REVISION OF THE GENUS *MURUNDUCARIS* (COPEPODA: HARPACTICOIDA: PARASTENOCARIDIDAE), WITH DESCRIPTIONS OF TWO NEW SPECIES FROM SOUTH AMERICA

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ABSTRACT

The genus *Murunducaris*, previously represented by a single species (*M. juneae*) collected in a hillside flush marsh near Brasília, Brazil, is revised here. The description of *M. juneae* is emended. Three additional species are assigned to the genus, and its geographical distribution is considerably expanded. *Murunducaris noodti* n. sp., from the vicinity of Arequipa (Peru), and *M. loyolai* n. sp., from the island of the city of Florianópolis (Santa Catarina, Brazil) are new to science. *Murunducaris dactyloides* (formerly *Parastenocaris dactyloides*), from the Tapajós River, near the city of Santarém (Pará, Brazil) is redescribed and its assignment to this genus is supported by synapomorphies. The diagnosis of the genus *Murunducaris* is emended. The phylogenetic affinities of species of *Murunducaris* to other members of the family are briefly discussed.

KEY WORDS: Copepoda, Harpacticoida, Murunducaris, Parastenocarididae, neotropics, South America

INTRODUCTION

Copepods of the family Parastenocarididae are typical freshwater organisms, being especially well adapted to interstitial life in the hyporheic zones of rivers, as well as to life in continental aquifers. Currently, the family is divided into 29 valid genera, but most of them are not monophyletic groups (Schminke, 1976a). In South America, the family is represented by several endemic groups, of which the most species-rich genera are *Remaneicaris* Jakobi, 1972; *Potamocaris* Dussart, 1979, and *Forficatocaris* Jakobi, 1969 (Corgosinho and Martínez Arbizu, 2005).

Murunducaris Reid, 1994 was proposed to accommodate a new species, *Murunducaris juneae* Reid, 1994, collected in a hillside flush marsh near Brasília, Brazil. Such marshes contain poorly drained hydromorphic soils (Ranzani, 1971) and are flooded up to several months during the rainy season because of the proximity of the groundwater table. These biotopes are widespread in the highlands of central Brazil (Reid, 1993) as well as in other areas of "cerrado" (Brazilian savanna).

Study of the collections of Friedrich Kiefer and Wolfram Noodt as well as examination of new samples taken in southern Brazil revealed the presence of some hitherto undescribed species attributable to the genus *Murunducaris*. This allowed us to revise the genus and provide an emended diagnosis with emphasis on synapomorphies. *Murunducaris juneae* and *M. dactyloides* (Kiefer, 1967) n. comb. are redescribed, and the proposed assignment of *M. dactyloides* n. comb. to *Murunducaris* is justified based on synapomorphies. Additional new species, from near the cities of Florianópolis (state of Santa Catarina, Brazil) and Arequipa (Peru), are described. The phylogenetic position of the genus within the family is briefly discussed.

MATERIALS AND METHODS

Type material of *Murunducaris juneae* was obtained from the collection of the Museum of Zoology of the University of São Paulo (MZUSP), Brazil. Type material of *Murunducaris dactyloides* comb. nov. was obtained from the Kiefer Collection in the Staatliches Museum für Naturkunde in Karlsruhe (SMNK), Germany. *Murunducaris noodti* n. sp. was obtained from the Noodt Collection in the DZMB (Deutsches Zentrum für Marine Biodiversitätsforschung)/ Senckenberg Forschungsinstitut und Naturmuseum, Germany. *Murunducaris loyolai* n. sp. was collected, using the Karaman-Chappuis method (Chappuis, 1942), from the sediments of a temporary lagoon on Joaquina Beach, in the city of Florianópolis, state of Santa Catarina, Brazil; the specimens are deposited in the Carcinological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil.

Adult females and males of *M. loyolai* were dissected in lactic acid and mounted on slides in glycerin. Drawings were made with a Leica DMR microscope, fitted with Nomarski interference contrast optics and a drawing tube, at 400x and 1000x magnification. The lengths of the specimens were measured from the tip of the rostrum to the posterior rim of the anal operculum.

The emended diagnosis represents the reconstructed groundpattern of *Murunducaris*. The term groundpattern is used in the sense of Grundmuster (Ax 1984, p. 156) and refers to all plesiomorphies and autapomorphies present at the stem species of the genus in question.

A table (Table 1) with some characters (presence and absence) that we believe important for the reconstruction of the phylogeny around *Murunducaris* is included for reference.

The terms furca and telson are used according to Schminke (1976b).

Abbreviations used are: A l= antennule, A2 = antenna, Ae = aesthetasc, ap = apomorphy, enp= endopod, exp= exopod, Md = mandible, Mx1 = maxillula, Mx2 = maxilla, Mxp = maxilliped, P1-P5= legs 1 to 5, pl = plesiomorphy.

Systematics

Parastenocarididae Chappuis, 1940 Murunducaris Reid, 1994

Emended Diagnosis.—Parastenocarididae with 8-segmented antennule in male (pl) and 7-segmented antennule in female (pl). Male antennule haplocer (pl). Mandible, maxillula and

Table 1. List of some important character mentioned in the text and respective taxa on which they occur. CSL4 = Cuneiform spinules on the proximal inner margin of exp1 of leg 4; SSL5 = Strong proximal spine of leg 5; DSL1 = Dimorphic inner basal spinule of leg 1; IPL5 = Intercoxal sclerite process of leg 5; PSL4 = Posterior outer spine of exp1 of leg 4; HIL5 = Hypertrophied intercoxal sclerite of leg 5; HSL5 = Hypertrophied distal spine of leg 5; RFS = Reduced furcal seta II; LSL5 = Loss of proximal spine of leg 5. "X" indicates where the character is present; interrogation sign indicates where the character is unknown.

