



Revision of *Brasilibathynellocaris* Jakobi, 1972 (Copepoda: Harpacticoida: Parastenocarididae) with redefinition of the genus

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Members of the genus *Brasilibathynellocaris* Jakobi, 1972 are typical neotropical Parastenocarididae. Their geographical distribution ranges from Central America to southern Brazil, with species occurring on both sides of the Andes mountain chain. The genus can be characterized and easily identified by the following characters: leg 4 with two strong spinules on anterior margin of coxa; exopod 1 (exp-1) short and with a proximal invagination on inner corner; leg 3 with exopod inwardly curved, ending in a long forceps formed by apophysis and thumb (both with a hyaline margin). In the present work we favour revalidation of *Brasilibathynellocaris*, arguing for its monophyly. *Pararemaneicaris* Jakobi, 1972 and *Paraforficatocaris* Jakobi, 1972 are new junior synonyms of *Brasilibathynellocaris*, as a result of transfer of their respective type species: *Brasilibathynellocaris cuscatlanensis* (Noodt, 1962) **comb. nov.**, and *Brasilibathynellocaris paranaensis* (Jakobi, 1972) **comb. nov.** Two monophyletic species groups, together constituting *Brasilibathynellocaris*, are newly proposed and diagnosed: the *Brasilibathynellocaris brasilibathynellae* group and the *Brasilibathynellocaris salvadorensis* group. Neotypes are designated for *B. brasilibathynellae* and *B. paranaensis* **comb. nov.** Redescriptions are provided for all known species of *Brasilibathynellocaris*.

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ADDITIONAL KEYWORDS: Central America – monophyly – Neotropics – neotype – *Paraforficatocaris* – *Pararemaneicaris* – revalidation – South America – synonym.

INTRODUCTION

Copepods of the family Parastenocarididae are very abundant and diverse in sandy banks of neotropical rivers. The fauna encompasses members of some very peculiar genera, some of them very diverse and distributed in the whole of South America. We can specially mention the genus *Remaneicaris* Jakobi, 1972, with 31 described species, occurring from El Salvador to Argentina. The second and third most diverse genera are *Forficatocaris* Jakobi, 1969 and *Pota-*

mocar Dussart, 1979. With 13 and six described species, respectively, they are so far endemic to South America and are very abundant in the tropics, with numerous undescribed species in the Amazon region (P. H. C. Corgosinho, unpubl. data).

Taxonomic knowledge of neotropical Parastenocarididae is very fragmentary. Until recently, all regionally occurring species were placed in the genera *Forficatocaris*, *Potamocaris*, *Murunducaris* Reid, 1994, *Paraforficatocaris* Jakobi, 1972, and *Parastenocaris* Kessler, 1913. The last two genera names have been applied to some neotropical species without consideration of possible taxonomic and phylogenetic

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problems associated with this application. Conversely, potentially monophyletic and validly applicable genera such as *Remaneicaris* Jakobi, 1972, *Brasilibathynellocaris* Jakobi, 1972, and *Siolicaris* Jakobi, 1972 were not adopted (see Corgosinho & Martínez Arbizu, 2005).

Parastenocaris has been used as a repository for species that belong to different evolutionary lineages. In accordance with Reid (1995) and Galassi & De Laurentiis (2004), use of the name *Parastenocaris* should be restricted to species around the *Parastenocaris brevipes* group, *Parastenocaris brevipes* Kessler, 1913 being the type species of the genus. Thus, the presence of *Parastenocaris* in South America should be gauged by the presence of the *Parastenocaris brevipes* group.

Another problem concerns recognition of the genus *Paraforficatocaris*, with *Paraforficatocaris paranaensis* Jakobi, 1972 as the type species. Its systematic position is discussed here.

With five described species [viz. *Brasilibathynellocaris brasilibathynellae* (Jakobi & Loyola e Silva, 1962), *Brasilibathynellocaris paranaensis* (Jakobi, 1972) comb. nov., *Brasilibathynellocaris panamericana* (Noodt, 1962), *Brasilibathynellocaris cuscatlanensis* (Noodt, 1962) comb. nov., and *Brasilibathynellocaris salvadorensis* (Noodt, 1962)], *Brasilibathynellocaris* ranks fourth in diversity amongst the neotropical genera; it is distributed from Central America (El Salvador) to southern Brazil. *Brasilibathynellocaris brasilibathynellae* is the most austral species, occurring in groundwaters on Santa Catarina island (Florianópolis, Santa Catarina state, Brazil), whereas *B. panamericana* is the most widespread one, occurring from El Salvador to Peru, in both freshwater and continental brackish water habitats.

In the present work, we favour revalidation of *Brasilibathynellocaris* based on arguments for its monophyly. As a contribution towards generic revision, we redescribe all included species: *B. brasilibathynellae*, *B. panamericana*, *B. cuscatlanensis* comb. nov., *B. salvadorensis*, and *B. paranaensis* comb. nov. In addition, we provide differential diagnoses for two newly recognized monophyletic species groups within the genus, and briefly discuss some possible relationships with other genera and species.

MATERIAL AND METHODS

The original material of *Parastenocaris brasilibathynellae* Jakobi & Loyola e Silva was loaned from the US National Museum of Natural History (USNM; Washington, DC). The vial labelled USNM 104409 was supposed to contain the holotype, but in spite of an exhaustive search the specimen was not found. Hence, we dissected and slide-mounted a male from

Jakobi & Loyola e Silva's sample USNM 104411, from the original type locality, which is designated as the neotype below. A female from the latter sample was dissected and slide-mounted as well.

For *Paraforficatocaris paranaensis* Jakobi the original name-bearing syntype series consisted of 'numerous males, females and juveniles' (translated from the German original, Jakobi, 1972b: 245). Our searches for this material were unsuccessful as well. Consequently, we designate as neotype below, a male collected in July 1999, using the Karaman–Chappuis method (Chappuis, 1942), at the original locus typicus. The iron bridge crossing the river at the entrance to Porto de Cima village, mentioned by Jakobi (1972b: 242) is still present; thus we are quite sure to have sampled the same place as Jakobi, with a margin of error of only some metres. The samples containing the male neotype and other specimens were washed through a 100 µm mesh, stained with Rose Bengal, and fixed with formalin at a final concentration of 4% formaldehyde.

For redescrptions of the remaining species, we studied the Noodt collection at the Senckenberg Research Institute, Dept. Deutsches Zentrum für Marine Biodiversitätsforschung (Wilhelmshaven, Germany). Unfortunately, Noodt did not designate name-bearing types for the species of the *Parastenocaris panamericana* group (*Brasilibathynellocaris* species) studied by him (Noodt, 1962). Moreover, several organisms were mounted together that do not always belong to a single species per slide (Noodt, 1962: 226–227). Often it was not possible to identify which limbs had been drawn by Noodt. As a result of the poor condition of some original preparations, redescrptions had to be based on several specimens from different slides.

A copepodid V specimen of *B. salvadorensis* was obtained from a Noodt sample containing individuals preserved in 4% formalin. Specimens from formalin samples were dissected in lactic acid and mounted on slides with glycerine. Drawings were made with a Leica DMR microscope equipped with Nomarski interference contrast, using a drawing tube and 400× and 1000× magnification.

For the reconstruction of phylogenetic relationships the method of phylogenetic systematics was used (Hennig, 1966; Ax, 1984; Wägele, 2005). The analysis was carried out by hand, using Hennigian principles (Meier, 1992; Wägele, 2005) and Hennig's criterion of parsimony (putative parsimony; Hennig, 1966; Wägele, 2004, 2005).

The poor knowledge of phylogenetic relationships within South American parastenocaridids has made it difficult to find the sister group of *Brasilibathynellocaris*. Therefore, polarization of character states for the present analysis was carried out by comparison

with the expected groundpattern for *Brasilibathynellocaris*, and considering all other parastenocaridids as the outgroup. The ontogenetic criterion for evaluation of character state polarity was also applied here. The term groundpattern is used in the sense of 'Grundmuster' (Ax, 1984: 156) and refers to all plesiomorphies and autapomorphies present at the stem species ('Stammart' *sensu* Ax, 1984) of the genus in question.

Additionally, the computer program supporting parsimony (cladistic parsimony) PENNY, an integrated part of the phylogeny inference package PHYLIP 3.67 (Felsenstein, 2007), was used in integration with the PHYLEDIT 2.0.1 (de Haro, 2002) interface. The PENNY program finds all most parsimonious phylogenies for discrete-character data with two states, for the Wagner-, Camin–Sokal-, and mixed parsimony criteria using the branch-and-bound method of exact search. In this study we used both Wagner and Camin–Sokal algorithms. The latter allows 0 → 1 character changes but not 1 → 0 changes. This last transformation is also supported by Wagner parsimony. Character states were polarized a priori. Thus, zero (0) represents the plesiomorphic condition, one (1) the apomorphic condition. The default output of PENNY for the Wagner algorithm is an unrooted tree. However, Figure 24 (A and B) presents rooted trees. The program WINCLADA (Nixon, 1999) was employed for construction of the trees.

The terms 'furca' and 'telson' are used according to Schminke (1976). The term 'thumb' refers to the outer spine of leg 3 of the male, homologous to the outer spine of exopod 1 (exp-1) of leg 3. For details on the development of the male leg 3 and for homologization of structures, see Glatzel (1991).

Abbreviations used: A1, antennule; A2, antenna; Ae, aesthetasc; ap, apomorphy; enp, endopod; exp, exopod; L, length; Md, mandible; Mx1, maxillule; Mx2, maxilla; Mxp, maxilliped; pl, plesiomorphy.

FAMILY PARASTENOCARIDIDAE

GENUS *BRASILIBATHYNELLOCARIS* JAKOBI, 1972

Brasilibathynellocaris Jakobi, 1972 – Jakobi (1972a: 143).

Pararemanecaris Jakobi, 1972, syn. nov. – Jakobi (1972a: 144).

Paraforficatocaris Jakobi, 1972, syn. nov. – Jakobi (1972b: 245).

Type species: Brasilibathynellocaris brasilibathynellae (Jakobi & Loyola e Silva, 1962).

Diagnosis: Parastenocarididae with dorsal integumental windows on cephalothorax and second to fifth urosomites of male (pl). Furca with seven setae (pl);

setae I–III originating from almost same region (pl), anterior to seta VII (pl); seta II reduced in size, sometimes indiscernible (ap?). A1 eight-segmented in male (pl), seven-segmented in female (pl). Maxilla with two endites, proximal endite with one seta (pl), distal one with one spiniform and two slender setae (pl). Leg 2 endopod sexually dimorphic (pl?); long outer spine on exp-1 (ap?). Basis of male leg 3 with a strong spinule on inner margin (ap?) and a row of short and stout spinules near insertion of endopod (pl?); exopod inwardly curved, strong, ending in a long forceps formed by apophysis and outer spine of exp-1 of leg 3 (the thumb), both with a hyaline margin (ap); endopod represented by slender seta (pl). Coxa of male leg 4 with two long and strong spinules on anterior margin (ap); exp-1 reduced in length and with proximal invagination on inner corner (ap); endopod sexually dimorphic (pl). Leg 5 rectangular, with an inner process, an intercoxal plate, a basal seta, and two distal setae inserted on outer margin; no proximal exopodal seta adjacent to outer basal seta (ap?).

Species groups included: *Brasilibathynellocaris* can be divided into two monophyletic groups (Fig. 24), which are newly proposed here:

SPECIES GROUPS

BRASILIBATHYNELLOCARIS BRASILIBATHYNELLAE GROUP

Diagnosis: *Brasilibathynellocaris* with leg 2 endopod sexually dimorphic (pl), very long in male (ap) and as long as exp-1. Male leg 4 exp-1 without anterior row of strong spinules (ap).

Species included: *Brasilibathynellocaris brasilibathynellae*; *B. paranaensis* comb. nov.

BRASILIBATHYNELLOCARIS SALVADORENSIS GROUP

Diagnosis: *Brasilibathynellocaris* with leg 2 endopod sexually dimorphic (pl), more ornamented in male, shorter than exp-1 in both sexes (pl). Male leg 4 exp-1 with anterior row of strong spinules (pl); endopod with a hyaline region (ap).

Species included: *Brasilibathynellocaris salvadorensis*; *B. panamericana*; *B. cuscatlanensis* comb. nov.

BRASILIBATHYNELLOCARIS BRASILIBATHYNELLAE (JAKOBI & LOYOLA E SILVA, 1962) (FIGS 1–5)

Parastenocaris brasilibathynellae Jakobi & Loyola e Silva – Jakobi & Loyola e Silva (1962: 390); Jakobi (1972b), Rouch (1986), Dussart & Defaye (1990), Reid (1998).

