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A new genus of Parastenocarididae Chappuis, 1940 (Copepoda: Harpacticoida) from the Amazonian Region, Brazil, with close affinity to *Murunducaris* Reid, 1994

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ABSTRACT

Santaremicaris gen. nov. is proposed to accommodate *Santaremicaris amazonensis* sp. nov., a new species collected by Noodt from the hyporheic zone of the Amazonas River at Santarém, Brazil, and *Parastenocarididae santaremensis* Noodt, 1963, which is redescribed and designated as the type species of the new genus. The new genus is recorded also from several localities of the Amazonian hydrographic basin. *Santaremicaris* gen. nov. is well supported by clear autapomorphies, e.g., 1) the absence of distal spinules on the endopod of the second swimming leg of the male, which is ornamented with strong outer spinules along the first 2/3 of the segment and armed with a long distal seta the insertion area of which covers almost the whole width of the segment; 2) the presence of a triangular, short and strongly sclerotized endopod on the fourth swimming leg of the male; and 3) the presence of a long and slim male fifth leg ending in a long distal spiniform process, with irregular margins, armed with only three setigerous

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elements on the outer margin, and reaching the middle of the subsequent urosomal segment or beyond it. The new genus is closely related to *Murunducaris* Reid, 1994, with males sharing conspicuous ornamentation on the inner margin of the first swimming leg basis, represented either by an enlarged spinule accompanied by minute accessory spinules or by a row of strong spinules. In addition, the males of both *Murunducaris* and *Santaremicaris* gen. nov. share an enlarged intercoxal sclerite with a median process on the fifth leg.

KEYWORDS

Amazonian basin, Fontinalicaridinae, groundwater, hyporheos, Neotropics

INTRODUCTION

Knowledge of taxonomy and phylogenetic affinities within the family Parastenocarididae is advancing in recent years. Several new genera were described (*i.e.*, *Simplicaris* Galassi and De Laurentiis, 2004; *Monodicaris* Schminke, 2009; *Asiacaris* Cottarelli, Bruno and Berera, 2010; *Dussartstenocararis* Karanovic and Cooper, 2011; *Iticocaris* Corgosinho, Martínez Arbizu and Previatelli, 2012a; *Horstkurttcaris* Karanovic and Lee, 2012; *Cottarellicaris* Schminke, 2013; *Himalayacaris* Ranga Reddy, Totakura and Corgosinho, 2014; *Indocaris* Ranga Reddy, Totakura and Shaik, 2016; *Eirinicaris* Corgosinho, Schizas, Previatelli, Rocha and Santos-Silva, 2017b; *Colombocaris* Gaviria, Defaye and Corgosinho, 2017; and *Noodtcaris* Gaviria, Defaye and Corgosinho, 2017). The classic work of Jakobi (1972) was revisited and many genera were redefined and reestablished [*i.e.*, *Remaneicaris* Jakobi, 1972 (Corgosinho and Martínez Arbizu, 2005); *Brasilibathynelloccaris* Jakobi, 1972 (Corgosinho et al., 2010a); *Kinnecaris* Jakobi, 1972 (Schminke, 2008); *Siolicaris* Jakobi, 1972 (Corgosinho et al., 2012b); *Proserpinicaris* Jakobi, 1972 (Karanovic, Cho and Lee, 2012); *Stammericaris* Jakobi, 1972 (Schminke, 2013), *Parastenocaris* Kessler, 1913 (Karanovic and Lee, 2012)]. Consequently, *Pararemaneicaris* Jakobi, 1972 and *Paraforficatocaris* Jakobi, 1972 were synonymized with *Brasilibathynelloccaris* (see Corgosinho et al., 2010a); *Nipponicaris* Jakobi, 1972 and *Pannonicaris* Jakobi, 1972 were synonymized with *Proserpinicaris* (see Karanovic, Cho and Lee, 2012); *Biwaecaris* Jakobi, 1972, *Oshimaensicaris* Jakobi, 1972, *Enckellicaris* Jakobi, 1972, and *Brinckicaris* Jakobi,

1972 were synonymized with *Parastenocaris* (see Karanovic and Lee, 2012); *Cafferocaris* Jakobi, 1972 was synonymized with *Kinnecaris* (see Schminke, 2013); and *Phreaticaris* Jakobi, 1972 was synonymized with *Stammericaris* (see Schminke, 2013). Despite the work of Karanovic and Lee (2012) in redefining the genus *Parastenocaris*, with the exception of the species belonging to the *Parastenocaris brevipes*-group, the genus *Parastenocaris* still remains as a repository of loosely related species of unclear phylogenetic affinities within the subfamilies Fontinalicaridinae Schminke, 2010 and Parastenocaridinae Chappuis, 1940 (see Schminke, 2010).

The Neotropical fauna of Parastenocarididae is composed of about 74 described species and 11 genera (Walter and Boxshall, 2020). *Potamocaris* Dussart, 1979, *Forficatocaris* Jakobi, 1969, *Murunducaris* Reid, 1994, *Brasilibathynelloccaris*, *Iticocaris*, *Eirinicaris*, and maybe *Remaneicaris* (see discussion about *Parastenocaris ahaggarica* Bozic, 1978 in Corgosinho et al., 2017a) are endemic to the Neotropical region. *Siolicaris* appears as the single genus with a hypothetical Gondwanian distribution. Most of the Neotropical genera are in Fontinalicaridinae, whereas *Eirinicaris* and *Remaneicaris* are the only representatives of Parastenocaridinae present in the region. However, specimens belonging to the monophyletic genus *Parastenocaris*, as redefined by Karanovic and Lee (2012), were found in samples from Mongaguá (state of São Paulo) and Morretes (state of Paraná), southern Brazil (unpublished data).

In this work we describe a new genus and species of Fontinalicaridinae closely related to *Murunducaris*. *Parastenocaris santaremensis* Noodt, 1963 is redescribed and designated as the type

species of the new genus. The phylogenetic position of *Murunducaris* and *Santaremicaris* gen. nov. within Fontinalcaridinae is still unsolved, pending a further robust phylogenetic analysis. However, in this work we discuss the phylogenetic relationships of *Murunducaris* and *Santaremicaris* gen. nov. with other genera and species within and outside the Neotropical region.

MATERIAL AND METHODS

The type material of *Santaremicaris santaremensis* (Noodt, 1963) comb. nov. and *S. amazonensis* sp. nov. were obtained from the Noodt Collection deposited at the DZMB (Deutsches Zentrum für Marine Biodiversitätsforschung)/Senckenberg am Meer, Wilhelmshaven, Germany. The material of both species was collected in the hyporheic zone of the Amazonas River at Santarém, state of Pará, Brazil (Fig. 1). Several specimens (dissected or undissected), not always belonging to the same species, were mounted on single slides. It was often not possible to identify

which limbs were previously illustrated by Noodt. As a result of the poor condition of some original slides, the redescription of *S. santaremensis* comb. nov. had to be based on several specimens from different slides. The description of *S. amazonensis* sp. nov. was based on a dissected male and an intact male mounted on a single slide along with a dissected male of *S. santaremensis* comb. nov., a dissected female and an intact female of *S. santaremensis* comb. nov., and a juvenile. The position of the voucher specimens of *S. amazonensis* sp. nov. are marked on the slide. Noodt's collection has not received museum accession numbers yet, but it is organized in "slide storage maps", prepared by Noodt, and available at the DZMB Senckenberg am Meer Wilhelmshaven (Germany). The identification of each slide was based on a reference to the "slide storage maps" (M), their sequential number and the number of the slides (preparations) within each map. Hence, for example, M2-6 is the sixth slide stored on the second slide storage map of Noodt's collection.



Figure 1. Map indicating the type locality (Santarém, Pará, Brazil) of *Santaremicaris santaremensis* comb. nov., and *Santaremicaris amazonensis* sp. nov. Arrows mark the position of Santarém within Brazil and Amazon.

Drawings were prepared on a Leica DMR microscope, fitted with Nomarski interference contrast optics and a drawing tube, at 400× and 1000× magnification. The lengths of the specimens were measured from the tip of the rostrum to the posterior rim of furca. Habitus and sensilla distribution are illustrated based on specimens picked from unsorted samples collected by Noodt at the same type locality, and stored at the DZMB.

The diagnosis represents the reconstructed ground pattern of *Santaremicaris* gen. nov. The term ground pattern is used in the sense of “grundmuster” (Ax, 1984, p. 156) and refers to all plesiomorphies and autapomorphies present in the stem species of the genus in question. A table with the characters differing between the species of *Santaremicaris* gen. nov. is included for reference (Tab. 1).

The terms ‘furca’ and ‘telson’ are used according to Schminke (1976). For homology of the furcal setae I–III we have compared our specimens with other Neotropical species belonging to *Brasilibathynellocaris*, *Murunducaris*, and *Siolicaris*, which all have a reduced or diminutive seta II between the larger seta I and III (see Corgosinho *et al.*, 2008; 2010a; 2012b). Terminology and homology of maxillary structures follow Ferrari and Ivanenko (2008). Therefore, by the application of serial homology, the nomenclature of Huys and Boxshall (1991) for Mx2 (Fig. 1.5.5, p. 26) is modified as follows: praecoxa of Mx2 is hereafter recognized as syncoxa (praecoxa and coxa), coxa is considered as the basis, and the basis is recognized as the first endopodal segment with claw. Other morphological terms are used according to Huys and Boxshall (1991).

Table 1. Comparative list of characters for the males of *Santaremicaris santaremensis* comb. nov. and *Santaremicaris amazonensis* sp. nov.

Characters	<i>Santaremicaris santaremensis</i> comb. nov.	<i>Santaremicaris amazonensis</i> sp. nov.
Length of male	325µm	255µm
Ornamentation of the basis of P1	Strong spinule with marginal smaller ones.	Row of subequal long spinules.
Ornamentation of the P1 enp1	Irregular rows of spinules on the inner and outer margins.	Longitudinal row of subequal spinules on the inner and outer margins.
Ornamentation of the P2 enp	Spinules shorter than in the sister species	Spinules longer than in the sister species
Ornamentation of the coxa of P3	Present	Absent
Ornamentation of the basis of P3	Inner claw-like spinule close to the basis/coxa articulation, proximal to a curved row of spinules decreasing in size from proximal to distal region.	Only a V-shaped row of equal spinules on inner margin.
Shape and ornamentation of P3 exp-1	Straight and smooth on the inner and outer margin.	Irregular margin with a proximal tube pore and 2 proximal spinules on the outer margin.
Shape and ornamentation of the apophysis	Spatuliform and smooth.	Elongate, with a sharp edge and a distal hyaline lamella.
Length and shape of P3 thumb	Longer than apophysis, knife-like.	Shorter than apophysis, spiniform with an inner hyaline lamina.
Fine ornamentation of the P4 exp3	With a row of fine spinules in the distal outer margin.	With a strong and cuneiform spinule in the distal outer margin.
P4 enp ornamentation on the outer margin	Absent	Present
P4 enp sclerotization	Along inner margin, proximal margin and portion of the outer margin.	Along the inner margin.
Proximal row of spinules on the inner margin of the P4 exp1	Less developed than in the sister species.	More developed than in the sister species.
Distal row of spinules on the inner margin of the P4 exp1	More developed than in the sister species.	Less developed than in the sister species.
Shape of P5 intercoxal sclerite process	Claviform	Linguiform
P5 shape and ornamentation	With a proximal hump on the outer margin followed by smooth outer margin; distally ending in tapering distal process, with two or three spinules on the midline of the inner margin, with two spinules proximally inserted, close to an irregular inner margin.	Irregular outer margin, distal spiniform process thinner than in the sister species, more or less smooth inner margin with 5 spinules along the midline.

Abbreviations used: A1 = antennule, A2 = antenna, Ae = aesthetasc, Ap = apomorphy, Aop = anal operculum, Cph = cephalothorax, enp = endopod, exp = exopod, enp1–3 = endopodal segments 1–3, exp1–3 = exopodal segments 1–3, Fig. = figure, Figs. = Figures, Fu = furca, Gds = genital-double somite, Gf = genital field, Ms = modified seta, Md = mandible, Mf = modified spine, Mx1 = maxillule, Mx2 = maxilla, Mxp = maxilliped, P1–P5 = legs 1 to 5, Pl = plesiomorphy, Sy = synapomorphy, Ur(s) = urosomite(s), Ur1–5 = urosomites 1–5.

SYSTEMATICS

Harpacticoida Sars, 1903

Parastenocarididae Chappuis, 1940

Fontinalicaridinae Schminke, 2010

Santaremicaris gen. nov.

