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Contributions to the taxonomy of the Normanellidae (Copepoda, Harpacticoida): description of a new genus from the Brazilian continental shelf and re-assignment of *Pseudocletodes vararensis* Scott & Scott, 1893 (*ex* Nannopodidae)

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Abstract

A new genus and species of Normanellidae (Copepoda, Harpacticoida), *Paranaiara inajae* **gen. et sp. nov.**, is described from the continental shelf off the northern coast of São Paulo State, Brazil. The new genus differs from the type genus *Normanella* Brady, 1880 and *Sagamiella* Lee & Huys, 1999 in its presence of lamelliform caudal rami, a maxillulary endopod represented by 2 setae, an unarmed maxillipedal syncoxa, and reduced setation on P2 enp-2 (without outer spine) and P3 enp-2 (with only 2 inner setae). All these apomorphic character states are shared with the genus *Pseudocletodes* Scott & Scott, 1893, formerly placed in the family Nannopodidae (*ex* Huntemanniidae) and here assigned to the Normanellidae. *Pseudocletodes* can be differentiated from *Paranaiara* by the loss of the P1 endopod and of the inner seta on P2–P4 enp-1, the presence of only 2 inner setae on P2 enp-2 (instead of 3) and only 1 inner seta on P4 exp-3 (instead of 2), the presence of a second inner seta on P4 enp-2 (instead of 1), the morphology of the fifth pair of legs which are not medially fused and have only 3 endopodal elements (instead of 4) in the male, and the well developed caudal ramus seta V (instead of rudimentary). It is postulated that prehensility of the P1 endopod was secondarily lost in the common ancestor of *Paranaiara* and *Pseudocletodes*. An updated family diagnosis of the Normanellidae and a dichotomous identification key to the 22 currently valid species are presented.

Key words: Taxonomy, meiofauna, systematics, identification key, São Paulo State, Brazil

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Introduction

Lang (1944) established the subfamily Normanellinae in the Laophontidae to accommodate four genera: *Normanella* Brady, 1880, *Laophontopsis* Sars, 1908, *Cletopsyllus* Willey, 1935 and *Pseudocleta* Lang, 1944. Nicholls (1945) independently proposed the family Normanellidae for the genera *Normanella* and *Cletopsyllus* but this course of action was not accepted by Lang (1948). Some authorities nevertheless continued to attribute authorship of the family-group name to Nicholls (1945) (*cf.* Soyer 1966; Itô 1971, 1972).

Huys and Willems (1989) revised the taxonomic concept of the subfamily Normanellinae, relegated *Pseudocleta* to *genus incertae sedis* in the superfamily Laophontoidea, fixed *Laophontopsis* as the type genus of a new family Laophontopsidae and upgraded the Normanellinae to family level. Pending revisionary and phylogenetic studies the remaining genera were accommodated in two non-related subfamilies to reflect the diphyletic status of the family: Cletopsyllinae (*Cletopsyllus* and *Pseudocletopsyllus* Vervoort, 1964) and Normanellinae (*Normanella*). The Cletopsyllinae was recognised as a distinct family by Huys and Lee (1999). Lee and Huys (1999) subsequently revised the Normanellidae, recognizing two valid genera in the family. The genus *Normanella*, with 18 valid species in six lineages, has a wide geographical distribution and occurs in various sediment types and at different depths. *Sagamiella* Lee & Huys, 1999 has an exclusively abyssal distribution, having been reported from the Gulf of Biscay (Bodin 1968) and Sagami Bay, Japan (Lee & Huys 1999).

During an ecological study of the meiofauna of the continental shelf off the northern coast of São Paulo State a new genus and species of Normanellidae was discovered. *Paranaiara inajae* **gen. et sp. nov.** is not only the first record of the family in Brazilian waters but also provided us with the incentive to re-examine an enigmatic but apparently closely related species, *Pseudocletodes vararensis* Scott & Scott, 1893, which is currently placed in the Nannopodidae (*ex* Huntemanniidae). *Pseudocletodes vararensis* has only been recorded twice since its original description from the Moray Firth, Scotland. Scott and Scott (1896) reported it from dredgings near Sanda Lighthouse in the mouth of the River Clyde estuary, whereas Coull (1973) found several specimens of this species at five deep-sea stations off North Carolina. In an unpublished PhD dissertation on the meiofauna from the northern Gulf of Mexico deep sea, Baguley (2004) recorded two specimens of the genus, which he attributed to two undescribed species, *Pseudocletodes* sp. and *Pseudocletodes longicauda* [*nomen nudum*], respectively. This material has, however, never been examined any further.

Material and methods

Sediment samples were obtained during a study of the meiofaunal diversity along the northern coast of São Paulo State as part of the interdisciplinary project “Rational use of the coastal ecosystem from the Brazilian tropical region: São Paulo State” conducted by the Biological Oceanography Department – Oceanographic Institute, University of 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, in March and August, 1989. Description of the sampling methodology and physical and chemical analysis is given by Corbisier (1993). Coordinates and environmental parameters of the stations where the new genus occurred are compiled in Table 1.

Before dissection, the habitus was drawn from whole specimens temporarily mounted in lactophenol. Adhesive plastic discs were used to support the coverslip in temporary mounts. Specimens were dissected in lactic acid and the dissected parts were mounted on slides in lacophenol 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.

For scanning electron microscopy (SEM), specimens were dehydrated through a series of graded acetone, critical-point dried, mounted on stubs and sputter coated with palladium. The material was observed using a Philips XL 30 Field Emission Scanning Electron microscope.

Total body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. The descriptive terminology follows Huys et al. (1996). Abbreviations used in the text are: ae, aesthetasc; P1–P6, for swimming legs 1–6; exp, enp and benp for exopod, endopod and baseoendopod, respectively; exp (enp)-1 (-2, -3) to denote the proximal (middle, distal) segments of a ramus. The term 'acrothek' denotes the primitively trifid setal structure found on the apical margin of the distal antennulary segment (Huys & Iliffe 1998).

The type material of *Paranaiara inajae* **gen. et sp. nov.** is deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP) and the Natural History Museum, London (NHM).

Taxonomic account

Order Harpacticoida Sars, 1903

Family Normanellidae Lang, 1944

Amended diagnosis. Laophontoidea. Body elongate, subcylindrical, without clear distinction between prosome and urosome. Genital double-somite subdivided by an internal, transverse chitinous rib laterally and dorsally. Anal somite with well developed, rounded operculum. Genital field with gonopores fused medially forming genital slit; each covered by vestigial P6 bearing 2 setae; large copulatory pore located in median depression. Caudal rami cylindrical or lamelliform, elongate, with 7 setae.

Rostrum triangular or bell-shaped, defined at base. Antennule of female 5- or 6-segmented; with both pinnate and smooth setae and pinnate spines; with aesthetasc on segment 3 and (in *Normanella* and *Sagamiella* only) as part of an apical acrothek on the most distal segment. Antennule 7-segmented in male; subchirocer with geniculation between segments 5 and 6; with aesthetasc on segment 5 and digitiform projection on segment 6. Antenna with allobasis bearing 1–2 abexopodal setae and 1-segmented exopod with 3–4 setae; endopod with 6 distal elements and 2 spines laterally. Mandible with biramous palp; basis with 1–2 setae; exopod and endopod 1-segmented or fused to basis, with 1 and 4 setae, respectively. Maxillule with 1–2 basal endites; exopod 1-segmented and with 2 setae; endopod incorporated in basis and represented by 2–3 setae. Maxillary syncoxa with 3 endites, formula [1,3,3]; allobasis drawn out into claw with 1–2 accessory setae and 0–1 spines; endopod represented by 3 setae. Maxilliped prehensile, with 0 or 2 setae on syncoxa; basis unarmed; endopod 1-segmented, drawn out into claw bearing 1–2 accessory setae.

P1 basis with inner spine located at inner distal corner and an outer spine. Exopod 3-segmented, exp-2 with inner seta, exp-3 with 3 spines and 2 setae. Endopod absent (in *Pseudocletodes*) or 2-segmented; either prehensile with elongate enp-1 or not prehensile with enp-1 as long as enp-2; enp-1 with 0–1 seta; enp-2 with 1 lateral and 2 apical elements. P2–P4 with 3-segmented exopods and 2-segmented endopods; basis with outer spine (P2) or seta (P3–P4); spine and seta formulae as follows:

	Exopod	Endopod
P1	0.1.023	[0–1].120 or absent
P2	0.1.123	[0–1]. [2–3]2[0–1]
P3	0.1.223	[0–1].[2–3]21
P4	0.1.[1–2]23	[0–1].[1–2]21

Female fifth pair of legs not fused medially, defined at the base, intercoxal sclerite absent; exopod and baseoendopod separate; exopod oval, with 6 setae; endopodal lobe elongated, with 5 setae; basal seta arising

from short setophore. Male fifth pair of legs fused medially or separated (in *Pseudocletodes*); endopodal lobe with 2–4 elements; exopod with 4 setae; basal seta arising from short setophore. Male sixth pair of legs asymmetrical (but without noticeable left-right size difference), with dextral and sinistral configurations; each with 2–3 setae. Eggs retained in a single ventral sac.

Sexual dimorphism in antennule, P2 endopod (enp-2 distal setae reduced in male), P3 endopod (male enp-2 forming an apophysis; distal elements usually reduced in length), P5, P6 and in genital segmentation. Male clasps caudal rami of female during precopulatory mate guarding.

Marine, free-living.

Type genus: *Normanella* Brady, 1880 (type species by monotypy: *Normanella dubia* Brady, 1880). Note that the type species cannot be attributed to "Brady & Robertson, 1880" (in *e.g.* Lang 1948; Bodin 1997) or "Brady & Robertson in Brady, 1880" (in *e.g.* Lee & Huys 1999) since an outside person (*i.e.* other than an author of the work) can only be credited with authorship if he/she is alone responsible for the name and for satisfying the criteria of availability (ICZN Art. 50.1.1) (Huys 2009).

Other genera included: *Pseudocletodes* Scott & Scott, 1893; *Sagamiella* Lee & Huys, 1999; *Paranaiara* **gen. nov.**

Genus *Paranaiara* gen. nov.

Diagnosis. Normanellidae. Body elongate, subcylindrical, without clear distinction between prosome and urosome. Genital double-somite with internal transverse chitinous ribs laterally and dorsally. Anal somite with well developed rounded operculum. Genital field with median genital slit; vestigial P6 with 2 setae; copulatory pore large. Caudal rami lamelliform and elongate, with straight outer margin and convex inner margin; with 7 setae; setae IV–V rudimentary conical spines.

Rostrum triangular. Antennule 6-segmented in female, with pinnate spines on segments 2, 3, 5 and 6, and an aesthetasc on segment 3; 7-segmented and subchirocer in male, with geniculation between segments 5 and 6, and an aesthetasc on segment 5; acrothek consisting of 2 basally fused setae. Antennary allobasis with 2 abexopodal setae; exopod with 4 setae. Mandible with biramous palp; basis with 1 seta; exopod 1-segmented, defined at base, with 1 seta; endopod fused to basis, with 4 setae. Maxillule with 2 basal endites, proximal endite represented by 2 setae, distal endite by 3 distal setae; exopod with 2 setae; endopod represented by 2 setae. Maxillary syncoxa with 3 endites; accessory armature on allobasis consisting of 2 setae; endopod represented by 3 setae. Maxilliped prehensile, with unarmed syncoxa; palmar margin of basis without ornamentation; endopod drawn out into a claw bearing 1 long seta.

P1 endopod 2-segmented, not prehensile; enp-1 as long as enp-2, unarmed; enp-2 with 1 lateral and 2 distal setae. P4 exp-3 with 2 inner setae. P2–P4 enp-1 with inner seta. P2–P4 enp-2 with 3, 2 and 1 inner setae, respectively; P2 enp-2 outer spine absent. P3 enp-2 outer apical seta well developed in male but shorter than in female. P2–P4 spine and seta formulae as follows:

	Exopod	Endopod
P1	0.1.023	0.120
P2	0.1.123	1.320
P3	0.1.223	1.221
P4	0.1.223	1.121

Male fifth pair of legs fused medially, endopodal lobe with 2 setae and 2 spines; exopod with 4 setae. Male sixth pair of legs asymmetrical, with dextral and sinistral configurations, with 3 setae each. Single egg-sac.

Type and only species: *Paranaiara inajae* **gen. et sp. nov.**

Etymology. The generic name is derived from the Tupí-Guaraní (a South American Indian language) *parana* (meaning sea) and *iara* (meaning lady). Gender: feminine.

***Paranaiara inajae* sp. nov.**
(Figs 1–11)

Type locality. Brazil, São Paulo State, Ubatuba (23º37.2' S, 45º01.2' W), 41 m depth; for additional environmental parameters see Table 1 (station 18V).

Type material. Holotype female in ethanol (reg. no MZUSP 19054) from station 18V, March 1989. Undissected paratypes (in ethanol) deposited in MZUSP (reg nos 19055–19062) include 1 female from station 5V, March 1989; 1 female from station 7V, March 1989; 1 female and 2 males from station 16V, March 1989; 1 female from station 18V, March 1989; 1 female and 1 male from station 26V, March 1989; 1 female from station 5I, August 1989; 1 female and 2 males from station 18I, August 1989; 1 female from station 26I, August 1989. Additional undissected paratypes (in ethanol) deposited in NHM include 1 female from station 7V, March 1989 (reg. no 2008.3651); 2 males from station 16V, March 1989 (reg. nos 2008.3652–3653); 1 female from station 18V, March 1989 (reg. no 2008.3654); 2 females from station 26V, March 1989 (reg. nos 2008.3655–3656); 1 female from station 27V, March 1989 (reg. no 2008.3657); 2 females from station 18I, August 1989 (reg. nos 2008.3658–3659); and 1 female from station 27I, August 1989 (reg. no 2008.3660). Dissected paratypes in the collection of C.E.F. da Rocha (Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo): 1 female from station 5I, August 1989; 3 females from station 26I, August 1989; 4 males from station 27I, August 1989; and 2 females from station 28I, August 1989. All material collected by T. Corbisier.

TABLE 1. Coordinates and environmental parameters of sampling sites where *Paranaiara inajae* **gen. et sp. nov.** was recorded during the interdisciplinary project "Rational use of the coastal ecosystem from the Brazilian tropical region: São Paulo State" conducted by the Biological Oceanography Department – Oceanographic Institute, University of São Paulo. Stations were sampled across the inner continental shelf of São Paulo State between São Sebastião Island and Ubatumirim inlet, Ubatuba during March (V stations) and August 1989 (I stations). Lat. = latitude, Long. = longitude; Temp. = temperature; MZ = grain size; GS = sorting; C_{org} = organic carbon. Sediment type according to Shepard's (1954) classification.