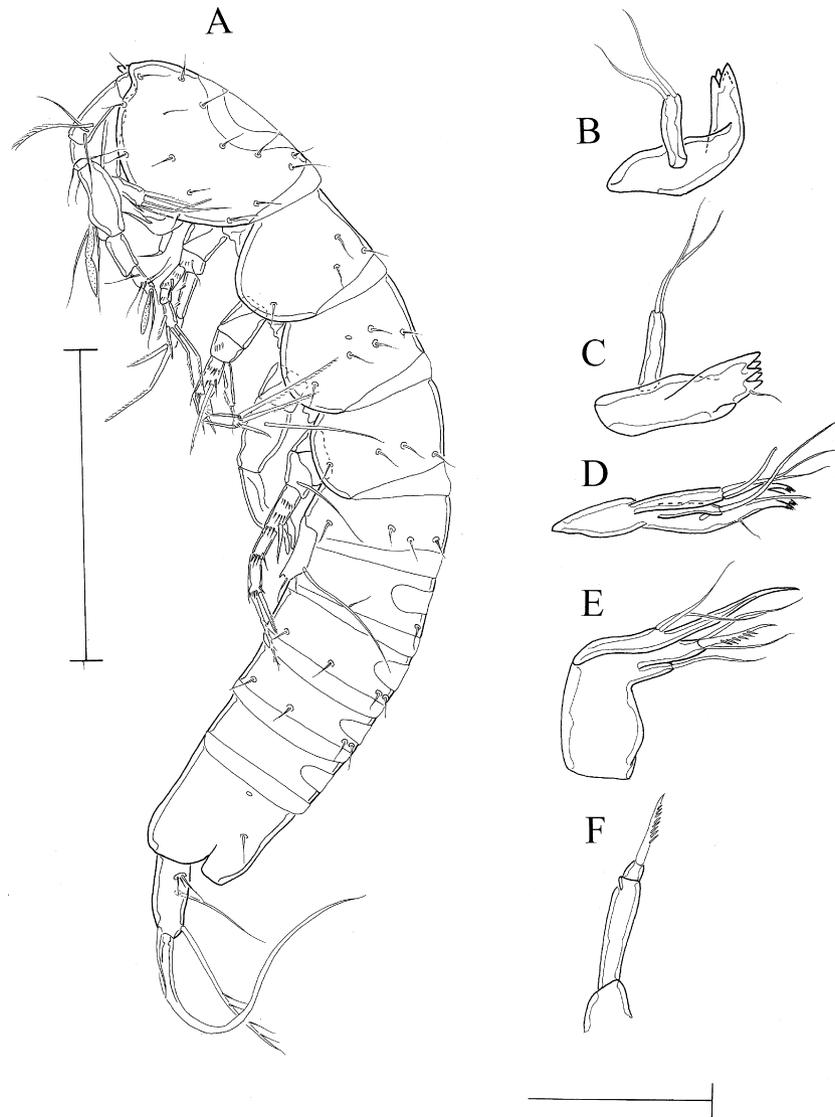


Figure 1. *Brasilibathynellocaris brasilibathynellae*, male. A, habitus, lateral. B, mandible, outer view. C, mandible, inner view. D, maxillule. E, maxilla. F, maxilliped. Scale bars: A = 100 µm, B–F = 20 µm.

Brasilibathynellocaris brasilibathynellae (Jakobi & Loyola e Silva) – Jakobi (1972a).

Parastenocaris brasili-bathynellae Jakobi & Loyola e Silva – Löffler (1981), incorrect spelling.

Material examined: USNM vial 104409 (no specimen; see Material and methods); USNM vial 104410 ('allotype female' of Jakobi & Loyola e Silva, 1962: 392); USNM vial 104411 [one male, designated neotype below; one female, now mounted on seven slides; deposited as paratypes at USNM. Although Jakobi & Loyola e Silva (1962: 392) did not give the collection number of the paratypes, here we assumed these specimens to be the 'two paratypes' mentioned in their publication.]

NEOTYPE DESIGNATION

With the holotype male permanently lost (see Material and methods), a neotype is designated here, in order to clarify the taxonomic status of *B. brasilibathynellae* (Jakobi & Loyola e Silva) and define this taxon objectively.

Neotype: Male, mounted on seven slides (USNM 1100477).

Type locality: Brazil, Santa Catarina state, Florianópolis, Santa Catarina Island, Lagôa village, in subterranean well water 'on the property of Mr. Olympio Pires' (Jakobi & Loyola e Silva, 1962: 395); identical to original type locality.

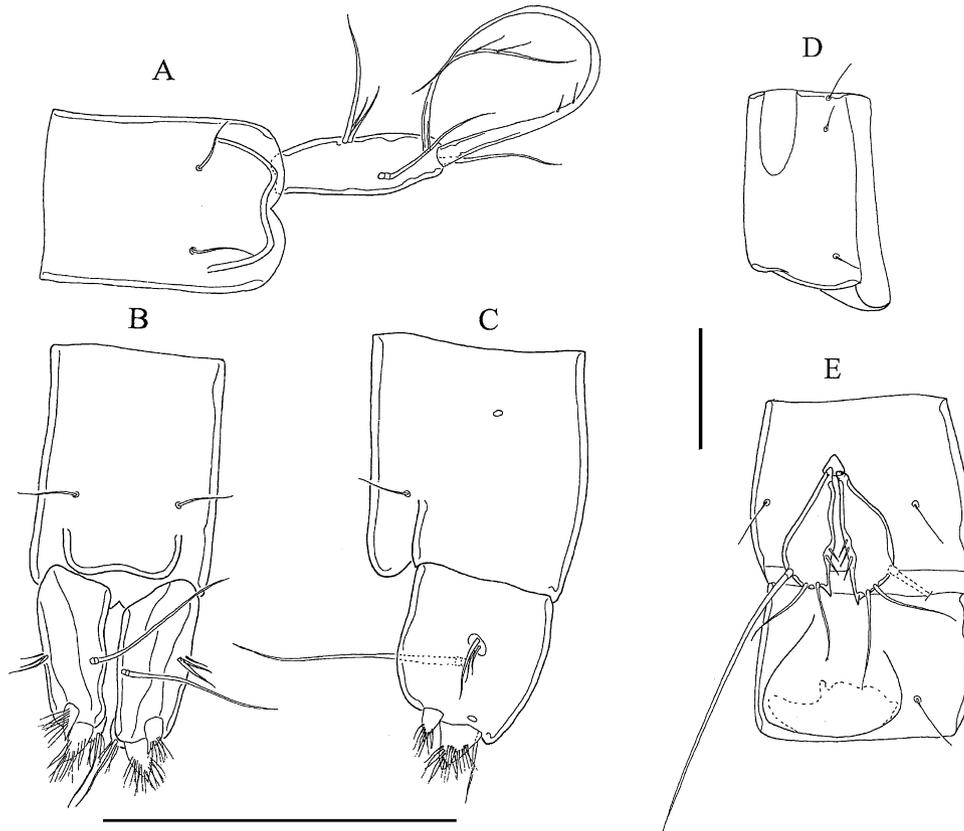


Figure 2. *Brasilibathynellocaris brasilibathynellae*. A, male telson, dorsal. B, female telson, dorsal. C, female telson, lateral. D, lateral view of male urosomite 2. E, ventral view of male urosomite 1 and 2. Horizontal scale bar for A–C = 50 μ m. Vertical scale bar for D–E = 20 μ m.

Table 1. Character matrix for phylogeny reconstruction in the genus *Brasilibathynellocaris*

Species	Character															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Other Parastenocarididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Brasilibathynellocaris brasilibathynellae</i>	1	1	1	0	0	1	1	0	0	0	1	0	1	0	0	0
<i>Brasilibathynellocaris paranaensis</i> comb. nov.	1	1	1	1	0	1	1	0	0	0	1	1	0	0	0	0
<i>Brasilibathynellocaris salvadorensis</i>	1	1	1	1	1	0	0	1	1	1	0	0	0	1	0	0
<i>Brasilibathynellocaris panamericana</i>	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	1
<i>Brasilibathynellocaris cuscatlanensis</i> comb. nov.	1	1	1	1	1	0	0	1	1	1	0	0	0	0	1	0

Character states polarized a priori; 0 = plesiomorphic; 1 = apomorphic.

Differential diagnosis: See Table 1. Comparison with the original description (Jakobi & Loyola e Silva, 1962) shows that this diagnostic combination of features is consistent with what is known of the former name-bearing holotype.

Description

Male: Habitus (Fig. 1A). Length 320 μ m (measured from tip of rostrum to distal rim of anal operculum). Rostrum not fused to cephalothorax, with a wide base

and two sensilla on tip. Cephalothorax with two concentric integumental windows on the dorsal margin, urosomites 2–5 with one dorsal integumental window. Dorsal pores on cephalothorax, first and third thoracic somites, and second and fourth urosomites. One pore on each side of telson. For sensilla on tergites, see Figure 1A. Telson smooth, anal operculum smooth and concave (Fig. 2A). Furca (Figs 2A, 3C) with seven setae; setae I, II, and III inserted proximally to the middle of furca, anterior to seta VII; seta II reduced,

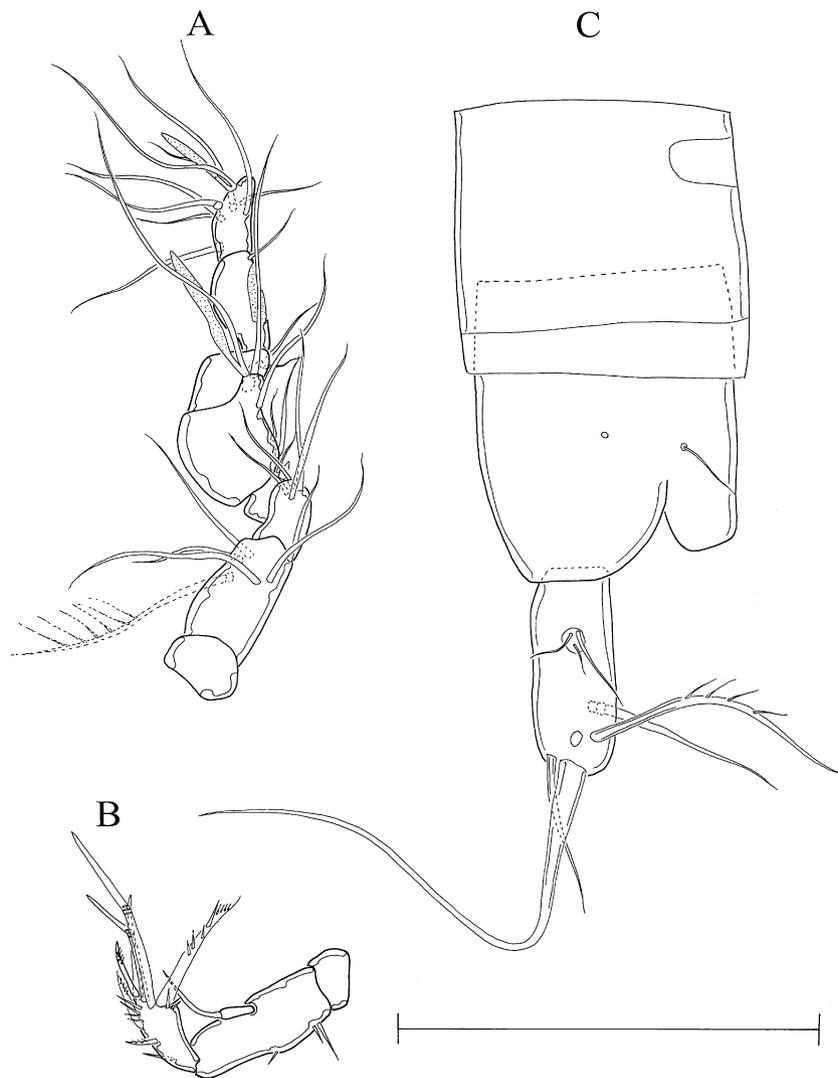


Figure 3. *Brasilibathynellocaris brasilibathynellae*, male. A, antennule. B, antenna. C, telson, lateral. Scale bar = 50 μ m.

not visible in some animals; seta IV subdistal, inserting dorsally, on outer margin of furca; seta V *c.* three times longer than furca, inserting on its distal margin; seta VI shorter than seta V, inserting beneath it; seta VII approximately same size as seta VI, socketed at base and inserting dorsally, on inner margin of furca. A1 (Fig. 3A) eight-segmented and prehensile; armature beginning with proximal segment: 0/6/4/2/5 + Ae/3 (one ventral hyaline spine and two setae)/2 (one outer hyaline spine and one distal seta)/9 + Ae; pinnate seta of first segment broken. A2 (Fig. 3B) with allobasis; abexopodal margin ornamented with two spinules, of unequal length, inserted proximally and one spinule inserted on its midlength; one-segmented exopod with one seta, and one-segmented endopod bearing seven setae. Mouthpart armature as follows: Md (Fig. 1B, C) coxal gnathobasis bearing one seta and a one-segmented palp with two setae; Mx1

(Fig. 1D) praecoxal arthrite with five elements (one dorsal surface seta, three claw-like pinnate spines and one slender seta), coxa with one seta, basis with three setae; Mx2 (Fig. 1E) syncoxa with two endites, proximal endite with one seta, distal endite with two slender setae and one pinnate spine, endopod with two setae, allobasis prolonged into inner claw; Mxp (Fig. 1F) subchelate, composed of syncoxa, basis, one-segmented endopod and one claw-like apical seta. Praecoxa of legs 1–4 is a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Fig. 4A–D). Leg 1 (Fig. 4A) coxa unarmed; basis with outer seta and one pore on anterior outer margin, four spinules on outer margin, and a distal row of seven small spinules between endopod and exopod; exopod three-segmented, exp-1 with outer spine, exp-2 unarmed, exp-3 with two outer spines and two geniculate setae of different lengths;