ZooBank: [urn:lsid:zoobank.org:act:27524A69-87E4-4634-A626-62D514F995A1](https://zoobank.org/act:27524A69-87E4-4634-A626-62D514F995A1)

Diagnosis. Small-sized Fontinalicaridinae (255–325 µm), with cylindrical habitus; body cuticle poorly chitinised; dorsal integumental window on Cph, Urs 3–5 in male and Urs 2–4 in female; boundary between prosome and urosome inconspicuous; Gf a wide concave plate, two times wider than narrow, with medial process and occupying anterior ventral half of female Gds. Last Urs of males and females with undulate distal frill. Fu cylindrical, divergent, about three times as long as wide, armed with six setae (Setae I, III, IV, V, VI, and VII), with distinct gap between setae I–III and VII, setae I and III inserted in proximal third of furca, seta VII in distal third; seta I longer than seta III, seta II absent, seta IV distally inserted on outer margin, longer than setae I, III, VI and VII, seta V the longest, about 4 times longer than Fu. Antennule eight-segmented in male and seven-segmented in female. A1 of the coiled type, segments V–VIII of males forming a functional unit for clasping the female. Coxal gnathobasis of md with distal row of teeth and seta; md palp one-segmented, with two distal setae. Mx1 praecoxal arthrite with five elements (surface seta thick and blunt, three claw-like pinnate spines, and

slender seta); coxal endite with one seta; basis with three setae. Mx allobasis with two endites; proximal endite with one seta; distal endite with two smooth setae and serrate spine; proximal endopodal segment drawn out into claw; distal endopodal segment with two setae. Mxp subchelate; syncoxa about 1/3 length of basis; enp drawn into spinulose claw. Basis of P1 sexually dimorphic in male, with modified robust spinule or row of strong spinules on inner margin; with outer seta. Male P2 enp with long distal seta, the insertion area of it covering almost the whole width of the segment, without distal ornamentation and with strong ornamentation on outer margin, along the first 2/3 of the segment. Male P3 with rectangular, smooth or ornamented coxa; basis rectangular or trapezoidal, approximately twice as long as wide, with long row of spinules on inner margin; with hook-like spinule on proximal inner margin or without it; enp absent; exp one-segmented, rectangular with regular margins or with irregular margins and tapering distally, longer than wide, slightly curved inwards, weakly ornamented on outer margin or smooth, with or without tube pore on inner margin; apophysis without distal seta or spine, spatuliform and shorter than thumb or slightly longer than thumb, the apophysis ending in a long tip with a rounded hyaline cushion at tip; thumb with or without hyaline inner margin. Female P3 enp unarmed, shorter than exp1 and acuminate distally. Male P4 basis unornamented, with outer seta and outer pore; inner margin of male P4 exp1 with distal and proximal row of spinules; enp short, triangular, not reaching middle of exp1, smooth or ornamented on outer margin, with strongly chitinized regions. Female P4 enp one-segmented, slightly longer than exp1 and bearing one distal and bipinnate spine fused to segment, ornamented with spinules on distal half, near the fusion of the spine and the enp. Male P5 a well-developed triangular plate reaching middle of next somite or slightly beyond; with irregular margins; inner margin with row of small spinules; distal portion ending in strong spiniform process; armature consisting of very long outer basal seta and two additional setae; intercoxal sclerite enlarged, triangular or a trapezoid plate, longer than wide, with distomedial cuticular process. Female P5 with small distal spiniform process, shorter than in male, long

outer seta and three well-developed lateral setae; with a small triangular intercoxal sclerite. P6 an unarmed concave plate with median hump covering Gf.

Type species. *Parastenocaris santaremensis* Noodt, 1963.

Composing species. *Santaremicaris santaremensis* (Noodt, 1963) comb. nov.; *S. amazonensis* sp. nov.

Etymology. The generic name refers to Santarém (Pará, Brazil), the municipality in which the new species were collected, combining this name with the ancient Greek substantive for shrimp, *καρίς* (*caris*).

Autapomorphies for the genus. Male second urosomite without integumental window. Last Ur of males and females with undulate distal frill. P2 enp without distal ornamentation, with long distal seta, the insertion area of it covering almost the whole width of the segment, and strong outer ornamentation along the first 2/3 of the segment. Basis of male P3 with long row of spinules on the inner margin. Absence of male P3 enp. Short, triangular and strongly chitinized male P4 enp. Long and slim male P5 with irregular margins, reaching the middle of the next urosomite or beyond, distal portion ending in a strong spiniform process, ornamented with spinules on the inner margin, armed with only three setigerous elements on the outer margin.

Santaremicaris santaremensis

(Noodt, 1963) comb. nov.

Figs. 2–8

Type material. M5-6. Slide containing two dissected males and some females.

Other examined material. M2-6; M2-8; M5-5 and undissected male and female picked from an unsorted sample collected by Noodt, at the same type location of *S. santaremensis* comb. nov. and stored at the DZMB. See material and methods for explanation of the codes.

Type locality. Hyporheic zone of the Amazonas River at Santarém (Pará, Brazil) (Noodt, 1963) (Fig. 1). Approximate coordinates: 02°25'S 54°42'W.

Other occurrences. Upper reaches of Negro River, lower reaches of the Tapajós and Tocantins Rivers.

Description of male (Figs. 2–4). Total length 285 μm (much shorter than measures given by Noodt, 1963, p. 144: 370–380 μm), measured from rostrum to end of furca. Rostrum not fused to cephalothorax, with wide base and two sensilla on tip (Fig. 2A, B). Cephalothorax and Urs 3–5 with dorsal integumental window (Fig. 2A, B), absent on Ur2. Pattern of sensilla as depicted (Fig. 2A, B); last Ur with distal frill undulate and thicker than those of previous Urs (Figs. 2A, B, 3C). Telson smooth (Fig. 3C), with proximal pore on lateral margins, with pair of sensilla adjacent to anal operculum, and without additional ornamentation; Aop slightly concave medially (Fig. 2A); Fu (Figs. 2A, B, 3C) cylindrical, approximately 2.5 times as long as wide, slightly enlarged distally in lateral view, slightly irregular on outer margin and convex on inner margin in dorsal view; presence of distal outer pore, and two lateral setae on proximal third; seta I longer than seta III, almost as long as setae VI and VII (Fig. 3C); seta II absent; seta IV distally inserted on outer margin, longer than setae I, III, VI and VII; seta V the longest, about four times longer than Fu; dorsal seta (VII) at distal third; all setae smooth except for unipinnate seta IV.

A1 (Fig. 3A): eight-segmented; of the coiled type with segments V to VIII forming functional unit for clasping female; armature as follows: I(0)/II(6)/III(4)/IV(1+1Ms)/V(4+(1+Ae))/VI(2+Ms)/VII(1+Ms)/VIII(7+ acrothec of 2+Ae).

A2 (Fig. 3B): allobasis without abexopodal armature, with small outer spinule proximally; one-segmented exp with long unipinnate seta; free endopodal segment with two proximal rows of spinules on inner margin, and transverse row of spinules subterminally; presence of two inner marginal spines and five terminal setae/spines, two of them geniculated.

Labrum triangular in lateral view.

Md: Coxal gnathobasis with distal row of teeth and seta; palp one-segmented, with two distal setae.

Mx1: Praecoxal arthrite with five elements (surface seta thick and blunt, three claw-like pinnate spines, and slender seta); coxal endite with one seta; basis with three setae.

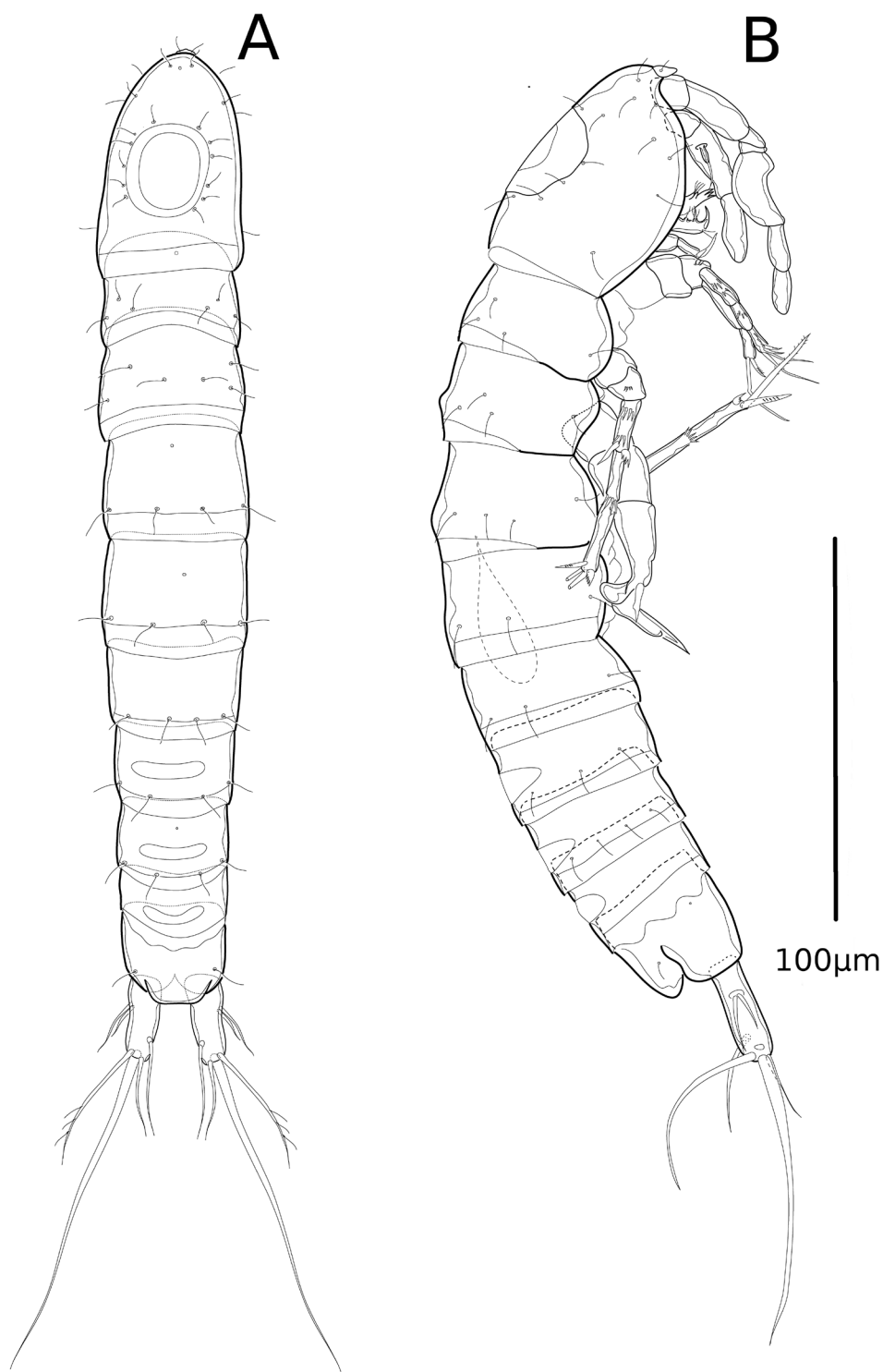


Figure 2. *Santaremicaris santaremensis* comb. nov., male. Dorsal (A) and lateral (B) habitus.

Mx: Allobasis with two endites; proximal endite with one seta; distal endite with two smooth setae and serrate spine; proximal endopodal segment drawn out into claw; distal endopodal segment with two setae.

Mxp: subchelate; syncoxa about 1/3 length of basis; enp drawn into spinulose claw.

P1 (Fig. 4A): coxa smooth. Anterior surface of basis with row of spinules on inner margin, distalmost enlarged; rows of spinules near insertion of enp and exp on anterior surface; and outer seta, outer pore and two outer spinules. Enp two-segmented: enp1 nearly as long as exp1 and exp2 combined, with two inner rows,

two outer rows and one distal row of spinules (Fig. 4A); enp2 with outer spine and long geniculate seta, with posterior hyaline frill. Exp three-segmented: exp1 with outer spine, rows of spinules on outer margin, proximal and distal to outer spine; exp2 unarmed, with row of outer spinules along outer margin; exp3 with outer row of spinules proximally, two outer spines and two geniculate apical setae.