Station	Lat. (S)	Long. (W)	Depth (m)	Temp. (º C)	MZ (Ø)	GS (φ)	Sand (%)	Silt (%)	Clay (%)	C_{org} (%)	$CaCO_3$ (%)	Sediment type
5V	23º40.8'	44º46.2'	53	15.3	4.61	1.86	63.10	25.45	11.45	1.00	17.00	Silty sand
7V	23º31.2'	44º51.0'	44	15.3	1.02	0.92	98.64	0.39	0.00	0.03	8.70	Sand
16V	23º45.5'	44º56.4'	52	15.8	4.94	1.63	46.14	43.84	10.02	1.07	16.70	Silty sand
18V	23º37.2'	45º01.2'	41	15.7	3.39	0.88	90.29	6.95	2.77	0.34	27.70	Sand
26V	23º50.4'	45º05.4'	44	15.5	4.06	1.18	67.62	24.91	7.47	0.55	14.00	Silty sand
27V	23º46.2'	45º07.8'	34	15.6	3.63	0.85	87.23	8.12	4.64	0.42	9.70	Sand
5I	23º40.7'	44º46.2'	53	19.8	3.38	1.08	84.05	11.55	4.40	0.75	18.80	Sand
18I	23º37.2'	45º01.3'	41	18.3	3.52	0.77	87.59	10.01	2.40	0.67	17.10	Sand
26I	23º50.5'	45º05.5'	45	20.5	4.15	1.18	72.42	21.23	6.36	1.26	15.00	Silty sand
27I	23º46.3'	45º07.7'	39	20.4	3.65	0.79	85.71	10.39	3.90	0.29	15.20	Sand
28I	23º42.0'	45º10.8'	27	21.6	3.46	0.72	90.64	6.10	3.27	0.98	10.70	Sand

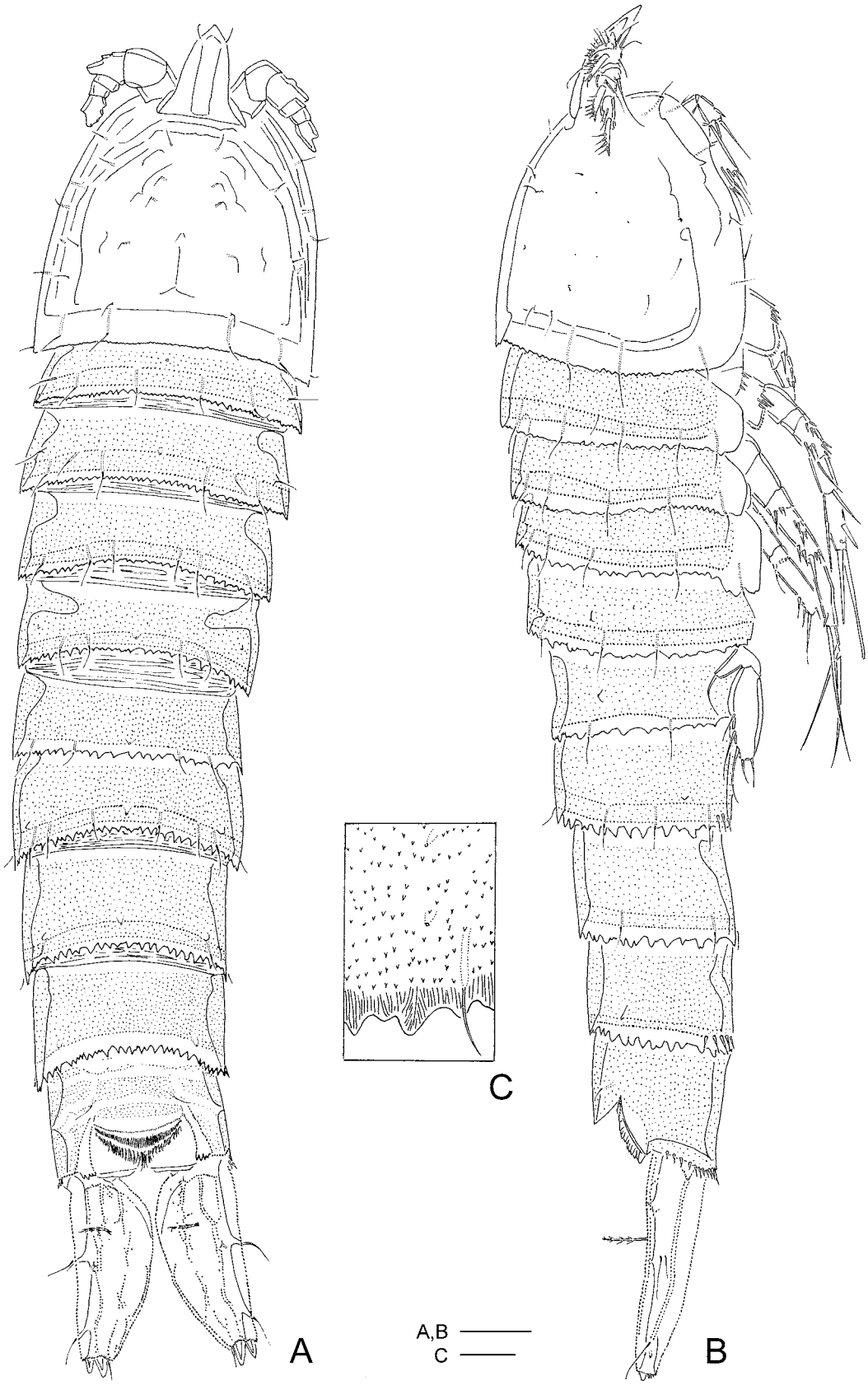

FIGURE 1. *Paranaiara inajae* **gen. et sp. nov.** (♀): (A) habitus, dorsal; (B) habitus, lateral; (C) detail of surface ornamentation on pedigerous somite, showing minute denticles, sensilla, integumental secretory pores and posterior margin reticulation, dorsal. Scale bars: 10 μm (C), 50 μm (A, B).

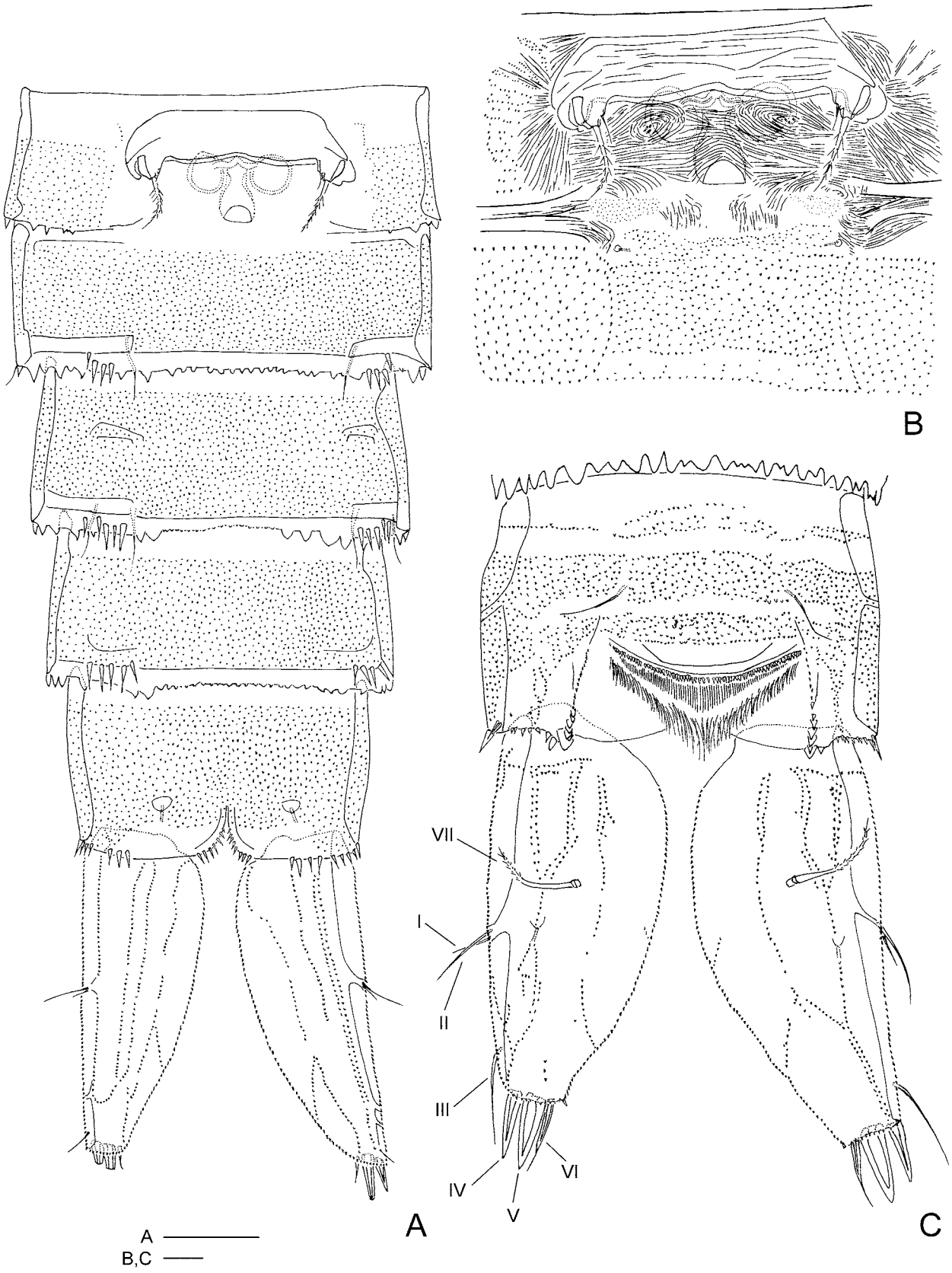

FIGURE 2. *Paranaiara inajae* **gen. et sp. nov.** (♀): (A) urosome, ventral [P5-bearing somite omitted]; (B) genital field; (C) anal somite and caudal rami, dorsal. Scale bars: 10 μm (B, C), 50 μm (A).

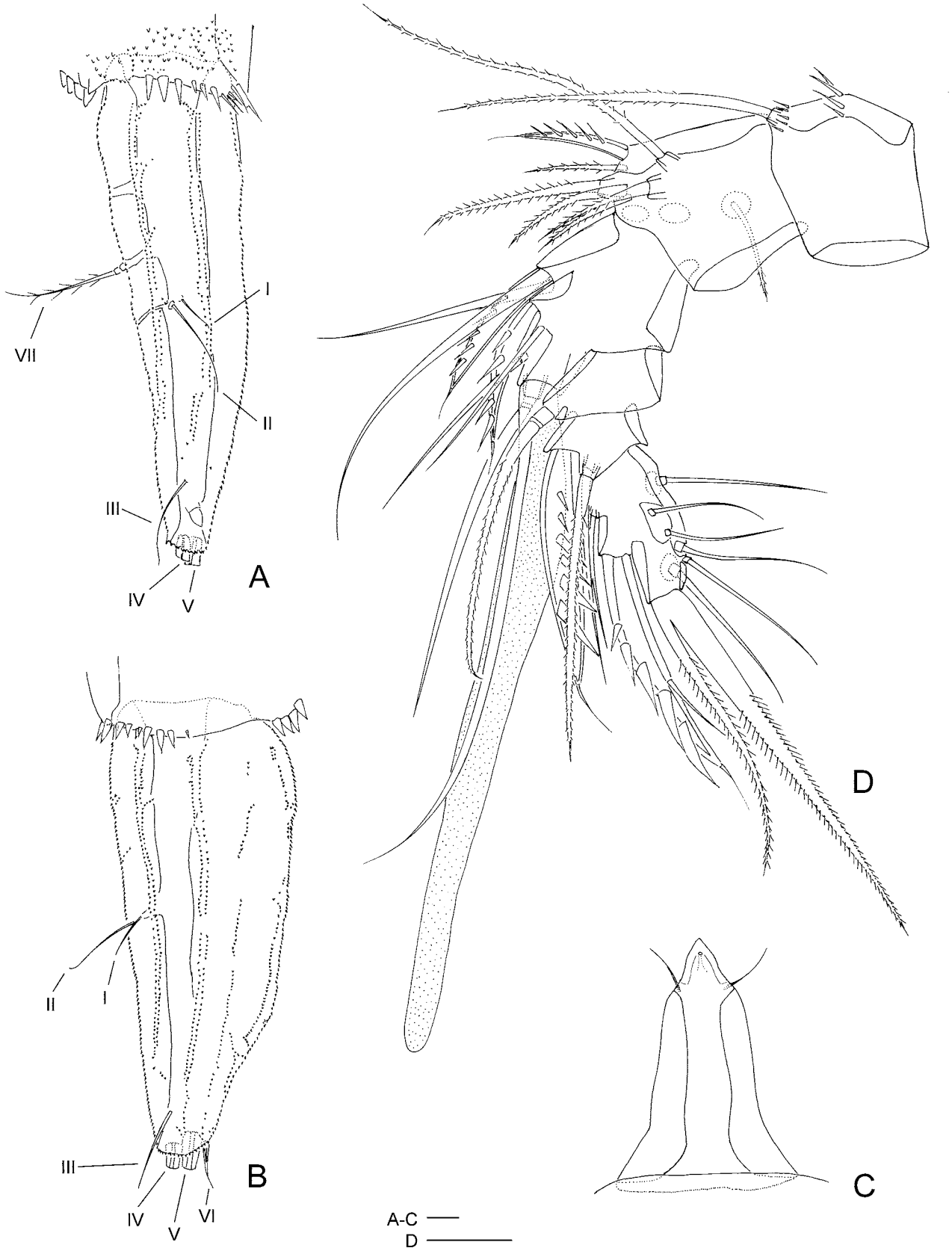

FIGURE 3. *Paranaiara inajae* **gen. et sp. nov.** (♀): (A) right caudal ramus, lateral; (B) right caudal ramus, ventral; (C) rostrum, dorsal; (D) antennule, ventral. Scale bars: 10 μm.

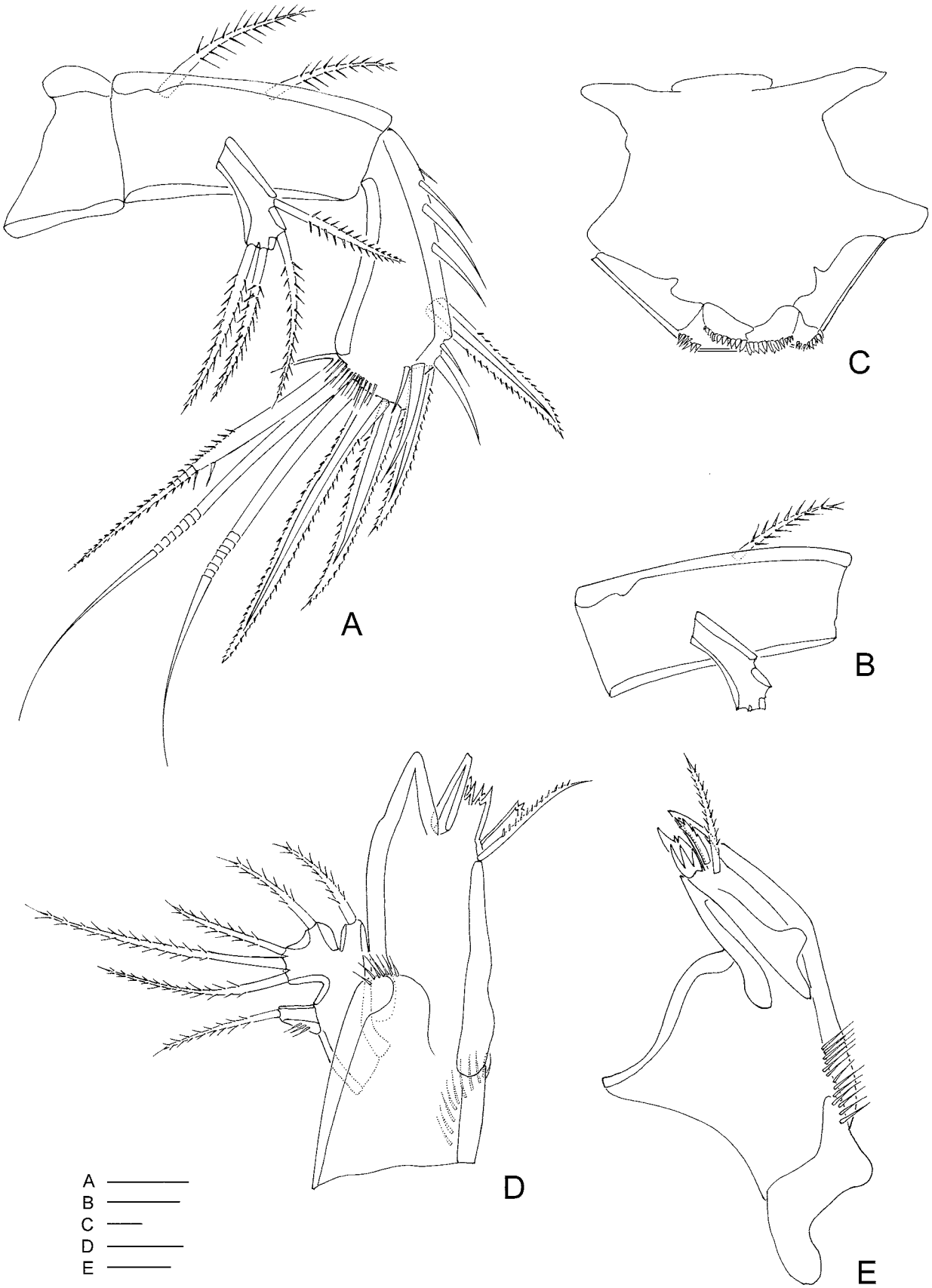

FIGURE 4. *Paranaiara inajae* **gen. et sp. nov.** (♀): (A) antenna; (B) antennary allobasis with aberrant abexopodal setation [exopodal armature omitted]; (C) labrum, anterior; (D) mandible; (E) mandibular gnathobase. Scale bars: 10 μm.