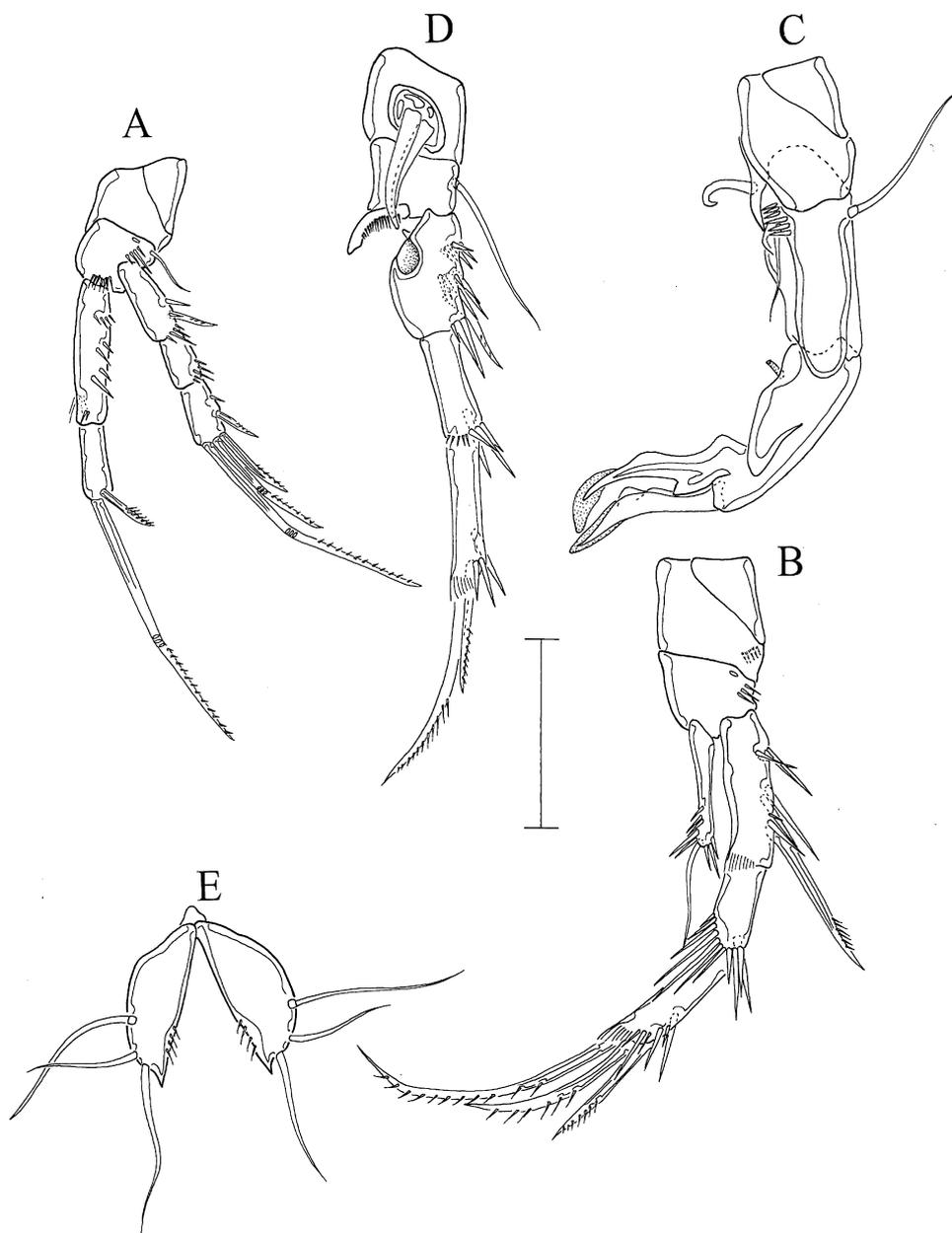


Figure 4. *Brasilibathynellocaris brasilibathynellae*, male. A, leg 1. B, leg 2. C, leg 3. D, leg 4. E, leg 5. Scale bar = 20 μ m.

endopod two-segmented, enp-1 as long as the combined length of first two exopod segments, with proximal transversal row of small spinules and longitudinal row of larger spinules on outer margin, enp-2 with one outer spine and one geniculate seta. Leg 2 (Fig. 4B) coxa unarmed, with one row of small spinules on posterior margin; basis without outer seta, an outer pore and ornamented with one row of spinules on outer margin; exopod three-segmented, exp-1 with a long outer spine and a hyaline frill on distal inner corner; exp-2 without armature and with two divergent rows of long spinules on its distal portion; exp-3 with three setae, hyaline frill on distal

inner corner and row of long spinules on outer margin; endopod one-segmented, as long as exp-1, with inner row of spinules along distal third, a distal seta and a row of three distal spinules. Leg 3 (Fig. 4C) coxa unarmed; basis with an outer seta, a strong inner spinule (hook-shaped) on proximal portion and a row of short and stout spinules near insertion of endopod; endopod represented by a slender seta; exopod inwardly curved, strong, ending in a long forceps formed by apophysis and thumb (both with a hyaline margin); proximally with tube pore on inner margin. Leg 4 (Fig. 4D) coxa with two long and strong spinules on anterior margin (around them we can observe a

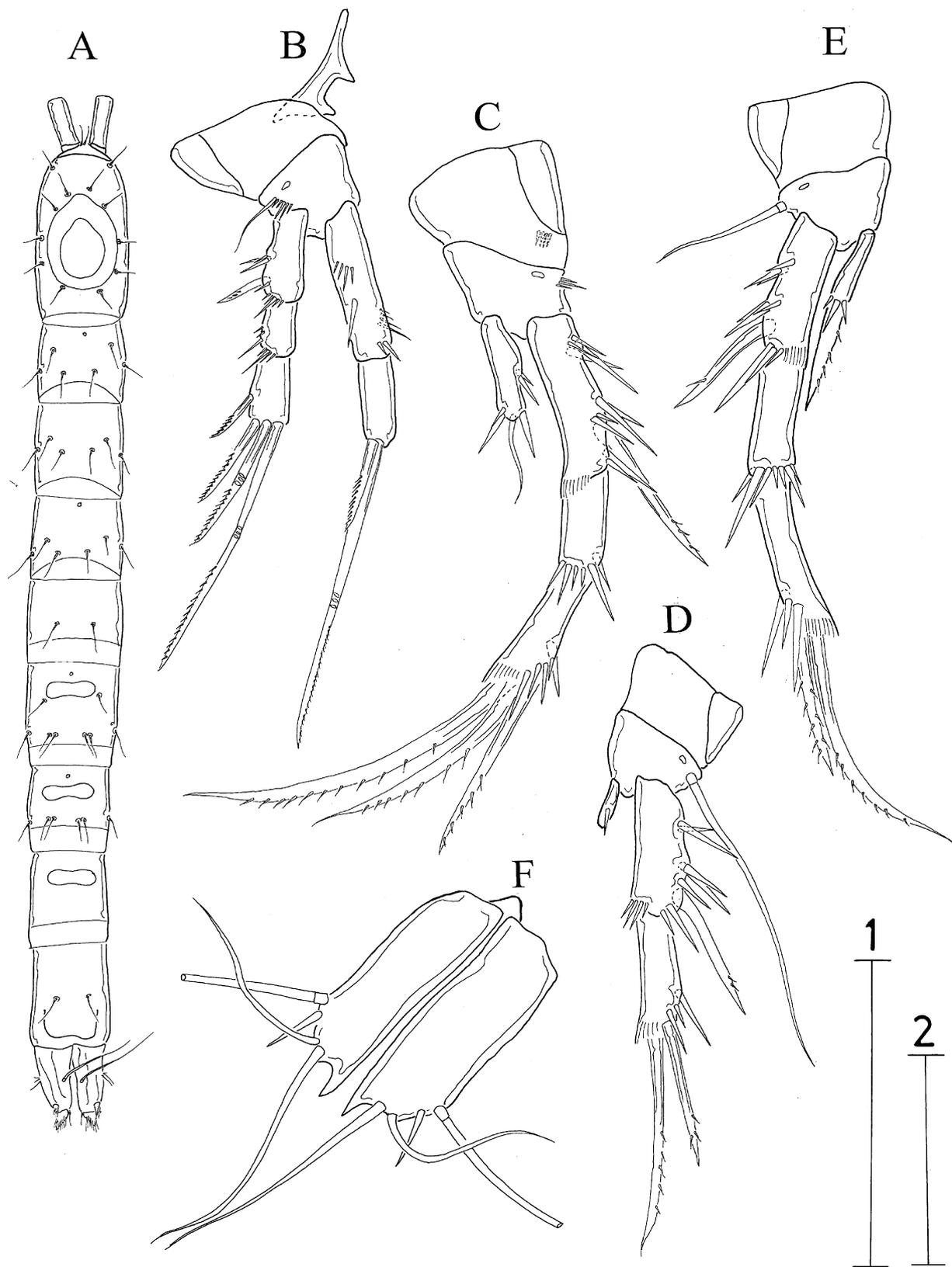


Figure 5. *Brasilibathynellocaris brasilibathynellae*, female. A, habitus, dorsal. B, leg 1. C, leg 2. D, leg 3. E, leg 4. F, leg 5. Scale bar 1 (for A) = 100 μ m, scale bar 2 (for B–F) = 20 μ m.

weakly chitinized zone); basis quadratic, with an outer seta; exp-1 reduced in length and with an invagination on proximal inner corner, outer margin strongly ornamented and with an outer spine; exp-2 unarmed, with a transversal row of long spinules on distal outer corner and a transversal row of smaller spinules on the distal margin; exp-3 with two distal setae, hyaline frill on distal inner corner and subdistal row of long spinules on outer margin; endopod horizontally displaced, with row of spinules along outer margin. Leg 5 trapezoidal, with an inner process, an intercoxal plate, an outer basal seta, two distal setae inserted on outer margin and a distal row of small spinules along inner margin (Figs 2E and 4E). Leg 6 is an unarmed, rounded and asymmetrical operculum covering the genital aperture (Fig. 2E), appearing as a triangular plate in lateral view (Fig. 2D).

Female: Sexually dimorphic in A1, leg 1–5, genital somite and furca. Habitus (Fig. 5A). Length 340 µm (measured from tip of rostrum to distal rim of anal operculum). Rostrum as in male. Cephalothorax with two concentric integumental window on the dorsal margin, second to fourth urosomite with one dorsal integumental window each. Dorsal pores on first and third thoracic somites, proximal region of the genital somite (homologous to male urosomites 2 and 3) and urosomites 3 (homologous to male urosomites 4). One pore on each side of telson (Fig. 2C). For sensilla on tergites see Figure 5A. Lateral sensilla patterns like in male (genital somite conserving the same sensilla patterns of the free male urosomites 2 and 3). Telson smooth, anal operculum smooth and concave (Figs 2B, C, 5A). Furca (Figs 2B, C, 5A) with seven setae; setae I–III inserted proximally to the middle of furca, anterior to seta VII; setae IV and V reduced to short, stout spines, with several setules on distal margin; setae VI and VII developed as in male; one lateral pore on distal region. A1 seven-segmented, not geniculate; armature beginning with proximal segment as in *B. panamericana* (Fig. 13D). A2 and mouthparts as in male. Praecoxa of legs 1–4 is a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Fig. 5B–E). Leg 1 (Fig. 5B) coxa unarmed; basis with outer seta and an outer pore, without row of spinules on its distal portion, between exopod and endopod; endopod two-segmented; enp-1 as long as the combined length of first two exopod segments, with a proximal row of small transverse spinules and one big spinule on outer margin; on inner margin with a distal row of small spinules; enp-2 and exp-1 to 3 as in male. Leg 2 (Fig. 5C) coxa unarmed, with one row of small spinules at posterior margin; basis without outer seta, with an outer pore and ornamented with one row of spinules on outer margin; exopod 3-segmented,

exp-1 with long outer spine and with a hyaline frill on distal inner corner; exp-2 without armature and with a distal row of long spinules; exp-3 with three setae, distal hyaline frill on inner corner and row of long spinules on outer margin; endopod one-segmented, shorter than in male, with two apical spinules, a distal seta and two spinules medially on the outer margin. Leg 3 (Fig. 5D) coxa unarmed; basis with a long outer seta and an outer pore; endopod represented by a short segment with a subdistal spinule; exopod two-segmented; exp-1 with an outer spine and an inner row of spinules on the distal corner; exp-2 with two setae, hyaline frill on distal inner corner and outer row of spinules. Leg 4 (Fig. 5E) coxa and basis unarmed; basis with an outer seta and an outer pore; endopod one-segmented, longer than exp-1, with a transverse row of spinules inserted medially, probably delineating original separation between endopod and distal seta, now incorporated into segment; exopod three-segmented, exp-1 normally developed, with an outer spine and a hyaline frill on distal inner corner; exp-2 unarmed, with a distal row of long spinules on outer corner and a distal transversal row of smaller spinules on distal inner corner; exp-3 with two distal setae, distal hyaline frill on inner corner, and three long spinules on outer margin. Leg 5 rectangular (Fig. 5F), with an inner process, an intercoxal plate, an outer basal seta, and three exopod setae on distal margin. Genital field as in *B. panamericana*. Genital operculum formed by two lateral and unarmed plates covering the gonopores. Single medially located copulatory pore.

BRASILIBATHYNELLOCARIS PARANAENSIS (JAKOBI, 1972) **COMB. NOV.** (FIGS 6–10)

Paraforficatocaris paranaensis Jakobi – Jakobi (1972b: 245); Reid (1982, 1998), Rouch (1986), Dussart & Defaye (1990).

Paraforficatocaris paranaense Jakobi – Jakobi (1972b: 245), incorrect (variant) original spelling.

Material examined: One male, designated neotype below.

NEOTYPE DESIGNATION

With the syntype series permanently lost (see Material and methods), a neotype is designated here, in order to clarify the taxonomic status of *B. paranaensis* (Jakobi) comb. nov. and define this taxon objectively.

Neotype: Male, mounted on seven slides (Instituto Nacional de Pesquisas da Amazônia = INPA, Manaus, Brazil; 1507a–g).