Таха	CSL4	SSL5	DSL1	IPL5	PSL4	HIL5	HSL5	RFS	LSL5
Murunducaris juneae	Х	Х	Х	Х	Х	Х	Х	Х	
M. loyolai sp. nov.	Х	Х	Х	Х	Х	Х	Х	Х	
M. noodti sp. nov.	Х	Х	Х	Х	Х	Х	Х	Х	
M. dactyloides comb. nov.	Х	Х	Х	Х	Х	Х	Х	Х	
P. santaremensis			Х	Х	Х	Х	Х	Х	
Parastenocaris sp. aff P. santaremensis			Х	Х	Х	Х	Х	Х	
P. fossoris					Х	Х	Х	Х	
P. crassicaudis					?	?	?	?	
Brasilibathynellocaris								Х	Х
P. itica								Х	Х
Siolicaris								Х	Х

maxilliped as in *M. loyolai* n. sp., not diverging from the groundpattern proposed for the family (Corgosinho et al. 2007a). Maxilla with 2 endites, proximal endite with 1 seta (pl), distal endite with 3 elements (pl), one of them transformed into a serrated spine (pl). Basis of leg 1 with sexually dimorphic spinule on inner margin (pl); endopod not sexually dimorphic (pl). Leg 2 endopod sexually dimorphic, stronger in males (pl). Leg 3 of males with proximal hump on inner margin (pl) and an apophysis ending in a claw (pl). Leg 4 of males with a long and lamelliform endopod (ap?), serrated on inner margin (ap?); outer spine of exp-1 inserted on posterior side of the segment (pl). Inner margin of exp-1 of leg 4 of males with proximal row of tiny, conical spinules (ap). Leg 5 with strong sexual dimorphism (pl), in male formed by a quadrate plate (ap), fused at base with intercoxal sclerite (ap), with hypertrophied distal spine (ap?) and strong proximal spine (ap); intercoxal sclerite strongly developed (pl), with process on ventral midline (pl). Furca with all 3 anterolateral setae located proximal to dorsal seta (pl).

Type Species.—*M. juneae*. Additional species: *M. loyolai* sp. nov., *M. dactyloides* comb. nov., and *M. noodti* sp. nov.

Murunducaris juneae Reid, 1994

An emended description of *M. juneae* is provided, based on direct observation of the type material.

Male, holotype, MZUSP 10470.— As described by Reid (1994), with the following modifications. Well-developed integumental windows on cephalothorax and 2nd, 3rd, 4th, and 5th urosomites. A1 with 8 segments (Fig. 1A); armature, beginning with proximal segment: 0/6/4/2/5+Ae/3/2/9+Ae. Mouthparts as described for *M. loyolai* sp. nov. Leg 1 basis with strongly developed inner spinule (Fig. 1B). Leg 3 (Fig. 1C) apophysis with curved distal spine, not incorporated into the segment. Leg 4 (Fig. 1D, D') with endopod outwardly curved (serrated margin turned toward outer margin). Leg 5 (Fig. 1E) with proximalmost spine strongly developed (arrowed). Female. As in original description.

Murunducaris loyolai n. sp.

Type Material.—Holotype, male dissected and mounted on seven slides (INPA 1514); allotype, female dissected and mounted on seven slides (INPA 1515).

Etymology.—The species is named in homage to Prof. Dr. Jaime de Loyola e Silva.

Type Locality.—Interstitial in sediments of a temporary lagoon on the beach of Joaquina, Florianópolis (27°37′05″S; 48°27′17″W).

Male (Fig. 2A, B).-Length 320 µm. Rostrum not fused to cephalothorax, with wide base and 2 sensilla on tip. For pattern of sensilla on somites see Figs. 2A, B. Dorsal pores on cephalothorax, 1st and 3rd thoracic somites and 1st to 4th urosomites (Fig. 2B). Lateral pore on telson (Fig. 2A). Cephalothorax and 2nd to 5th urosomites with dorsal integumental windows (Fig. 2A, B). Telson smooth, anal operculum smooth and convex (Fig. 2A, B). Furca (Fig. 2A, B) with 7 setae; setae I, II, and III located on proximal third, anterior to dorsal seta. A1 8-segmented and prehensile (Fig. 3A); armature, beginning with proximal segment: 0/6/4/2/ 5+Ae/3/2/9+Ae. A2 (Fig. 3B) with allobasis; 1-segmented exopod with 1 seta, and 1-segmented endopod bearing 7 setae. Mouthparts armature as follows: Md (Fig. 3C, D) with a coxal gnathobasis bearing 1 seta and a palp with 2 setae; Mx1 (Fig. 3E, F) with a praecoxal arthrite bearing 5 elements (1 dorsal surface seta, 3 claw-like pinnate spines and 1 slender seta), coxa with 1 seta and basis with 3 setae; Mx2 (Fig. 3G) with one setae on proximal endite, distal endite with 2 slender setae and pinnate spine, endopod with 2 setae; Mxp (Fig. 3H) 3-segmented, distal segment with 1 claw-like seta. Leg 1 (Fig. 4A) coxa unarmed, with proximal row of small spinules on its anterior side and posterior row of larger spinules distally on posterior margin; basis with outer seta, outer row of spinules, strong spinule on inner margin (arrowed), and distal row of small spinules, between endopod and exopod; first endopod segment same size as first 2 exopod segments together; exopod 3-segmented, exp-1 with outer spine, exp-2 unarmed, exp-3 with 2 outer spines and 2 geniculate setae; endopod 2-segmented, enp-1 with 2 large spinules on outer margin, enp-2 with outer spine and geniculate seta. Leg 2 (Fig. 4B) coxa unarmed, with posterior row of spinules on its outer margin; basis without outer seta and ornamented with row of spinules on outer margin; exopod 3-segmented, exp-1 with long outer spine and with hyaline frill on inner margin; exp-2 without armature and with row of spinules of unequal sizes on its



Fig. 1. Male of *Murunducaris juneae* Reid, 1994. Holotype, MZUSP 10470. Antennule (A), leg 1 (B), leg 3 (C), leg 4 (D and D'); D' shows the coxa and basis of the right leg, and D shows the entire leg with a damaged protopod; leg 5 (E). Scale = $25 \mu m$.