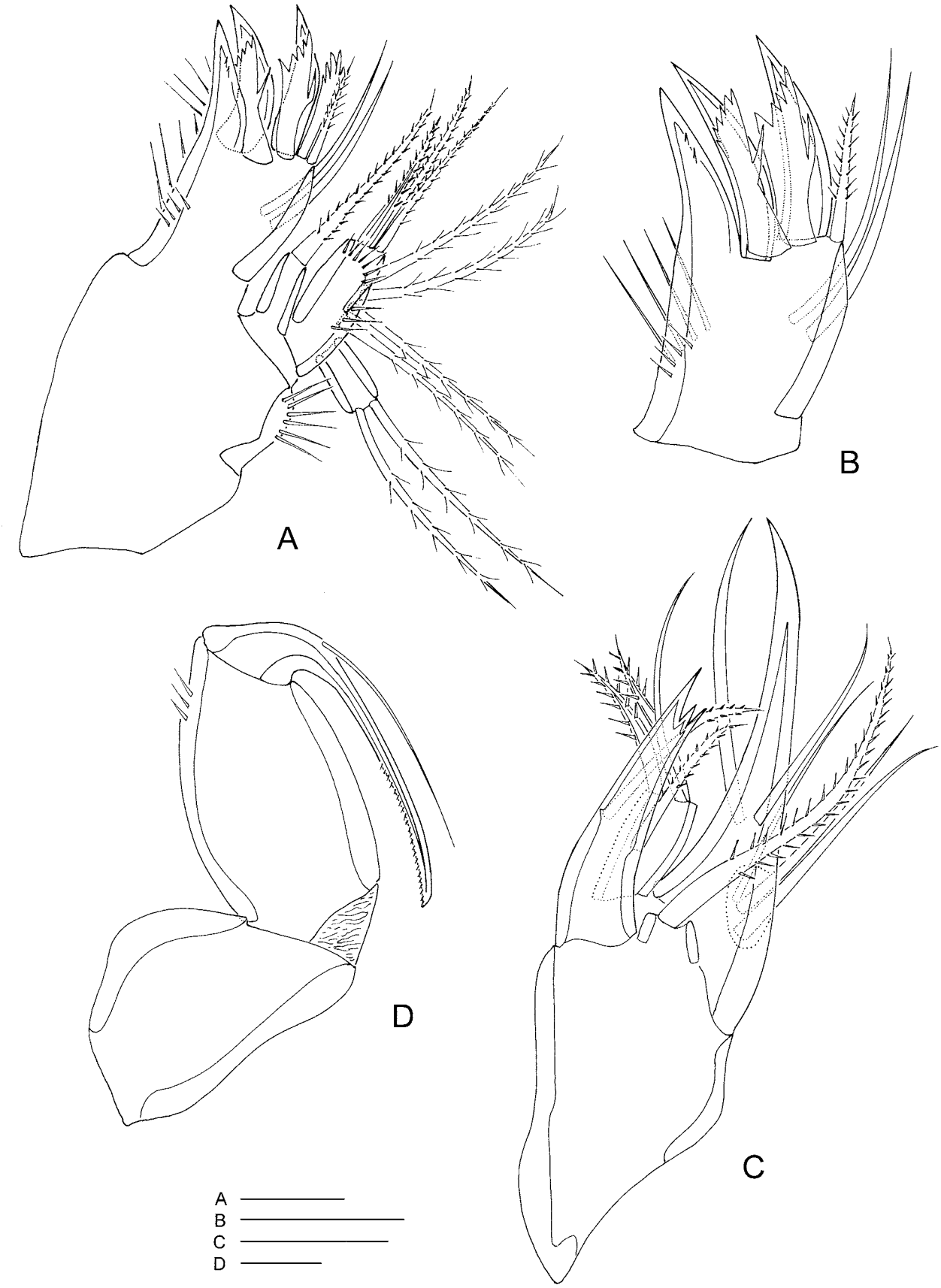

FIGURE 5. *Paranaiara inajae* **gen. et sp. nov.** (♀): (A) maxillule, posterior; (B) maxillulary arthrite, posterior; (C) maxilla, medial view; (D) maxilliped. Scale bars: 10 μm.

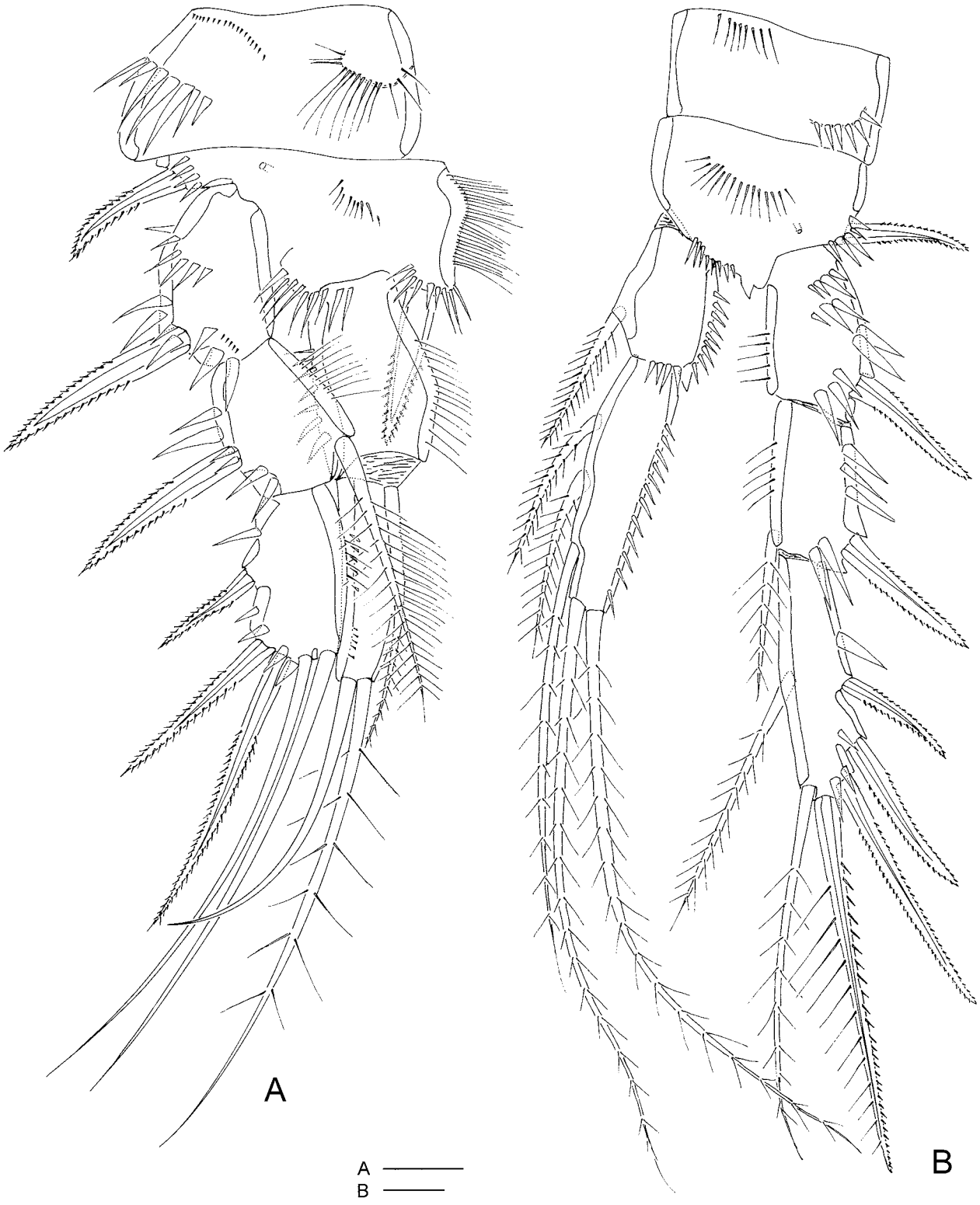

FIGURE 6. *Paranaiara inajae* **gen. et sp. nov.** (♀): (A) P1, anterior; (B) P2, anterior. Scale bars: 10 μm.

FIGURE 7. *Paranaiara inajae* **gen. et sp. nov.** (♀): (A) P3, anterior; (B) P4, anterior; (C) P5, anterior. Scale bars: 10 μm.

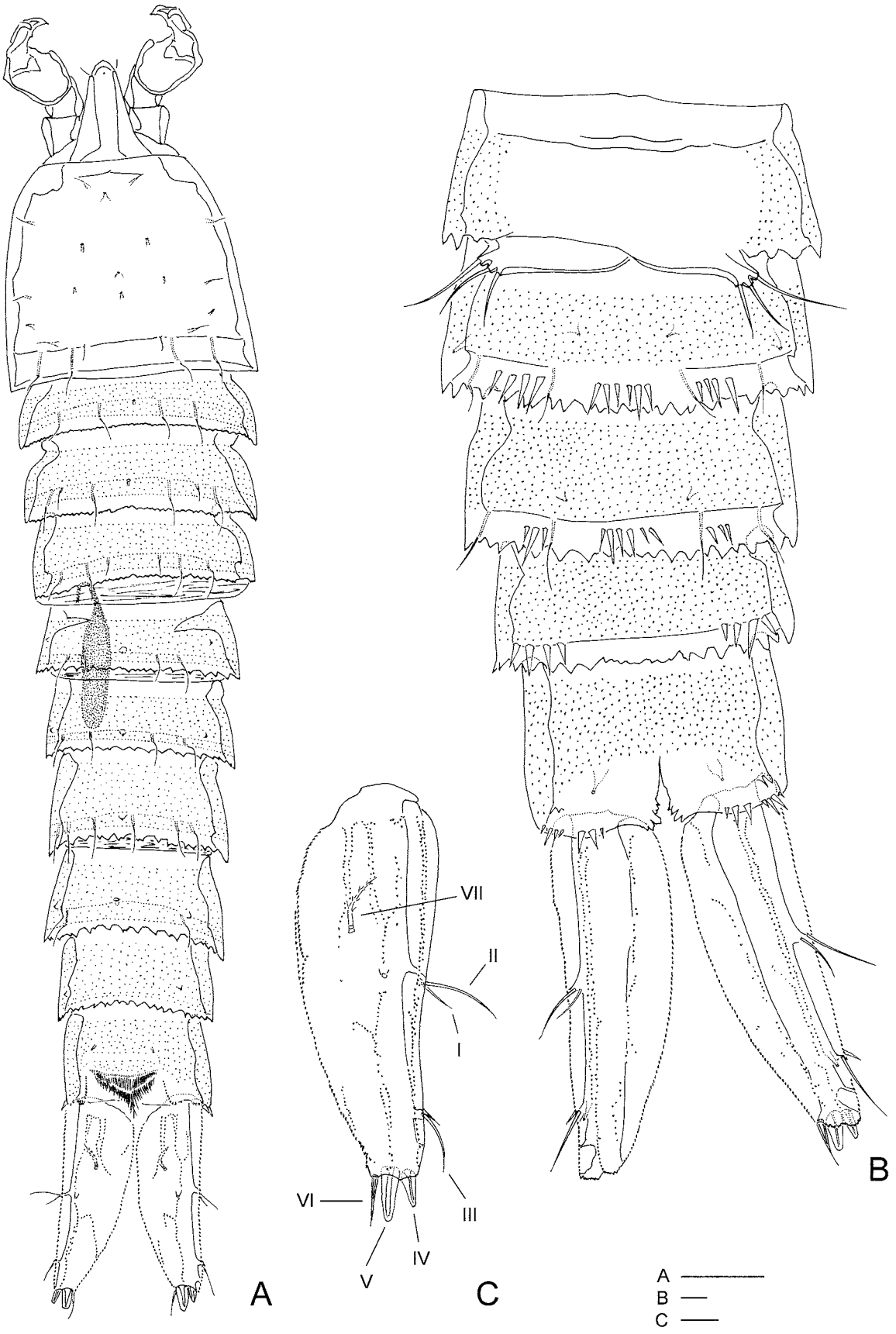

FIGURE 8. *Paranaiara inajae* **gen. et sp. nov.** (♂): (A) habitus, dorsal; (B) urosome, ventral [P5-bearing somite omitted]; (C) right caudal ramus, dorsal. Scale bars: 10 μm (B, C), 50 μm (A).

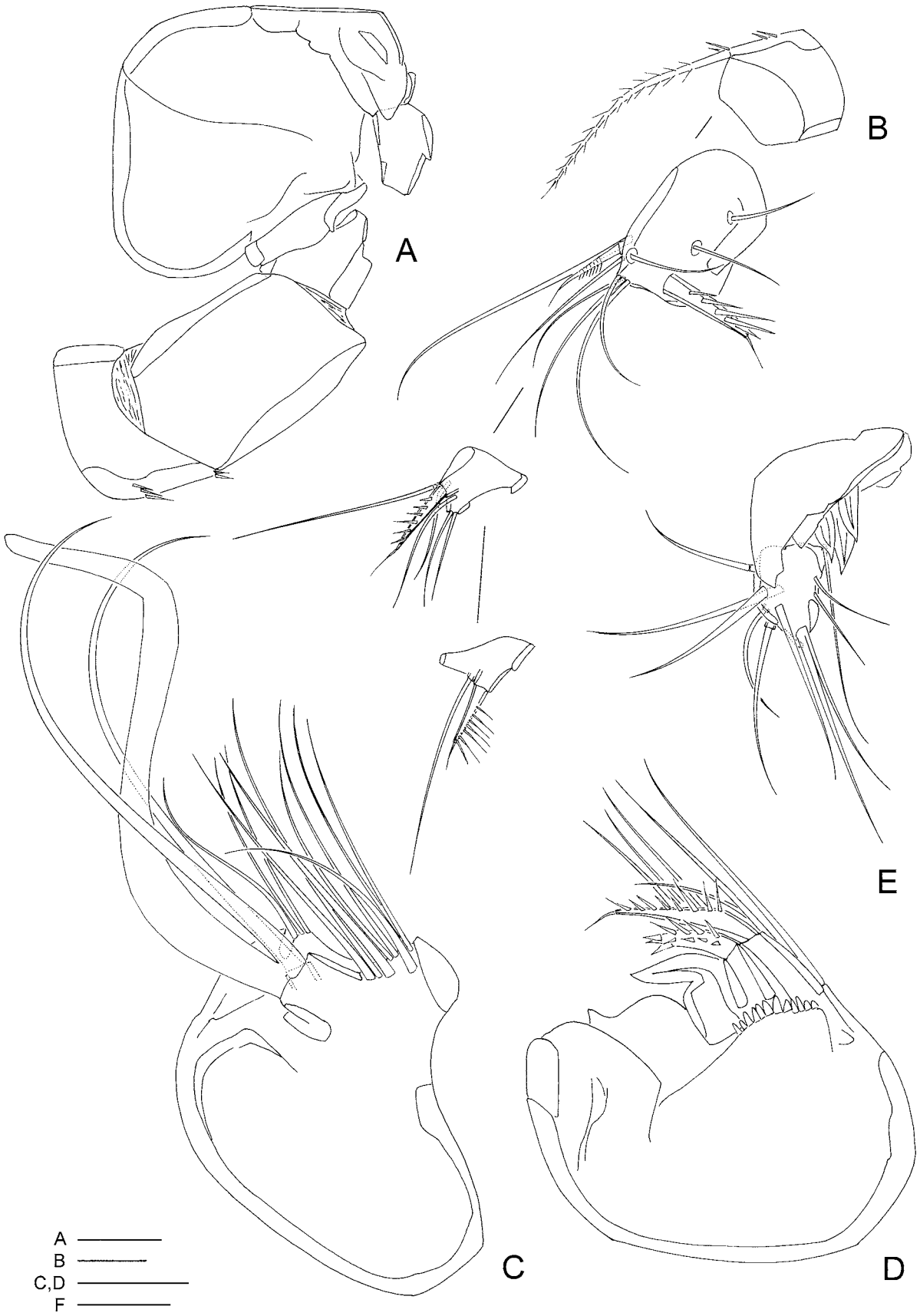

FIGURE 9. *Paranaiara inajae* **gen. et sp. nov.** (♂): (A) antennule, ventral [armature omitted]; (B) antennulary segments 1–4, ventral [disarticulated]; (C) antennulary segment 5, ventral; (D) antennulary segment 5, dorsal; (E) antennulary segments 6–7, ventral. Scale bars: 10 μm.