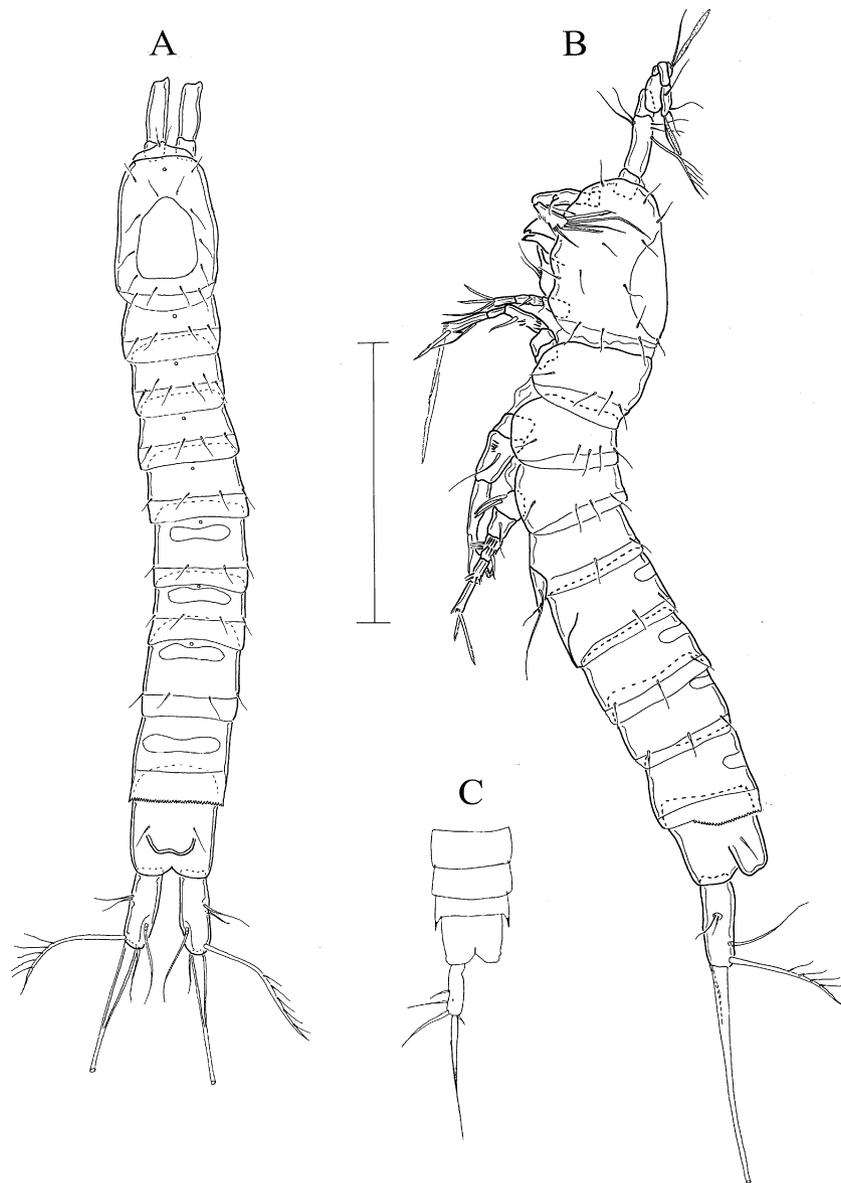


Figure 6. *Brasilibathynellocaris paranaensis* **comb. nov.**, male. A, habitus, dorsal. B, habitus, lateral. C, ventral view of three last urosomites, telson, and furca; from Jakobi (1972b). Scale bar: A, B = 100 μ m; C not to scale.

Type locality: Brazil, Paraná, city of Morretes, bank of Nhundiaquara River at steel bridge leading into Porto de Cima, coordinates 25°28'41"S, 48°49'37"W (identical to original type locality), July 1999.

Differential diagnosis: See Table 1. Comparison with the original description (Jakobi, 1972b) shows that this diagnostic combination of features is consistent with what is known of the former name-bearing syntype series.

Description

Male: Habitus (Fig. 6A, B). Length 270 μ m (measured from tip of rostrum to distal rim of anal operculum).

Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax with dorsal integumental window, second to fifth urosomites with one dorsal integumental window each. Dorsal pores on all segments except last urosomite. For sensilla on somites see Figure 6A, B. Last urosomite with serrated hyaline frill (Figs 6A, B, 7A) extending from lateral side to dorsal side (Fig. 7A). Telson smooth, anal operculum smooth and concave (Figs 6A, 7A). Furca (Figs 6A, B, 7A) with seven setae; setae I–III inserted proximally to the middle of furca, anterior to seta VII; seta II reduced, not visible in some animals; seta IV subdistal, inserting dorsally, on outer margin of furca; setae V long, inserting on distal margin of

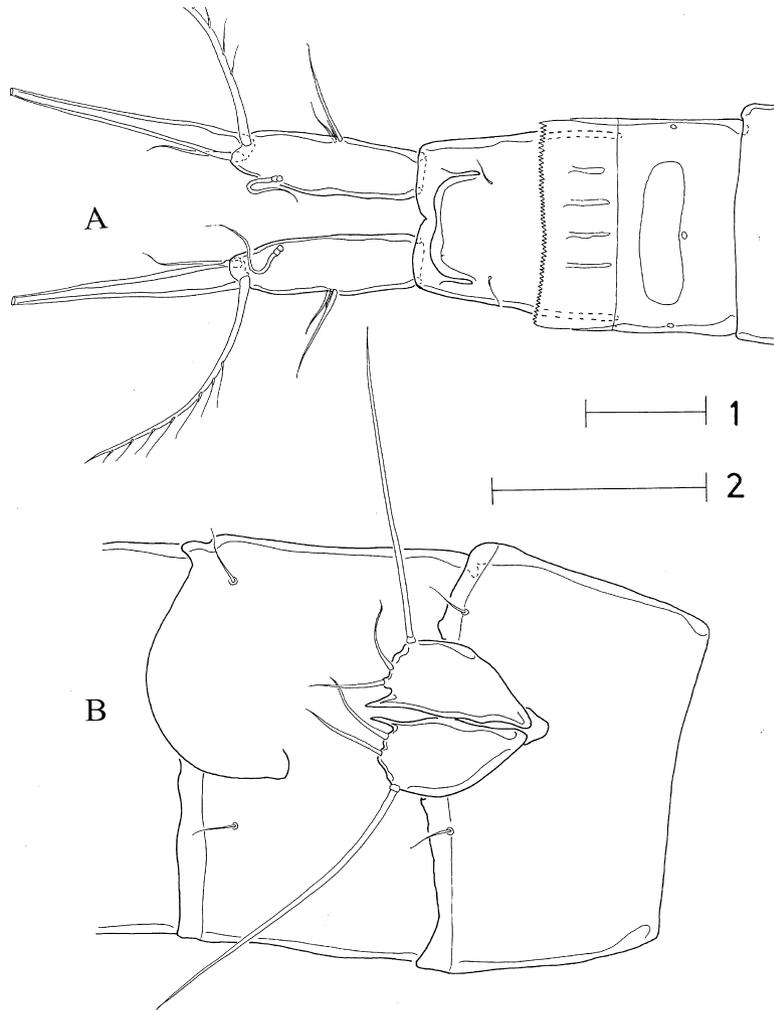


Figure 7. *Brasilibathynellocaris paranaensis* **comb. nov.**, male. A, telson with furca, and last urosomite showing a well-developed, distally serrated hyaline frill, supported by lateral cuticular extensions. B, first and second urosomites, ventral; first urosomite with leg 5. Scale bars = 20 μ m.

furca; seta VI shorter than seta V inserting beneath it; seta VII of about same length as seta VI, socketed at base and inserting dorsally, on inner margin of furca. A1 as in *B. brasilibathynellae*, eight-segmented and prehensile (Fig. 8A, A1–A7); armature beginning with proximal segment: 0/6/4/2/5 + Ae/3/2/9 + Ae. A2 (Fig. 8B) with allobasis; one-segmented exopod with one seta, and one-segmented endopod bearing seven setae. Md, Mx1, Mx2, and Mxp armature as in *B. brasilibathynellae*. Praecoxa of legs 1–4 is a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Figs 9A, B, 10A, C). Leg 1 (Fig. 9A) coxa unarmed; basis with an outer and an inner row of strong spinules, one pore and a row of eight small spinules distally set between endopod and exopod. Exopod three-segmented, exp-1 with an outer spine, exp-2 unarmed, exp-3 with two outer spines and two geniculate setae of different lengths; endopod

two-segmented, enp-1 with two long spinules on inner margin; enp-2 with one outer spine and one geniculate seta. Leg 2 (Fig. 9B, C) coxa unarmed; basis without outer seta and ornamented with one row of spinules on outer margin; exopod three-segmented, exp-1 with a long outer spine and a hyaline frill on distal inner corner; exp-2 without armature and with two divergent rows of long spinules on distal portion; exp-3 with three setae, distal hyaline frill on inner corner and row of long spinules along outer margin; endopod one-segmented, long, of same size as exp-1, with an inner row of spinules of increasing length along distal third, a distal seta, a longitudinal distal row of three short and one longer subapical one on outer margin, and a longitudinal row of proximal spinules on outer margin. Leg 3 (Fig. 10A, B) coxa unarmed; basis with an outer seta, an anterior pore, and an inner row of strong and conical spinules near

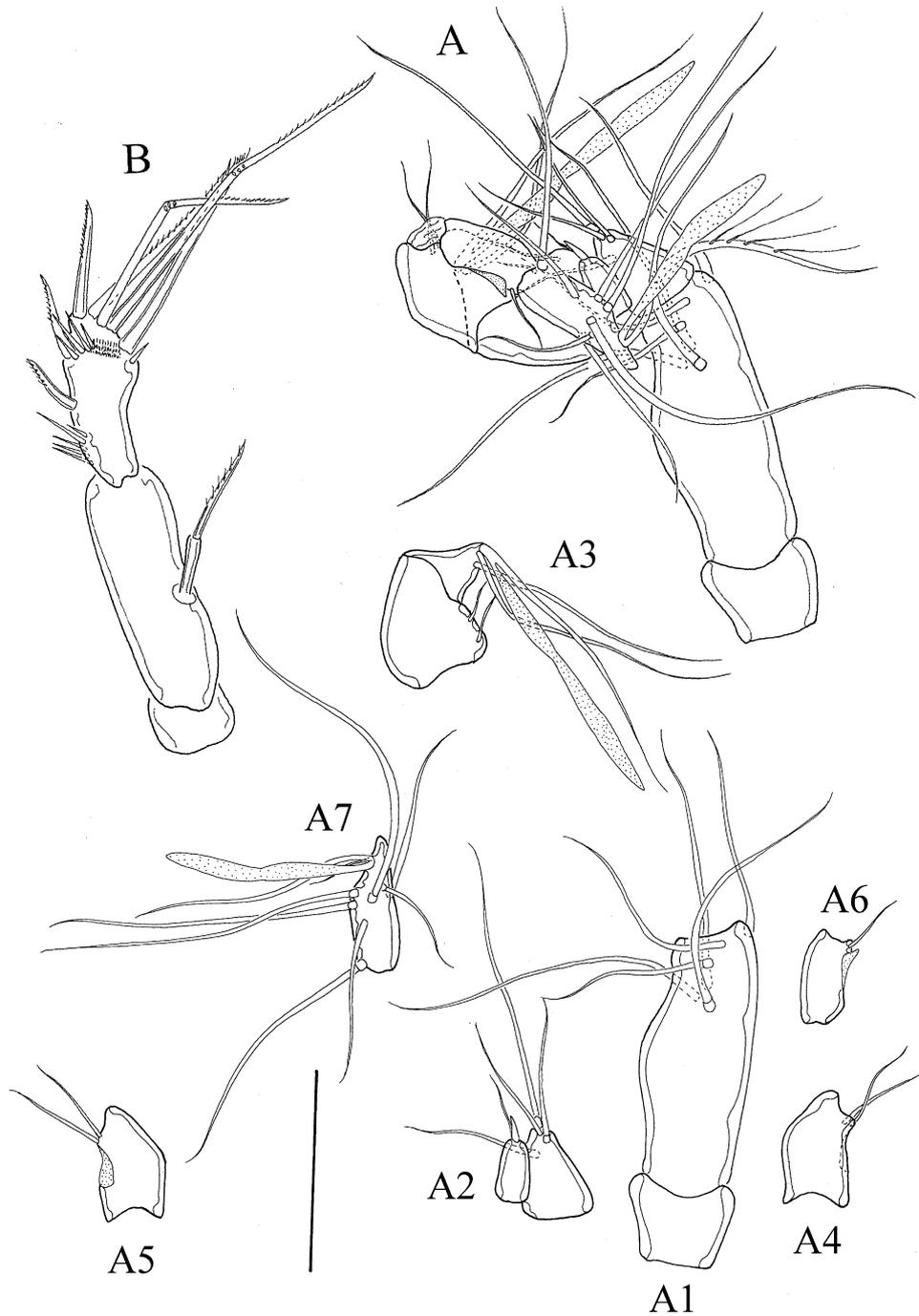


Figure 8. *Brasilibathynellocaris paranaensis* **comb. nov.**, male. A, antennule; geniculate view. A1–A7, antennule; exploded view. A1, first and second segments; A2, third and fourth segments; A3, fifth segment; A4 and A5, sixth segment, A4, posterior view, A5, anterior view; A6, seventh segment; A7, eighth segment. B, antenna. Scale bar = 20 μ m.

insertion of endopod; endopod represented by a slender seta; outer margin of basis with a long seta and a row of spinules; exopod inwardly curved, strong (with a proximal well-developed hyaline cushion), ending in a long apophysis (with a falciform hyaline tip); thumb longer than apophysis. Leg 4 (Fig. 10C, D)

coxa with two long and strong spinules on anterior side (around them we can observe a weakly chitinized zone); basis with an outer seta, rectangular, with an outer pore and a row of long spinules on posterior side; exp-1 reduced in length (Fig. 10C–E), strong, quadratic, and with a very pronounced invagination