Fig. 2. Male of Murunducaris loyolai n. sp., holotype, INPA 1514. A, lateral; B, dorsal. Scale = 100 $\mu m.$



Fig. 3. Male of *Murunducaris loyolai* n. sp., holotype, INPA 1514. A, antennule; B, antenna; C, mandible in posterior view, D, mandible in anterior view; E, maxillula in anterior view; $(\Phi = \cos a \text{ of maxillula}; \Psi = \text{basis of maxillula})$, F, maxillula gnathobasis in posterior view; G, maxilla; H, maxilliped. Scale = 20 μ m.



Fig. 4. Male of *Murunducaris loyolai* n. sp., holotype, INPA 1514. A, leg 1 (arrow indicate the transformed spinule on the inner margin of the basis), B, leg 2; C, leg 3; D, leg 4, E-G, leg 5, E, Posterior margin of leg 5, showing the limbs apart from each other and at the midline, the keyhole-like process, F, anterior margin of the right limb, showing the exact position of setae and spines, G, anterior view of leg 5, showing limbs in resting position. Scale = 20 µm.

distal portion; exp-3 with 3 setae, distal hyaline frill on inner corner, and row of long spinules on outer margin; endopod 1-segmented, with distal seta and anterior row of spinules. Leg 3 (Fig. 4C) coxa unarmed, with anterior row of spinules; basis with outer seta and row of stout spinules on its anterior margin, next to outer margin; endopod represented by spine; exopod straight, inner margin with proximal protrusion and medial concavity; thumb represented by strong spine; apophysis shorter than thumb and ending in curved spine. Leg 4 (Fig. 4D) coxa unarmed, with posterior row of spinules on outer margin; basis with outer seta and outer pore and distal spinule between endopod and exopod; exopod 3-segmented, exp-1 with outer spine inserted on posterior side, proximal row of 3 small spinules on inner margin, and row of distal setules on inner margin; exp-2 without armature and with row of distal spinules (smaller on inner margin); exp-3 with 2 setae and row of distal spinules on outer margin; endopod lamelliform, outwardly curved, outer margin with serrated lamella and subterminal row of setules; endopod with hump on distal third of inner margin, and 2 subdistal spinules. Leg 5 (Fig. 4E, F, G) quadrate, fused to intercoxal sclerite, with outer seta and 3 distal elements; distalmost spine hypertrophied and appearing as cuneiform process; proximalmost seta developed as strong spine, normally hidden behind distal spine and leg 5 plates; intercoxal sclerite strongly developed, with medial process similar in outline to a keyhole, and also with medial spinule set posteriorly to this process.

Female (Fig. 5A, B).-Length 340 µm. Rostrum not fused to cephalothorax, with wide base and 2 sensilla on its tip. For pattern of sensilla on somites see Fig. 5A, B. Dorsal pores on cephalothorax, 2nd and 3rd thoracic somites, and 1st to 3rd urosomites (Fig. 5B). Lateral pore on telson (Fig. 5A). Cephalothorax and 2nd to 4th urosomite with dorsal integumental windows (Fig. 5A, B). Telson smooth, anal operculum smooth and convex (Fig. 5A, B). Furca as in male. A1 7-segmented (Fig. 5C); armature beginning with proximal segment: 0/4/5/2+Ae/1/1/9+Ae. A2, Md, Mx1, Mxp, and Mx2 as in male. Leg 1 (Fig. 6A) coxa unarmed, with anterior row of small spinules, and 2 posterior rows of larger spinules; basis with outer seta, outer row of spinules, row of spinules on inner margin, and distal row of small spinules between endopod and exopod; enp-1 as long as first 2 exopodal segments; exopod 3-segmented, as in male; endopod 2-segmented, enp-1 with 2 pairs of large spinules on outer margin, enp-2 as in male. Leg 2 (Fig. 6B) coxa unarmed, with anterior row of spinules on its proximal portion and posterior row of spinules on outer margin; basis without outer seta and ornamented with 1 row of spinules on outer margin and 1 row on inner margin; exopod 3-segmented, as in male; endopod 1-segmented, with long distal seta, 2 adjacent spinules, and 2 anterior spinules. Leg 3 (Fig. 6C) coxa unarmed, with 1 pair of spinules on posterior margin; basis with outer seta and 3 spinules between it and exopod; endopod small, with 1 subdistal seta; exopod 2-segmented, exp-1 with outer spine and 3 distal spinules on inner margin, exp-2 with 2 setae. Leg 4 (Fig. 6D) coxa unarmed, with anterior row of spinules on its proximal margin and outer row of spinules posteriorly inserted; basis with outer seta and outer pore; exopod

3-segmented, exp-1 with outer spine inserted posteriorly; exp-2 without armature and with row of distal spinules; exp-3 with 2 terminal setae and row of distal spinules on outer margin; endopod with strong distal spine, 2 subdistal spinules, and 1 anterior spinule. Leg 5 (Fig. 6E) trapezoidal, not fused at base with intercoxal sclerite, with inner row of spinules; all 4 setae inserted on outer margin, distalmost seta stoutest. Genital field as in Fig. 6E. Genital operculum U-shaped (Fig. 6E).

Murunducaris noodti n. sp.

Parastenocaris arequipensis n. sp. Noodt, 1969: 669-671, Fig. 7.

Type Material.—Syntypes; male and female on the same slide preparation (Noodt Collection in DZMB/Senckenberg, labeled M6-5.