P2 (Fig. 4B): intercoxal sclerite a small unornamented trapezoidal plate, shorter than coxa,

concave proximally and distally; with proximal lateral projections. Coxa with anterior row of spinules. Basis without outer seta, with row of spinules on outer margin and outer pore on anterior surface. Enp one-segmented, 0.4 times as long as exp1, with distal seta as long as exp1, the insertion area of it covering almost the whole width of the segment; with strong spinules on outer margin, not reaching the distal 1/3, distal margin unornamented. Exp three-segmented: exp1 with outer row of spinules, hyaline frill distally on

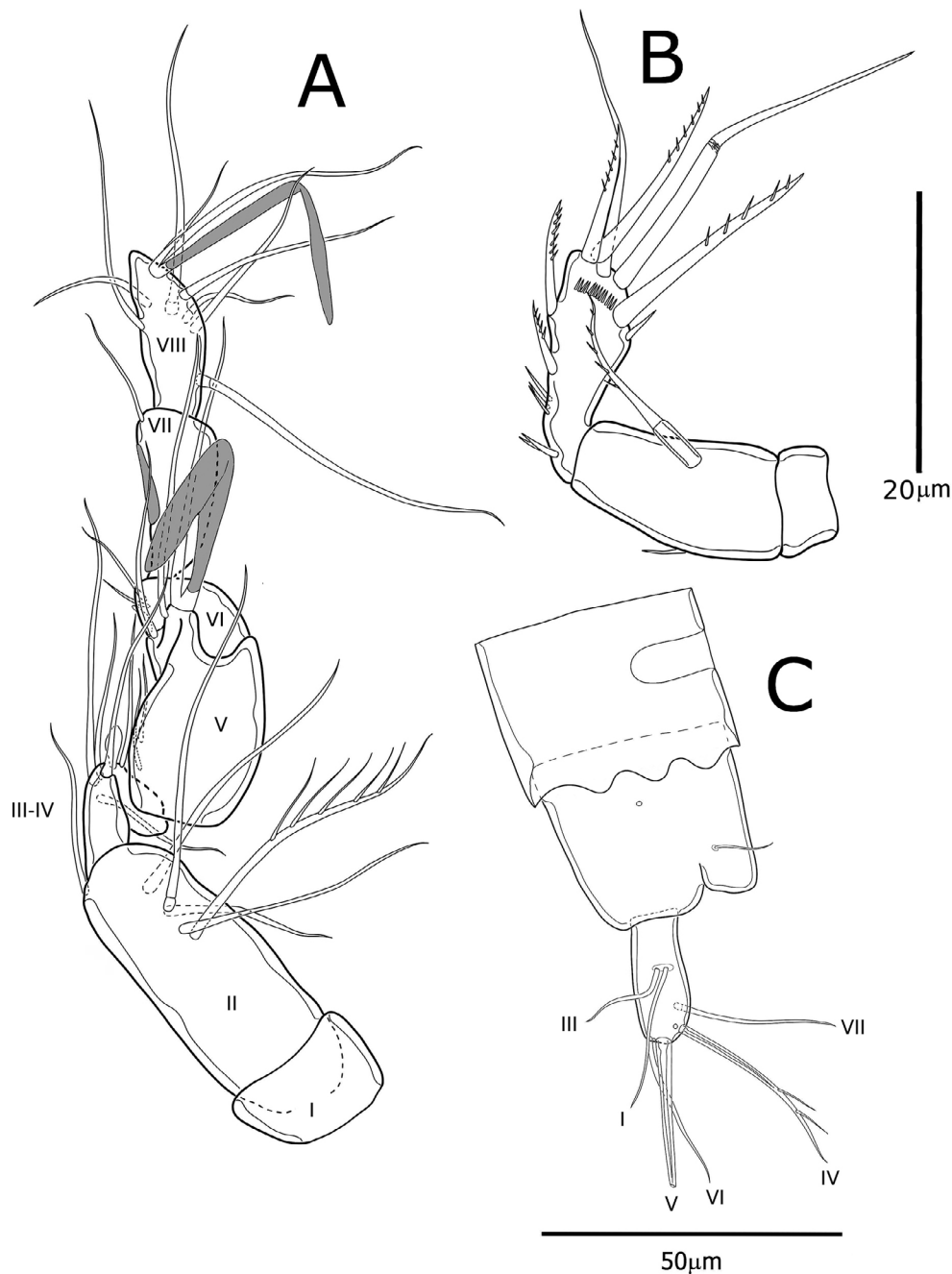


Figure 3. *Santaremicaris santaremensis* comb. nov., male. Antennule (A), antenna (B), and last urosomite, telson, and furca (C). Roman numerals identify the antennule segments and furcal setae. Vertical scale bar (A, B), horizontal scale bar (C).

inner corner, and outer spine reaching beyond distal edge of exp2; exp2 with distal row of strong spinules only; exp3 with outer distal row of spinules, hyaline frill at inner distal corner, unipinnate distal outer spine, unipinnate distal medial seta and distal inner seta (distal inner seta distally broken).

P3 (Fig. 4C): intercoxal sclerite a small unornamented trapezoidal plate as long as coxa, straight proximally, concave distally, with proximal

lateral projections. Coxa rectangular, with diagonal row of spinules on anterior face. Basis long, trapezoidal, bearing long outer seta and outer pore, hook-like spinule on proximal inner corner and row of spinules. Enp lacking. Exp one-segmented, rectangular, long, slightly curved inwards, smooth on outer margin, with long and spatuliform apophysis; thumb longer than apophysis, with medial hump and ending in long tip.

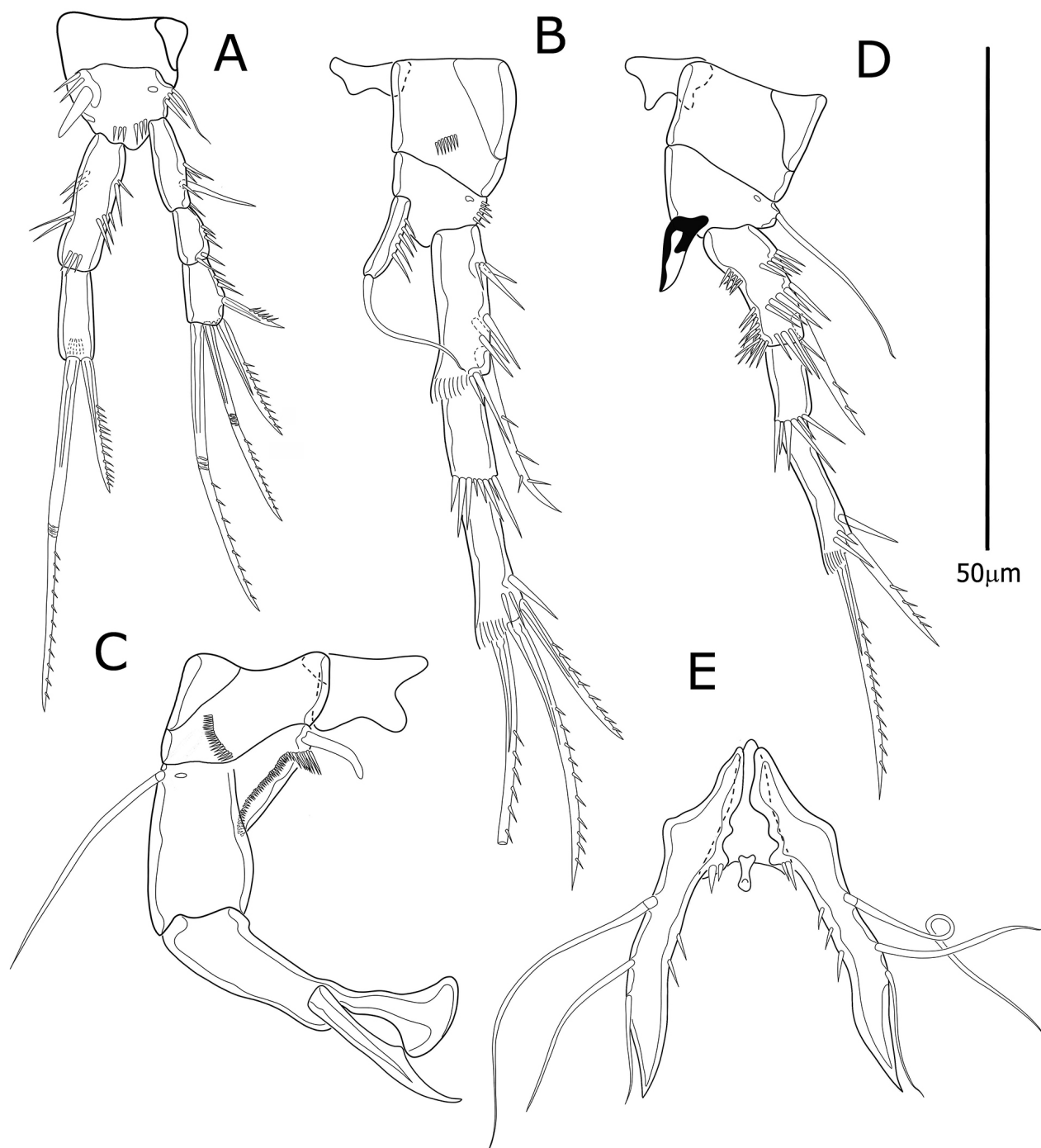


Figure 4. *Santaremicaris santaremensis* comb. nov., male. P1 (A), P2 (B), P3 (C), P4 (D), and P5 (E).

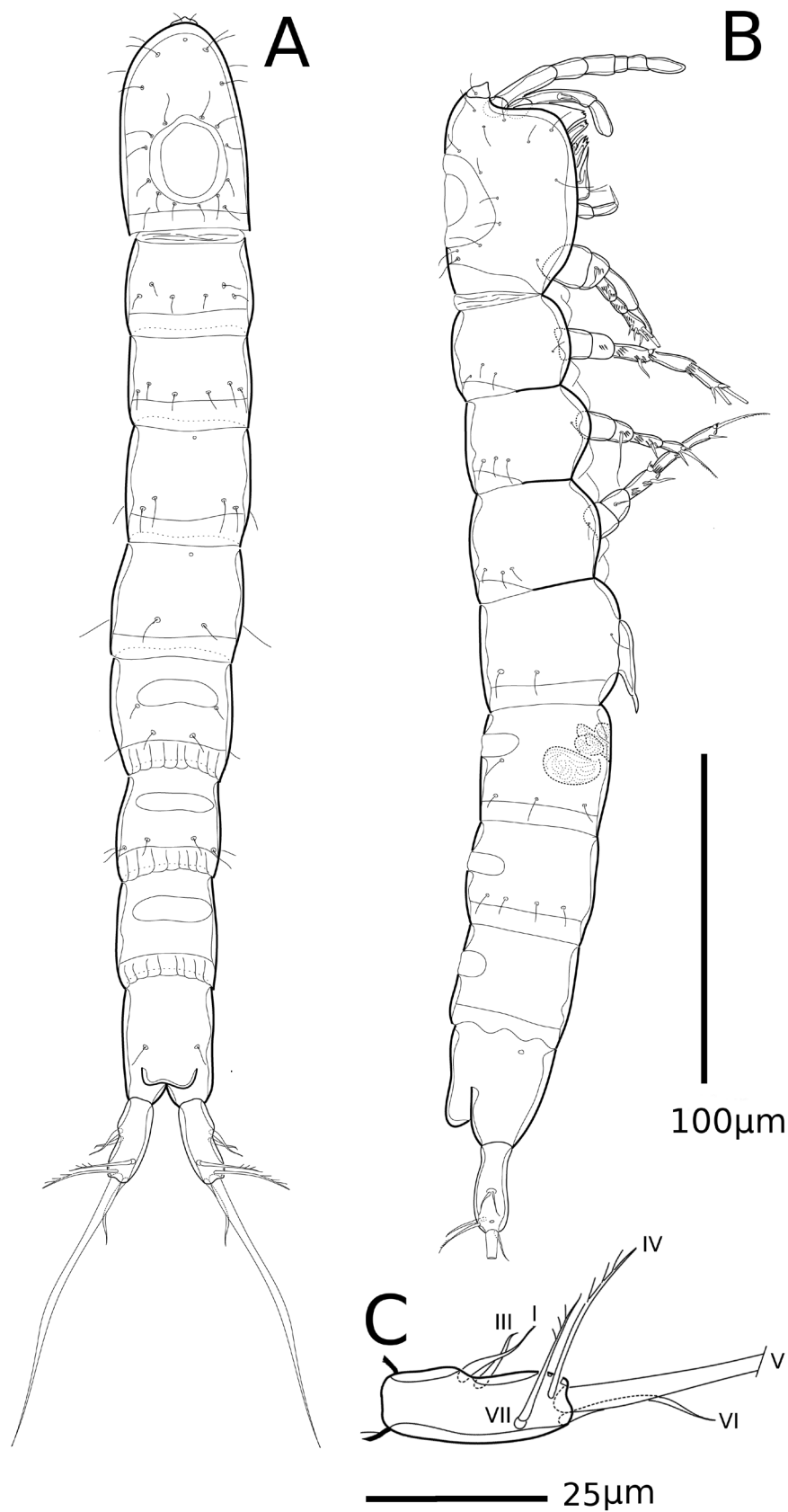


Figure 5. *Santaremicaris santaremensis* comb. nov., female. Dorsal (A), lateral (B) habitus, and left furca in dorsal view (C). Roman numerals identify furcal setae. Vertical scale bar (A, B), horizontal scale bar (C).