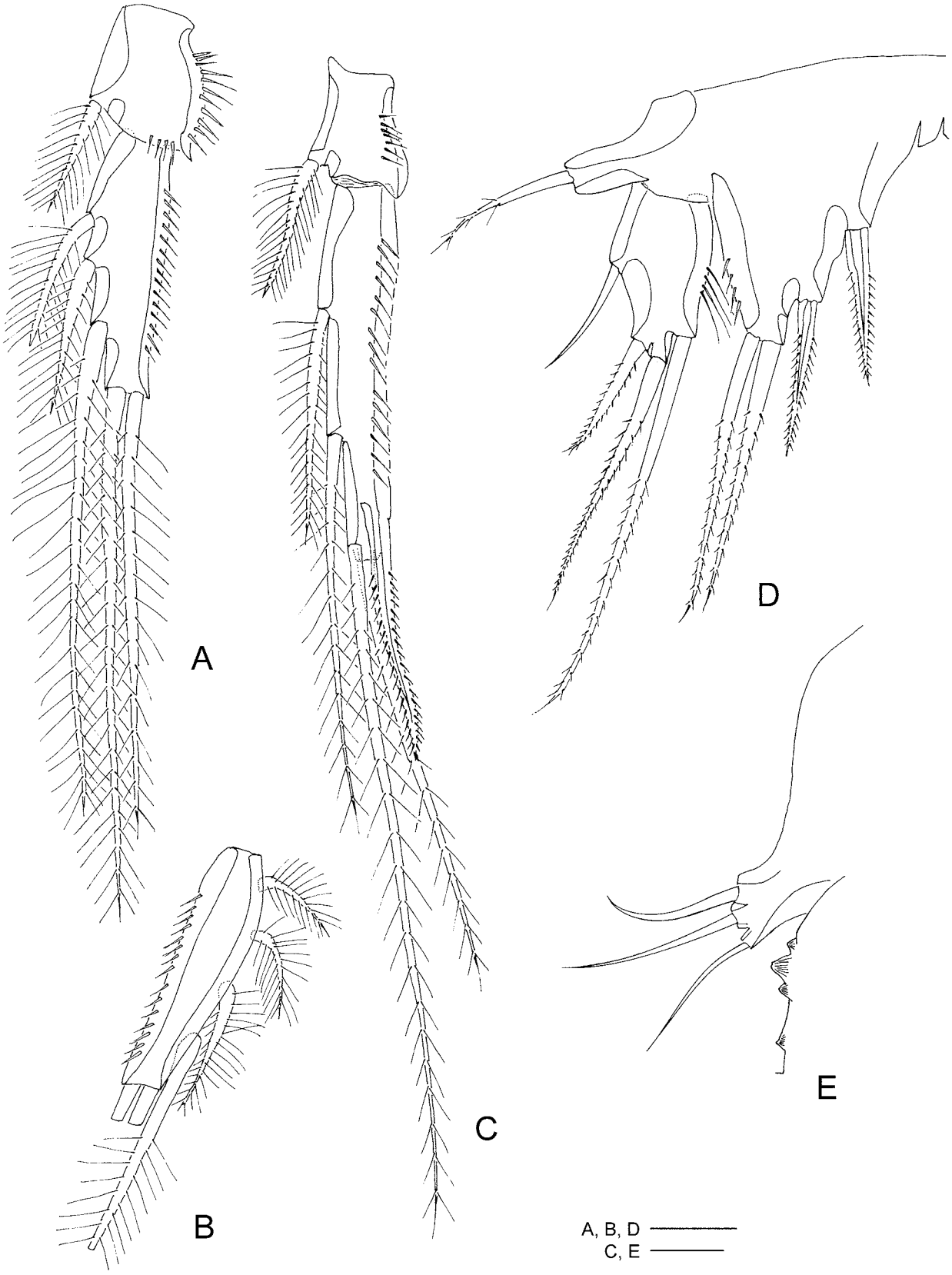

FIGURE 10. *Paranaiara inajae* **gen. et sp. nov.** (♂): (A) P2 endopod, anterior; (B) P2 endopod-2 with aberrant setation pattern [distal elements omitted]; (C) P3 endopod, anterior; (D) P5, anterior; (E) P6. Scale bars: 10 μm.

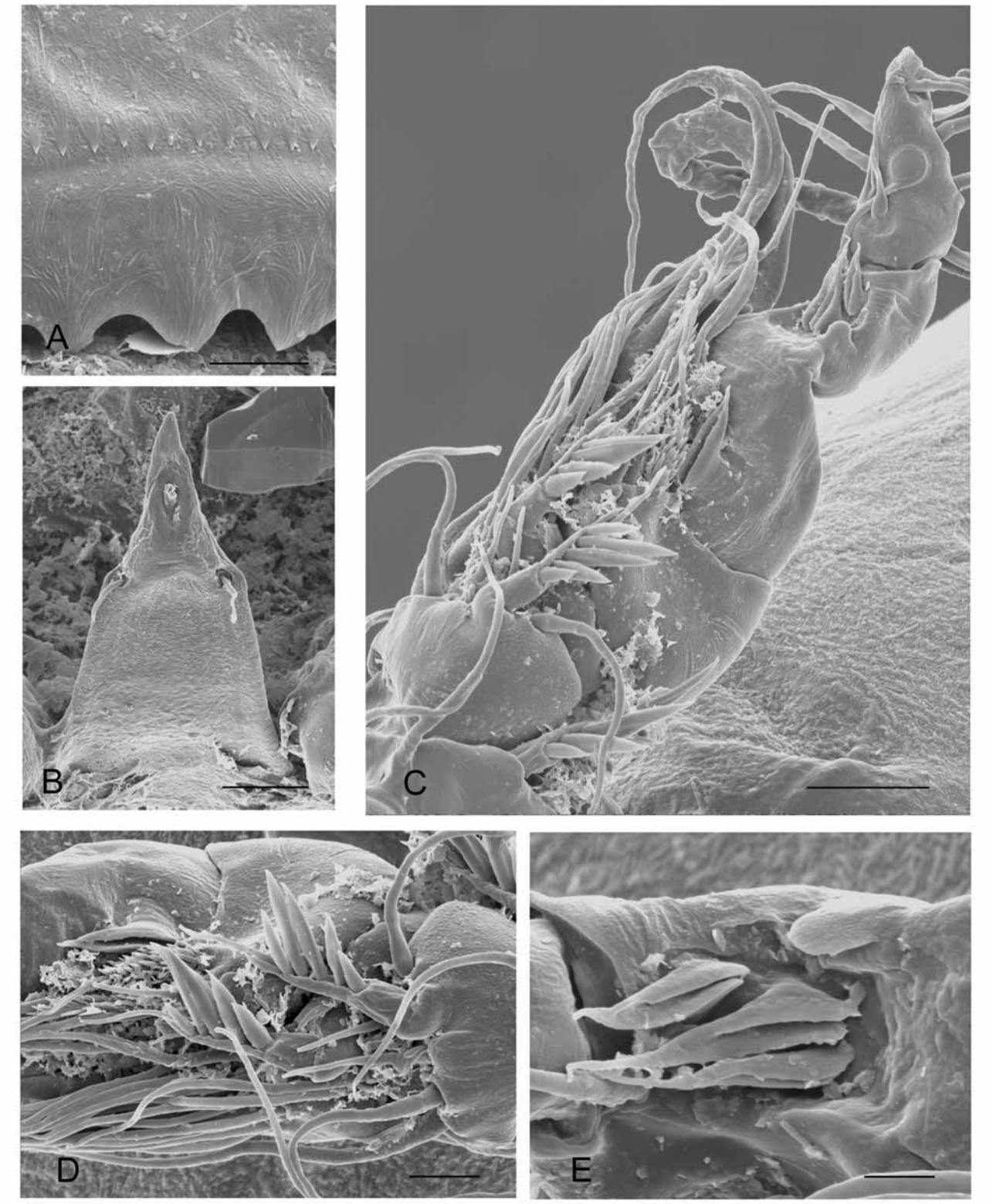

FIGURE 11. *Paranaiara inajae* **gen. et sp. nov.** (♂), scanning electron micrographs: (A) surface ornamentation of pedigerous somite, showing minute denticles and reticulation near posterior margin, dorsal; (B) rostrum, dorsal; (C) antennulary segments 4–7, anterodorsal; (D) antennulary segments 4–5, anterior; (E) antennulary segment 6, anterior. Scale bars: 2 μm (E); 5 μm (A, D), 10 μm (B, C).

Description. FEMALE (Figs 1–7). Total body length 725–1014 μm (*N* = 14; mean = 849 μm). Largest width measured at posterior margin of cephalic shield: 192 μm. Urosome slightly narrower than prosome (Fig. 1A–B).

Cephalic shield with serrulate posterior margin; pleural area well developed and rounded, with sensilla as illustrated in figures 1A–B; without areolation and without minute spinules as found on free body somites.

Pedigerous somites (Fig. 1A–B) covered with minute spinules and a pattern of sensilla and pores as illustrated; hyaline frill not developed; pleurotergites well developed, rounded, ventral portion without minute spinules; posterior margins serrate and with fine reticulation as shown in figure 1C.

Urosomites (Figs 1A–B; 2A) with surface ornamentation consisting of minute spinules dorsally and ventrally. Hyaline frill not developed but posterior margin distinctly serrate dorsally and ventrolaterally. Posterior margin of urosomites 2–4 crenulate midventrally and with a few lateroventral spinules.

Genital double-somite (Figs 1A–B; 2A) with original segmentation marked by transverse serrate surface ridge dorsally and dorsolaterally and a short surface suture ventrolaterally; completely fused ventrally. Genital field (Fig. 2B) with pattern of dense surface striations; copulatory pore large, located in midventral depression, without surrounding spinules. Gonopores fused medially forming a single genital slit covered on both sides by opercula derived from the sixth legs. P6 with a small protuberance bearing 1 pinnate outer seta and 1 minute inner seta.

Anal somite (Fig. 2A, C) with well developed rounded, denticulate anal operculum flanked by a row of small spinous processes. Anal opening with a fringe of fine setules and bordered by small spinules midventrally. Surface ornamentation consisting of a pair of sensilla dorsally and a pair of pores ventrally; posterior margin with few spinules ventrally and dorsally.

Caudal rami (Figs 2C; 3A–B) lamelliform and elongate, about 3 times as long as wide; with straight outer margin and convex inner margin. Each ramus with a dorsal pore medially, 1 tube-pore laterally and 7 setae: seta I naked, shortest and closely set to naked seta II; seta III naked and positioned ventrolaterally; setae IV and V represented by rudimentary, conical, smooth spines, not fused basally; seta VI naked; seta VII bi-articulate at its base and sparsely pinnate. Surface ornamentation of each ramus consisting of rows of minute denticles as shown in figures 2C, 3A–B. Posterior margin denticulate and with a ventral semi-circular extension covering bases of setae IV–VI.

Rostrum (Fig. 3C) triangular, prominent and tapering abruptly towards apex; completely defined at the base; with pair of tiny sensilla and a middorsal tube-pore near the apex; dorsal and ventral surface without ornamentation.

Antennule (Fig. 3D) short, 6-segmented, segment 3 the longest. Segment 1 with spinular rows around anterior margin and at base of seta. Segment 3 with aesthetasc fused basally to a seta and arising from a distinct pedestal. Armature formula: 1-[1 pinnate], 2-[7 pinnate + 1 pinnate spine (+ 2 elements missing in holotype, indicated by dorsal scars in Fig. 3D)], 3-[5 + 2 pinnate spines + (1 + ae)], 4-[1 pinnate], 5-[1 + 1 pinnate + 1 pinnate spine], 6-[7 + 1 pinnate spine + acrothek]. Acrothek consisting of 1 slender and 1 strong pinnate seta. Pinnate spines on segments 5 and 6 very large and with coarse spinules.

Antenna (Fig. 4A) 3-segmented comprising coxa, allobasis and and free distal segment of endopod. Coxa small, without ornamentation. Basis and proximal endopod segment completely fused, forming an elongate allobasis bearing 2 abexopodal pinnate setae. Exopod 3 times longer than wide, with 2 pinnate setae laterally and 2 pinnate setae apically. Free endopod segment as long as allobasis, abexopodal margin with a row of long spinules and distal margin with a row of fine spinules; lateral armature consisting of 2 pinnate spines; distal armature consisting of 2 pinnate spines and 3 geniculate setae, outermost one being pinnate and fused basally to a short seta.

Labrum (Fig. 4C) well developed, with spinular ornamentation along distal margin. Paragnaths not observed.

Mandible (Fig. 4D–E) with well developed gnathobase bearing several multicuspidate teeth around distal margin and 1 pinnate seta at dorsal corner. Palp small, biramous but only the exopod is defined at its base. Basis with 1 pinnate seta. Exopod 1-segmented, small, with 1 plumose seta apically and a few spinules along outer margin. Endopod fused to basis, with 1 lateral and 3 distal plumose setae.

Maxillule (Fig. 5A–B) with large praecoxa bearing a few short distal spinules around outer margin; arthrite strongly developed, with 2 naked setae on anterior surface and 7 spines/setae around distal margin,

innermost one fused at its base (Fig. 5B). Coxa with cylindrical endite bearing 1 pinnate seta. Basis with 2 endites, represented by 2 plumose and 3 pinnate setae, respectively; with a row of spinules on posterior surface. Endopod incorporated with basis, represented by 2 plumose setae. Exopod 1-segmented, with 2 sparsely plumose setae.

Maxilla (Fig. 5C) with 3 endites on syncoxa; praecoxal endite small and cylindrical, with one pinnate seta; proximal coxal endite with one multicuspidate spine fused to endite, and 2 pinnate setae; distal coxal endite with 2 pinnate spines and 1 naked seta. Allobasis drawn out into strong, slightly curved claw. Accessory armature consisting of 2 naked setae. Endopod represented by 3 naked setae.

Maxilliped (Fig. 5D) without armature or ornamentation on syncoxa. Basis with a few spinules near outer distal corner. Endopod drawn out into a long pinnate claw; accessory armature consisting of a long naked seta. Swimming legs P1–P4 (Figs 6A–B; 7A–B) with 3-segmented exopods and 2-segmented endopods.

P1 (Fig. 6A) with a well developed coxa bearing strong spinules along outer margin, minute denticles near outer distal corner and fine setules on anterior surface. Basis with setules along inner margin; anterior surface with a pore and 4 spinular rows as figured; armature consisting of strong, pinnate outer and inner spines. Exopodal segments with strong spinules along outer margin and outer distal corner; exp-2 and -3 also with setules along inner margin; exp-1 with 1 stout pinnate outer spine; exp-2 with pinnate outer spine and plumose inner seta (extending beyond distal margin of exp-3); exp-3 with 3 pinnate outer spines and 2 geniculate distal setae. Endopod 0.85 times as long as exopod; segments with setules along inner margin and spinules along outer margin as figured; enp-1 slightly shorter than enp-2, unarmed. Enp-2 with 1 plumose and 1 strong naked setae apically, and 1 plumose inner seta.

P2–P4 (Figs 6B; 7A–B). Coxa and basis with spinular rows along outer margin. Coxa with 1 (P4) or 2 (P2–P3) rows of setules/spinules on anterior surface. Basis with spinules near insertion of endopod near base of outer spine/seta; anterior surface with setular row in P2; with outer bipinnate spine (P2) or sparsely plumose seta (P3–P4). Exopodal segments with strong spinules along outer margin and outer distal corner; exp-1 and -2 also with fine setules along inner margin. Endopodal segments with spinules along outer margin (except P4 enp-1); P2 enp-2 twice as long as enp-1, endopod reaching to proximal third of exp-3; P3 enp-2 3 times as long as enp-1, endopod reaching to distal margin of exp-2; P4 enp-2 2.3 times longer than enp-1, endopod reaching to middle of exp-2. Spine and setal formula as for genus.

P5 (Fig. 7C) baseoendopod with a short outer setophore bearing a short, plumose basal seta; with one pore near proximal margin. Endopodal lobe elongate, extending beyond distal margin of exopod, with 3 pinnate setae along inner margin and 2 pinnate setae apically; outer margin with spinules; inner margin with spinules, setules and 2 tube-pores as figured. Exopod oval, tapering distally, inner and proximal outer margins with setules; with 1 naked and 2 pinnate setae along outer margin, 2 naked setae around apex and 1 naked seta along inner margin.