Etymology.—The species is named in homage to the German copepodologist and collector, Dr. Wolfram Noodt. Noodt labeled this slide as "*Parastenocaris arequipensis*," and mentioned the name in a general article on biogeography (Noodt, 1969); however, he never published a species description. As a nomen nudum, this name is not available according to Articles 8 and 11 of the ICZN (1999). We take this opportunity to express our debt for his extensive collections and studies on South American parastenocaridids.

Type Locality.—No special annotations were made on the slide, or given by Noodt (1969). Probably, as indicated by the name originally written by Noodt on his slide preparations and the circle indicating the collection locality on the map in Fig. 7 of Noodt (1969), this species comes from Arequipa, Peru, or its vicinity.

Male.-Length 445 µm. Telson smooth, anal operculum smooth and convex (Fig. 9E). Furca (Fig. 9E) with 7 setae; setae I, II, and III located on distal third, at level of dorsal seta. A1 8-segmented and prehensile (Fig. 7A); armature beginning with proximal segment: 0/6/4/2/5+Ae/3/2/9+Ae. A2 and mouthparts as in M. loyolai. Leg 1 (Fig. 7B) coxa unarmed; basis with a distal row of spinules, between endopod and exopod and a strong spinule on inner margin, inserting beneath an anterior basal process; exp-1 as long as first 2 exopod segments; exopod 3-segmented, as in M. loyolai; endopod 2-segmented, enp-1 with 2 pairs of large spinules on outer margin, enp-2 with 2 spinules on proximal portion and 2 spinules distally inserted. Leg 2 (Fig. 7C) coxa unarmed; basis without outer seta and ornamented with row of spinules on outer margin; exopod 3-segmented, exp-1 with long outer spine and hyaline frill on inner margin; exp-2 without armature and with distal row of spinules; exp-3 with 3 setae, hyaline frill on inner distal corner, and row of long spinules on outer margin; endopod 1-segmented, with distal seta, 2 distal spinules, and row of spinules on outer distal margin. Leg 3 (Fig. 8A) coxa unarmed, with posterior transverse row of spinules; basis with outer seta and row of spinules distal to it; endopod not observable, probably represented by single seta or spine; exopod inwardly curved, inner margin with proximal hump, outer margin with proximal row of spinules and 2 additional distal spinules; thumb represented by strong spine; apophysis shorter than



Fig. 5. Female of *Murunducaris loyolai* n. sp., allotype, INPA 1515. A, lateral view of habitus; B, dorsal view of habitus; C, antennule. A and B, Scale $1 = 100 \ \mu m$; C, Scale $2 = 20 \ \mu m$.



Fig. 6. Female of *Murunducaris loyolai* n. sp., allotype, INPA 1515. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, ventral view of the somite bearing leg 5 and the genital double-somite showing the U-shaped genital operculum. Scale = $20 \mu m$.



Fig. 7. Male of *Murunducaris noodti* n. sp., syntype, Noodt Collection (M6-5). A, antennule; B, leg 1; C, leg 2 (Ω, incompletely illustrated inner seta; 'Ω, full inner seta). Scale= 20 µm.



Fig. 8. Male of *Murunducaris noodti* n. sp., syntype, Noodt Collection (M6-5). A, leg 3 (arrow indicates the transformed distal seta of the apophysis); B, leg 4; C, leg 5 in lateral view. Scale = $20 \mu m$.

thumb, ending in long curved spine (arrowed), about three times as long as apophysis. Leg 4 (Fig. 8B) coxa unarmed; basis with outer seta and outer pore, distal margin with long spinule between endopod and exopod; exopod 3-segmented, exp-1 with outer spine inserted posteriorly and proximal row of 9 tiny spinules on inner margin, but no setules, spinules, or hyaline frill on inner corner; exp-2 without armature and with row of distal spinules; exp-3 with 2 terminal setae and row of spinules on outer distal margin. Leg 5 (Fig. 8C) quadrate, fused to intercoxal sclerite, with an outer seta and 3 distal elements; distalmost spine hypertrophied, appearing as a bulb with a distal crown; proximalmost seta developed as a strong spine; intercoxal sclerite strongly developed, ornamented with a medial process similar to that found in *M. juneae*.

Female.—A1 as in female of *M. loyolai* A2, mouthparts, telson, and furca as in male, leg 1 and leg 2 as in male. Leg 3 (Fig. 9B) much as in M. loyolai sp. nov. but with short endopod, 1-segmented, with small distal spine and tiny subdistal spinule. Leg 4 (Fig. 9C) coxa unarmed; basis with outer seta and outer pore; exopod 3-segmented, exp-1 with outer spine and distal row of spinules on inner corner; endopod 1-segmented, with row of 3 spinules near insertion of terminal spine (it is difficult to discern whether this "spine" is incorporated into the segment). Leg 5 (Fig. 9A) trapezoidal, with all 4 setae set on outer margin. A distinct form of *M. noodti* sp. nov. was also collected by Noodt in the same locality. Noodt labelled it as a subspecies of Parastenocaris arequipensis, viz., P. arequipensis phyllophora. However it is identical to the "typica" form, differing only in the shape of the furca (Fig. 9D). Herein we refer to it as a variety and not as a subspecies, postulating that it may be an ecotype.

Murunducaris dactyloides (Kiefer, 1967) n. comb.

Parastenocaris dactyloides Kiefer, 1967: 131-133, Abb. 1-14. Remaneicaris dactyloides Jakobi, 1972: 142, Tab. I.

Type Material.—In his original description, Kiefer (1967) mentioned that the type material was deposited in his collection or in the biological collection of the National Institute for Amazonian Research (INPA, Brazil). However, none of this material was ever sent to INPA, and it is now located in the Kiefer Collection at the Staatliches Museum für Naturkunde in Karlsruhe (SMNK), Germany.

Holotype.—Dissected male, mounted on two slides, labeled with the numbers 7465 and 7466. Allotype: undissected female labeled with the number 7475. Paratypes: undissected males mounted on three different slides, labeled 7467, 7915, and 7917.

