae]. Although the males of both genera are unknown, the male of the closely related “Genus X” shows that the segments distal to the geniculation in the male antennule are free. The presence of a single compound segment distal to the geniculation is a synapomorphy uniting the Laophontopsidae and Cristacoxidae.

The coxal projections on legs 1–4 in *Laophontisochra* and *Acuticoxa* may be indicative of a relationship with some genera currently included in the Huntemanniidae. Por (1986a: 421) established the family Huntemanniidae for the genera *Nannopus* Brady, 1880, *Huntemannia* Poppe, 1884 [type], *Pontopolites* T. Scott, 1894, *Metahuntemannia* Smirnov, 1946, *Beckeria* Por, 1986b and possibly *Pseudocletodes* Scott & Scott, 1893. Unfortunately, it has remained unnoticed that Brady (1880: 100) had already established a new subfamily Nannopinae within the Harpacticidae for *Nannopus* Brady, 1880 (type genus) and *Platychelipus* Brady, 1880 (now placed in the Laophontidae). According to the Principle of Coordination applied to family-group names (ICZN Art. 36.1) Brady (1880) is deemed also to have simultaneously established the coordinate family name Nannopidae. Since the family-group name Huntemanniidae was used by Por (1986a) to include the genus *Nannopus*, it must sink as a junior synonym of Nannopinae Brady, 1880. Huys (2009) pointed out that the second part of the generic name *Nannopus* is derived from the Greek stem *πους*, meaning foot, and hence the family name must be corrected to Nannopodidae. Since Por’s (1986a) proposal, Dahms and Pottek (1992) have relegated *Beckeria* to a junior subjective synonym of *Metahuntemannia*, Kihara and Huys (2009) have assigned *Pseudocletodes* to the Normanellidae and two genera have been added to the family, *Rosacletodes* Wells, 1985 and *Pottekia* Huys, 2009. The former was proposed by Wells (1985) as a new replacement name for the cletodid genus *Echinocletodes* Pallares, 1982 (type species *E. kuehnemanni* Pallares, 1982), a junior homonym of *Echinocletodes* Lang, 1936 (type species *Cletodes armata* T. Scott, 1903; cf. Huys *et al.* 1996a: 75), and is of particular interest here. Bodin (1997) did not assign the genus to any of the families defined by Por (1986a) while George (2008) considered *A. kuehnemanni* (Pallares, 1982) a *species incertae sedis* in the Argestidae. Both Huys *et al.* (1996a) and Wells (2007) listed it as a genus in the Huntemanniidae.

Pallares’ (1982) description of *Rosacletodes kuehnemanni*, based on material from Tierra del Fuego (Argentina), clearly shows spinulose projections on the coxae of P1–P4 which are virtually identical to the structure found on the coxa of P1 in *L. maryamae*. Such structures were also recently described for *Huntemannia jadensis* Poppe, 1884 by Kornev and Chertoprud (2008). There is also a gross resemblance in