MALE (Figs 8–11). Body more slender than in female. Body length 652–913 μm (*N* = 10; mean = 808 μm). Largest width measured at distal margin of P3-bearing somite: 128 μm. Urosome narrower than prosome (Fig. 8A). Rostrum distinct at base as in female (Fig. 11B). Cephalic shield with smooth posterior margin; ornamentation consisting of sensilla and pores as figured. Pedigerous somites covered with small denticles (Fig. 11A); with serrate posterior margin and delicate reticulation (Fig. 11A). Surface ornamentation of urosome (Fig. 8A–B) consisting of patches of minute spinules, sensilla and pores. Posterior margins with weaker serrations than in female; with ventral spinule rows. Caudal rami (Fig. 8B–C) more slender than in female, with additional tube-pore and spinules near base of seta III.

Antennule (Figs 9A–E; 11C–E) 7-segmented. Subchirocer with geniculation between segments 5 and 6. Segment 1 with 2 rows of spinules along anterior margin. Segment 4 represented by small sclerite (Fig. 9B). Segment 5 largest and swollen, with partial surface suture (Figs 9C–D; 11C–D). Segment 6 forming dorsal spinous process overlying anterior part of segment 7 (Fig. 9E). Armature formula: 1-[1 pinnate], 2-[9 + 1 pinnate +1 pinnate spine], 3-[5 + 1 pinnate spine], 4-[1 + 1 pinnate spine], 5-[18 + 2 pinnate spines + 1 fused spine + (1 + ae)], 6-[1 + 3 modified elements], 7-[8 + acrothek]. Pinnate spines on segments 2–4 with coarse

spinules (Fig. 11C–D). Modified elements on segment 6 fused at base and transversally elongate (Fig. 11E). Acrothek consisting of 2 short, basally fused, naked setae.

P2 endopod (Fig. 10A) 2-segmented; both apical setae of enp-2 distinctly shorter than in female.

P3 endopod (Fig. 10C) 2-segmented and modified. Enp-2 more slender and longer than in female; outer margin with a subdistal, straight, bipinnate apophysis (homologous with outer spine of enp-2 of female). Inner seta of enp-1 and both distal inner and outer distal seta of enp-2 shorter than in female.

Fifth pair of legs (Fig. 10D) fused medially; defined at base. Baseoendopod with a short outer setophore bearing a plumose basal seta. Endopodal lobe triangular, much shorter than in female, not reaching distal margin of exopod; with 2 inner pinnate spines and 2 apical pinnate setae; with a row of small spinules along outer margin. Exopod about twice as long as maximum width; ornamented with a few fine setules along inner margin; armature consisting of 1 long pinnate inner seta, 1 pinnate apical seta and 2 outer elements (proximal one naked, distal one pinnate).

Sixth pair of legs (Figs 8B; 10E) asymmetrical, represented on both sides by a small plate; right plate distinct from the somite but left one is fused with it. Outer distal corner produced into a cylindrical process bearing 3 naked setae.

Variability. One female paratype showed only the distal abexopodal seta (derived from the proximal endopod segment) on the allobasis of the left antenna (Fig. 4B). One male paratype displayed three short plumose setae along the inner margin of the left P2 enp-2 (Fig. 10B).

Etymology. The specific name *inajae* is dedicated to the senior author's mother, Inajá Batista Kihara.

Genus *Pseudocletodes* Scott & Scott, 1893

Diagnosis. Normanellidae. Body elongate, subcylindrical, without clear distinction between prosome and urosome. Genital double-somite with internal transverse chitinous ribs laterally and dorsally. Anal somite with well developed rounded operculum. Genital field with median genital slit; vestigial P6 with 2 setae; copulatory pore large. Caudal rami lamelliform and elongate, with virtually straight outer margin and convex inner margin; with 7 setae; setae IV–V moderately developed, setiform.

Rostrum bell-shaped. Antennule 6-segmented in female, with large pinnate spines on segments 5 and 6, and an aesthetasc on segment 3; 7-segmented and subchirocer in male (after Scott and Scott (1893: Plate XII, Fig. 12), with geniculation between segments 5 and 6, and aesthetasc on segment 5; acrothek unconfirmed. Antennary allobasis with 2 abexopodal setae; exopod with 3–4 setae. Mandible with biramous palp; basis with 1 seta; exopod 1-segmented, defined at base, with 1 seta; endopod fused to basis, with 4 setae. Maxillule with 2 basal endites, proximal endite with 2 and distal endite with 3 setae; exopod with 2 setae; endopod represented by 2 setae. Maxillary syncoxa with 3 endites; accessory armature on allobasis consisting of 1 seta; endopod represented by 3 setae. Maxilliped prehensile; with unarmed syncoxa; palmar margin of basis without ornamentation; endopod drawn out into claw bearing 1 long seta.

P1 endopod absent. P4 exp-3 with 1 inner seta. P2–P4 enp-1 without inner seta. P2–P4 enp-2 with 2 inner setae; P2 enp-2 outer spine absent. P3 enp-2 inner and apical setae well developed in male but shorter than in female. P2–P4 spine and seta formulae as follows:

	Exopod	Endopod
P1	0.1.023	absent
P2	0.1.123	0.220
P3	0.1.223	0.221
P4	0.1.123	0.221

Male fifth pair of legs not fused medially, endopodal lobe with 3 setae; exopod with 4 setae. Male sixth pair of legs asymmetrical, with dextral and sinistral configurations, with 3 setae each. Single egg-sac.

Type and only species: *Pseudocletodes vararensis* Scott & Scott, 1893 (fixed by monotypy in the subgenus *Cletodes* (*Pseudocletodes*)).

***Pseudocletodes vararensis* Scott & Scott, 1893**
(Figs 12–20)

Type locality. Scotland, Moray Firth; among *Filograna implexa* Berkeley, 1835 (Polychaeta, Serpulidae).
Material examined. Syntype female in ethanol, subsequently dissected on 9 slides (reg. nos NHM 1911.11.8.45174–175); syntype male in ethanol, subsequently dissected on 9 slides. (reg. nos NHM 1911.11.8.45174–176).

Redescription. FEMALE (Figs 12–18). Total body length 871 µm (*N* = 1). Body slender. Largest width measured at posterior margin of cephalic shield: 171 µm. Urosome slightly narrower than prosome (Fig. 12A–B).

Cephalic shield with smooth posterior margin, pleural area well developed and rounded, posterolateral angles minutely crenate, ornamentation consisting of sensilla as illustrated in figures 12A–B; without minute spinules as found on free body somites.

Pedigerous somites (Fig. 12A–B) covered with minute spinules and with sensillar pattern as illustrated. All prosomites without defined hyaline frill; pleurotergites well developed and rounded; posterior margin serrate.

All urosomites (Figs 12A–B; 13A) with surface ornamentation consisting of minute spinules dorsally and ventrally; posterior margin distinctly serrate dorsally and laterally; ventral posterior margin as shown in figure 13A.

Genital double-somite (Figs 12A–B; 13A) with original segmentation indicated by a transverse, serrate surface ridge dorsally and dorsolaterally, and a short surface suture ventrolaterally; completely fused ventrally. Genital field (Fig. 13B) with large copulatory pore located in a median depression. Gonopores fused medially forming a single genital slit covered on both sides by opercula derived from the sixth legs. P6 with a small protuberance bearing one pinnate outer seta and one naked inner seta.

Anal somite (Fig. 13A–C) with well developed, denticulate anal operculum flanked by a row of spinous processes. Anal opening with a fringe of small denticles, and bordered by spinules ventrally. Surface ornamentation consisting of a pair of sensilla dorsally and a pair of pores ventrally; posterior margin with row of spinules.

Caudal rami (Figs 13C; 14A–B) lamelliform and elongate, about twice as long as wide; with virtually straight outer margin and convex inner margin. Each ramus with a dorsal pore (between setae II and VII), 2 ventral tube-pores near distal margin and seven setae: seta I naked, shortest and closely set to naked seta II; seta III naked and positioned ventrolaterally; setae IV and V not fused basally, pinnate and with fracture plane (seta V longest, about 1.5 times as long as ramus); seta VI bare; seta VII bi-articulate at its base and sparsely plumose. Surface ornamentation consisting of minute spinules and rows of small denticles as shown in figures 13C, 14A–B; a few spinules present around bases of setae I–III and near inner distal corner. Posterior margin partially serrate and with a ventral extension covering the bases of setae IV–VI.

Rostrum (Fig. 14C) triangular, apex pointed; completely defined at base; with 1 pair of tiny sensilla and 1 middorsal tube-pore near the apex; dorsal surface smooth.

Antennule (Fig. 14D) 6-segmented, segment 3 longest. Segment 1 with spinular row around anterior margin and at base of seta. Segment 3 with aesthetasc fused basally to a seta and arising from a distinct pedestal. Armature formula: 1-[1 pinnate], 2-[4 + 5 pinnate + 1 pinnate spine (+ 1 element missing, indicated by dorsal scar in Fig. 14D)], 3-[3 + 1 pinnate + 2 pinnate spines + (1 + ae)], 4-[1], 5-[2 + 1 pinnate spine], 6-[4 + 1 pinnate spine (+ 2 elements missing, indicated by dorsal scars in Fig. 14D) + acrothek]. Structure of

acrothek unknown (position indicated by arrow in Fig. 14D). Pinnate spines on segments 5 and 6 very large and with coarse spinules.

Antenna (Fig. 15A) 3-segmented comprising coxa, allobasis and free distal endopod segment. Basis and proximal endopod segment completely fused, forming an elongate allobasis bearing 2 abexopodal pinnate setae. Exopod almost 2.5 times longer than wide, with 1 pinnate seta laterally, and 2 pinnate setae apically. Endopod 1.5 times longer than allobasis, outer margin with a row of long spinules and distal margin with a row of fine spinules; lateral armature consisting of 2 pinnate spines, distal armature consisting of 2 pinnate spines and 3 geniculate setae, outermost one being pinnate and fused basally to a short seta.

Labrum (Fig. 15B) well developed, with spinular ornamentation along distal margin.

Paragnaths (Fig. 15B) well developed lobes, with spinular ornamentation along distal and inner margins.

Mandible (Fig. 15C) with well developed gnathobase bearing several multicuspidate teeth around distal margin and 1 basally fused pinnate seta at dorsal corner. Palp small, biramous but only the exopod is defined at its base. Basis with 1 pinnate seta. Exopod 1-segmented, small, with 1 pinnate seta apically and few spinules along outer margin. Endopod fused to basis, with 1 lateral and 3 distal pinnate setae.

Maxillule (Fig. 15D) with large praecoxa bearing a few long spinules around distal outer margin; arthrite strongly developed, with 2 naked setae on anterior surface and 8 spines/setae around distal margin. Coxa with cylindrical endite bearing 1 pinnate seta. Basis with 2 endites, represented by 2 plumose and 1 naked + 2 pinnate setae, respectively; with rows of spinules on anterior surface. Endopod incorporated with basis, represented by 2 plumose setae. Exopod 1-segmented, with 2 sparsely plumose setae.

Maxilla (Fig. 16A). Syncoxa with very long outer spinules and three endites; praecoxal endite small and cylindrical, with one pinnate seta; proximal coxal endite with one pinnate spine fused to endite, and 2 naked setae; distal coxal endite with 1 spine and 2 naked setae. Allobasis drawn out into a strong, slightly curved claw. Accessory armature consisting of 1 naked seta. Endopod represented by 3 naked setae.

Maxilliped (Fig. 16B) with 2 spinule rows on syncoxa. Basis with a few spinules near outer distal corner. Endopod drawn out into a long pinnate claw; accessory armature consisting of a long naked seta.

Swimming legs P1–P4 (Figs 16C; 17A–B; 18A) with well developed praecoxae ornamented with spinules along outer distal corner.

P1 (Fig. 16C) with large coxa bearing strong spinules along outer margin, and minute denticles and fine setules on anterior surface. Basis with a well developed, flattened, pinnate spine at inner distal corner and stout pinnate outer spine; with very long setules along inner margin and large spinules along distal margin and around base of spines. Exopod 3-segmented; all segments with strong spinules along outer margin and around outer distal corner; exp-1 with 1 stout pinnate outer spine; exp-2 with 1 pinnate, outer spine and 1 sparsely plumose inner seta; exp-3 with 3 pinnate spines along outer margin, 2 pinnate setae apically and 1 sparsely plumose inner seta (note that the presence of the latter element is an aberration; for normal condition see male: Fig. 20B). Endopod absent.

P2–P4 (Figs 17A–B; 18A) coxa with strong spinules along outer margin, and minute denticles and/or fine setules on anterior surface. Basis with long setules along inner margin (P2 only) and with spinules near insertion of endopod and at base of outer pinnate spine (P2) or plumose setae (P3–P4). Exopods 3-segmented; all segments with strong spinules along outer margin and near outer distal corner; with long setules along inner margin of exp-1 and -2. Endopods 2-segmented, with scattered spinules along outer margin as figured. P2 enp-2 twice as long as enp-1; endopod reaching to just beyond distal margin of exp-2. P3 enp-2 almost 3 times as long as enp-1; endopod reaching to proximal third of exp-3. P4 enp-2 6 times as long as enp-1, endopod reaching to just beyond distal margin of exp-2. Spine and setal formula as for the genus.

P5 (Fig. 18B) baseoendopod with short, outer setophore bearing plumose basal seta; with one pore near articulation with exopod. Endopodal lobe elongate, extending to distal margin of exopod, with 3 pinnate setae along inner margin and 2 pinnate setae apically; outer and inner margins with long setules; with tube-pore between distal inner and inner apical setae. Exopod elongate-oval, tapering distally, inner margin with very long setules, outer margin with short setules; with 4 pinnate setae along outer margin, 1 pinnate seta apically and 1 subapical inner element (missing on both sides; insertion site marked by arrow in Fig. 18B).

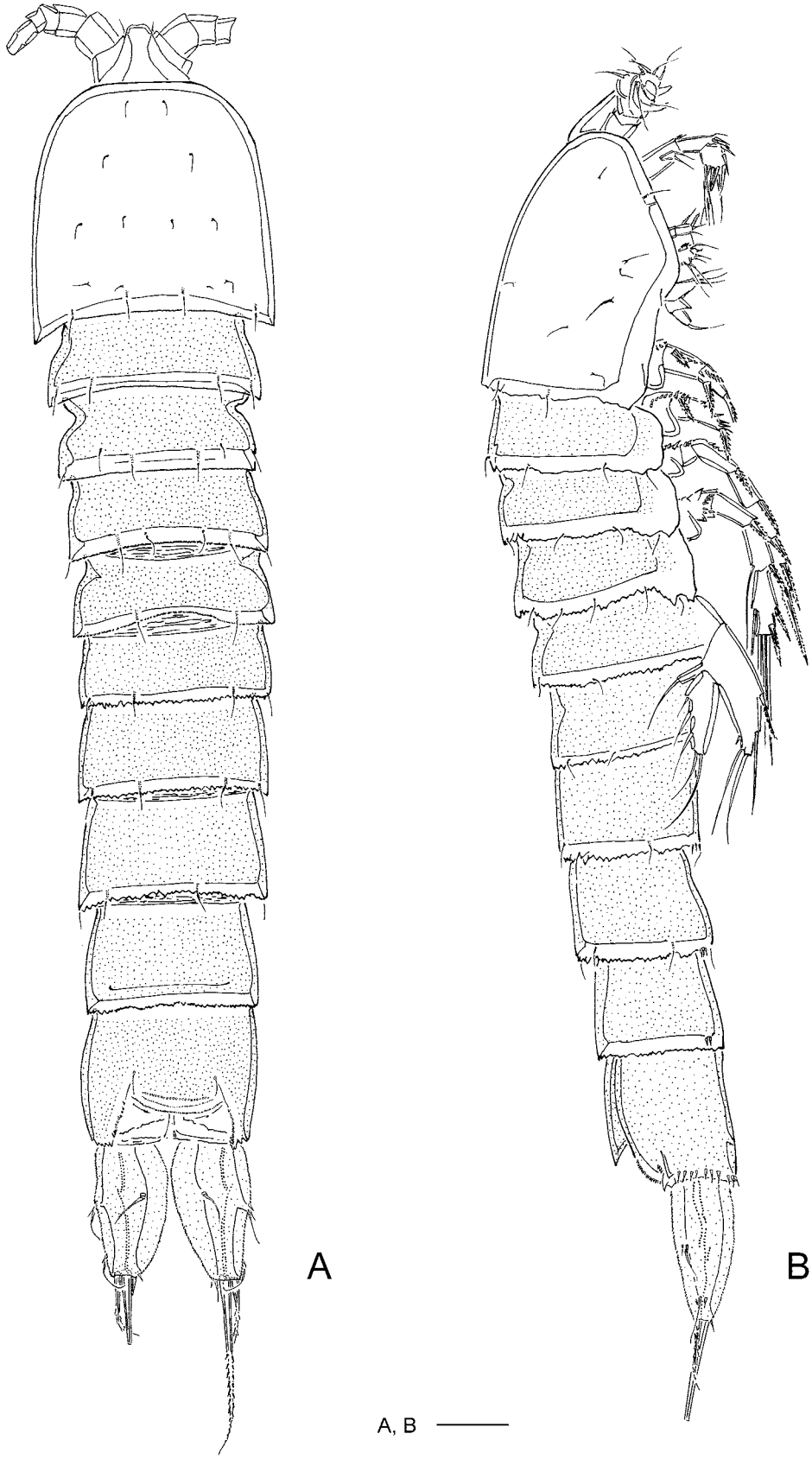

FIGURE 12. *Pseudocletodes vararensis* Scott & Scott, 1893 (♀): (A) habitus, dorsal; (B) habitus, lateral. Scale bar: 50 μm.