Type Locality.—Interstitial groundwater of a sandy beach of the Tapajós River near the city of Santarém, state of Pará, Brazil. See Kiefer (1967) for further details.

Male.—Length 360 μ m. Rostrum not fused to cephalothorax, with a wide base and 2 sensilla on the tip. Cephalothorax and 2nd to 5th urosomite with dorsal integumental windows. Telson with 2 strong spinules inserted ventrally next to midline; anal operculum smooth and convex (Fig. 10B). Furca (Fig. 10B) with 7 setae; setae I, II, and III located on proximal third, anterior to dorsal seta. A1 8-segmented and prehensile (Fig. 10A); armature, beginning with proximal segment: 0/6/4/2/5+Ae/3/2/9+Ae. A2 and mouthparts as in M. loyolai. Leg 1 (Fig. 11A) coxa unarmed; basis with outer seta, outer row of spinules, strong spinule on inner margin, and distal row of small spinules between endopod and exopod; enp-1 as long as first 2 exopods; exopod 3-segmented, exp-1 with outer spine, exp-2 unarmed, exp-3 with 2 outer spines and 2 geniculate setae; endopod 2-segmented, enp-1 with 2 rows of spinules on outer margin, enp-2 with outer spine and geniculate seta. Leg 2 (Fig. 11B) coxa unarmed, with anterior row of spinules; basis without outer seta and ornamented with row of spinules on outer margin; exopod 3-segmented, exp-1 with long outer spine and hyaline frill on inner corner; exp-2 without armature and with distal row of spinules of unequal size; exp-3 with 3 setae, hyaline frill on inner distal corner, and row of long spinules on outer margin; endopod 1-segmented, slightly dimorphic, with distal seta, 2 distal spinules, and row of spinules on outer margin. Leg 3 (Fig. 11D) coxa unarmed; basis with outer seta and anterior row of strong spinules on outer margin; endopod represented by spine; exopod inwardly curved, proximal third with hump on inner margin; outer margin with row of spinules on proximal third; thumb represented by short spine; apophysis longer than thumb and ending in curved spine. Leg 4 (Fig. 11C) coxa unarmed, with 2 strongly developed spinules inserted on anterior side, next to inner margin; basis unarmed and with modified spinule near endopod insertion; exopod 3-segmented, exp-1 with outer spine inserted posteriorly and proximal row of 6 small spinules on inner margin; exp-2 without armature and with row of distal spinules; exp-3 with 2 setae and distal row of spinules on outer margin; endopod lamelliform, straight, outer margin serrated. Leg 5 (Fig. 11E, F) quadrate, fused to intercoxal sclerite, with an outer seta and 3 distal elements; distalmost spine hypertrophied, appearing as rectangular process when relaxed (with distal protuberance similar to a mandibular "cutting" edge); proximalmost seta also developed as strong spine, but normally hidden by distal spine and leg 5 plates; intercoxal sclerite strongly developed, ornamented with median spiniform process.

Female.-Length 370 µm. Rostrum not fused to cephalothorax, with wide base and 2 sensilla on tip. Cephalothorax and 2nd to 4th urosomite with dorsal integumental windows. Telson, furca, A2, mouthparts, and leg 1 (Fig. 12A) as in male. A1 7-segmented, as in female of M. loyolai sp. nov. Leg 2 (Fig. 12B) exopod as in male; endopod with distal seta, 2 distal spinules, and 2 subdistal spinules on outer margin. Leg 3 (Fig. 12C) coxa unarmed; basis with outer seta and 3 spinules below it; endopod small, armed with 1 subdistal "spine"; exopod 2-segmented, exp-1 with outer spine and 3 spinules distally inserted on inner corner, exp-2 with 2 setae. Leg 4 (Fig. 12D) coxa unarmed, with anterior row of spinules; exopod 3-segmented, exp-1 with outer spine and distal row of 4 spinules around inner margin; exp-2 without armature and with row of distal spinules; exp-3 with 2 setae and 3 distal spinules on outer margin; endopod 1-segmented, with 2 spinules, probably



Fig. 9. *Murunducaris noodti* n. sp., female, syntype, Noodt Collection (M6-5). A, leg 5 (A); B, coxa, basis and first exopod segment of leg 3; C, coxa, basis and first exopod segment of leg 4; D, lateral view of telson with a transformed, leaf-shaped furca; E, lateral view of male telson, with a normal furca. Scale = $20 \mu m$.



Fig. 10. Male of *Murunducaris dactyloides* (Kiefer, 1967) n. comb., holotype. A, antennule (Kiefer Collection No. 7465, SMNK); B, ventral view of telson (Kiefer Collection No. 7466, SMNK). Scale 1, Fig. A = $25 \ \mu m$; Scale $2 = 100 \ \mu m$, Fig. B.



Fig. 11. Male of *Murunducaris dactyloides* (Kiefer, 1967) n. comb., holotype (Kiefer Collection No. 7465, SMNK). Leg 1 (A), leg 2 (B), leg 3 (C); leg 4 (D, Kiefer Collection No. 7465, SMNK), ventral view of leg 5 (Kiefer Collection No. 7466, SMNK) showing the limbs in resting position (F) and the posterior side of the right limb (E). Scale = $20 \mu m$.



Fig. 12. Female of *Murunducaris dactyloides* (Kiefer, 1967) n. comb., allotype (Kiefer Collection No. 7475, SMNK). Leg 1 (A), leg 2 (B), leg 3 (C), leg 4 (D) and ventral view of the somite bearing leg 5 and genital double-somite showing the U-shaped genital operculum (E). Scale = $20 \mu m$.

indicating region of insertion of missing distal seta. Leg 5 (Fig. 12E) trapezoidal, with all 4 setae inserted on outer margin. Genital field as illustrated in Figure 12E. Genital operculum U-shaped (Fig. 12E).