P4 (Fig. 4D): intercoxal sclerite a small unornamented trapezoidal plate, shorter than coxa, straight proximally, concave distally, with proximal lateral projections. Coxa smooth. Basis not ornamented, with outer pore on anterior surface; outer seta long, reaching beyond distal margin of exp1. Enp triangular, with strongly chitinized areas, short, approximately 0.7 times as long as exp1, smooth and acuminate. Exp three-segmented: exp1 with outer

row of spinules in proximal third; rows of spinules proximally and distally to outer spine reaching distal edge of exp2; inner margin with row of spinules from median to distal margin replacing hyaline frill, with additional row of spinules in proximal third; exp2 with distal row of strong spinules; exp3 with distal row of spinules on outer margin, inner hyaline frill at distal corner, unipinnate outer spine, and distal unipinnate seta nearly twice as long as outer seta.

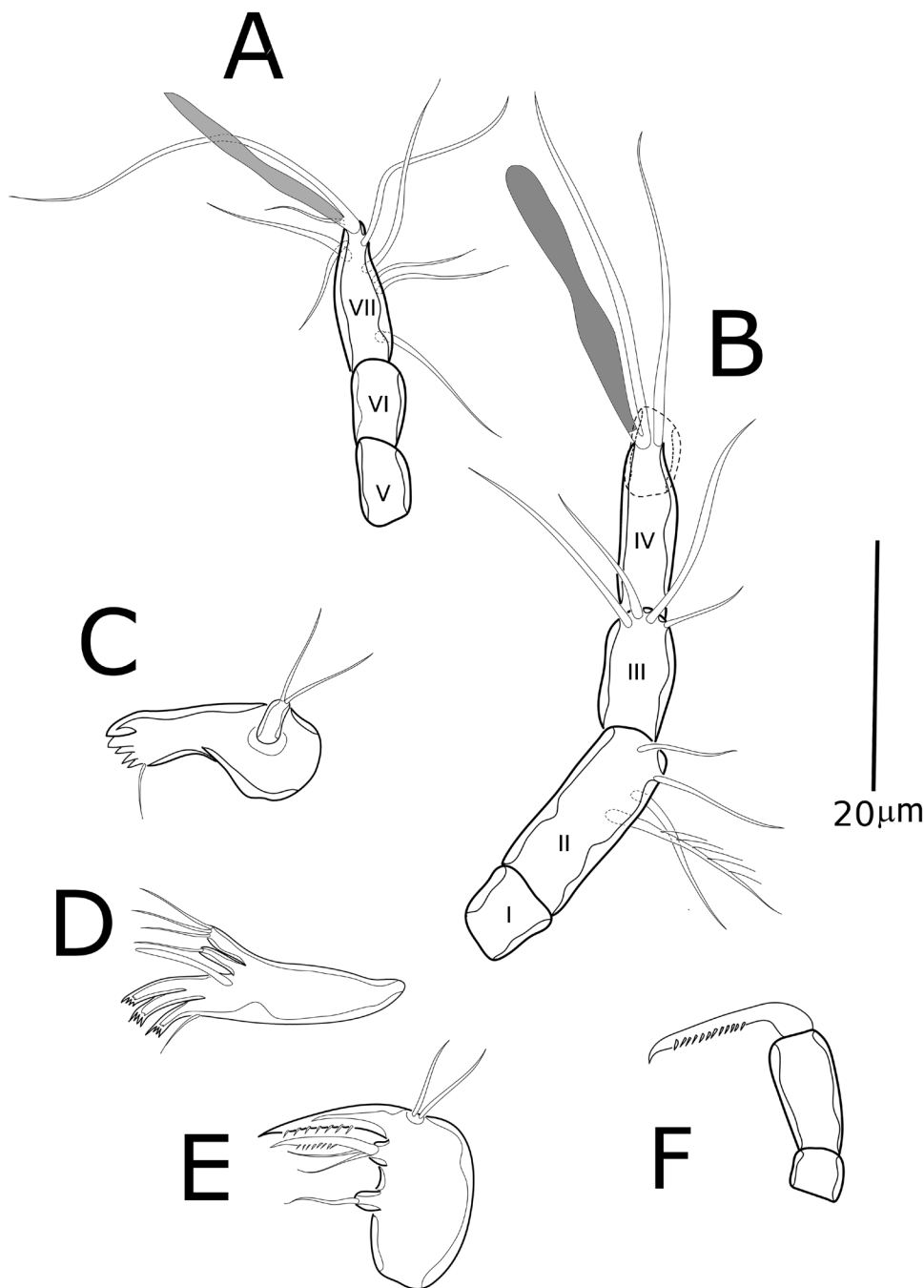


Figure 6. *Santaremicaris santaremensis* comb. nov., female. Antennule (**A** and **B**), mandible (**C**), maxillula (**D**), maxilla (**E**), and maxilliped (**F**). Roman numerals identify the antennule segments.

P5 (Fig. 4E): intercoxal sclerite a large triangular plate reaching the proximal 1/3 of the limb, with distomedial claviform cuticular process. P5 consisting of well-developed triangular plate reaching middle of subsequent Ur; proximal 1/3 with irregular inner margin and outer hump, medially with concave inner

margin and convex outer margin; distally with convex inner margin and concave outer margin; inner margin bearing row of small spinules; distal portion spiniform; armature consisting of very long outer basal seta and 2 additional setae;

P6 represented by unarmed cuticular flap.

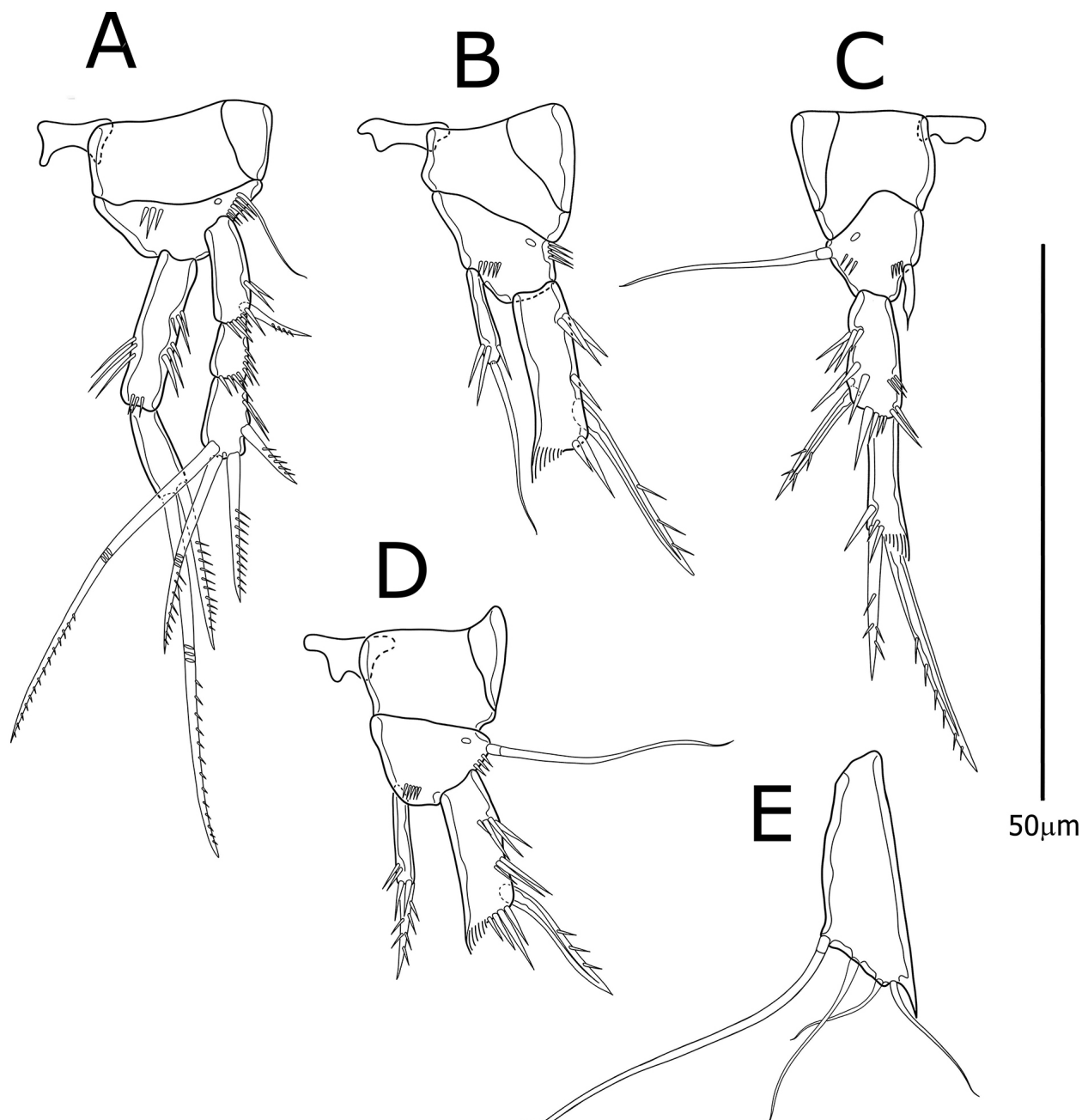


Figure 7. *Santaremicaris santaremensis* comb. nov., female. P1 (A), protopodite, exp 1, and enp of P2 (B), P3 (C), protopodite, exp 1, and enp of P4 (D), P5 (E).

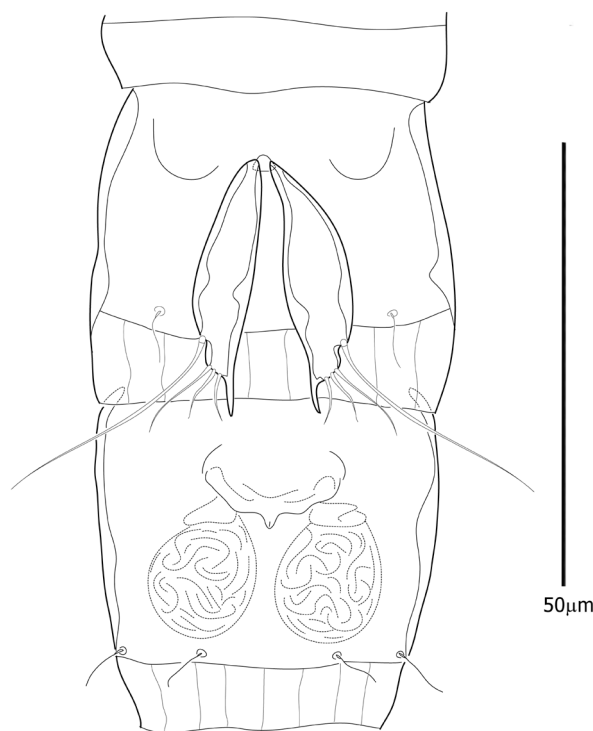


Figure 8. *Santaremicaris santaremensis* comb. nov., female. First urosomite with PS and genital double-somite with genital field.

Description of female (Figs. 5–8). Length 351 μ m (slightly shorter than measurements given by Noodt, 1963, p. 144: 350–380 μ m), measured from tip of rostrum to end of furca. Sexual dimorphism expressed in A1, P1, P2, P3, P4, P5 and Gds. Cph and Urs2 (Gds), 3, and 4 with dorsal integumental windows. Urs2–4 with undulate distal frill on dorsal view, Ur4 with undulate distal frill on lateral view. Telson as in male, except for the more concave Aop (Fig. 5A). Fu (Fig. 5A–C) cylindrical, approximately 2.5 times longer than wide, slightly enlarged distally in lateral view, convex on inner margin in dorsal view, concave in the outer margin, with distal outer pore, and two lateral setae at end of proximal third. Fu armature as follows: seta I and III subequal, both about twice shorter than setae IV and VII; seta II absent; seta IV almost as long as setae VI and VII, subterminally inserted on outer margin; seta V the longest, 3.4 times longer than Fu; dorsal seta (VII) at distal third; all setae smooth, except for unipinnate setae IV and VII.