the general morphology of the swimming legs (P2–P4) between *Rosacletodes* and *Laophontisochra*, including the strongly reduced endopods (represented by a single seta in *Rosacletodes*) and exopods (at most 2-segmented in the ♀), the enlarged outer spine on P2–P4 exp-1 (proximal outer spine if only one segment expressed), and the outer basal seta originating from an articulated setophore (this is shown for at least P4–P5 in *R. kuehnmanni* and *L. maryamae* and has as yet to be confirmed for P2–P3). Additional similarity is found in the plesiomorphic condition of the mandibular palp (2-segmented, 2 basal setae, exopod represented by single seta, endopod by 3) and the apomorphic reduction of caudal ramus seta V. *Rosacletodes* shows several plesiomorphic character states not found in *Laophontisochra* or *Acuticoxa* such as the 5-segmented ♀ antennule (with aesthetasc on segment IV), the trisetose antennary exopod and the biramous ♀ P5 with six elements on the endopodal lobe and five on the exopod. Prehensibility of the P1 endopod as displayed in the nannopodid genera *Laophontisochra* and *Acuticoxa* is a morphological adaptation that has evolved secondarily and convergently in response to changing environments in many other harpacticoid families such as the Ectinosomatidae (e.g. Hicks & Schriever 1983), Pseudotachidiidae (e.g. Hicks 1988), Cylindropsyllidae (e.g. Huys & Willems 1993) and Leptastacidae (Huys *et al.* 1996b). The non-prehensile P1 endopod in *Rosacletodes* has an identical segmentation and armature pattern as that of the prehensile ramus in both *Laophontisochra* and *Acuticoxa*, the only difference being the much shorter proximal endopod segment in *Rosacletodes*. Prehensibility of the P1 endopod is here considered a synapomorphy (in conjunction with the 4-segmented ♀ antennule, reduced antennary exopod, geniculate endopodal claw on the maxilliped, etc.) supporting the sistergroup relationship between *Laophontisochra* and *Acuticoxa* within a larger encompassing clade characterized by coxal projections on the swimming legs. This clade further includes *Rosacletodes*, *Huntemannia* and “Genus X”, all of which show varying degrees of coxal modification in leg 1, being most extreme in the latter genus (P.H.C. Corgosinho & M. Büntzow, pers. commn). Based on the arguments presented above, *Laophontisochra* and *Acuticoxa* are here formally assigned to the Nannopodidae.

The family Nannopodidae is heterogeneous at present; in particular, both *Metahuntemannia* and *Pottekia* (= *Talpina*) are radically divergent from the other nannopodid genera. The sexual dimorphism expressed on the P4 endopod (distal inner seta of ♀ modified into a serrate curved spine in ♂; cf. *Pottekia pectinata* (Dahms & Pottek, 1992)) clearly indicates an affinity with genera such as *Bathycamptus* Huys & Thistle, 1989; *Micropsammis* Mielke, 1975; and *Isthmiocaris* George & Schminke, 2003 (and almost certainly the closely related *Perucamptus* Huys & Thistle, 1989 – male unknown at present!) (George & Schminke 2003; Huys & Thistle 1989; Mielke 1975), all of which are currently assigned to the subfamily Hemimesochrinae in the Canthocamptidae (Wells 2007). Pending a revision of the latter family, *Metahuntemannia* and *Pottekia* are here tentatively assigned to the Hemimesochrinae.

## Key to genera of Nannopodidae

- 1 Exopods of P2–P4 3-segmented ..... 2
- Exopods of P2–P4 2-segmented ..... 3
- 2 Rostrum bell-shaped, anterior margin with multiple rows of long setules <sup>1</sup>; P1 endopod distinctly shorter than exopod; P2 endopod 2-segmented, exp-2 with 2–3 setae..... *Nannopus* Brady, 1880
- Rostrum triangular, without setular ornamentation; P1 endopod extending beyond distal margin of exp-3; P2 endopod 1-segmented with 1 apical seta ..... *Pontopolites* T. Scott, 1894
- 3 Antennule ♀ 4-segmented; P1 endopod prehensile, distinctly longer than exopod ..... 4
- Antennule ♀ 5-segmented; P1 endopod not prehensile, distinctly shorter than exopod ..... 5
- 4 P2–P4 with outer spinous projection on coxa; P5 exopod and baseoendopod fused in ♀, forming a single plate with 8 setae/spines ..... *Acuticoxa* **gen. nov.**
- P2–P4 without coxal processes; P5 biramous in ♀ ..... *Laophontisochra* George, 2002
- 5 Rostrum with setular ornamentation around apex; antennule ♀ with aesthetasc on segment 3; distal exopod segment of P1 with innermost seta much longer than inner distal spine and penicillate apically .... *Huntemannia* Poppe, 1884
- Rostrum without setular ornamentation around apex; antennule ♀ with aesthetasc on segment 4; distal exopod segment of P1 with innermost seta much shorter than inner distal spine and not penicillate at tip..... *Rosacletodes* Wells, 1985

<sup>1</sup> See Huys and Boxshall (1991: Fig. 3.15.4.B) for detailed structure.

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