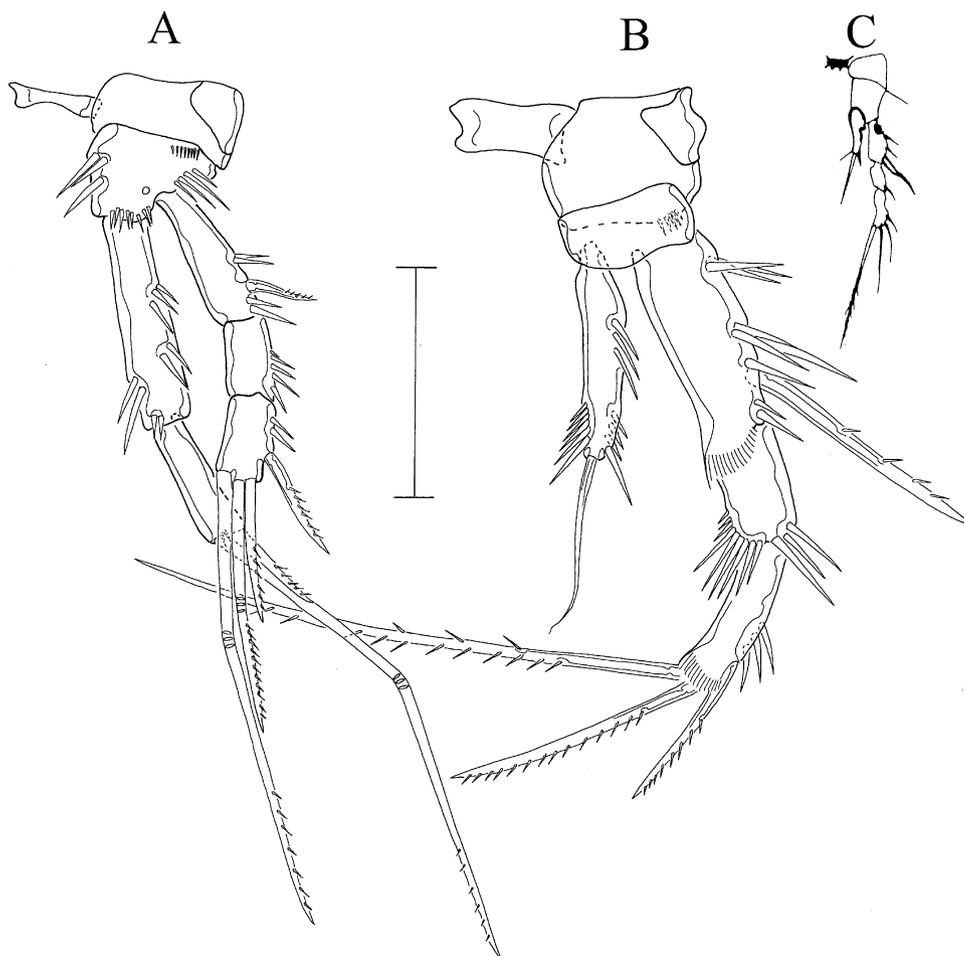


Figure 9. *Brasilibathynellocaris paranaensis* **comb. nov.**, male. A, leg 1. B, leg 2. C, leg 2; from Jakobi (1972b). Scale bar: A, B = 20 μ m; C not to scale.

on proximal inner corner, outer margin strongly ornamented and with an outer spine; exp-2 unarmed, with distal row of long spinules on distal outer corner and two small spinules distally inserted; exp-3 with two distal setae of different lengths, distal hyaline frill on inner corner and three long spinules on distal outer margin; enp reduced to a curved segment, inserted horizontally and bending downwards in the outer part, ending with enlarged tip, with row of spinules along apical margin. Leg 5 trapezoidal (Fig. 7B), with an inner process, an intercoxal plate, an outer basal seta, and two distal setae inserted on distal margin. Leg 6 is an unarmed, rounded, and asymmetrical operculum covering the genital aperture (Fig. 7B).

Female: We could not study any female, but some remarks can be made about Jakobi's (1972b) description. He mentioned a leg 3 with three exopod segments and three unequal setae on exp-3, whereas no female parastenocaridid possesses such features. It is clear, therefore, that Jakobi confused legs 2 and 3.

BRASILIBATHYNELLOCARIS PANAMERICANA (NOODT, 1962) (FIGS 11–13)

Parastenocaris panamericana Noodt – Noodt (1962: 228); Löffler (1981).

Brasilibathynellocaris panamericana (Noodt) – Jakobi (1972a).

Parastenocaris panamericana panamericana Noodt – Rouch (1986), Dussart & Defaye (1990).

Material examined: Syntypes from sample S 176 (Noodt, 1962); from this sample, Noodt prepared four slides now stored at DZMB (Noodt collection, box 6, slide nos. 37–40), all of them carrying more than one individual and both sexes; we were unable to discern unequivocally which animal was actually drawn by Noodt. Redescription is based on dissected males on slides 38–40 and on females on slides 37, 39, and 40.

Collecting locality: El Salvador, groundwater in bank of Rio Guasala (next to Jiboa river) on road between San Salvador and Zacatecoluca. Note that Noodt

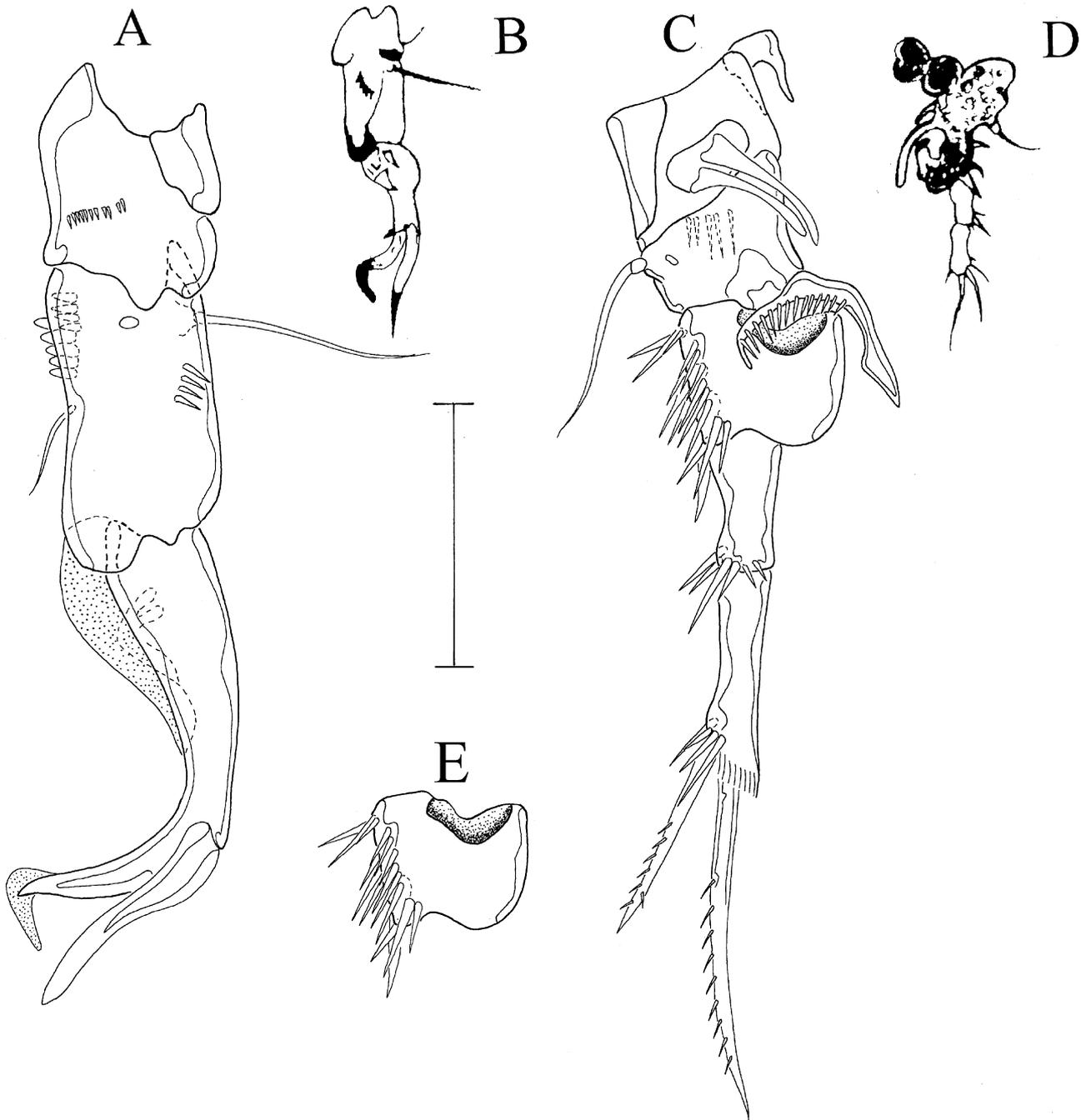


Figure 10. *Brasilibathynellocaris paranaensis* **comb. nov.**, male. A, leg 3. B, leg 3; from Jakobi (1972b). C, leg 4. D, leg 4; from Jakobi (1972b). E, leg 4 exopod 1. Scale bar: A, C, E = 20 μ m; B, D not to scale.

(1962: 228) called this locality (of sample S 176) the 'locus typicus', but that this did not explicitly exclude the many additional specimens he listed from other samples from his type series of *Parastenocaris pan-americana* (ICZN, 1999: Art. 72.4.6). Consequently, all those specimens are syntypes of equal nomenclatural standing, and all corresponding localities together form the type locality (ICZN, 1999: Art. 76.1).

Description

Male: Habitus in dorsal view and length as in Noodt (1962: 229, fig. 12). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax with dorsal integumental window, second to fifth urosomites with one dorsal integumental window each (Noodt, 1962, loc. cit.). Telson smooth (Fig. 11A); anal operculum smooth and slightly concave (Noodt,

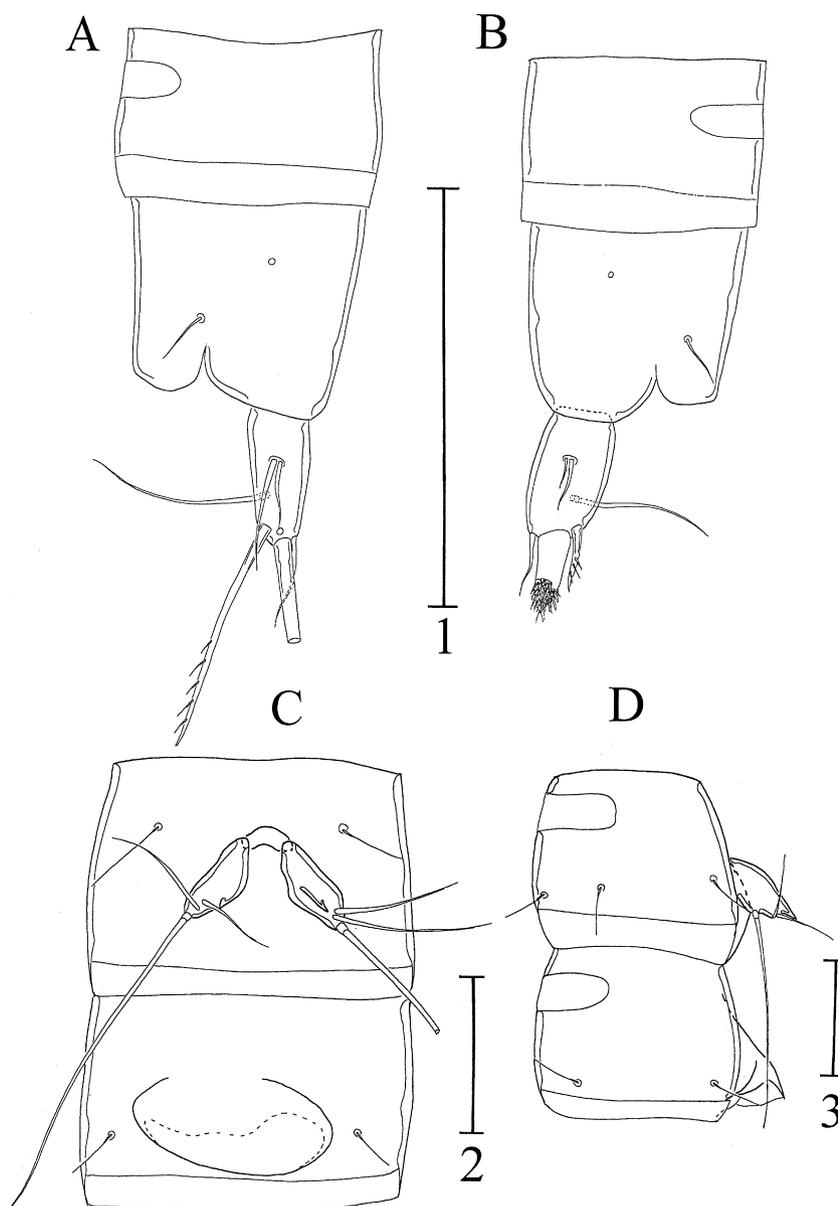


Figure 11. *Brasilibathynellocaris panamericana*. A, male telson, lateral. B, 'forma truncata', female telson, lateral. C, ventral view of the first and second urosomites of male. D, lateral view of the first and second urosomite of male. Scale bar 1 (for A–B) = 50 μ m. Scale bar 2 (for C) = 20 μ m. Scale bar 3 (for D) = 20 μ m.

1962: 229, fig. 2). Furca (Fig. 11A) with six visible setae and a distal pore on outer margin; setae I and III inserted proximally to the middle of furca, anterior to seta VII; seta II reduced or absent, not visible; seta IV subdistal, inserting dorsally, on outer margin of furca; setae V long (Noodt, 1962: 229, fig. 1), inserting on distal margin of furca; seta VI shorter than seta V inserting beneath it; seta VII of about same size as seta VI, socketed at basis and inserting dorsally, on inner margin of furca. A1, A2, and mouthparts as in *B. brasilibathynellae*. Praecoxa of legs 1–4 is a dis-

tinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Fig. 12A–D). Leg 1 (Fig. 12A) coxa unarmed; basis with outer seta and one pore on anterior outer margin, three spinules on outer margin, and a row of eight small spinules distally, between endopod and exopod. Endopod two-segmented; enp-1 as long as the combined length of first two exopod segments, with two outer rows of spinules and a distal row of spinules on inner margin; enp-2 with one outer spine, one geniculate seta, and a posterior hyaline frill. Exopod three-segmented, exp-1