DISCUSSION

The two new species described here differ from each other and from *M. juneae* and *M. dactyloides* by the following characters of the males: shape of leg 3; lengths of the apophysis, claw, and thumb; size of the spinule between the exopod and endopod of leg 4; shape of the endopod of leg 4; number of spinules on the proximal region of the inner margin of the exp-1 of leg 4; shape of the distal spinule of leg 5; and shape of the intercoxal sclerite process of leg 5.

In accordance with Corgosinho et al. (2007a), the mouthparts seem to be very conservative within parastenocaridids. For example, Md, Mx1 and Mxp are quite similar and small differences do not involve changes in number of setae and spines (Corgosinho et al. 2007a). Reid (1994) reported 2 setae on the proximal syncoxal endite of Mx2 present in *M. juneae*. This condition can be observed in all *Remaneicaris* species, and was also described for *P. ahaggarica* Bozic, 1978. However, observation of the type material of *M. juneae* revealed that this species has only one seta on the first syncoxal endite, as observed for most of the species within the family and illustrated for *M. loyolai* (Fig. 3G).

According to Reid (1994), the principal diagnostic features of the genus Murunducaris are: "the posterior insertion of the spiniform setae in both sexes (sc. on the first segment of the exopod of leg 4; authors' amendment) and, in the male, the fifth leg with massive, fused basipods, each with a large subconical terminal spine and the posteriorly recurved process located on the ventral midline of the basis." Observations of other species now assigned to Murunducaris [M. dactyloides (Kiefer, 1967), M. noodti, and M. loyolai] as well as of other closely related species outside the genus, such as Parastenocaris santaremensis Noodt, 1963, P. fossoris Fryer, 1956, and P. crassicaudis Chappuis, 1955 (Corgosinho, personal observation), revealed that some of the diagnostic characters proposed by Reid (1994) are, in fact, plesiomorphies. Although they cannot be used to define a monophyletic group around M. juneae, these plesiomorphies were very informative in a more inclusive analysis, helping us to propose a more robust hypothesis about the phylogenetic position of the genus Murunducaris within Parastenocarididae. The assignment of *M. dactyloides* (Kiefer, 1967) to *Remaneicaris* by Jakobi (1972) was not supported by Corgosinho and Martínez Arbizu (2005). This species does not have the typical autapomorphies proposed for this genus, such as the lack of an intercoxal sclerite on leg 5 and a subdistal seta on the outer margin of leg 4 exp-3. Rather, it shares with its congeners in Murunducaris the potential autapomorphies outlined above in the extended diagnosis of the genus.

One interesting character, not previously observed, is the presence of a strong spinule on the inner margin of the basis of leg 1 of males. It is present not only in the species of *Murunducaris*, but also in *P. santaremensis* (Fig. 13A) and in a new species close to *P. santaremensis* (recently discovered by the first author in the Rio Negro, Amazon

basin). This inner dimorphic spinule of Murunducaris and P. santaremensis may well be confused with a spiniform seta, homologous to the dimorphic seta present in ameirids. However, under optical microscopy, this structure appears compact, without an inner duct that is evidenced by the presence of a cuticular layer on the margins of spines and setae. Moreover, it inserts anteriorly on the inner margin of the basis, emerging from the outer surface of the cuticle and not passing through an orifice in the integument. Additionally, observation of the type species of the genus Murunducaris as well as of the other species studied for this report has revealed that, in males, a supplementary ornamentation is present near the insertion of the dimorphic spinule (one on each side of the dimorphic spinule in M. loyolai and M. dactyloides); whereas in the females, only a row of small spinules and no seta in the corresponding position can be observed. A different condition can be observed in the male of another species closely related to P. santaremensis (here Parastenocaris sp. aff. P. santaremensis) found in the Noodt collection (Fig. 13B). In this species, the ornamentation of the inner margin of the basis of leg 1 is not composed by a strong dimorphic, cuneiform spinule followed by untransformed spinules, but occurrs in this species as a single row of 6 strong spinules on the inner margin of leg 1. Since there is no homology between spines and spinules, as previously supposed by Galassi and De Laurentiis (2004) for Forficatocaris and at least P. bidens (Noodt, 1955) (cf. Ahnert, 1994) within the genus Potamocaris, thus the presence of only spinules on the inner margin of the basis of leg 1 of Parastenocaris sp. aff. P. santaremensis and Murunducaris females leads us to assume that the condition observable in males of Murunducaris is not necessarily a dimorphic spine or seta, but a dimorphic spinule.

The presence of a seta on the inner margin of the basis of leg 1 and its supposed secondary loss in some independent lineages within Parastenocarididae was used by Galassi and De Laurentiis (2004) as a working hypothesis to explain the presence of this structure within the family. Indeed, this structure has been observed in several species of Parastenocarididae from different evolutionary lineages. For example, Corgosinho et al. (2007a and b) described an inner seta on the basis of leg 1 of R. ignotus (Dussart, 1983). Corgosinho et al. (2007a and b) observed that the condition present in this species is in the groundpattern of the family, and should be interpreted as a plesiomorphy. In other members of Parastenocarididae it can be seen, in accordance with Galassi and De Laurentiis (2004), in some species that are not closely related, e.g., P. tumida, P. mangyans Bruno and Cottarelli, 1999, P. silvana Cottarelli, Bruno and Berera, 2000, P. corsica Cottarelli, Bruno and Berera, 2000, P. ranae Stoch, 2000, P. federici Stoch, 2000 and P. trichelata Reid, 1995. To these species we add here P. hippuris Hertzog, 1938, P. vicesima Klie, 1935 (Corgosinho, personal observation), P. inferna Schminke, 1971, P. glareola Herzog, 1936, P. aedes Hertzog, 1938 and P. ursulae Schminke, 1971. All these species belong to a larger, monophyletic group that is characterized, among other features, by the presence of a transformed penultimate segment on A1 of males (Schminke 1993). Murunducaris,