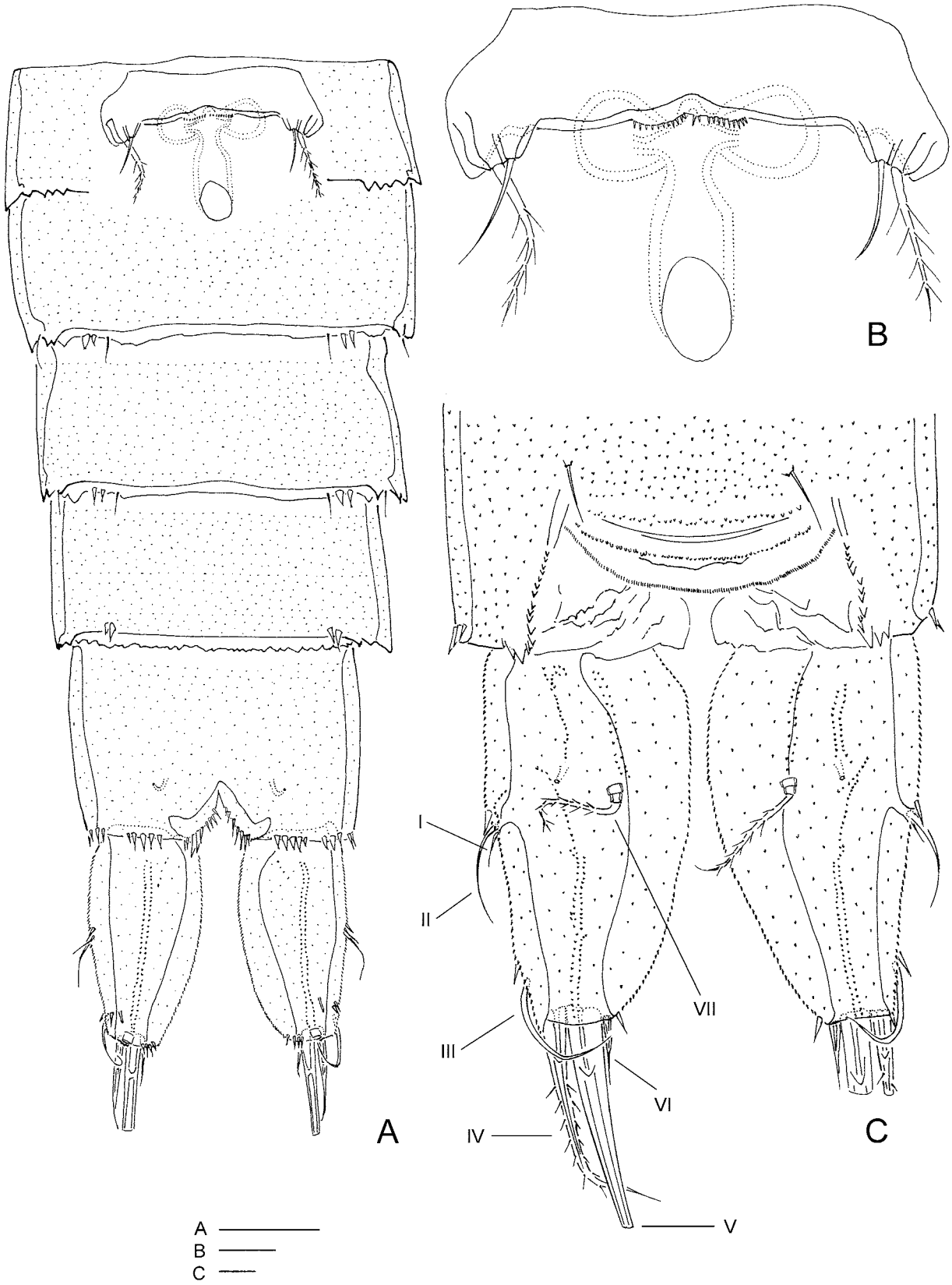

FIGURE 13. *Pseudocletodes vararensis* Scott & Scott, 1893 (♀): (A) urosome, ventral [P5-bearing somite omitted]; (B) genital field; (C) anal somite and caudal rami, dorsal. Scale bars: 10 μm (B, C), 50 μm (A).

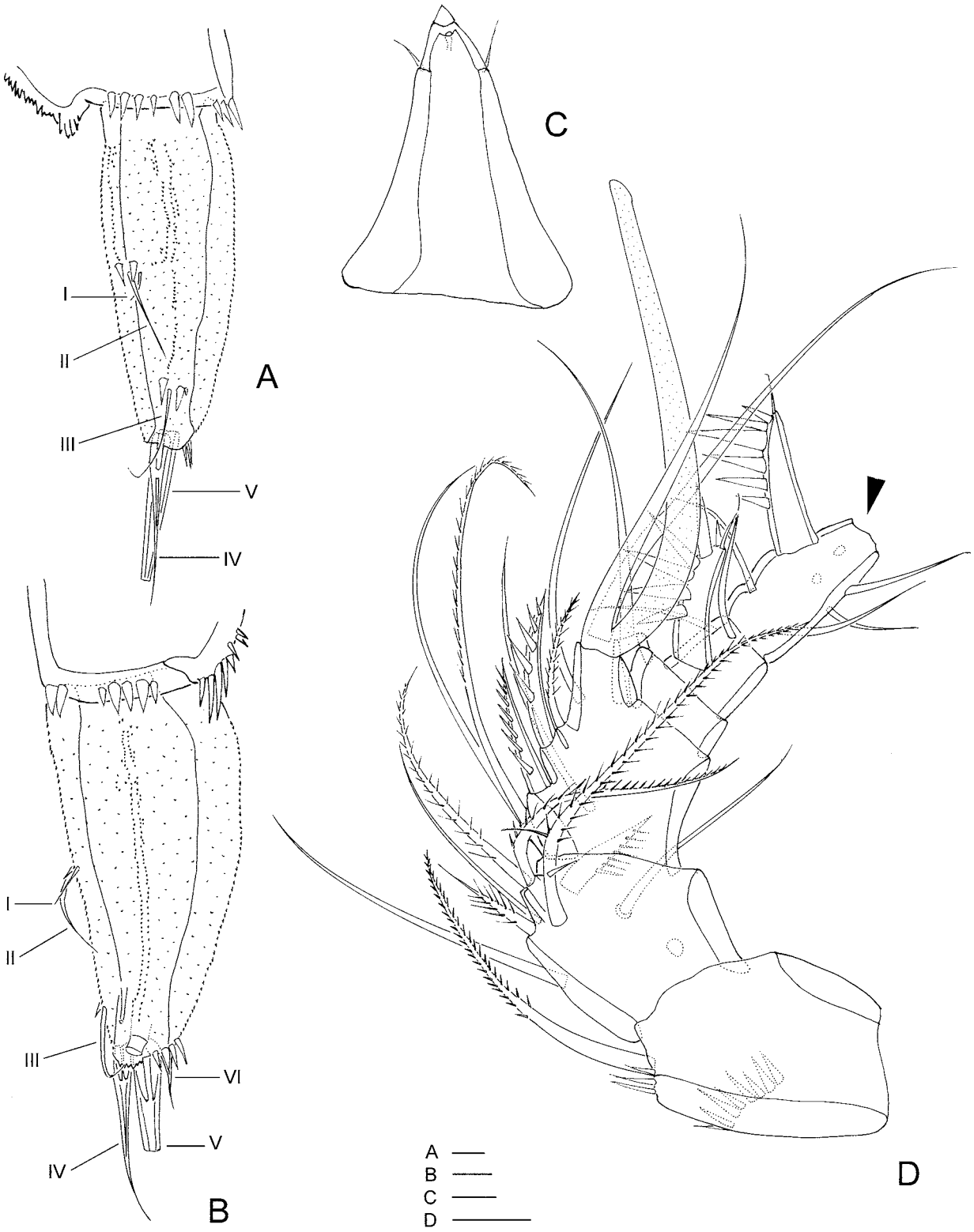

FIGURE 14. *Pseudocletodes vararensis* Scott & Scott, 1893 (♀): (A) right caudal ramus, lateral; (B) right caudal ramus, ventral; (C) rostrum, dorsal; (D) antennule, ventral [arrows indicate missing apical elements]. Scale bars: 10 μm.

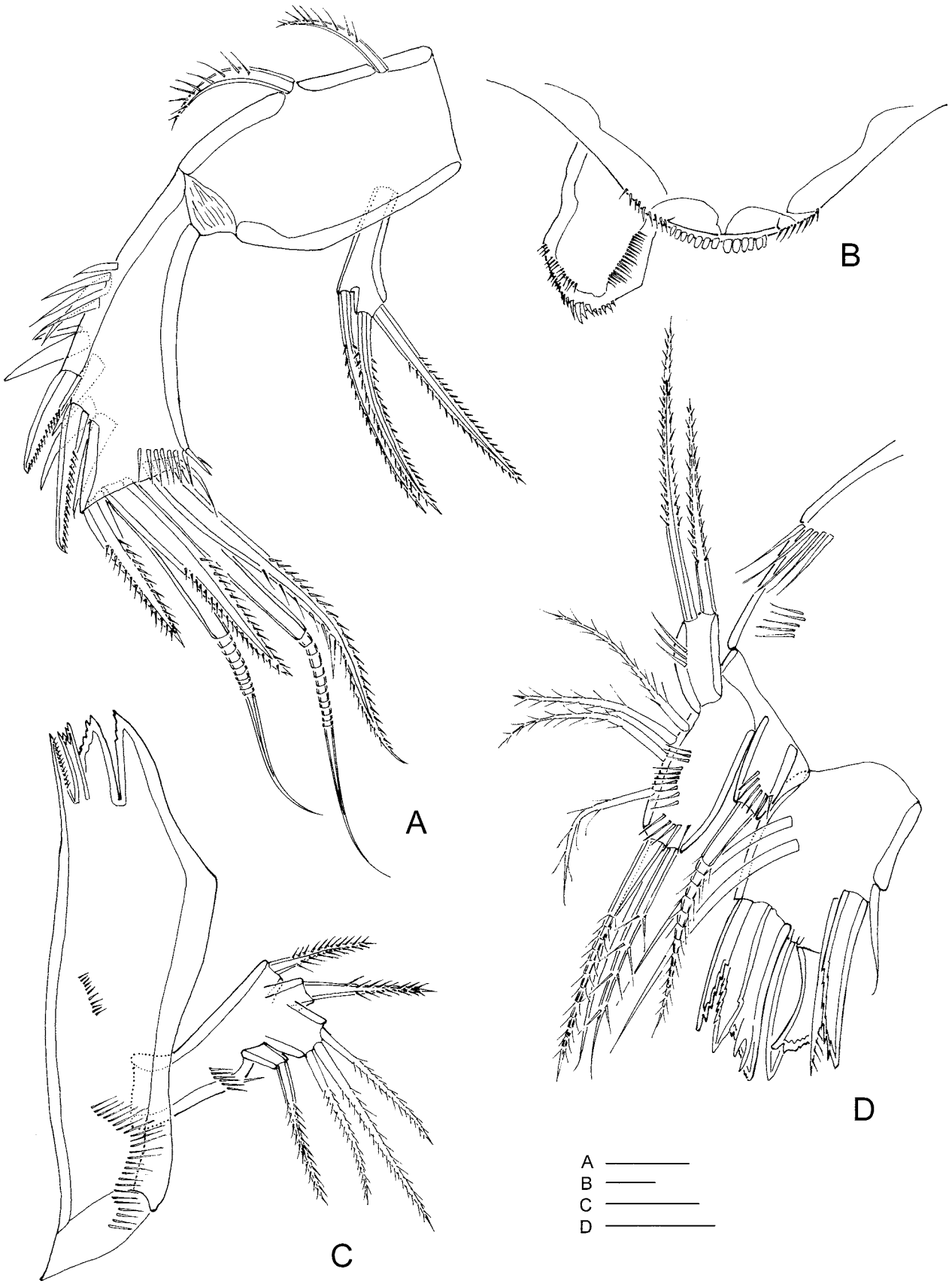

FIGURE 15. *Pseudocletodes vararensis* Scott & Scott, 1893 (♀): (A) antenna; (B) labrum with paragnath, anterior; (C) mandible; (D) maxillule, anterior. Scale bars: 10 μm.

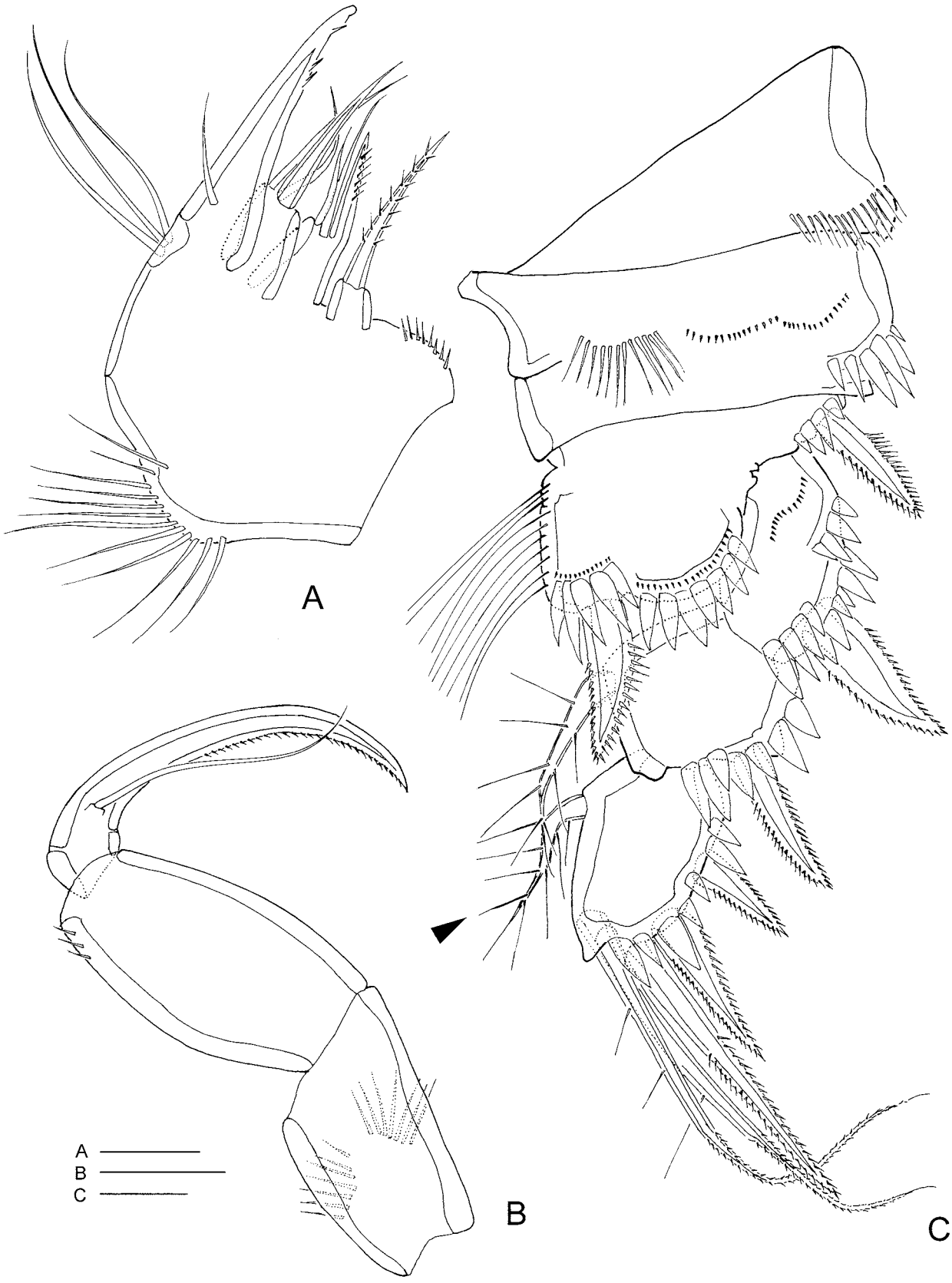

FIGURE 16. *Pseudocletodes vararensis* Scott & Scott, 1893 (♀): (A) maxilla; (B) maxilliped; (C) P1, anterior [arrow indicating aberrant supernumerary seta]. Scale bars: 10 μm.