A1 seven-segmented (Fig. 6A, B); armature as follows: I(0)/II(4)/III(4)/IV(1+ (1+ae))/V(0)/VI(0)/VII(7+ (2+ae)).

A2 as in male.

Md (Fig. 6C), Mx1 (Fig. 6D), Mx (Fig. 6E), Mxp (Fig. 6F) as described for male.

P1 (Fig. 7A): intercoxal sclerite a small unornamented trapezoidal plate, shorter than coxa, concave proximally and distally. Coxa as in male; basis with row of spinules on inner margin not as developed as in male, without row of spinules near insertion of enp and exp, and with five outer spinules; exp1–3 as in male; enp1 lacking proximal row of spinules on inner margin, enp2 as in male.

P2 (Fig. 7B): intercoxal sclerite a small unornamented trapezoidal plate, shorter than coxa, slightly concave proximally and distally, with proximal lateral projection. Coxa smooth; basis with row of spinules near insertion of enp, outer pore and outer row of spinules; outer margin of exp1–3 as in male; enp thinner than in male, without outer ornamentation along the proximal 2/3, with subdistal spinules, two on inner margin, one on outer margin, with thin and long distal seta, as long as exp1, the insertion area not as wide as in the male.

P3 (Fig. 7C): intercoxal sclerite a small unornamented trapezoidal plate, shorter than coxa, proximally straight and irregular distally. Coxa smooth; basis with outer pore, row of spinules distal to long outer seta, and row of spinules near insertion of enp; exp two-segmented, exp1 enlarged, with strong spinules in proximal third, proximally and distally to outer spine, distal row of strong spinules and row of small spinules on inner margin; exp2 with subdistal row of spinules on outer margin, with inner hyaline frill, outer bipinnate spine and distal unipinnate seta; enp one-segmented, 0.5 times as long as exp1, unarmed, acuminate distally.

P4 (Fig. 7D): intercoxal sclerite a small unornamented trapezoidal plate, shorter than coxa, almost straight proximally, concave distally, with proximal lateral projection. Coxa smooth; basis with row of spinules distally to outer seta, and row of spinules near enp insertion; exp1 without ornamentation on inner margin and with a distal inner hyaline frill, outer margin with row of spinules in proximal third, proximally and distally to outer spine; exp2–3 as in male; P4 enp one-segmented, slightly longer than exp1 and bearing one distal and bipinnate spine fused to segment; with two spinules on inner margin, medial and anterior spinules inserted at base of spine.

P5 (Fig. 7E–8): well developed, a simple trapezoidal plate; distal margin ending on spiniform process, without inner ornamentation, reaching distal margin of the Gds; armature composed of proximal, long and articulated seta, two medial setae, and distal seta. Intercoxal sclerite a small triangular plate.

P6 (Fig. 8): unarmed concave plate with median hump covering Gf.

***Santaremicaris amazonensis* sp. nov.**

ZooBank: [urn:lsid:zoobank.org:act:976B796E-DE41-494F-BC5D-21BCD727878B](https://zoobank.org/act:976B796E-DE41-494F-BC5D-21BCD727878B)

Figs. 9, 10

Type material. Only one intact male and one dissected male of *S. amazonensis* sp. nov. present in the slide M2-6 are designated as the syntypes. The dissected male of *S. santaremensis* comb. nov., the intact and the dissected female of *S. santaremensis* comb. nov., and the juvenile mounted in the same slide are not part of the type series.

Other examined material. Undissected male picked from an unsorted sample collected by Noodt, at the same type location of *P. santaremensis* comb. nov. and stored at the DZMB. See material and methods for explanation of the codes.

Type locality. Hyporheic zone of the Amazonas River at Santarém (Pará, Brazil) (Fig. 1). Approximate coordinates: 02°25'S 54°42'W.

Etymology. The specific name refers to the Amazonian biome in which the new species was found.

Description of male (Figs. 9, 10). Length 351 μm, measured from rostrum to end of furca. Rostrum not fused to cephalothorax, with wide base and two sensilla on tip (Fig. 9A, B). Cephalothorax and Urs3–5 with dorsal integumental window (Fig. 9A, B), last Ur with undulate distal frill. Patterns of sensilla as depicted (Fig. 9A, B). Telson with pair of sensilla adjacent to anal operculum, without additional ornamentation and with proximal lateral pore. Fu cylindrical (Fig. 9A–C), about 2.5 times as long as wide, slightly enlarged distally in lateral view, slightly irregular on outer margin and slightly convex on inner

margin in dorsal view, with distal outer pore, and two lateral setae in proximal third. Armature of Fu as follows (Fig. 9A–C): seta I shorter than seta III, seta II absent, seta III shorter than seta IV; seta IV inserted distally on outer margin, almost as long as seta VII, dorsal seta VII inserted at distal third, longer than seta VI; seta V the longest, more than 3 times longer than furca; all setae smooth.

A1 and A2 as in *S. santaremensis* comb. nov.

Labrum triangular in lateral view. Md, Mx1, Mx2 and Mxp as described for *S. santaremensis* comb. nov.

P1 (Fig. 10A): intercoxal sclerite a small unornamented trapezoidal plate, shorter than coxa, straight proximally, concave distally, with proximal lateral projection. Coxa smooth. Basis with row of strong spinules on inner margin, row of minute spinules near insertion of enp and distal to outer seta. Enp two-segmented: enp1 longer than exp1 and exp2 combined, with one inner row, two outer rows and one terminal row of spinules; enp2 with outer spine, long geniculate seta, and posterior hyaline frill. Exp three-segmented: exp1 bearing outer spine, proximal and distal rows of spinules on outer margin; exp2 unarmed, with row of outer spinules; exp3 with outer row of spinules proximally, two outer spines and two geniculate apical setae.

P2 (Fig. 10B): as in *S. santaremensis* comb. nov., except for presence of spinules on anterior surface of basis, near enp insertion, and stronger spinules on outer margin of enp.

P3 (Fig. 10C): Coxa quadratic. Basis rectangular, with long outer seta, outer pore, and V-shaped row of spinules on inner margin. Enp lacking. Exp unisegmented, irregular in shape, long, slightly curved inwards, with cuticular humps on medial and proximal inner margin, inner tube pore near articulation with basis, and with two proximal outer spinules; apophysis long, sigmoid, narrowing in long tip with distal hyaline cushion; thumb shorter than apophysis, with long tip and hyaline inner margin.

P4 (Fig. 10D): similar to *S. santaremensis* comb. nov., except for presence of row of spinules on outer margin of enp; stronger proximal row of spinules on exp1 inner margin, and weaker distal row of spinules on exp1 inner margin.

P5 (Fig. 10E): intercoxal sclerite a large trapezoidal plate reaching the proximal 1/3 of the limb, with distomedial linguiform cuticular process. P5 consisting of well-developed triangular plate reaching middle of subsequent Ur; with irregular outer margin, slightly bulging proximally; inner margin

almost straight, with row of small spinules; distal portion ending in strong and thin spiniform process; armature consisting of very long outer basal seta and two additional setae inserted on distalmost hump.

P6 represented by unarmed cuticular flap.

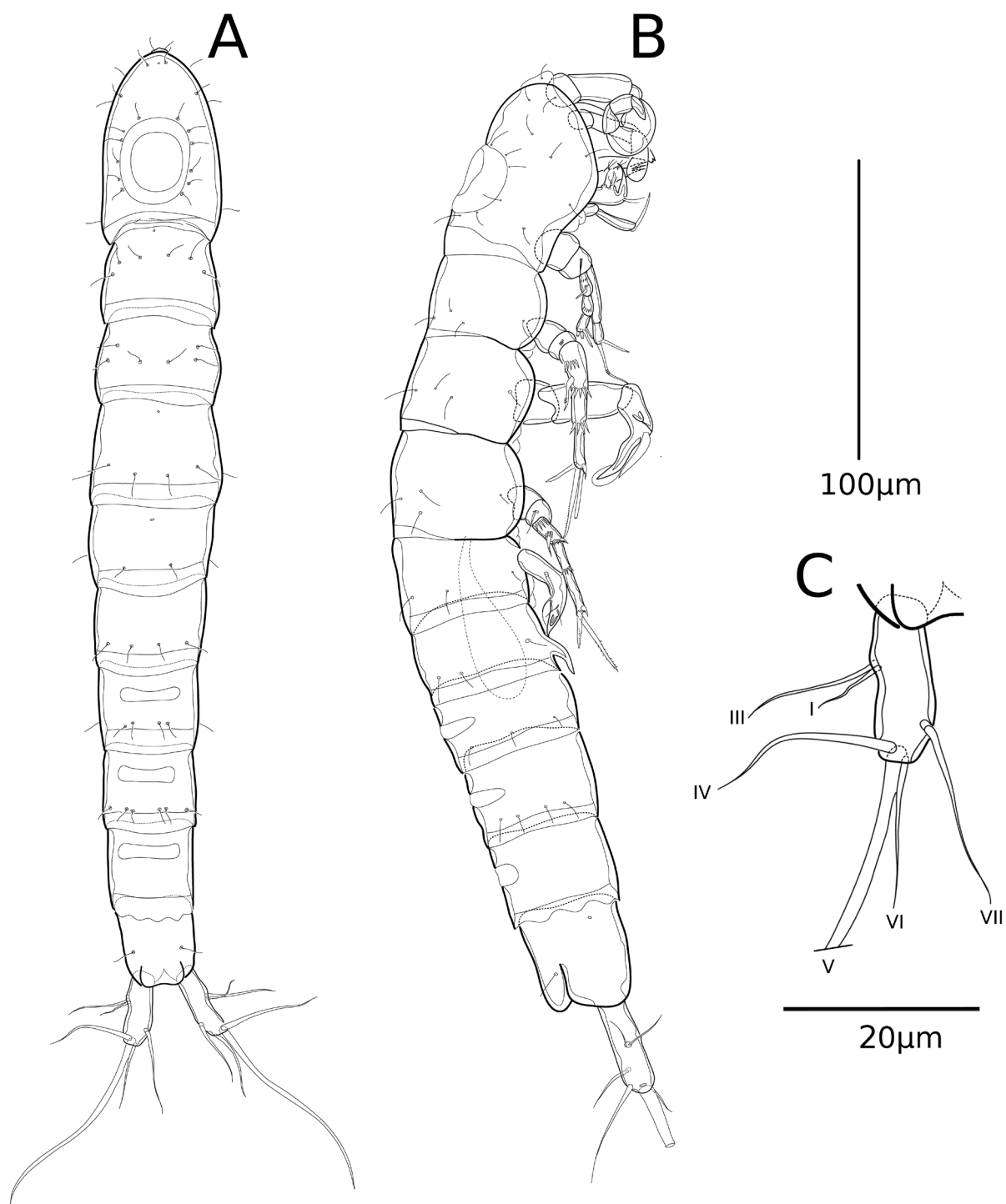


Figure 9. *Santaremicaris amazonensis* sp. nov., male. Dorsal (A), lateral (B) habitus, and right furca in dorsal view (C). Roman numerals identify furcal setae. Vertical scale bar (A, B), horizontal scale bar (C).