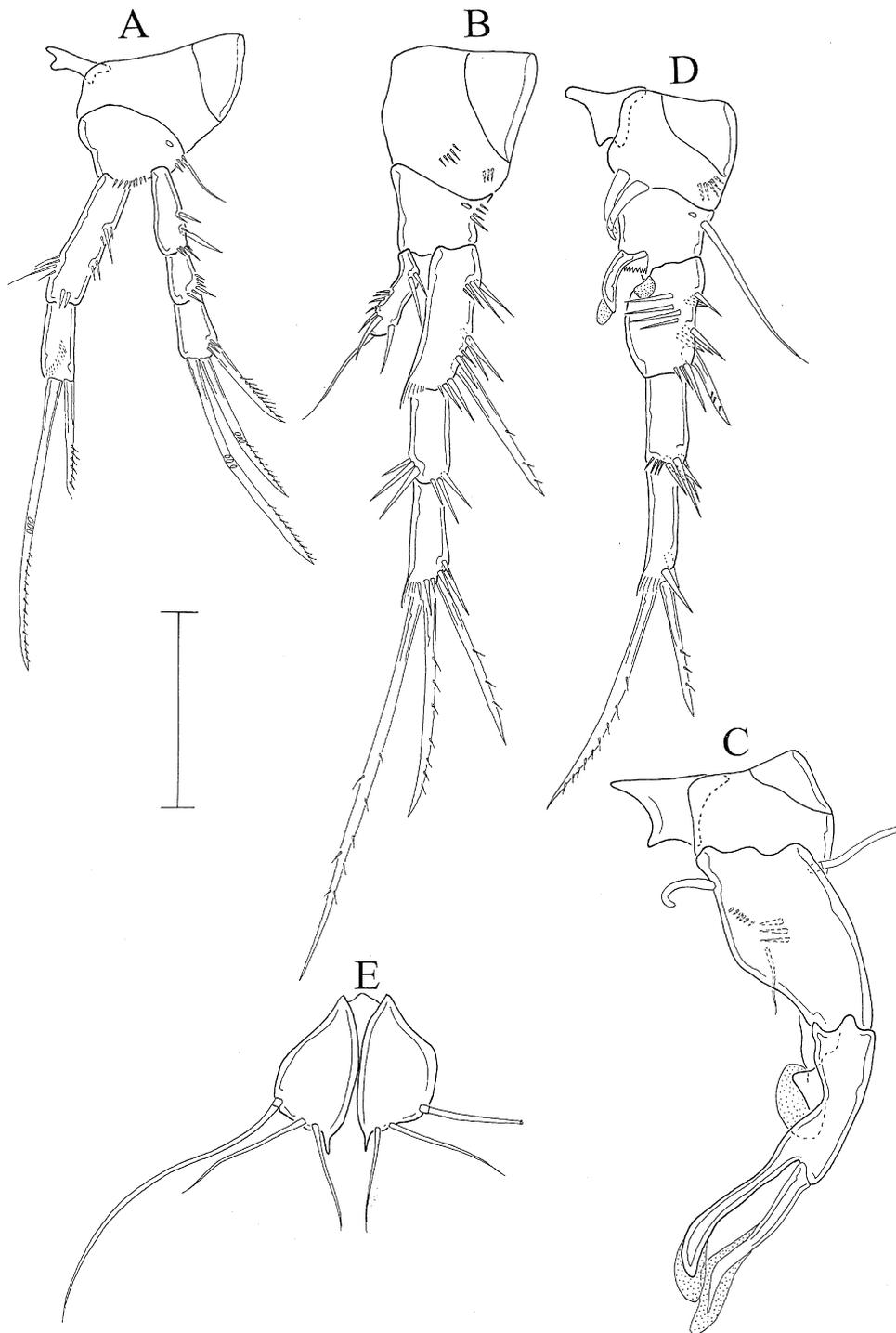


Figure 12. *Brasilibathynellocaris panamericana*, male. A, leg 1. B, leg 2. C, leg 3. D, leg 4. E, leg 5. Scale bar = 20 μ m.

with outer spine, exp-2 unarmed, exp-3 with two outer spines and two geniculate setae of different lengths. Leg 2 (Fig. 12B) coxa unarmed, with row of small spinules on posterior margin and row of spinules on anterior margin; basis without outer seta, with outer pore and one row of spinules on outer

margin; exopod three-segmented, exp-1 with a long outer spine and a hyaline frill on distal inner corner; exp-2 without armature and with two divergent rows of long spinules arranged distally; exp-3 with three setae of different lengths, distal hyaline frill at inner corner and row of long spinules on outer distal

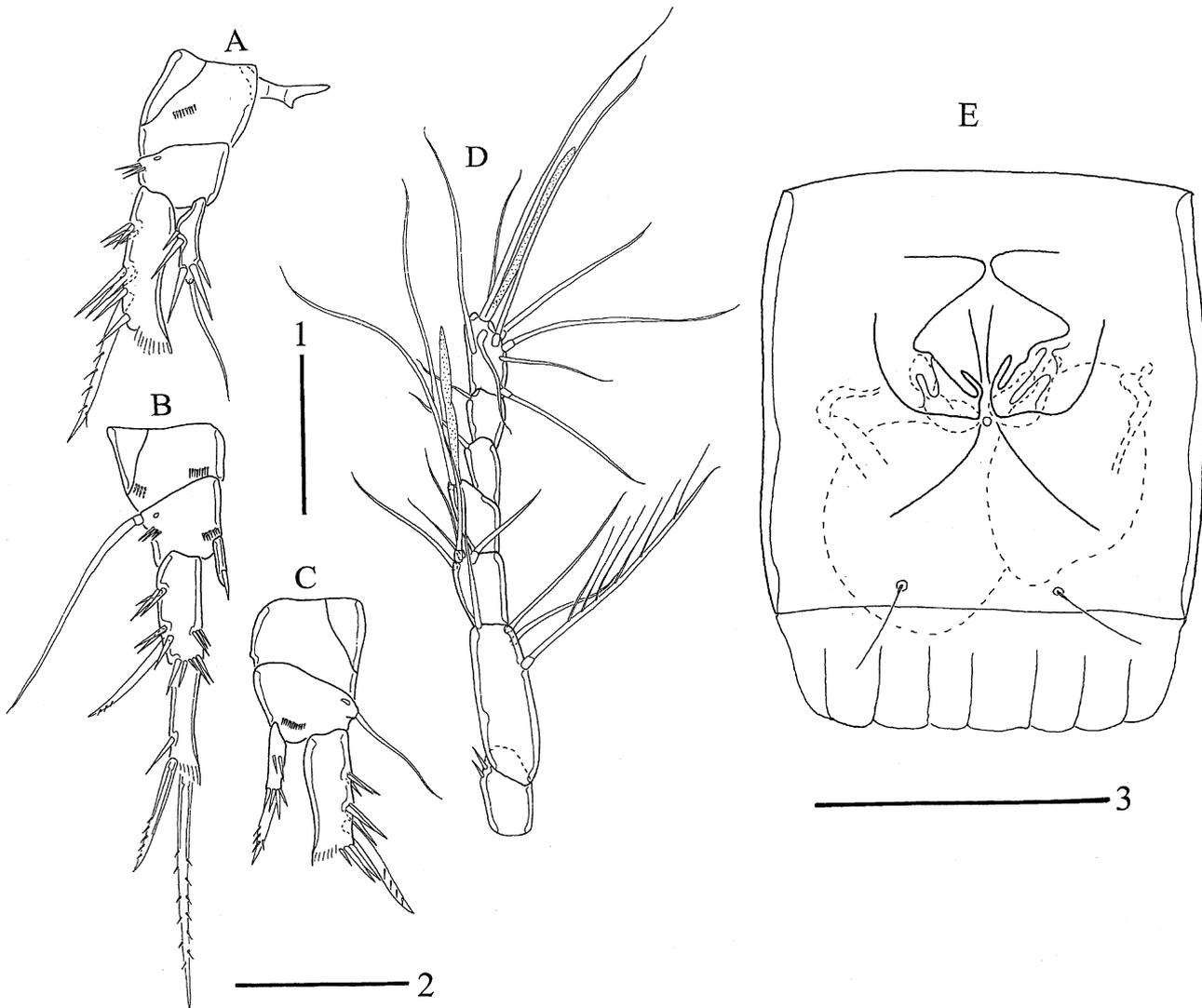


Figure 13. *Brasilibathynellocaris panamericana*, female. A, coxa, basis, endopod, and exopod 1 of leg 2. B, leg 3. C, coxa, basis, endopod, and exopod 1 of leg 4. D, antennule. E, female genital field. Scale bars 1 (for A–C), 2 (for D), 3 (for E) = 20 μm .

margin; endopod one-segmented, shorter than exp-1, with a row of spinules along inner margin, one long and subdistal spinule on each side of segment, two long spinules proximally inserted on outer margin and a distal seta. Leg 3 (Fig. 12C) coxa unarmed; basis with an outer seta (broken in the illustration), an inner strong (hook-shaped) spinule on proximal portion and two rows of spinules of different sizes near insertion of endopod; endopod represented by a slender seta; exopod inwardly curved, strong, ending in a long forceps formed by long apophysis and thumb (both with a hyaline margin); proximally with a hyaline 'cushion' on inner margin. Leg 4 (Fig. 12D) coxa with two long and strong spinules on anterior margin; basis quadratic, with an outer seta and an

outer pore; exp-1 reduced in length and with an invagination on proximal inner corner; anteriorly with a row of four long spinules; outer margin strongly ornamented and with an outer spine; exp-2 unarmed, with a transversal row of long spinules distally inserted on outer corner and a distal row of small spinules on inner corner; exp-3 with two distal setae of different lengths and two big spinules distally inserted on outer margin; endopod falciform, with a serrated lamella on outer margin and a subdistal hyaline 'tongue' on inner margin. Leg 5 trapezoid, with an inner process, an intercoxal plate, an outer basal seta, and two distal setae inserted on outer margin (Figs 11D, 12E); in different shape on Figure 11C because of lateral displacement of the

limbs. Leg 6 is an unarmed, rounded, and asymmetrical operculum covering the genital aperture (Fig. 11C), appearing as a triangular plate in lateral view (Fig. 11D).

Female: Sexually dimorphic in A1, legs 2–5, genital somite and furca. Length as in Noodt (1962). Integumental windows as in *B. brasilibathynellae*. Telson smooth, anal operculum smooth and slightly concave (Noodt, 1962: 229, fig. 1). Furca as in male, but with seven visible setae; setae I–III inserted proximally to the middle of furca, anterior to seta VII; seta II very reduced. A1 seven-segmented (Fig. 13D), not geniculate; armature beginning with proximal segment as follows: 0/4/5/2 + Ae/1/1/9 + Ae. A2 and mouthparts as in male. Praecoxa of legs 2–4 is a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Fig. 13A–C). Leg 1 as in male. Leg 2 (Fig. 13A) coxa unarmed, with one row of small spinules on anterior margin; basis without outer seta, with outer pore and ornamented with one row of spinules on outer margin; exopod three-segmented, exp-1 with long outer spine and with a hyaline frill on the distal inner corner, exp-2 and exp-3 as in male; endopod one-segmented, less ornamented than in male. Leg 3 (Fig. 13B) coxa unarmed, with a posterior and an anterior row of spinules; basis with a long outer seta, an outer pore, a row of spinules between outer seta and exopod, and a row of spinules before insertion of endopod; endopod represented by a short segment with a subdistal spinule; exopod two-segmented; exp-1 with an outer spine and two transversal inner rows of spinules, inserted one distally and subdistal; exp-2 with two apical setae, an hyaline frill on distal inner corner and an outer subdistal spinule. Leg 4 (Fig. 13C) coxa unarmed; basis with an outer seta, an outer pore, and a row of spinules near insertion of endopod; endopod one-segmented, longer than exp-1, with a row of transverse spinules medially inserted, probably delineating original separation between endopod and pinnate distal seta, now incorporated into segment, and two basal spinules; exopod three-segmented, exp-1 normally developed, with an outer spine and a hyaline frill on distal inner corner; exp-2 and exp-3 as in males. Leg 5 rectangular, with an inner process, an intercoxal plate, an outer basal seta and three distal exopodal setae (Noodt, 1962: 229, fig. 10). Genital field as illustrated in Figure 13E. Genital operculum formed by two lateral and unarmed plates covering the gonopores. Single medially located copulatory pore.

BRASILIBATHYNELLOCARIS PANAMERICANA
'FORMA TRUNCATA'

Parastenocaris panamericana f. *truncata* – Noodt (1962: 230); Rouch (1986), Dussart & Defaye (1990).

Material examined: Specimens from sample S 114 (Noodt, 1962); from this sample, Noodt prepared 12 slides now stored at DZMB (Noodt collection, box 6, slide nos. 9–20); only slides 9–13 carry members of *B. panamericana* 'f. *truncata*', as follows: three males each (nos. 9, 10); four, three, and one female, respectively (nos. 11–13).

Collecting locality: El Salvador, groundwater from beach of a small rocky sea bay near La Fochota (south of La Union).

Diagnosis: Males of *B. panamericana* 'f. *truncata*' are similar to those of the nominotypical form in all characters. Females differ in the following characters: furca (Fig. 11B; see also Noodt, 1962: 229, figs 15, 16, and 232, figs 26–28) seta IV reduced to a slender spine; seta V reduced to a stout spine, with several setules arranged distally; other setae developed as in male. Leg 5 rectangular, with an inner process, an intercoxal plate, an outer basal seta, but lacking the most proximal exopodal seta, as in male Noodt (1962: 231, fig. 19).

BRASILIBATHYNELLOCARIS SALVADORENSIS
(NOODT, 1962) (FIGS 14–19)

Parastenocaris salvadorensis Noodt – Noodt (1962: 233); Rouch (1986), Dussart & Defaye (1990).

Brasilibathynellocares salvadorensis (Noodt) – Jakobi (1972a).

Material examined: Syntypes from sample S 175 (Noodt, 1962); from this sample, Noodt prepared nine slides now stored at DZMB (Noodt collection, box 6, slide nos. 28–36); only slides 28–33 carry members of *B. salvadorensis* s.s., as follows: four males (slide no. 28), one neotenic male (29), three females (30), five females (31), nine females (32), four females (33). Additional material: male copepodid V dissected and mounted on six slides (labelled SI to SVI) and deposited in DZMB (Noodt collection, box A); the exact locality of this sample is not mentioned and unknown, as the vial, which contains male and female adults and juveniles of *B. salvadorensis*, is labelled with the species name only.

Collecting locality: El Salvador, groundwater from bank of Rio Zacatiapa, on road between San Salvador and Zacatecoluca. See note in 'Collecting locality' section under *B. panamericana*.