FIGURE 17. *Pseudocletodes vararensis* Scott & Scott, 1893 (♀): (A) P2, anterior; (B) P3, anterior. Scale bar: 10 µm.

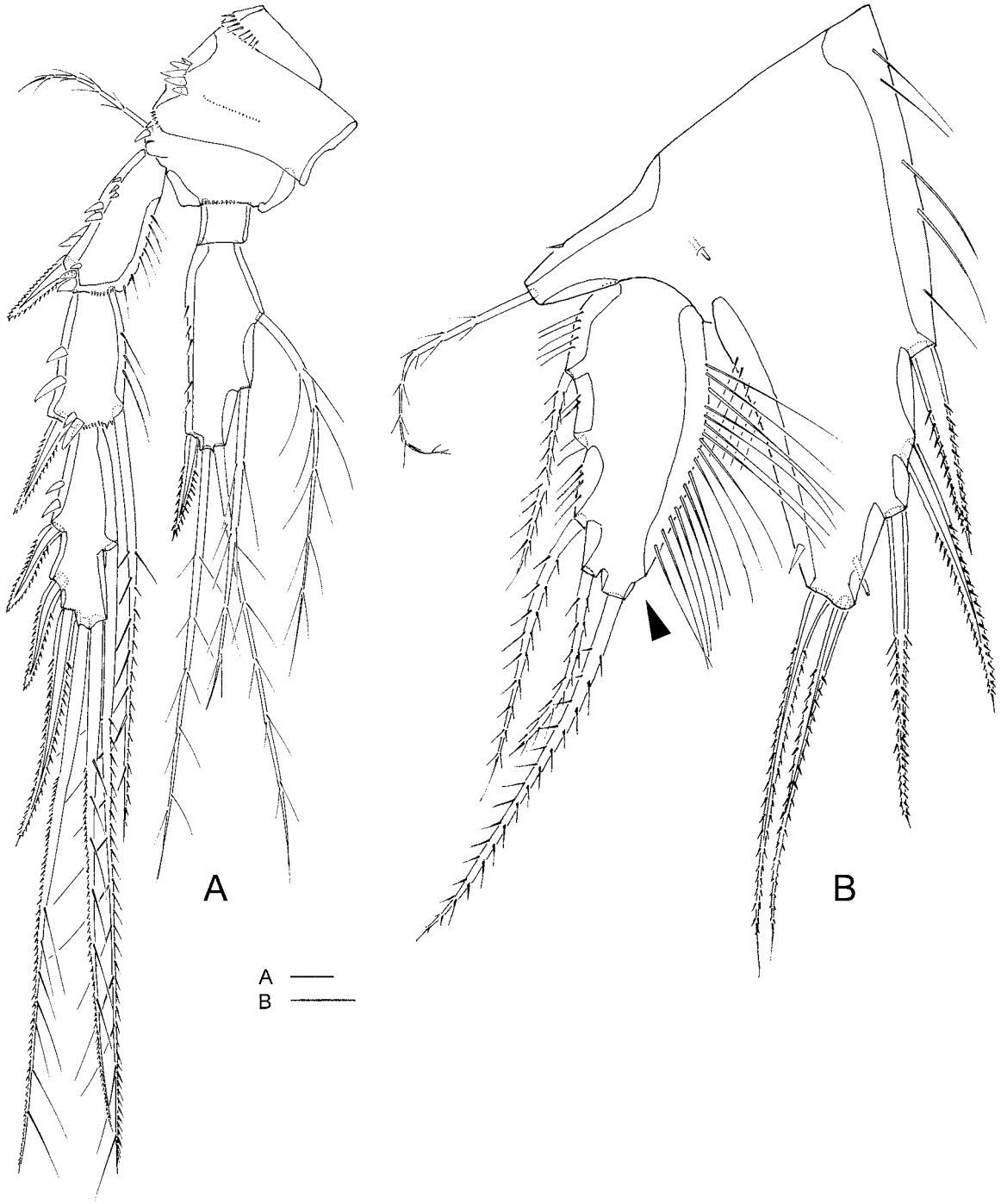

FIGURE 18. *Pseudocletodes vararensis* Scott & Scott, 1893 (♀): (A) P4, anterior; (B) P5, anterior [arrow indicating insertion scar of dislodged seta]. Scale bars: 10 μm.

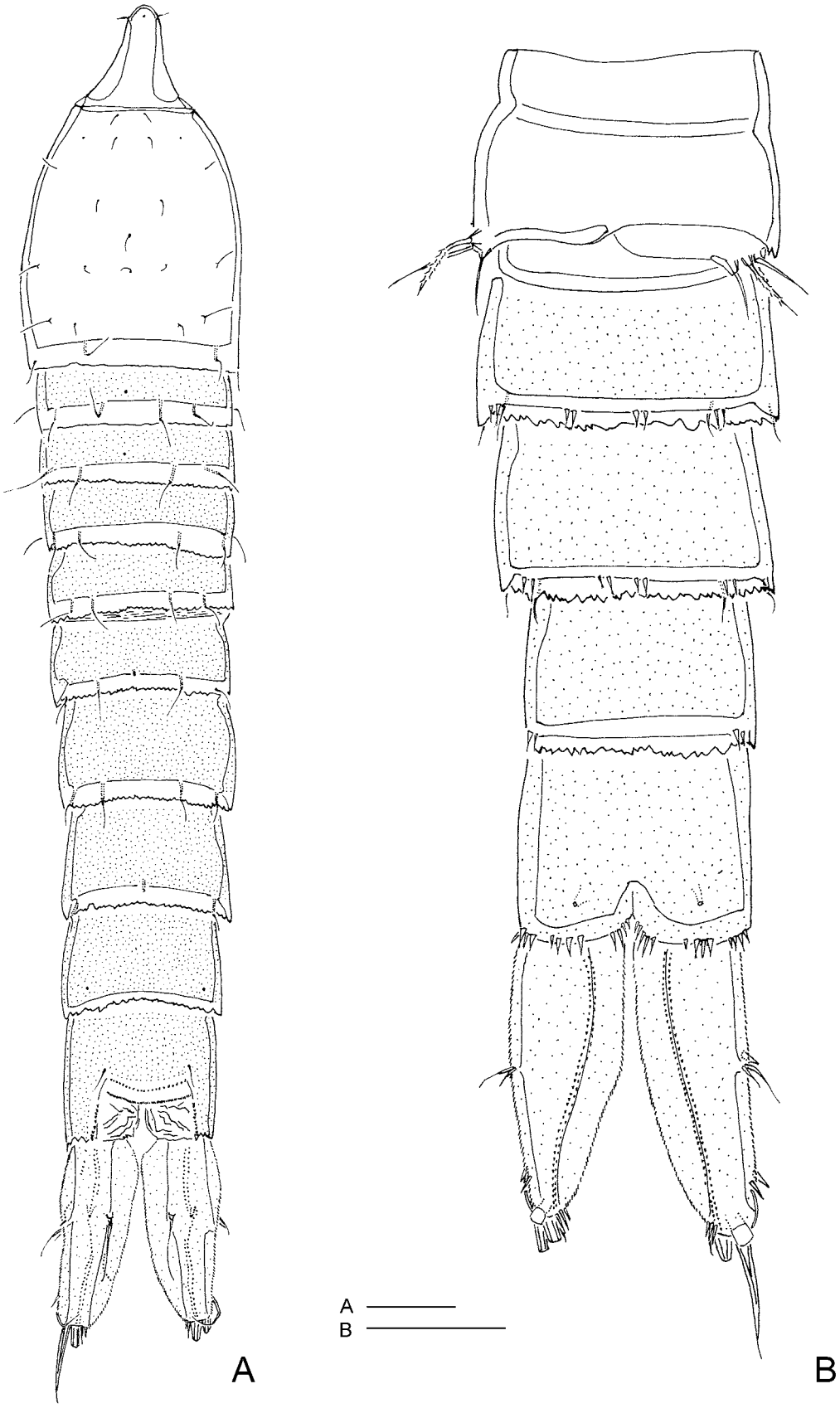

FIGURE 19. *Pseudocletodes vararensis* Scott & Scott, 1893 (♂): (A) habitus, dorsal; (B) urosome [P5-bearing somite omitted], ventral. Scale bars: (A, B) 50 μm.

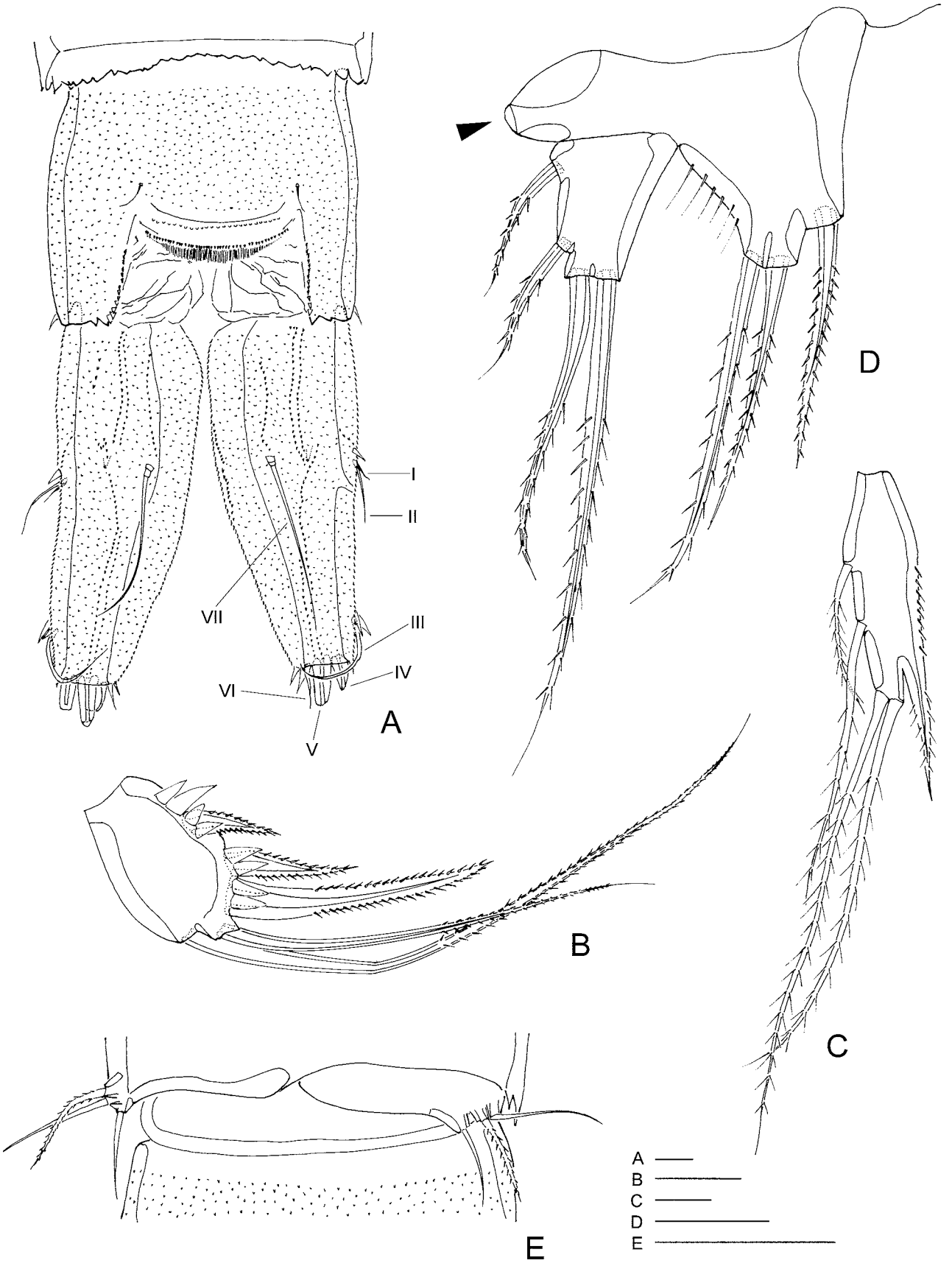

FIGURE 20. *Pseudocletodes vararensis* Scott & Scott, 1893 (♂): (A) anal somite and caudal rami, dorsal; (B) P1 exp-3, anterior; (C) P3 enp-2, anterior; (D) P5, anterior [arrow indicating insertion scar of dislodged outer basal seta]; E. sixth legs, anterior. Scale bars: 10 μm.

MALE (Figs 19–20). Body more slender than in female. Body length 728 µm (*N* = 1). Largest width measured at medial portion of cephalic shield: 125 µm. Urosome slightly narrower than prosome (Fig. 19A). Cephalic shield (Fig. 19A) with posterior margin weakly serrate; with pattern of sensilla and pores as figured. Pedigerous somites covered with minute spinules. Prosomites with serrate posterior margin. Urosome (Fig. 19A–B) with surface ornamentation consisting of patches of minute spinules, sensilla and pores as figured; posterior margins irregularly serrate and with spinules. Caudal rami (Fig. 20A) more slender than in female.

Antennules missing in the only male available.

P1 exopod 3-segmented. Exp-3 with 3 pinnate outer spines and 2 pinnate setae apically (Fig. 20B).

P3 endopod (Fig. 20C) 2-segmented, modified. Enp-2 more slender than in female; outer margin produced into a subdistal pinnate apophysis (homologous with outer spine of enp-2 in female); proximal inner seta distinctly shorter than in female; distal inner and both apical setae slightly shorter than in female.

Fifth pair of legs (Fig. 20D) not fused medially; defined at base. Baseoendopod with a short setophore bearing an outer basal seta (missing on both sides; original insertion site marked by arrow in Fig. 20D). Endopodal lobe well developed, triangular; with 2 pinnate setae apically and 1 pinnate inner seta. Exopod about 1.2 times as long as maximum width, with 2 pinnate apical setae and 2 pinnate outer setae.

Sixth pair of legs (Fig. 20E) asymmetrical, represented on both sides by a small plate (fused to ventral wall of supporting somite along one side, articulating at base and covering gonopore along other side); outer distal corner produced into a cylindrical process bearing 1 pinnate middle seta flanked by 2 naked setae.

Variability. Except for the aberrant armature pattern on P1 exp-3 of the female syntype no additional variability was observed. Both syntypes showed only 3 setae on the antennary exopod (both left and right antennae) whereas Scott and Scott (1893: Plate XII-Fig. 6) figured an additional lateral seta. Given that 4 setae is the norm in the superfamily Laophontoidea in general, and the family Normanellidae in particular it is not unlikely that the 4-setae condition is the typical one in *P. vararensis*.

Discussion

Comparison between Scott and Scott's (1893) original text and illustrations of *Pseudocletodes vararensis* Scott & Scott, 1893 and our redescription based on syntype material revealed a number of differences which can partly be attributed to deficiencies in the original description:

(a) antennary exopod with four setae (this is conceivably the typical condition – see above under variability);

(b) antennary endopod with long seta near proximal corner of abexopodal margin (such a seta has not been observed before in harpacticoids);

(c) mandibular palp without exopod (represented by a minute segment in our material; Fig. 15C) and with endopod defined at base (fused to basis in our material; Fig. 15C); the exopod is present in all normanellids described to date, and the suture line between basis and endopod is often difficult to discern if the palp is not mounted in the right position;

(d) maxilliped with seta on syncoxa but without armature on endopod (in both syntypes the syncoxa was unarmed and the endopod had a long accessory seta; Fig. 16B); it is likely that the accessory seta was dislodged in the specimen examined by Scott and Scott (1893), however we found no scars indicating the presence of a syncoxal seta;

(e) palmar margin of maxillipedal basis with distinct spinule row (without ornamentation in our material; Fig. 16B); and

(f) endopodal lobe of male P5 longer than in our material (Fig. 20D).