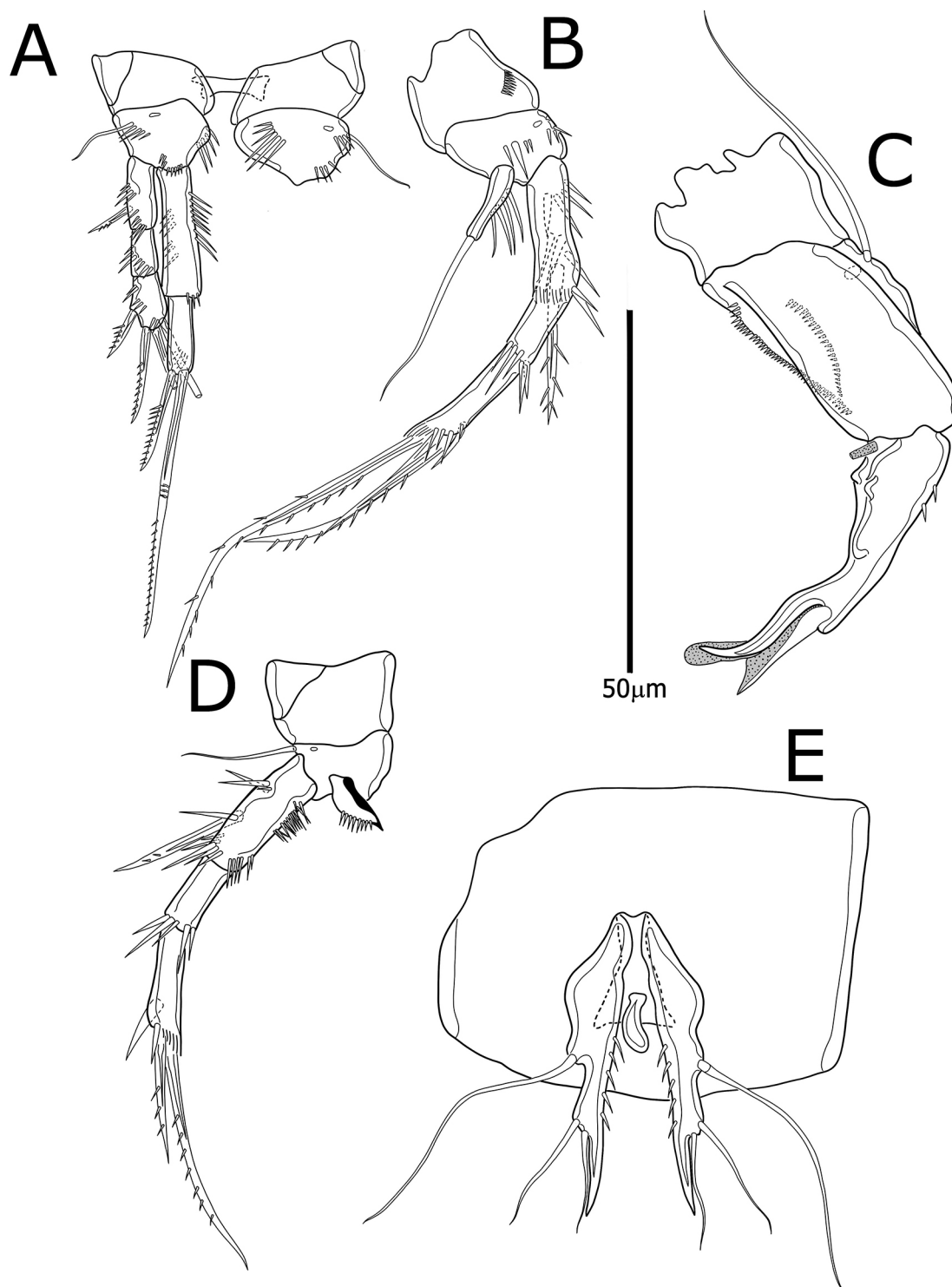


Figure 10. *Santaremicaris amazonensis* sp. nov., male. P1 (A), P2 (B), P3 (C), P4 (D), and P5 (E).

DISCUSSION

Most of the characters proposed by Schminke (2010) cannot be satisfactorily used as diagnostic for the Neotropical Fontinalicaridinae (*i.e.*, *Brasilibathynellocaris*, *Colombocaris*, *Eirinicaris*,

Forficatocaris, *Itiocaris*, *Murunducaris*, *Noodtcaris*, *Potamocaris*, *Remaneicaris*, *Siolicaris*).

According to Schminke (2010), in the Fontinalicaridinae, a) the terminal seta of the male P3 is separate from the apophysis; b) the end of female P3 has no terminal seta and is a relatively short element

with a rounded apex, carrying spinules terminally and subterminally; c) the basis of male P4 has an inner row of spinules and is ornate between the exp and enp insertions; d) the P5 of both sexes are much larger and triangular, and extend back well beyond the own somite; and e) in the furca, the group of three lateral setae and the dorsal seta are at a distance from one another, the dorsal seta being located distally, the three lateral setae proximally.

However, within the Neotropical Fontinalicaridinae the unfused spine on male P3 apophysis is present in *Noodtcaris kubitzkii* (Noodt, 1972) and *Noodtcaris tapajoensis* (Noodt, 1963), but it is modified in these species as a hyaline spine in *N. kubitzkii* or it is a blunt spine in *N. tapajoensis*. In the remaining *Noodtcaris* species, the spine is fused to the apophysis. The referred spine is not fused to the apophysis in *Potamocaris* and *Forficatocaris*, but its loss as an articulated element or fusion to the apophysis occurs within *Potamocaris*. The modification of the spine into a hyaline spine occurs in some species of *Potamocaris* and *Forficatocaris*. Only *Murunducaris* has the typical unfused spine, although strongly modified in *Murunducaris noodti* Corgosinho, Martínez Arbizu and Reid, 2008. *Siolicaris* has an unarmed apophysis, with the exception of *Siolicaris sandhya* (Ranga Reddy, 2001) (Corgosinho *et al.*, 2012b). The apophysis is also unarmed on *Iticocaris* and *S. amazonensis* sp. nov., but bears a distal hyaline cushion, which we consider homologous to a spine, in *Brasilibathynelloccaris* and *S. santaremensis* comb. nov. The female P3 enp is absent in *Potamocaris*, *Siolicaris* and at least in the Colombian species of *Noodtcaris* (the female of *N. tapajoensis* is unknown). When the enp is present on the female P3, it is generally short, unarmed, and with blunt tip, but it is bifid on *Murunducaris dactyloides* (Kiefer, 1967), bears a distal seta on *Murunducaris loyolai* Corgosinho, Martínez Arbizu and Reid, 2008, and has an acuminate tip in *S. santaremensis* comb. nov. The basal accessory spinule or a row of spinules between enp and exp of male P4 is generally present in *Potamocaris* and *Forficatocaris*. This character is absent in *Murunducaris juneae* Reid, 1994, *Colombocaris isabellae* Gaviria, Defaye and Corgosinho, 2017, *Noodtcaris columbiensis* (Noodt, 1972), *Brasilibathynelloccaris*, *Siolicaris partim* and *Iticocaris*. The P5 morphology shows a plethora of

transformations in shape, size, and armature within the Neotropical Fontinalicaridinae. It is dimorphic in shape and armature in *Potamocaris*, *Forficatocaris*, *Murunducaris*, and *Santaremicaris* gen. nov. (maybe also in *Colombocaris*, but the female is unknown), with extreme and non-homologous transformations occurring in *Murunducaris* and *Forficatocaris*. The P5 is rather short in *Siolicaris* and *Brasilibathynelloccaris*. The typical fontinalicaridid P5 as described by Schminke (2010) is present in *Iticocaris* and *Noodtcaris* only. The most consistent diagnostic character is the insertion of the lateral setae of the furca (setae I, II, III) anteriorly to the dorsal one (seta VII). This character differs only in *Potamocaris*, where the lateral and dorsal setae are distally inserted, at the same transverse plane.

Therefore, it is evident that most of the diagnostic characters are very plastic within Neotropical fontinalicaridids, and the inclusion of the new genus within this subfamily must be on the grounds of derived characters shared with *Murunducaris* plus the insertion of the lateral furcal setae anteriorly to the dorsal one, and the presence of a short, not spiniform, and unarmed female P3 enp.

A robust phylogenetic hypothesis on the position of the monophylum *Murunducaris/Santaremicaris* gen. nov. within Fontinalicaridinae is not possible without a broader morphological and molecular study with sufficient taxon sampling. However, some evidence indicates a closer proximity between *Potamocaris*, *Forficatocaris*, *Murunducaris*, *Santaremicaris* gen. nov., *Parastenocaris fossoris* Fryer, 1956, *Parastenocaris crassicaudis* Chappuis, 1955, *Parastenocaris nigerianus* Chappuis, 1959, *Parastenocaris jeanninei* Dumont, 1981, *Parastenocaris kimi* Dumont, 1981, *Parastenocaris aberrans* Apostolov, 2004, and maybe *Proserpinicaris phyllura* (Kiefer, 1938) (*incertae sedis*). For details, see discussion below.

Characters shared between Santaremicaris gen. nov. and Murunducaris.

The new genus shares with *Murunducaris* (1) the presence of strong ornamentation on the inner margin of the basis of P1 in males (Sy), (2) the presence of a large male P5 intercoxal sclerite (Sy) with medial cuticular process (Sy), and (3) a proximal row of spinules on the inner margin of the male P4 expl

(Sy). The characters are described for the two genera in details below:

(1) Strong ornamentation on the inner margin of the basis of P1 in males. The presence of an inner spine on the basis of P1 is a widespread character of Harpacticoida (Huys and Boxshall, 1991; Willen, 2000; Seifried, 2003). Within Harpacticoida a strongly dimorphic spine is an apomorphy for at least the Ameiridae Boeck, 1865 and the Diosaccinae Sars, 1906. One characteristic of armature elements such as setae and spines is their hollow core, in which a single nerve enters (Fahrenbach, 1962). Setules, spinules and cilia are solid projections of the cuticle, lacking cellular components (Fahrenbach, 1962), and they do not cross the cuticle; this seems to be the condition present in *Murunducaris* and *S. santaremensis* comb. nov. In all *Murunducaris* species there is a strong and long spinule, sometimes followed by smaller accompanying spinules on the inner margin of the basis of the male P1 (Corgosinho *et al.*, 2008). The same character is observed in *S. santaremensis* comb. nov. However, in *S. amazonensis* sp. nov., there is a row of strong and subequal spinules on the inner margin of the male P1. In a series of transformation, we consider that a row of long spinules as present in *S. amazonensis* sp. nov. precedes the condition present in *S. santaremensis* comb. nov. and *Murunducaris*; the condition in *S. amazonensis* sp. nov. representing the retention of a plesiomorphic condition. A weak ornamentation, with short, not enlarged spinules is observed in females of *Murunducaris* and *S. santaremensis* comb. nov. The female is unknown for *S. amazonensis* sp. nov. and the female P1 of *M. noodti* is mistakenly described as being equal to the male P1 (Corgosinho *et al.*, 2008). In the female of *M. noodti* the basis of the P1 does not have the modified inner spinule, which is present in the males of the genus *Murunducaris*. We consider that this is convincing evidence supporting that the large basal spinule observed for *Murunducaris* and *S. santaremensis* comb. nov. is not homologous to the seta or spine, sometimes found in Parastenocaridinae. Within this family, when a seta or spine occurs on the inner margin of the basis of P1, it is normally present in both males and females. To our knowledge, such armature was never described for a Fontinalicaridinae species, occurring convergently only in some groups

of species within the Parastenocaridinae. When a seta occurs on the inner margin of the P1 basis within Parastenocarididae, it is not dimorphic in shape, differing at most in length (*e.g.*, *Eirinicaris antonioi* Corgosinho, Schizas, Previattelli, Rocha and Santos-Silva, 2017b). The absence of a modified medial spine in the male P1 basipodite is considered a synapomorphy for *Psammonitocrella* Huys, 2009 and Parastenocarididae (see Martínez Arbizu and Moura, 1994; Corgosinho *et al.*, 2020), and is a condition present in the ground pattern of the Fontinalicaridinae. *Murunducaris* and *Santaremicaris* gen. nov. are derived genera within the Fontinalicaridinae. If future studies reveal that what we consider a transformed spinule is in fact a transformed spine, it must be considered a synapomorphy for these genera, resulting from the re-expression of a plesiomorphic condition not found within the *Psammonitocrella*/Parastenocarididae monophylum. For additional information on this character see Corgosinho *et al.* (2008).

(2) Presence of an enlarged male P5 intercoxal sclerite with medial cuticular process. The male intercoxal sclerite of *Murunducaris* and *Santaremicaris* gen. nov. is the strongest evidence supporting the sister group relationship of these genera. This character was described for the first time by Reid (1994) and further confirmed by Corgosinho *et al.* (2008) for three additional species of *Murunducaris* and *S. santaremensis* comb. nov. The intercoxal sclerite is enlarged, quadratic or trapezoidal, with a cuticular process of various shapes depending on the species (*e.g.*, hook-like, spiniform, club-shaped or linguiform) occurring between the limbs and occupying a medial or distal position in the intercoxal sclerite. This character is shared by *Murunducaris* and *Santaremicaris* gen. nov., exclusively. Further studies are necessary to verify if this character is present in *Pa. fossoris* and *Pa. crassicaudis*, two species that are considered closely related to *Murunducaris* and *S. santaremensis* comb. nov. (Corgosinho *et al.*, 2008).

(3) Proximal row of spinules on the inner margin of the male P4 exp1. Males of *Murunducaris* and *Santaremicaris* gen. nov. have a proximal row of spinules on the inner margin of the P4 exp1. Within the Fontinalicaridinae, the Neotropical *Forficatocaris*, the African *Pa. fossoris*, *Pa. crassicaudis* (see Fischer,

1998), *Pa. nigerianus*, *Pa. jeanninei*, and *Pa. kimi*, the European *Proserpinicaris phyllura* (*incertae sedis*) (see Glatzel, 1991), and maybe *Pa. aberrans* have a proximal inner row of acuminate spinules in the P4 exp1. In the absence of a complete phylogenetic analysis of the Fontinalicaridinae, we consider this ornamentation as synapomorphic for *Murunducaris* and *Santaremicaris* gen. nov. only.