Description

Male: Length as in Noodt (1962). Rostrum not fused to cephalothorax, with a wide base and two sensilla on tip. Cephalothorax with dorsal integumental window,

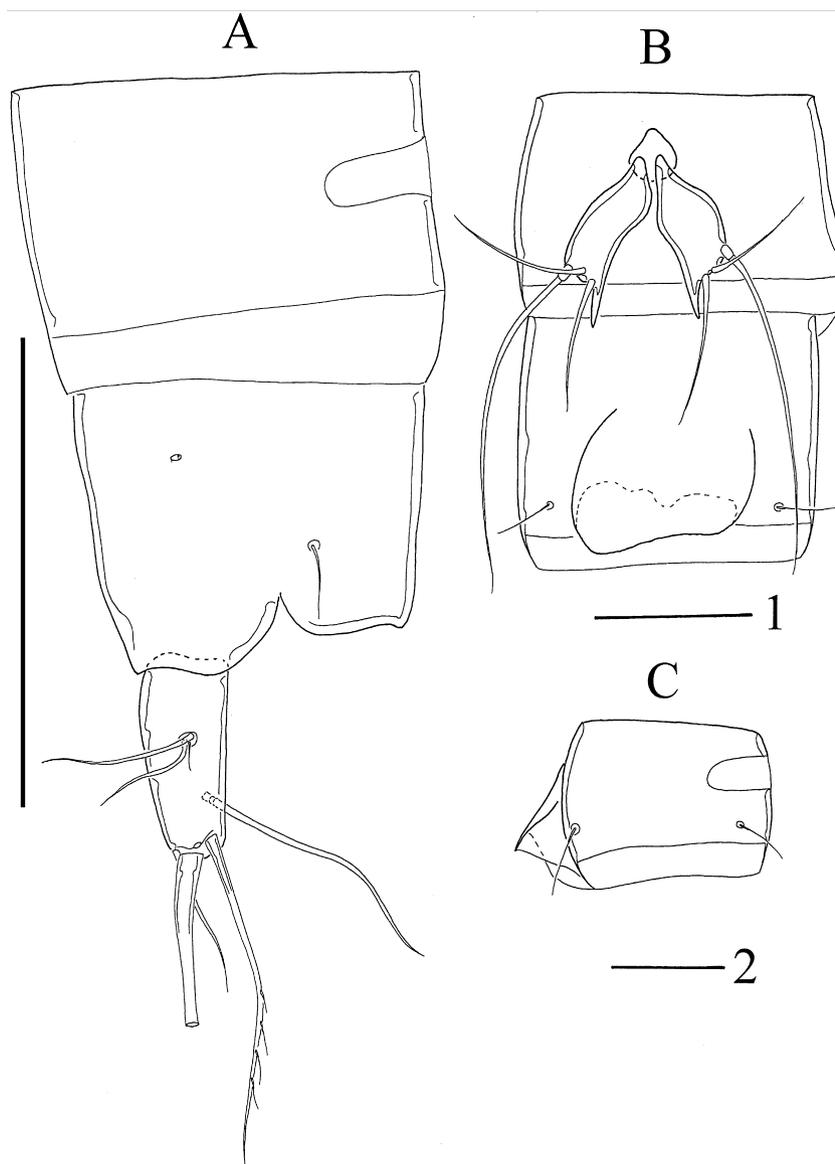


Figure 14. *Brasilibathynellocares salvadorensis*. A, lateral view of male telson. B, ventral view of first and second urosomite of male. C, lateral view of second urosomite of male. Vertical scale bar (for A) = 50 μ m. Scale bar 1 (for B) = 20 μ m. Scale bar 2 (for C) = 20 μ m.

second to fifth urosomites with one dorsal integumental window each. Telson smooth (Fig. 14), anal operculum smooth and slightly concave (Noodt, 1962: 234, fig. 30). Furca (Fig. 14) with seven setae; setae I–III inserted proximally to the middle of furca, anterior to seta VII; seta II very reduced; seta IV subdistal, inserting dorsally, on outer margin of furca; setae V very long, inserting on distal margin of furca (Noodt, 1962: 234, fig. 30); seta VI much shorter than seta V inserting beneath it; seta VII of about same size as seta VI, socketed at basis and inserting dorsally, on inner margin of furca. A1 (Fig. 15A) eight-segmented and prehensile; armature beginning with proximal

segment: 0/6/4/2/5 + Ae/3/2/9 + Ae. A2 and mouthparts as in *B. brasilibathynellae*. Praecoxa of legs 1–4 is a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Figs 15B, 16A–C). Leg 1 (Fig. 15B) coxa unarmed; basis with outer seta and one pore on anterior outer margin, three spinules on outer margin, and a row of eight small spinules distally inserted between endopod and exopod; exopod three-segmented, exp-1 with outer spine, exp-2 unarmed, exp-3 with two outer spines and two geniculate setae of different lengths; endopod two-segmented, enp-1 as long as the combined length of first two exopod segments, with two outer

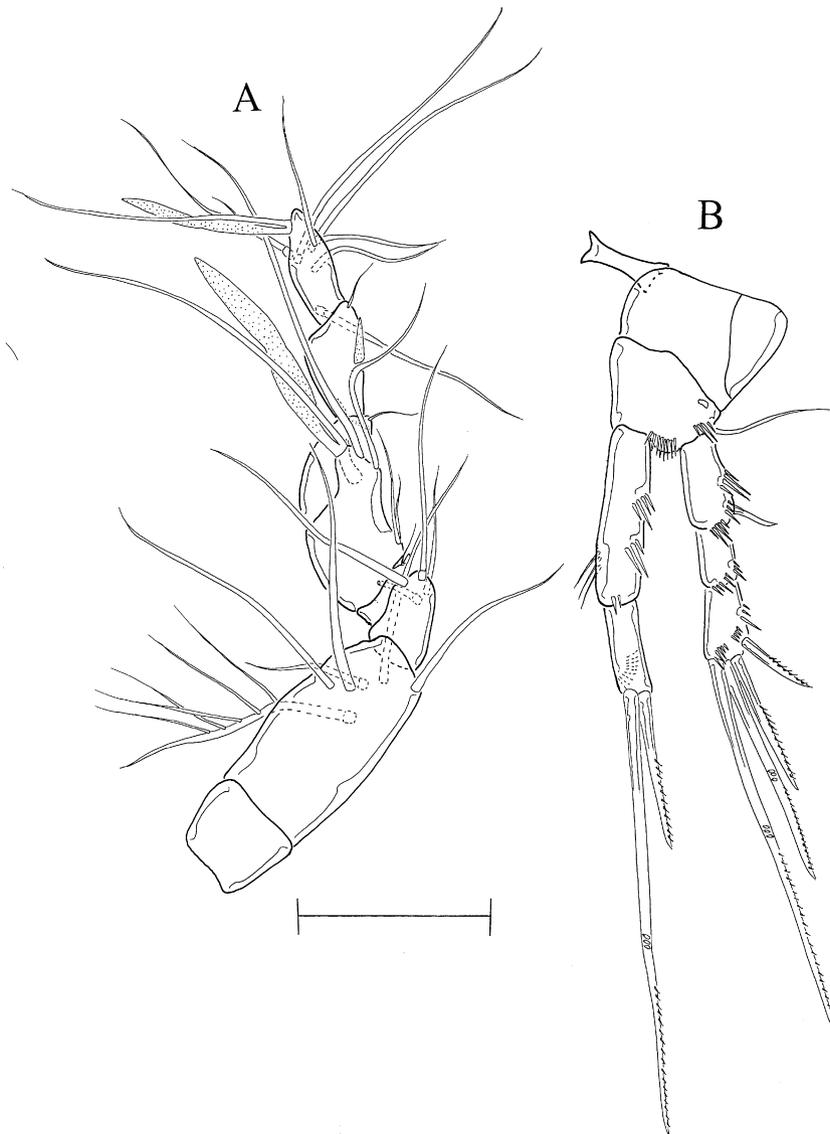


Figure 15. *Brasilibathynellocaris salvadorensis*, male. A, antennule. B, leg 1. Scale bar = 20 μ m.

transversal rows of spinules and a distal longitudinal row of spinules on inner margin, enp-2 with one outer spine, one geniculate seta, and a posterior hyaline frill. Leg 2 (Fig. 16A) coxa unarmed, with one row of small spinules on anterior margin; basis without outer seta and ornamented with one longitudinal row of spinules and one pore on outer margin; exopod three-segmented, exp-1 with a long outer spine and a hyaline frill on distal inner corner; exp-2 without armature and with two divergent transversal rows of long spinules inserted distally (hair-like spinules on distal inner corner); exp-3 with three setae, distal hyaline frill at distal inner corner and row of long spinules on outer distal corner; endopod one-segmented, shorter than exp-1, with a longitudinal row of five short spinules on inner basal margin, one

longitudinal row of four spinules of increasing length on inner distal margin, one apical setae, one subapical strong spinule on outer margin, and a transversal row of three long spinules at one-third of the outer margin. Leg 3 (Fig. 16B) coxa unarmed; basis with a long outer seta, an inner strong (hook-shaped) spinule on proximal portion, and two rows of spinules of different sizes near insertion of endopod; endopod represented by a slender seta; exopod inwardly curved, strong, ending in a long forceps formed by apophysis and thumb (both with a hyaline margin); proximally with a hyaline 'cushion'. Leg 4 (Fig. 16C) coxa with two long and strong spinules on anterior side (around them we can observe a weakly chitinized zone) and a row of small spinules posteriorly inserted; basis with an outer seta, an outer pore, and a row of spinules on outer margin;

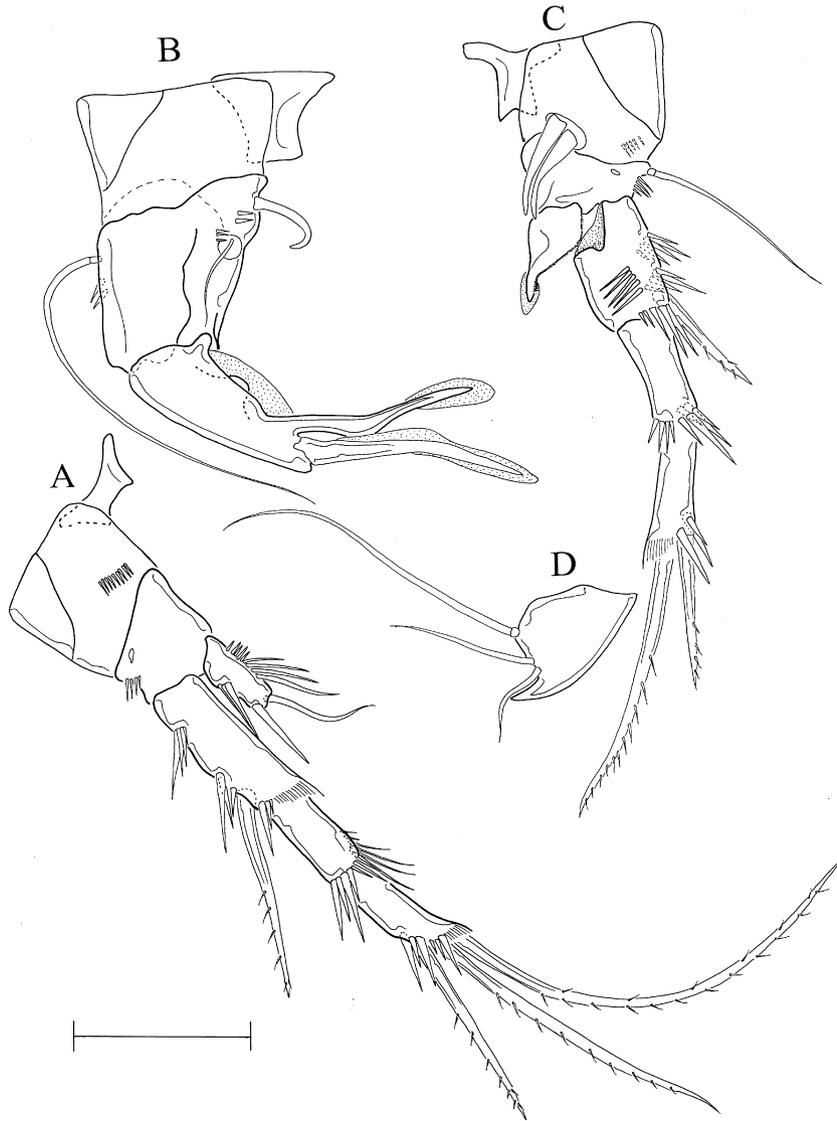


Figure 16. *Brasilibathynellocares salvadorensis*, male. A, leg 2. B, leg 3. C, leg 4. D, leg 5. Scale bar = 20 μ m.

exp-1 reduced in length and with an invagination on proximal inner corner, anteriorly with a row of four strong spinules; outer margin strongly ornamented and with an outer spine; exp-2 unarmed, with a distal row of long spinules on outer corner and a row of smaller spinules on distal inner corner; exp-3 with two distal setae of different length and with three big spinules on distal outer corner; endopod subtrapezoidal, quadratic on proximal margin and prolonged in an inner blunt tip with distal hyaline margin. Leg 5 trapezoidal, with an inner process, an intercoxal plate, an outer basal seta, and two distal setae (Figs 14B, 16D). Leg 6 is an unarmed, rounded, and asymmetrical operculum covering the genital aperture (Fig. 14B), appearing as a triangular plate in lateral view (Fig. 14C).