An additional difference which cannot be explained by imperfect observation is the discrepancy in size. According to Scott and Scott (1893) the body length (of presumably the female) is 1140 µm while our female syntype measured only 870 µm.

According to Scott and Scott's (1893: 240) text description and Wilson's (1932: 564) key, the P1 endopod in *Pseudocletodes* Scott & Scott, 1893 is replaced by a "dagger-shaped spine". Comparison with the closely related genus *Paranaiara* **gen. nov.** however, demonstrates that this element represents the inner basal spine and that the endopod is genuinely missing. Evidence for this is found in the precise distribution of the large spinules along the distal margin of the basis, being present around the base of the spine, and between its point of origin and the insertion of the endopod (compare Figs 6A and 16C). The complete reduction of the P1 endopod is a rare phenomenon in the Harpacticoida, thus far being found only in a few genera belonging to the families Paramesochridae (*Kunzia* Wells, 1967; *Meiopsyllus* Cottarelli & Forniz, 1995) and Cletodidae (*Monocletodes* Lang, 1936a; *Scintis* Por, 1986b).

Scott and Scott (1893) were not explicit in their generic assignment of *Pseudocletodes vararensis*. They placed the species in a new subgenus *Pseudocletodes* which they considered most similar to *Cletodes* Brady, 1872 but at the same time stated that the morphology of P1 (absence of endopod) is "… so much at variance with the characters of that genus as to render its position in *Cletodes* untenable". Lang (1936a: 451) upgraded *Pseudocletodes* Scott & Scott, 1893 to generic level and pointed out that it was a senior homonym of *Pseudocletodes* Sars, 1920 (type species: *Pseudocletodes typicus* Sars, 1920) (family Adenopleurellidae) for which he proposed the new replacement name *Pseudoplatychelipus* Lang, 1936a (itself being a junior objective synonym of *Sarsocletodes* Wilson, 1924).

In his revision of the Cletodidae, Lang (1936a) subdivided the family into four genus-groups ("Reihe" in German, or lineages) and assigned *Pseudocletodes* to the *Argestigens*-Reihe together with 13 other genera. Lang (1944, 1948) eventually abandoned his "Reihe" concept but Por (1986a), building on suggestions proposed in Becker's (1972) PhD dissertation, revived it by reallocating the cletodid genera to five families, one subfamily and a category called "Canthocamptidae *incertae sedis*". In the family Huntemanniidae (valid name: Nannopodidae; *cf.* Huys 2009) he accommodated the genera *Nannopus* Brady, 1880; *Huntemannia* Poppe, 1884; *Pontopolites* T. Scott, 1894; *Metahuntemannia* Smirnov, 1946; *Beckeria* Por, 1986b; and, provisionally, *Pseudocletodes*. Por (1986a) claimed that the differently built P5 in the latter made its position somewhat uncertain.

Huys and Kihara (in preparation) scrutinized the monophyly of the Nannopodidae (*ex* Huntemanniidae) and concluded that only *Nannopus*, *Huntemannia*, *Rosacletodes* Wells, 1985, *Laophontisochra* George, 2002 and an as yet unpublished new genus (Huys & Kihara, in preparation) can be retained in the family, whereas *Metahuntemannia* and *Dahmsopottekina* Özdikmen, 2009 (= *Talpina* Dahms & Pottek, 1992) should tentatively be assigned to the Canthocamptidae (subfamily Hemimesochrinae). *Pseudocletodes* cannot be assigned to either of these families but shows instead a clear affinity to the Normanellidae in the morphology of the antennule (ancestral segments 3–4 fused forming compound segment in female; armature pattern, in particular the position of pinnate spines; presence of digitiform process on segment 6 partly covering segment 7 in male), antenna (exopod with 4 setae; armature pattern on free endopod), mandible (biramous), maxillule (exopod 1-segmented with 2 setae; 2 basal endites; endopod incorporated), P1 exopod (exp-2 with inner setae; exp-3 with 3 spines and 2 setae) and the swimming leg sexual dimorphism. In particular the male P3 endopod provides unequivocal evidence supporting the inclusion of *Pseudocletodes* in the Normanellidae, *i.e.* the endopod is 2-segmented (enp-2 is not subdivided into two pseudosegments as in *e.g.* Laophontidae, Orthopsyllidae and Cristacoxidae) with the mucroniform apophysis arising from the outer distal corner, being the homologue of the outer pinnate spine of the female, and the apical setae reduced in length (*cf.* Lee & Huys 1999: 259). Although the P1 endopod is absent in *Pseudocletodes*, its morphology in the closely related genus *Paranaiara* (2-segmented with 1 lateral and 2 distal elements on enp-2) provides additional indirect evidence for its assignment to the Normanellidae.

Paranaiara and *Pseudocletodes* share a sister-group relationship within the Normanellidae based on the following presumed synapomorphies [plesiomorphic character states given in square brackets]:

(a) caudal rami lamelliform [cylindrical];

(b) maxillulary endopod represented by 2 setae [3 setae];

(c) maxilliped with unarmed syncoxa and without spinules on palmar margin of basis [syncoxa with 1 seta; basis with palmar spinules];

(d) P2 enp-2 without outer spine [outer spine present]; and

(e) P3 enp-2 with 2 inner setae [with 3 inner setae].

Both genera have large spinulose spines on segments 5–6 of the female antennule but this character is also present in the *dubia*-lineage of the genus *Normanella* (Lee & Huys 1999). *Pseudocletodes* can be differentiated from *Paranaiara* by the loss of the P1 endopod and of the inner seta on P2–P4 enp-1, the presence of only 2 inner setae on P2 enp-2 (instead of 3) and only 1 inner seta on P4 exp-3 (instead of 2), the presence of a second inner seta on P4 enp-2 (instead of 1), the morphology of the fifth pair of legs in the male which are not medially fused and have only 3 endopodal elements (instead of 4), and the well developed caudal ramus seta V (instead of rudimentary). The major morphological differences between the four known normanellid genera are summarized in Table 2.

Pseudocletodes and *Paranaiara* show a number of plesiomorphic character states that have not been documented before in the other normanellid genera.

TABLE 2. Morphological differences between normanellid genera.

	Normanella	*Sagamiella*	*Pseudocletodes*	*Paranaiara* **gen. nov.**
Antennule ♀	5- or 6-segmented	6-segmented	6-segmented	6-segmented
Antennulary acrothek	2 setae + ae	2 setae + ae	?	2 setae
Antennary exopod	4 setae	3 setae	3–4 setae	4 setae
Antennary allobasis	1 abexopodal seta	1 abexopodal seta	2 abexopodal setae	2 abexopodal setae
Mandibular basis	2 setae	1 seta	1 seta	1 seta
Mandibular endopod	discrete	fused to basis	fused to basis	fused to basis
Maxillulary basis	2 endites	only proximal one present	2 endites	2 endites
Maxillulary endopod	3 setae	3 setae	2 setae	2 setae
Maxillary allobasis	2 accessory setae + spine	1 accessory seta	1 accessory seta	2 accessory setae
Maxillipedal syncoxa	2 setae	2 setae	unarmed	unarmed
P1 endopod	prehensile, 2-segmented	prehensile, 2-segmented	absent –	non-prehensile, 2-segmented
P1 enp-1 inner seta	present	present	–	absent
P2–P4 enp-1 inner seta	present	present	absent	present
P2 enp-2 outer spine	present	present	absent	absent
P2 enp-2 inner setae	2–3	2	2	3
P3 enp-2 inner setae	3	3	2	2
P3 enp-2 apical setae ♂	strongly reduced	strongly reduced	well developed	well developed
P4 enp-2 inner setae	2	2	2	1
P4 exp-3	2 inner seta	2 inner setae	1 inner seta	2 inner setae
P5 baseoendopods ♂	medially fused	medially fused	free	medially fused
P5 endopodal lobe ♂	2 elements*	2 elements	3 elements	4 elements
P6 ♂	3 setae	2 setae	3 setae	3 setae
Caudal ramus shape	cylindrical	cylindrical	lamelliform	lamelliform
Caudal seta V	well developed	well developed	well developed	vestigial

*: some variability has been recorded in some species (*e.g. N. tenuifurca* and *N. sarsi*: *cf.* Lee & Huys 1999)

In both genera the antennary allobasis displays two setae on the abexopodal margin, one being derived from the basis and the other from the incorporated proximal endopodal segment; in *Normanella* and *Sagamiella* only the endopodal seta is expressed as is the case in all other known members of the Laophontoidea.

Huys and Lee (1999) discussed the various modifications of setal elements on the male P3 endopod in the superfamily Laophontoidea and regarded the strong reduction of the two apical elements on enp-2 (represented by 2 setule-like elements in male) in both *Normanella* and *Sagamiella* as an autapomorphy of the Normanellidae. In *Pseudocletodes* and *Paranaiara* this sexual dimorphism is not as pronounced as in the other genera. The apical setae (only the outer apical one in the latter genus) are indeed shorter but still well developed in the male (Figs 10C, 20C).

Although some intraspecific variability has been observed in the number of endopodal elements on the male P5 (*Normanella tenuifurca*, *N. sarsi*; *cf.* Lee & Huys 1999: Figs 16D, 22D) the normal condition in both *Normanella* and *Sagamiella* appears to be two apical spines/setae. In *Pseudocletodes* and *Paranaiara* the endopodal lobe displays 3 and 4 elements, respectively, due to the expression of 1–2 lateral spines.

Finally, *P. vararensis* is the only normanellid known thus far in which the male fifth legs are not medially fused.

The phylogenetic significance of the short, non-prehensile P1 endopod in *Paranaiara* is difficult to assess since it could either be the result of secondary shortening and associated loss of prehensility (a character possibly already present in the common ancestor of *Paranaiara* and *Pseudocletodes* and leading to the complete loss of the endopod in the latter) or represent the plesiomorphic state of the laophontoidean ancestor. Since the latter scenario would imply a convergent evolution of the prehensile endopod in the Normanellidae and its sister-group (encompassing all remaining laophontoidean families) we prefer the subsequent loss of prehensility in the common ancestor of *Paranaiara* and *Pseudocletodes* as the most parsimonious option. Within the Laophontoidea such loss appears to have evolved independently in the Adenopleurellidae (Huys 1990).

An updated diagnosis of the family Normanellidae is presented above, incorporating the new data resulting from the present paper.

Species in the genus *Normanella* often differ only by small differences in body ornamentation and in proportions of the appendages. Since many records are now considered doubtful or indeterminable, any identification must be verified against the best available description (Lee & Huys 1999; Wells 2007). Since Lee and Huys' (1999) revision of *Normanella*, three new species have been added from the Gulf of Mexico (Lee *et al.* 2003). *Normanella minuta sensu* Willey (1930), *N. semitica* Monard, 1935a, *N. quarta* Monard, 1935b, *N. serrata* Por, 1959, *N. serrata sensu* Božić (1964), *N. minuta* (?) *sensu* Bodin (1972) and *N. serrata sensu* Marinov and Apostolov (1985) were all considered *species inquirendae* by Lee and Huys (1999) and are not included in the key below.

Key to species of Normanellidae

1 P1 endopod absent ..... *Pseudocletodes vararensis* Scott & Scott, 1893
- P1 endopod 2-segmented 2
2 P1 endopod prehensile, with elongate enp-1 bearing inner seta and short enp-2; male P5 with 2 elements on endopodal lobe 3
- P1 endopod not prehensile, enp-1 as long as enp-2 and without inner seta; male P5 with 4 elements on endopodal lobe ..... *Paranaiara inajae* **gen. et sp. nov.**
3 Antennary exopod with 3 setae; male P6 with 2 setae ..... *Sagamiella* Lee & Huys, 1999 … 4
- Antennary exopod with 4 setae; male P6 with 3 setae ..... *Normanella* Brady, 1880 … 5
4 Caudal ramus twice as long as wide, subrectangular..... *S. aberrans* (Bodin, 1968)[1]
- Caudal ramus 2.5 times as long as wide, ovoid ..... *S. latirostrata* Lee & Huys, 1999
5 P2 enp-2 with 2 inner setae..... 6
- P2 enp-2 with 3 inner setae..... 7
6 P4 enp-2 with 4 setae/spines (outer spine absent) ..... *N. reducta* Noodt, 1955
- P4 enp-2 with 5 setae/spines (outer spine present)..... *N. bifida* Huys & Lee, 1999
7 P4 enp-2 with 4 setae/spines (outer spine absent) ..... *N. mucronata sensu* Marinov (1977)
- P4 enp-2 with 5 setae/spines (outer spine present) 8
8 Caudal ramus with strongly developed, proximally dilated seta V, lacking internal fracture plane; rostrum distinctly pointed 9
- Caudal ramus with normally developed or reduced seta V, always with internal fracture plane; rostrum of different shape 10
9 Rostrum with short apical portion, distance between sensilla and apex about 18% of rostrum length; caudal ramus seta V distinctly lanceolate in proximal half and with flagellate distal third; female P5 exopod with middle and distal outer setae clearly separated, and distance between insertion site of middle outer seta and apex about 1/4 of outer margin length ..... *N. confluens* Lang, 1965

- Rostrum with long apical portion, distance between sensilla and apex at least 1/4 of rostrum length; caudal ramus seta V gradually tapering distally; female P5 exopod with middle and distal outer setae closely set, and distance between insertion site of middle outer seta and apex about 1/8 of outer margin length..... *N. mucronata* Sars, 1909

10 Caudal ramus at least 3 times as long as maximum width 11
- Caudal ramus shorter 12

11 Caudal ramus shorter than 4 times maximum width ..... *N. paratenuifurca* Lee & Huys, 1999
- Caudal ramus longer than 4 times maximum width ..... *N. tenuifurca* Lee & Huys, 1999

12 Cephalic shield without surface areolation in either sex 13
- Cephalic shield with distinct surface areolation in both sexes 14
- Cephalic shield with weakly developed areolation pattern between dorsal longitudinal ridges in female, without surface areolation in male ..... *N. texana* Lee, Montagna & Han, 2003

13 Rostrum with straight lateral margins; caudal ramus about twice as long as wide, with setae IV–V well developed; male P2 enp-2 outer apical seta minute, shorter than outer spine ..... *N. minuta* (Boeck, 1873)
- Rostrum with distinctly concave lateral margins; caudal ramus shorter than twice the width; setae IV–V reduced; male P2 enp-2 outer apical seta small, longer than outer spine ..... *N. dubia* Brady, 1880

14 Caudal ramus slightly longer than wide ..... *N. bolini* Lang, 1965
- Caudal ramus at least twice as long as maximum width 15

15 Female P5 endopodal lobe distinctly shorter than exopod 16
- Female P5 endopodal lobe extending to or beyond distal margin of exopod 19

16 Female antennule 6-segmented ..... *N. chanhoi* Lee, Montagna & Han, 2003
- Female antennule 5-segmented 17

17 Rostrum with pointed apex; female P5 exopod elongate (greatest width proximally) 18
- Rostrum with blunt apex; female P5 exopod oval (greatest width about halfway) ..... *N. similis* Lang, 1936b

18 Rostrum areolate; female antennule with spinous protuberance on segment 2, and segment 3 partly subdivided by surface suture originating from posterior margin; male P5 endopodal lobe well developed, reaching to middle of exopod; caudal ramus about twice as long as wide ..... *N. brevispina* Lee, Montagna & Han, 2003
- Rostrum smooth; female antennule without spinous protuberance on segment 2, and segment 3 not subdivided; male P5 endopodal lobe weakly developed, not reaching to middle of exopod; caudal ramus about twice as long as wide ..... *N. pallaresae* Lee & Huys, 1999

19 Female P5 exopod with clear step halfway outer margin; male P5 exopod with 5 (?) setae ..... *N. sarsi* Lee & Huys, 1999
- Female P5 exopod without clear step halfway outer margin; male P5 exopod with 4 setae 20

20 Female P5 exopod flask-shaped, with proximal swelling along inner margin ..... *N. obscura* Lee & Huys, 1999
- Female P5 exopod not flask-shaped, with straight inner margin 21

21 Caudal ramus 2.5 times as long as wide; female P5 exopod slender, 4.3 times as long as basal width ..... *N. incerta* Lang, 1934
- Caudal ramus twice as long as wide; female P5 exopod shorter, 3.5 times as long as basal width ..... *N. porosa* Noodt, 1964

[1] Note that Wells' (2007: 573) statement that the caudal ramus "…is twice as long as broad in *S. latirostrata* but only about 1.5 times as long as broad in *S. aberrans*", is an inadvertent slip of the pen.

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