Fig. 13. Leg 1 (A), leg 4 (C) and leg 5 (E) of *Parastenocaris santaremensis* (Noodt collection Mappe 2, slide 6). Leg 1 (B) and leg 4 (D) of *Parastenocaris* sp. "aff. *santaremensis*" (undescribed species; Noodt collection Mappe 2, slide 6). Scale = $20 \mu m$.

however, belongs to a distantly related monophyletic group around the fontinalis-group Lang, 1948 (sensu Martínez Arbizu, 1997). Within this group, no other species has been described with a similar spiniform or setiform element on the inner margin of the basis of leg 1. In view of the evidences offered above, a better hypothesis would be to consider the inner seta on the basis of leg 1 as a plesiomorphic character, being lost in the stem line of a larger monophyletic group around the *fontinalis*-group. Additionally, even within the species listed by Galassi and De Laurentiis (2004) and the others added by us in this work, it seems that an inner seta appears in other, less closely related species. This scattered occurrence does not provide strong support for the idea that a seta on the inner margin of the basis of leg 1 has been lost independently within the family. Also, since we cannot base our hypothesis on the assumption that most researchers overlooked this seta in the past, it is more parsimonious to assume that it has arisen independently within the family.

All the species of Murunducaris have a more or less pronounced dimorphism in the endopod of the leg 2 of males. This condition is more developed in M. juneae, M. loyolai, and M. noodti, appearing in M. juneae as a foliaceous structure. In M. dactyloides, it is less conspicuous. A similar kind of sexual dimorphism can also be seen, for example, in species of Brasilibathynellocaris Jakobi, 1972, Parastenocaris itica Noodt, 1962, P. santaremensis, P. fossoris, P. crassicaudis (Corgosinho, personal observation), and in the species close to P. fontinalis, e.g., P. hispanica Martínez Arbizu, 1997. Other species of South American parastenocaridids, such as Siolicaris jakobii (Noodt, 1963), S. siolii (Noodt, 1963) (Corgosinho, personal observation), and the species belonging to the genera Potamocaris and Forficatocaris (Ahnert, 1994) do not have this character. This condition seems to be present also in the *columbiensis*-group of Noodt (1972), but this is difficult to evaluate and needs to be reinvestigated. It is interesting that some of the species that have a dimorphic leg 2 endopod also have a reduced seta II on the furca, i.e., Brasilibathynellocaris, Murunducaris, P. itica, P. santaremensis and P. fossoris, which is sometimes difficult to see, or even absent (Brasilibathynellocaris and P. itica). However, a less reduced seta II on the furca seems to be present in the group around *P. fontinalis*; whether this seta is reduced in P. crassicaudis is unclear. It is difficult to say if the dimorphism of leg 2 endopod is a character that can define a monophyletic group within the family; however, it may define some monophyletic units within the South American parastenocaridids. For example, within the species that have a reduced seta II on the furca, e.g., species of Brasilibathynellocaris, Murunducaris, Siolicaris, Parastenocaris jakobii, P. itica, and P. santaremensis, there is a group of species that have lost the distal seta on the male leg 5, viz., Brasilibathynellocaris, Siolicaris, and P. itica. Within this group, Brasilibathynellocaris and P. itica show sexual dimorphism in the male leg 2 (sharing very similar morphology of the male leg 3). However, the leg 4 structure of Brasilibathynellocaris and the lack of sexual dimorphism in the leg 4 endopod of males of P. itica raise doubts about the monophyletic condition of a group formed by P. itica

plus *Brasilibathynellocaris*. On the other hand, *Murunducaris*, *P. santaremensis*, and the African species *P. fossoris* and *P. crassicaudis* also have a dimorphic leg 2 endopod. These species show some interesting homologies, which are probably good synapomorphies. From the information presently available, it is difficult to establish whether dimorphism in the endopod of leg 2 may have appeared several times, or whether it has been lost several times within the family.

The leg 3 of the male of *M. loyolai* is very similar to the corresponding leg of *M. juneae*, appearing as a strong exopod, nearly straight, with a medial concavity, a short apophysis (not reaching the distal edge of the thumb), and armed with a short, curved claw. In both *M. dactyloides* and *M. noodti* the exopod appears as a slender appendix, but differs in the size of the thumb, apophysis claw is short and the short thumb does not extend beyond the proximal third of the apophysis; in *M. noodti*, the apophysis is shorter than the thumb, and the apophysis claw is about half the length of the exopod.

A proximal hump on the inner margin of the male leg 3 is present in all species of Murunducaris. Within South America, this character has been observed only in members of Murunducaris and of the columbiensis-group (Parastenocaris sensu lato; for definition of Parastenocaris sensu stricto see Reid, 1995). Outside South America, in a group more closely related to Fontinalicaris Jakobi, 1972, this character is present at least in the species around P. fontinalis, P. aquaeductus Chappuis, 1925 (see Delamare-Deboutteville, 1958), P. kabyloides Enckell, 1965 and species around it, P. torokae Pónyi, 1957, and P. lacustris Chappuis, 1957. This character seems to be present also in some other species not closely related to the species mentioned above, most of them belonging to the minutagroup, genus Parastenocaris sensu lato. According to Martínez Arbizu (1997), the sister group of the fontinalisgroup is formed, probably, by the species around P. aquaeductus plus P. kabyloides, but there is no evidence that this group formed by P. aquaeductus plus the species around P. kabyloides and P. fontinalis form a monophylum with Murunducaris. The same can be said when we consider the columbiensis-group and the species P. torokae and P. *lacustris*. It is more probable that this proximal hump is a symplesiomorphy, or has appeared independently, being a character of low phylogenetic signal. In fact, as was mentioned above, Murunducaris seems to be more related phylogenetically to P. santaremensis, P. crassicaudis, and P. fossoris, with which it shares a hypertrophied leg 5 intercoxal sclerite and probably a hypertrophied distal spine on leg 5. Within this group, only Murunducaris has a distal claw on the leg 3 apophysis (a plesiomorphic character within Parastenocarididae), whereas the species close to P. santaremensis as well as P. crassicaudis and P. fossoris share the more advanced condition.