Characters separating Santaremicaris gen. nov. from Murunducaris

The new genus differs from *Murunducaris* by (4a) the presence of ornamentation on the inner margin of the P1 enp1 of male and female (Pl) (also present in *M. juneae*), (4b) such ornamentation is represented by stiff and long spinules (Ap); (5a) the absence of distal spinules on the enp of the male P2 (Ap), (5b) which is ornamented with strong outer spinules (Ap) and (5c) armed with long distal seta (Ap); (6) absence of a distal spine on the apophysis of male P3 (Ap); (7a) presence of a long row of spinules on the inner margin of the basis of male P3 (Ap), (7b) which has no trace of enp or seta indicating the enp (Ap); (8) presence of a triangular, short and sclerotized enp in the male P4 (Ap); (9) Presence of an inner distal row of spinules on the male P4 exp1; (10a) presence of a long and slim male P5 (Pl), (10b) with irregular margins (Ap), (10c) ornamented on the inner margin (Pl), (10d) ending in a long tip (probably representing a fused distal atrophied spine; Ap?), and (10e) with only three setigerous elements on the outer margin (Ap); (11) absence of an integumental window in the male second urosomite (Ap).

(4a–b) Presence of long and stiff spinules on the inner margin of the P1 enp1. The presence of an inner ornamentation on the enp1 of P1 is considered to be a plesiomorphic condition (Corgosinho *et al.*, 2007b). Within the Fontinalicaridinae genera, this ornamentation is observed in *Fontinalicaris* (see Martínez Arbizu, 1997; Schminke, 2010), *Proserpinicaris* (see Karanovic *et al.*, 2012; Karanovic and Lee, 2012; Totakura *et al.*, 2014), *Brasilibathynellocaris* (except in the male of *Brasilibathynellocaris brasilibathynellae* (Jakobi and Loyola e Silva, 1962) see Corgosinho *et al.*, 2010a), *Iticocaris* (see Corgosinho *et al.*, 2012a), *Siolicaris* (except in *Siolicaris sioli* (Noodt, 1963), see Corgosinho

et al., 2012b), *Colombocaris* (see Gaviria *et al.*, 2017), *Noodtcaris* (see Noodt, 1972; Gaviria *et al.*, 2017), and *Santaremicaris* gen. nov. Within *Forficatocaris* and *Potamocaris* one or more spinules are modified in the male, this being a synapomorphy shared by both genera; females retain the plesiomorphic condition. Within *Murunducaris*, it is absent in all species, except for *M. juneae* (see Corgosinho *et al.*, 2008). The presence of a row of spinules on the inner margin of the P1 enp1 appears to be a widespread characteristic. This condition is present in Fontinalicaridinae and Parastenocaridinae (see Ranga Reddy *et al.*, 2014, fig. 9 and Corgosinho *et al.*, 2017b). However, the spinules present in *Santaremicaris* gen. nov. are longer and more numerous than in other Neotropical species. Within *Brasilibathynellocaris*, stiff spinules are present only in one species, *Brasilibathynellocaris paranaensis* Jakobi and Loyola e Silva, 1962 (Corgosinho *et al.*, 2010a). In *Noodtcaris*, only *N. tapajoensis* (see Gaviria *et al.*, 2017) has this character. Therefore, we consider the presence of stiff spinules in *M. juneae*, *B. paranaensis*, and *N. tapajoensis* as convergent to the condition observed in *Santaremicaris* gen. nov.

(5a–c) Ornamentation and armature of male P2 enp. The condition found in *S. santaremensis* comb. nov. and *S. amazonensis* sp. nov. is unique within the family, not to mention within the Neotropical Fontinalicaridinae, and consists of a clear synapomorphy uniting both species. In males of *Santaremicaris* gen. nov. the distal seta is longer than usual, and its insertion occupies almost the whole distal margin of the enp. Additionally, the ornamentation is strong and limited to the outer margin only, with no distal or inner ornamentation. A P2 enp highly dimorphic in shape, also differing in ornamentation is not a widespread character within the Parastenocarididae. In most genera and species the P2 enp is very similar in female and male, differing in fine ornamentation only. The morphology, normally, is represented by an enp not too short or longer than half of the exp1, with a small distal seta, with an insertion not as wide as the distal margin of the segment, with some few distal spinules and some few outer and maybe inner spinules. Within the Parastenocaridinae it is reduced to a small enp with a distal seta in *Monodicaris*, but is normally developed in most species within this subfamily. Within the

Fontinalicaridinae it is long and strongly ornamented in males of *B. brasilibathynellae* and *B. paranaensis*, occurring as a derived condition within this genus (Corgosinho et al., 2010a). It is claviform, strongly ornamented, with a distal seta and accompanied by a distal spinule bearing a hyaline margin in *S. sandhya*, but normally developed in the remaining *Siolicaris* species described so far. All the species of *Murunducaris* have some dimorphism in the P2 enp. A foliaceous P2 enp is more developed in *M. juneae*, *M. loyolai*, and *M. noodti*. In *M. dactyloides* it is less conspicuous. A similar kind of sexual dimorphism can be observed in *Iticocaris itica* (Noodt, 1962), *Pa. fossoris*, and *Pa. crassicaudis*, and in species closely related to *Fontinalicaris fontinalis* (Schnitter and Chappuis, 1915) (e.g., *Fontinalicaris hispanica* Martínez Arbizu, 1997). A similar condition seems to be present in *Noodtcaris*, but this is difficult to evaluate based only on the original descriptions. Corgosinho et al. (2008) mentioned that a dimorphism of the P2 enp is absent in *Forficatocaris*, but the study of new and undescribed species (unpublished data), and the reexamination of the literature and some type material revealed that the P2 enp is thick and/or long with some few minute spinules along the inner margin of the distal 1/3 in some males of *Forficatocaris* (e.g., *Forficatocaris evelinae* Noodt, 1972; *Forficatocaris lilianae* Noodt, 1972; *Forficatocaris odeteae* Moreira, Eskinazi-Sant'Anna and Previattelli, 2019).

(6) Male P3 apophysis lacking distal spine. According to Schminke (2010), there is no distal spine on the apophysis of a Parastenocaridinae. The presence of this armature in Fontinalicaridinae and its absence in Parastenocaridinae is considered a plesiomorphic and an apomorphic condition, respectively (Corgosinho et al., 2017b). Within the Fontinalicaridinae, an apophysis with a distal spine occurs in *Fontinalicaris*, *Proserpinicaris partim*, *Murunducaris*, some species of *Forficatocaris* and *Potamocaris*, *S. sandhya* and *Siolicaris xyrophora* (Noodt and Galhano, 1969), *N. tapajoensis* and *N. kubitzkii*, and other fontinalicaridids still included in the genus *Parastenocaris*, such as *Pa. fossoris*, and perhaps in the Portuguese *Proserpinicaris cruzi* (Noodt and Galhano, 1969) (*incertae sedis*). In all these cases, except for *S. sandhya* and *S. xyrophora*, which are derived species within *Siolicaris*, the armature is

considered the retention of a plesiomorphic character. The apophysis with a clear incorporated spine occurs in the Colombian *N. columbiensis*, *Noodtcaris roettgeri* (Noodt, 1972), and in some *Proserpinicaris* species. The spine is completely absent in the Neotropical *Brasilibathynellocaris*, *Siolicaris*, *Iticocaris itica*, some *Potamocaris* species, *Santaremicaris* gen. nov., *Parastenocaris staheli* Menzel, 1916, the African *Pa. crassicaudis*, *Pa. kimi*, *Pa. nigerianus*, and *Pa. jeanninei*, the Spanish *Proserpinicaris cantabrica* (Chappuis, 1937) (*incertae sedis*), *Parastenocaris calliroe* Cottarelli, 1969 (Sardinia), and *Parastenocaris sardoa* Cottarelli and Torrisoni, 1977 (Sardinia). This is a heterogeneous group of genera and species probably belonging to different evolutionary lineages, some of them not directly related to each other. Hence, it is more parsimonious to consider the loss of the distal spine occurring several times within the Fontinalicaridinae. Within the Neotropical zone, the loss of the distal spine of the male P3 apophysis would have occurred independently within the monophylum *Potamocaris/Forficatocaris*, because the presence of the distal spine is in the ground pattern of this clade. It occurs again in the putative monophylum *Brasilibathynellocaris/Iticocaris/Siolicaris*, and once in the lineage of *Santaremicaris* gen. nov. within the monophylum *Murunducaris/Santaremicaris* gen. nov.

(7a–b) male P3 basis with a long row of spinules on the inner margin and enp absent. Within the Fontinalicaridinae an inner row of spinules on the basis of the male P3 is present in *N. tapajoensis*, *Pa. crassicaudis*, *Pa. fossoris*, *Pa. nigerianus*, *Pa. kimi*, *Pa. sardoa*, *Pa. calliroe*, *Proserpinicaris phyllura* (*incertae sedis*), and some *Proserpinicaris* (e.g., *Proserpinicaris admete* (Cottarelli, Fasano, Mura and Saporito, 1980); *Proserpinicaris ima* (Cottarelli, 1989), *Proserpinicaris kalypto* (Pesce, Galassi and Cottarelli, 1988); *Proserpinicaris proserpina* (Chappuis, 1938)), *S. xyrophora*, and maybe in *Pr. cruzi* (*incertae sedis*). Within *Potamocaris* and *Forficatocaris* the inner row of spinules is fused into a process (“Vorsprung”), which is a synapomorphy uniting these genera. Inner basal ornamentation of the male P3 is absent in *Colombocaris*, *Iticocaris*, *Murunducaris*, *Noodtcaris*, *Siolicaris*, *Pa. staheli*, *Fontinalicaris sensu* Martínez Arbizu (1997), *Pa. jeanninei*, *Parastenocaris matopoica* Wells, 1964, *Pa. aberrans*, *Pr. cantabrica* (*incertae*

sedis), and other *Proserpinicaris* (e.g., *Proserpinicaris corgosinhoi* Totakura, Ranga-Reddy and Shaik, 2014; *Proserpinicaris imjin* Karanovic, Cho and Lee, 2012; *Proserpinicaris moravica* (Sterba, 1965); *Proserpinicaris nipponensis* (Chappuis, 1955); *Proserpinicaris ondali* (Lee and Chang, 2009); *Proserpinicaris wangpi* Karanovic, Cho and Lee, 2012; *Proserpinicaris young* Karanovic, Cho and Lee, 2012). The male P3 enp is not illustrated or it is absent in *Lacustricaris budapestiensis* (Török, 1935), *Parastenocaris lacustris* Chappuis, 1958 (*incertae sedis*) (Chappuis and Delamare Deboutteville, 1958), *Pa. aberrans*, *Pa. nigerianus*, *Pa. matopoica*, *Pa. jeanninei*, *Pa. staheli* and some *Proserpinicaris*.

It seems that an inner basal ornamentation evolved independently within the Fontinalicaridinae and its presence is not necessarily connected to the presence of the enp in some species such as *Pa. calliroe*, *Pa. nigerianus*, and at least *Pr. ima* within *Proserpinicaris*. Neither the absence of ornamentation is associated with the absence of the enp in all cases. However, the enp is sometimes represented by a small spine or seta, which makes its identification difficult and it was possibly omitted in some old descriptions. The absence of both enp and ornamentation undisputedly occurs in *Colombocaris*, *Iticocaris*, *M. juneae* and *M. dactyloides*.

In the ground pattern of *Murunducaris* the male P3 basis is represented by an unadorned segment with a spiniform enp. Instead, a basis without an enp and with a long row of spinules on the inner margin is present only in the ground pattern of *Santaremicaris* gen. nov. We believe that the condition present in *Santaremicaris* gen. nov. is homologous to what we observed in *Pa. fossoris*, *Pa. crassicaudis*, *Pa. kimi*, and *Pa. nigerianus*. In these species, the ornamentation does not occupy the whole inner surface of the basis and the enp is posteriorly inserted to it. We hypothesize that this is a plesiomorphic condition. In *Santaremicaris* gen. nov. the basis of the male P3 is elongated, ornamented with a long row of minute spinules along the inner margin, and the enp is absent; this being considered an autapomorphy supporting this genus.