The posterior insertion of the outer spine of exp-1 of leg 4 was considered a very important diagnostic character for the genus by Reid (1994). This character is also present in *P. santaremensis* (Fig. 13C) and *P. fossoris* (Corgosinho personal observation); its presence in *P. crassicaudis* needs

to be checked. Our hypothesis is that this structure evolved prior to the origin of the South American *Murunducaris* species, and thus cannot be used to justify the monophyletic condition of this genus, at least if we consider as *Murunducaris* only those species whose males have a quadratic leg 5 basi-endopod with a strong proximal spine near the outer basal seta and a hypertrophied distal spine not fused to the basoendopod (*M. dactyloides, M. noodti, M. loyolai*, and *M. juneae*).

One of the most striking characteristics of the genus Murunducaris is the presence of a large, subconical, terminal spine on the leg 5 of males. In the species that compose this genus, this spine seems not to be incorporated into the segment, despite the original description of Reid (1994), that this structure was continuous with the subjacent limb. This kind of transformation is unique to Murunducaris. However, observation of the leg 5 of P. santaremensis (and undescribed species around it; Fig. 13E), P. crassicaudis, and P. fossoris revealed a very interesting condition. For example, in *P. fossoris* the distal margin of the leg 5 is represented by a very ornamented triangular region (Fischer 1998; p. 40, fig. 15A and p. 44, plate 1C, D), and on the outer margin, there are only two setae between this "ornamented structure" and the articulated setae of the basis. No conspicuous suture occurs between this "ornamented process" and the rest of the limb. In P. crassicaudis (see Fischer 1998; p. 66, fig. 30A, B), a strong spine appears on the distal margin of leg 5, but a clear suture indicates the point of insertion of this spine. In P. santaremensis (Fig. 13E), there are only two setae on the outer margin, between a triangular process and the articulated setae of the basis. If it is proved that this triangular process is a hypertrophied distal spine that later fused to the segment; a condition similar to that seen in *P. fossoris*, the non-fused condition found in Murunducaris should therefore be considered a plesiomorphy, and the hypertrophy of the distal spine, a synapomorphy for a taxon formed by *Murunducaris*, plus P. santaremensis (and the species around it) and at least P. fossoris. The condition observed in P. crassicaudis can be interpreted as plesiomorphic. However, further study is necessary to assess whether this is the result of character reversion, since we believe that the presence of a upwardly curved spinule on the inner margin of the enp-1 of leg 1 of the male of P. crassicaudis (Fischer 1998: p. 64, fig. 28A) and P. fossoris (Fischer 1998: p. 36, fig. 11A) is a very good synapomorphy for these species.

A final characteristic feature of *Murunducaris* is the presence of a proximal row of conical spinules on the inner margin of the exp-1 of the leg 4 of males. In other species of this family, a similar ornamentation appears in different locations along the inner margin of exp-1 of leg 4. However, it seems that most of these ornamentations are not homologous. For example, in *M. dactyloides* and *M. noodti* the exp-1 of the leg 4 of males has no hyaline frill, and a row of conical spinules appears in the proximal region. In *Brasilibathynellocaris*, some species have an anterior row of strong spinules on exp-1 of the leg 4 of males, and no hyaline frill. A subdistal row of strong spinules occurs also in the *fontinalis*-group (sensu Martínez Arbizu, 1997), while a distal row of spinules can be seen also in the group around

P. kabyloides and P. aquaeductus. In view of these facts, one might imagine that these spinules, in the different genera, are a modified hyaline frill. However, both M. juneae and M. loyolai clearly have an inner hyaline frill, evidencing the true condition of the row of conical spinules in Murunducaris. In other groups, it seems that the hyaline frill has undergone modification, appearing transformed into an inner row of spinules. For example, observation of a neotenic male of Brasilibathynellocaris salvadorensis (Noodt, 1962) (Corgosinho personal observation; Noodt Collection, box 6, slide number 29; DZMB/ Senckenberg Forschungsinstitut und Naturmuseum, Wilhelmshaven, Germany) revealed that the anterior row of strong spinules present on the exp-1 of the leg 4 of males is homologous to a hyaline frill, appearing in this specimen as a distal row of spinules on the inner corner of the exp-1. In P. santaremensis (Fig. 13C) and in Parastenocaris sp. aff. P. santaremensis (Fig. 13D), a proximal row of strong spinules on the inner margin of the leg 4 exp-1 of males is located proximal to a modified "hyaline frill" (Fig. 13C, D).

ACKNOWLEDGEMENTS

We thank the Deutscher Akademischer Austauschdienst "DAAD", the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM), and the Forschungsinstitut Senckenberg for financial support of the senior author. We are in debt to the DZMB-Senckenberg Forschungsinstitut and the Instituto Nacional de Pesquisas da Amazônia for logistical support during this study. We thank Dr. Thomas Glatzel, University of Oldenburg, for allowing us to study his personal collection of Parastenocarididae. We are in debt to Dr. Marcos Tavares from the Museu de Zoologia da Universidade de São Paulo (MZUSP) for the loan of the type specimen of Murunducaris juneae. This study would not have been possible without examination of Dr. Wolfram Noodt's type material; we are therefore especially in debt to Dr. Ahmed Ahnert, who curated Noodt's material after he passed away and placed it at our disposal for the present study. Finally, we would like to express our sincere thanks to the anonymous referees and the editorial board of JCB for constructive comments that resulted in improvements to the original manuscript.

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RECEIVED: 18 June 2007. ACCEPTED: 24 March 2008.