(8) Triangular, short and sclerotized enp of the male P4. A short and sclerotized enp of the male P4 is a unique feature of *Santaremicaris* gen. nov. No other Fontinalicaridinae has these combined features. A superficially similar enp is observed in *Pr. nipponensis*

Chappuis, 1955, and *Pa. nigerianus*. However, based on the illustrations of these species, we can say nothing about sclerotization. Sclerotized male P4 enp appear in the monophylum *Potamocaris/Forficatocaris*, especially in *Forficatocaris*. However, the morphology of the P4 enp in *Forficatocaris* is so different from that of *Santaremicaris* gen. nov. that any hypothesis of homology must be abandoned. The male P4 enp in the remaining fontinalicaridids have a variety of shapes, i.e., long and lamelliform, foliaceous and hirsute, spiniform, short and cuneiform, or even absent. In *Murunducaris*, the sister group of *Santaremicaris* gen. nov., the male P4 enp is long, lamelliform with outer ornamentation as in *M. dactyloides* and *M. noodti* or slightly bent inwards, with ornamentation mostly distributed outwardly as in *M. juneae* and *M. loyolai*. However, in no *Murunducaris* species is the enp sclerotized. Therefore, we consider the triangular, short and sclerotized enp of the male P4 as autapomorphic for *Santaremicaris* gen. nov.

(9) Presence of an inner distal row of spinules on the male P4 exp1. During the ontogeny of most Parastenocarididae, a distal inner row of spinules on the male P4, still present in the copepodid V (see Glatzel, 1991; Corgosinho et al., 2010a) is homologous to the adult hyaline frill. The presence of the inner hyaline frill in the adults is considered a plesiomorphic condition of the Parastenocarididae, and the retention of the juvenile character in the adult (a distal inner row of spinules) is the apomorphic condition.

A distal inner row of spinules is present in *S. santaremensis* comb. nov. and in *S. amazonensis* sp. nov. The same character is also observed in *Forficatocaris*, *Pa. fossoris*, *Pa. crassicaudis*, *Pa. jeanninei*, *Pa. kimi*, *Pa. nigerianus*, *Pr. phyllura* (*incertae sedis*), *Fontinalicaris* (*Parastenocaris fontinalis*-group sensu Martínez Arbizu, 1997; Fig. 5A, B), and *Proserpinicaris*.

(10a–e) Shape, ornamentation, and armature of the male P5. The shared presence of an enlarged male P5 intercoxal sclerite with a cuticular process between the limbs in both *Santaremicaris* gen. nov. and *Murunducaris* justify a sister group relationship between these genera. An enlarged intercoxal sclerite was reported by Corgosinho et al. (2008) for *Pa. fossoris* and *Pa. crassicaudis*, but this condition is not illustrated by Fischer (1998). The same condition

may be present in *Pa. aberrans* from the Northern Pyrenees in France (Apostolov, 2004).

One of the most striking characters of the genus *Murunducaris* is the presence of a large, subconical, terminal and unfused spine on the P5 of males (Corgosinho et al., 2008). This transformation is unique for *Murunducaris*. However, the observation of the P5 of *S. santaremensis* comb. nov., *S. amazonensis* sp. nov., *Pa. crassicaudis*, *Pa. fossoris*, *Pa. aberrans*, and *Pa. jeanninei* revealed very interesting conditions. In *Pa. fossoris*, the distal margin of the P5 is represented by a much-ornamented triangular region (Fischer, 1998; Fig. 11A), and on the outer margin, there are only two setae between this ornamented structure and the articulated setae of the basis. A similar P5 of male, but without the distal ornamentation, is described for *Pa. matopoica*. In *Pa. crassicaudis* (see Fischer, 1998; Fig. 11B) and *Pa. jeanninei*, a strong spine appears on the distal margin of P5, but a clear suture indicates the point of insertion of this spine. In *Pa. aberrans*, the

distal spine may be what Apostolov (2004) depicts as an inner hyaline lamella. In *S. santaremensis* comb. nov. and *S. amazonensis* sp. nov., there are only three setae on the outer margin and a distal spiniform process. This distal spiniform process may be a fused distal spine, homologous to the distal ornamented process of *Pa. fossoris*. We consider that the unfused condition of the distal spine of *Murunducaris*, *Pa. crassicaudis*, *Pa. jeanninei*, and *Pa. aberrans* is a plesiomorphy. Autapomorphies of *Santaremicaris* gen. nov. are long male P5 with irregular margins and with a putative fused distal spine.

(11) Male second Ur without integumental window. It is very difficult to discuss the phylogenetic significance of the urosomal integumental windows on the Urs of Parastenocarididae. In most cases they are not described or are considered absent. Recently its phylogenetic and taxonomic importance was highlighted by Corgosinho and Martínez Arbizu (2005) and Corgosinho et al. (2007a; 2007b) and

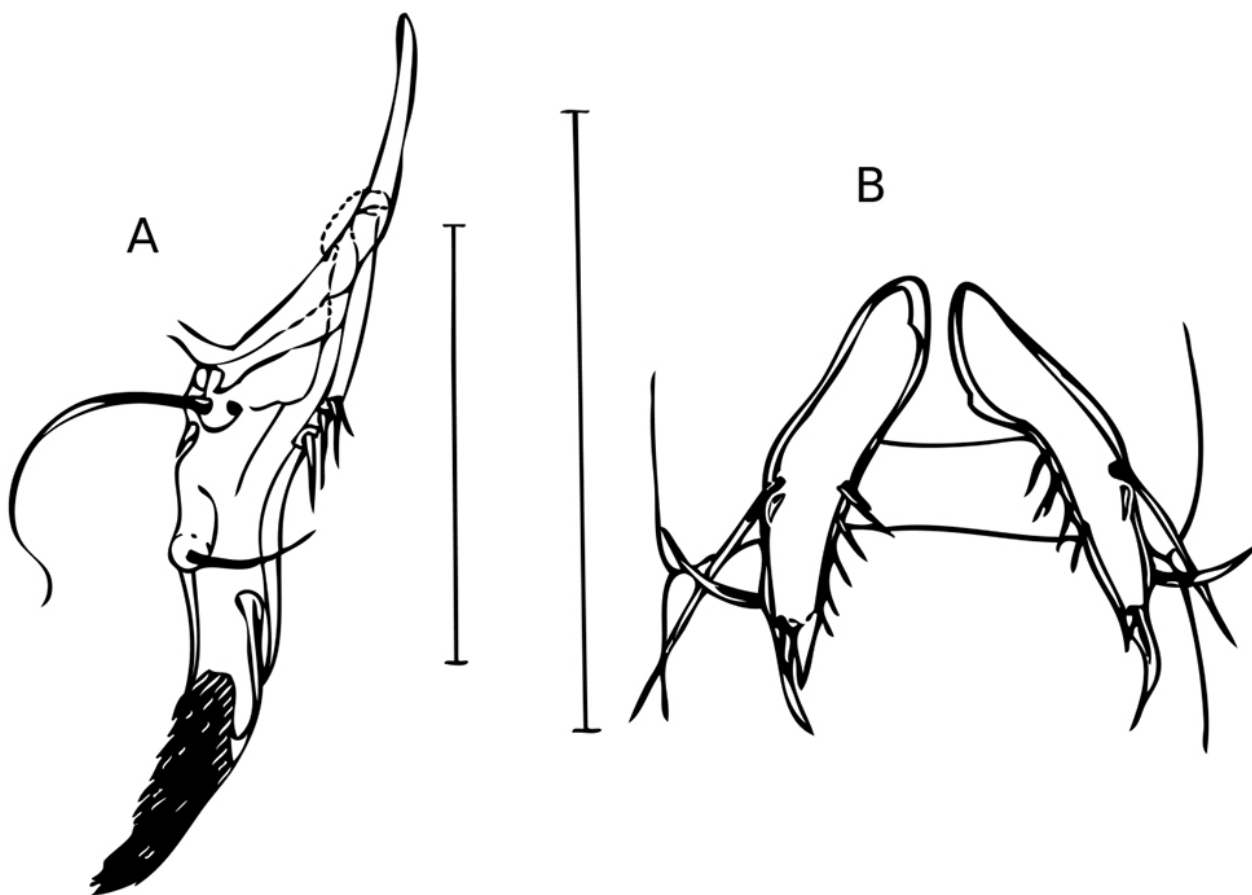


Figure 11. *Parastenocaris fossoris*, male P5 (A). *Parastenocaris crassicaudis*, male P5 (B). Scale bars 50 μ m. After Fischer (1998). Reproduction authorized by Dr. Lutz Fischer and Dr. Thomas Glatzel.

Schminke (2008; 2009). The most plesiomorphic pattern is the presence of dorsal integumental windows from Ur2 to Ur5 in male and Ur2 to Ur4 in females. This is considered the ground pattern for the Parastenocarididae by Corgosinho *et al.* (2007a). To our knowledge, lateral integumental windows have evolved only within the Parastenocaridinae, in *Remaneicaris* (Corgosinho and Martínez Arbizu, 2005 and Corgosinho *et al.*, 2007b, 2010b, 2017a), *Kinnecaris* (Schminke, 2008; Bruno and Cottarelli, 2015), and *Monodicaris*. Therefore, the ground pattern of Parastenocarididae is retained in Fontinalicaridinae. In the absence of contrary evidence, the loss of the integumental window on the Ur2 segment in male is considered as an autapomorphy of *Santaremicaris* gen. nov.

The curved hook on the inner margin of the basis of male P3.

A curved hook on the inner margin of the basis of male P3 could be considered a modified enp in *Santaremicaris* gen. nov. With exception of *Remaneicaris* (see Corgosinho *et al.*, 2007b), in which the enp is one-segmented, in the remaining Parastenocarididae the enp, when present, is represented by a seta or spine. According to Corgosinho *et al.* (2010a), with the exception of *B. paranaensis*, all *Brasilibathynellocaris* species have a curved hook proximally inserted on the inner margin of male P3, similar to what is observed in *S. santaremensis* comb. nov. Within *Brasilibathynellocaris*, the curved hook is proximal to the seta representing the enp (Corgosinho *et al.*, 2010a). In addition, both in *Santaremicaris* gen. nov. and *Brasilibathynellocaris* the hook-like structure is not hollow, which is evidence that the curved hook is a spinule, instead of a modified spine. This character could be present in the common ancestor of *Brasilibathynellocaris*, *Murunducaris*, and *Santaremicaris* gen. nov. *Brasilibathynellocaris* could have retained the ancestral character (secondarily lost in *B. paranaensis*), whereas it was lost in the *Murunducaris/Santaremicaris* gen. nov. lineages, reappearing in *S. santaremensis* comb. nov. The expression of this character in *S. santaremensis* comb. nov. could be the result of the reactivation of a silent gene. Therefore, considering all the characters discussed in

this contribution, it is difficult to discuss the evolution of the curved hook on the inner margin of the basis of male P3 without a proper phylogenetic analysis. We cannot exclude the possibility of convergent evolution.

Santaremicaris gen. nov. has a rectangular basis in the male P3 (two times longer than wide). A similar basis is described for *Iticocaris* and *Brasilibathynellocaris*, whereas *Siolicaris*, *Potamocaris*, *Forficatocaris*, and *Murunducaris* have a shorter basis. Despite the similarities mentioned above between *Brasilibathynellocaris*, *Iticocaris* and *Santaremicaris* gen. nov., to date, there is no strong evidence supporting a close affinity between these genera. Instead, the unique morphology of the P5 intercoxal sclerite and the armature of the P5 itself points to another direction.

Distinguishing characters between S. santaremensis comb. nov. and S. amazonensis sp. nov.

Santaremicaris santaremensis comb. nov. and *S. amazonensis* sp. nov. differ in body length, and the following male characters: a) ornamentation of the basis of P1; b) fine ornamentation of the enp1 of P1; c) fine ornamentation of the P2 enp; d) ornamentation of the coxa and basis of P3; e) shape and ornamentation of the P3 exp1; f) shape and ornamentation of P3 apophysis; g) length and shape of P3 thumb; h) fine ornamentation of P4 enp and exp1; i) fine ornamentation of the P4 exp3; j) shape of the intercoxal process on P5; and k) finally shape and fine ornamentation of P5. For the conditions of each character, see [Tab. 1](#).

FINAL CONSIDERATIONS

It is still premature to say which group of species is closely related to *Murunducaris* and *Santaremicaris* gen. nov. However, as discussed above, there are some shared characters such as the presence of a proximal and distal row of spinules on the inner margin of male P4 exp1 (the latter eventually lost in some *Murunducaris*, *Potamocaris*, and *Pa. aberrans*) that could support a close relationship between *Potamocaris*, *Forficatocaris*, *Murunducaris*, *Santaremicaris* gen. nov., *Pa. fossoris*, *Pa. crassicaudis*, *Pa. nigerianus*, *Pa. jeanninei*, *Pa. kimi*, *Pa. aberrans*, and maybe *Pr. phyllura (incertae sedis)*.

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