Female: Sexually dimorphic in A1, legs 2–5, genital somite, and furca. Length as in Noodt (1962). Integumental windows as in *B. brasilibathynellae*. Telson smooth, anal operculum smooth and slightly concave (Noodt, 1962: 234, fig. 29). Furca as in male, with seven setae; setae I–III inserted proximally to the middle of furca, anterior to seta VII; setae 2 reduced or absent. A1 as in female of *B. panamericana* (Fig. 13D). A2 and mouthparts as in male. Praecoxa of legs 2–4 is a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Fig. 17A–C). Leg 1 as in male. Leg 2 (Fig. 17B) coxa unarmed, with one row of small spinules on posterior margin; basis without outer seta and ornamented with one row of spinules and one pore on outer margin; exopod three-segmented,

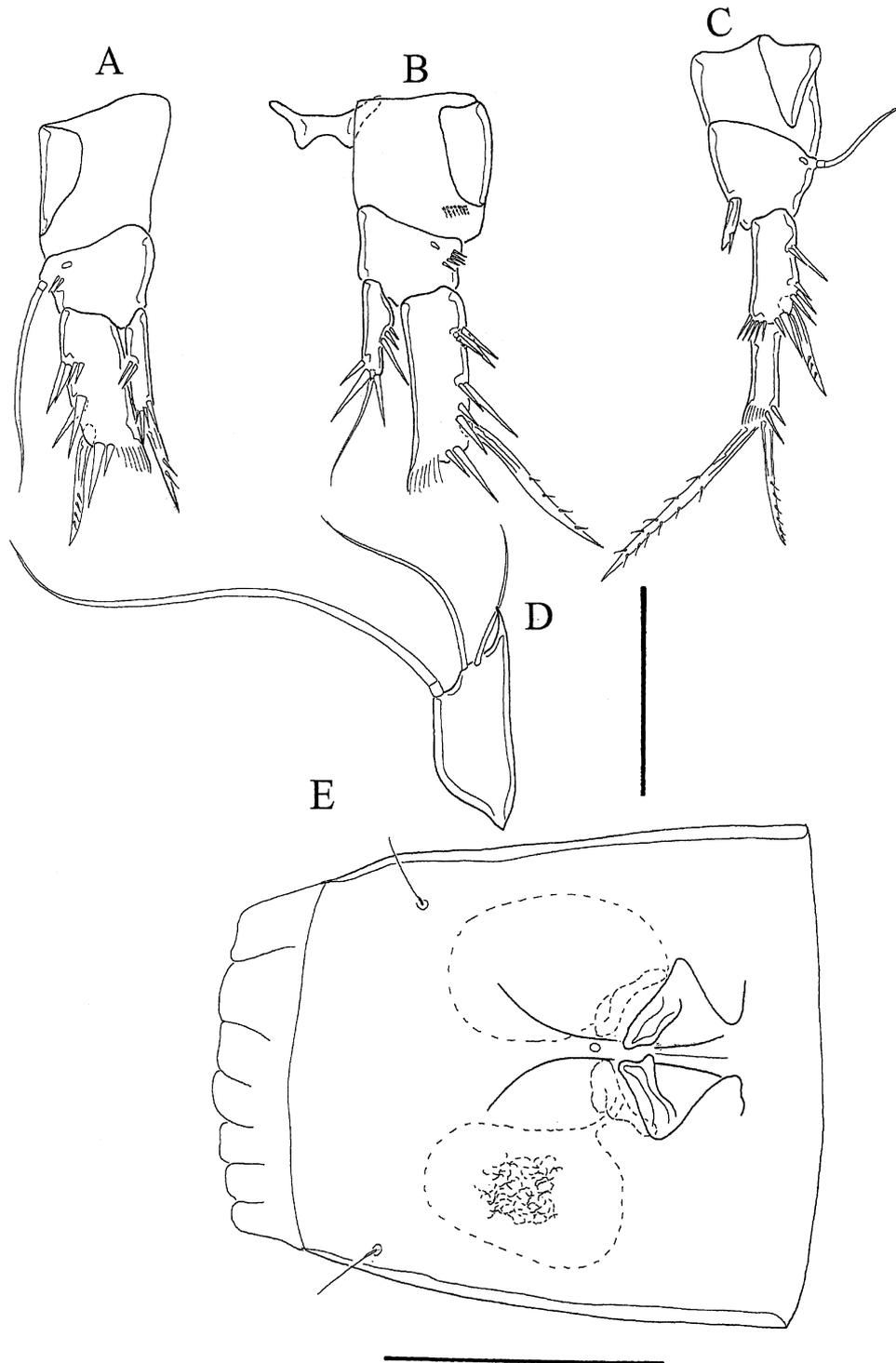


Figure 17. *Brasilibathynellocaris salvadorens*, female. A, coxa, basis, endopod, and exopod 1 of leg 4. B, coxa, basis, endopod, and exopod 1 of leg 2. C, leg 3. D, leg 5. E, female genital field. Vertical scale bar (for A–D) and horizontal scale bar (for E) = 20 μ m.

exp-1 with long outer spine and with a hyaline frill on distal inner corner, exp-2 and exp-3 as in male; endopod one-segmented, less ornamented than in male. Leg 3 (Fig. 17C) coxa unarmed; basis with an

outer seta and an outer pore; endopod represented by a short segment with a subdistal spinule; exopod two-segmented; exp-1 with an outer spine and one on the distal corner; exp-2 with two setae, a hyaline

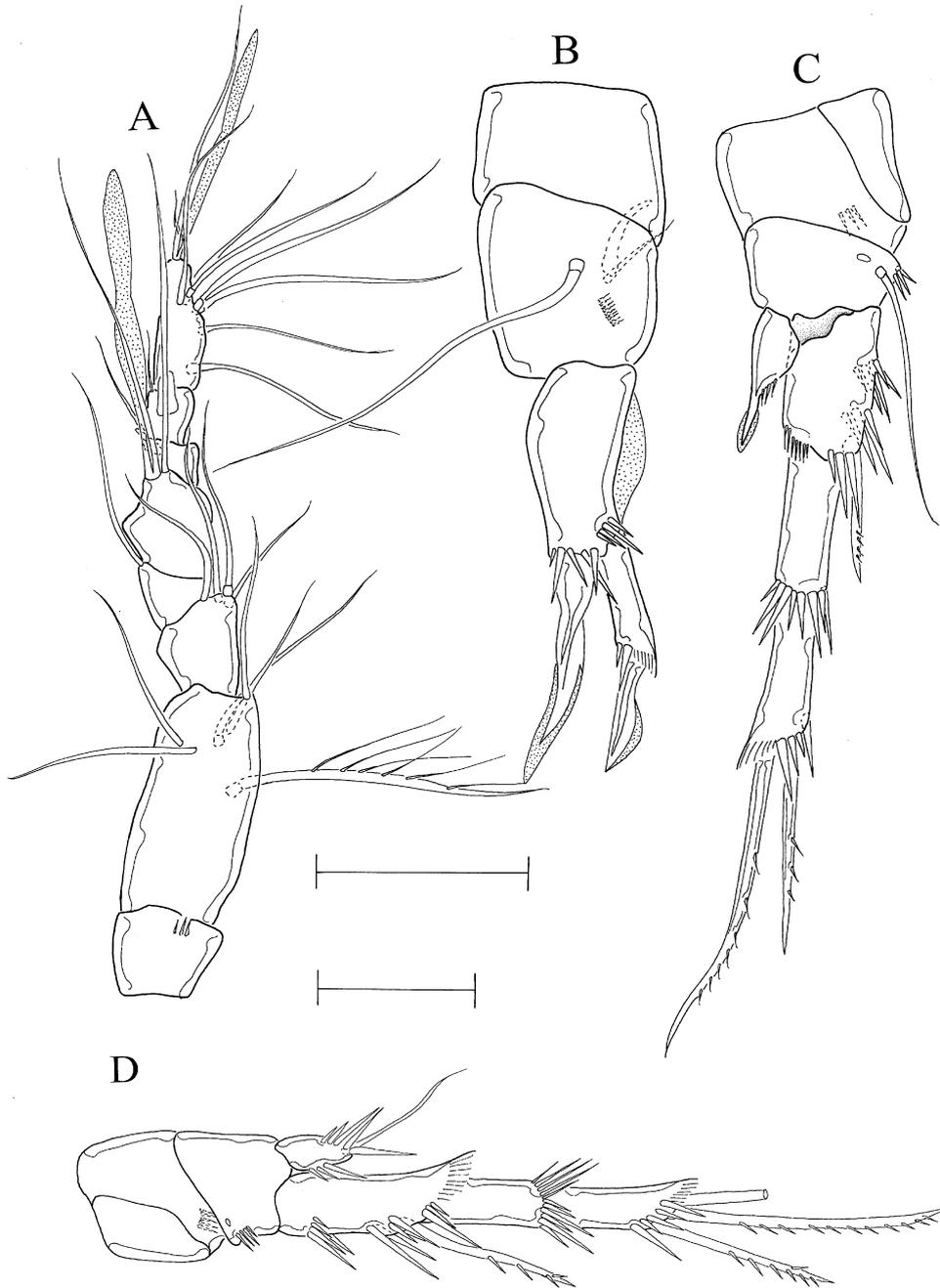


Figure 18. *Brasilibathynellocaris salvadorensis*, neotenic male. A, antennule. B, leg 3. C, leg 4. D, leg 2. Scale bars (upper for A–C, lower for D) = 20 μ m.

frill on the distal inner corner, and two spinules on distal outer corner. Leg 4 (Fig. 17A) coxa and basis unarmed; basis with an outer seta, an outer pore and two spinules below it; endopod one-segmented, longer than exp-1, with a transverse row of spinules medially inserted, probably delineating the original separation between endopod and pinnate distal seta, now incorporated into segment; exopod three-segmented, exp-1 normally developed,

with an outer spine and a hyaline frill on distal inner corner; exp-2 and exp-3 as in male. Leg 5 trapezoidal, with an inner process, an intercoxal plate, an outer basal seta, and two distal setae inserted on outer margin (Fig. 17D). Genital field as illustrated in Figure 17E. Genital operculum formed by two lateral and unarmed plates covering the gonopores. Single medially located copulatory pore.

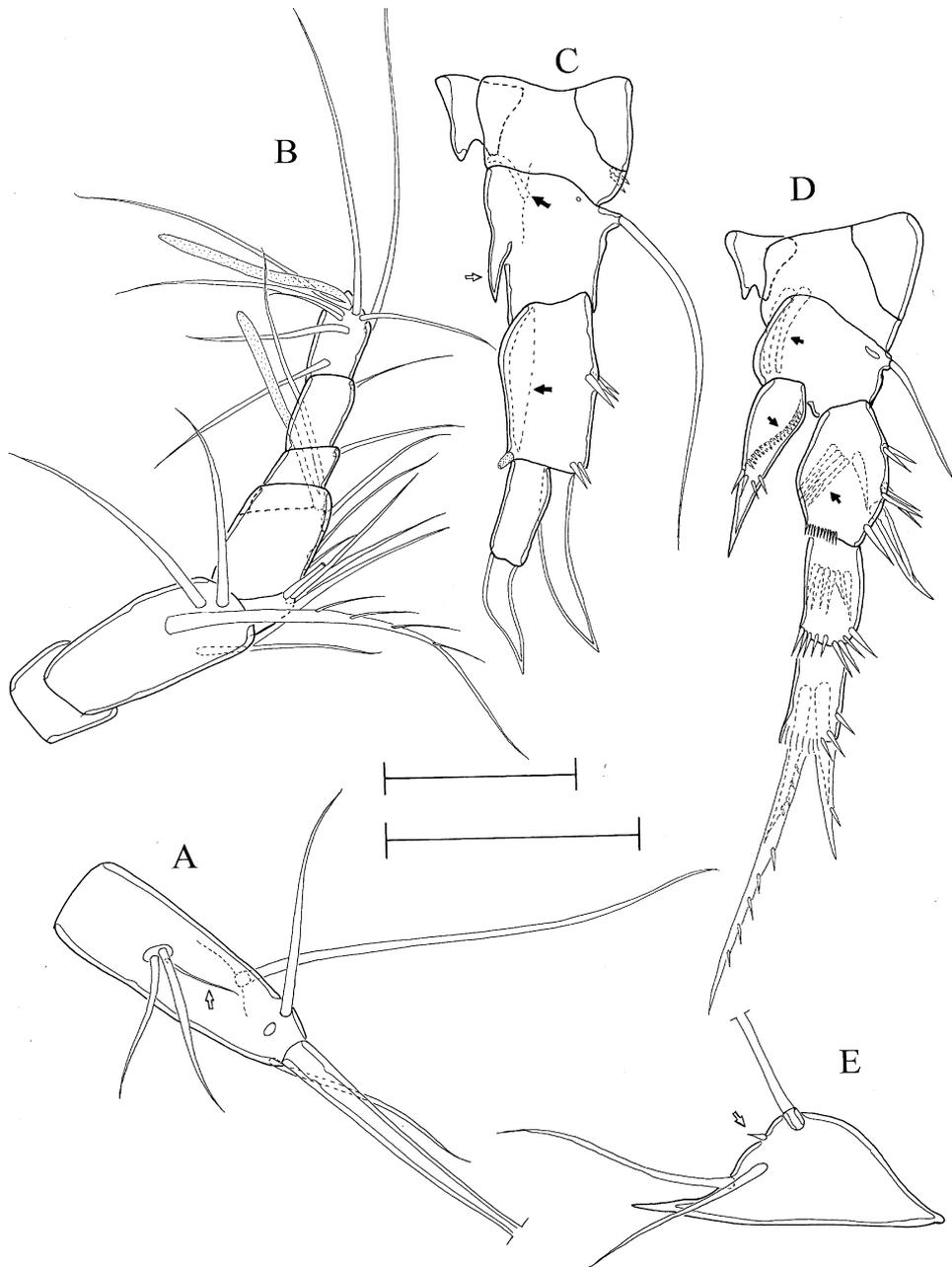


Figure 19. *Brasilibathynellocaris salvadorensis*, male of copepodid V. A, furca. B, antennule. C, leg 3. D, leg 4. E, leg 5. Solid arrows point to structures of the adult developing inside the copepodid; open arrows point to structures of the copepodid that will be reduced or absent in the adult. Scale bars (upper for A–D, lower for E) = 20 µm.

BRASILIBATHYNELLOCARIS SALVADORENSIS
'FORMA LANCEOLATA'

Parastenocaris salvadorensis f. *lanceolata* – Noodt (1962: 235); Rouch (1986), Dussart & Defaye (1990).

Material examined: Noodt (1962) reported material from samples S 310 and S 311, which was collected from different spots at the same site; we found no material from S 310, thus observations were based on ten females from S 311.

Collecting locality: El Salvador, Laguna de Ilopango near San Salvador, groundwater from sandy beach at Balneario Apulo.

Diagnosis: Females of *B. salvadorensis* f. *lanceolata* differ from the nominotypical form only in the furca (Noodt, 1962: 236, figs 40, 41).

Description of neotenic male of *B. salvadorensis*
Neotenic male with five urosomites and telson. No distinct difference in shape and armature of furca.

A2, legs 1 and 5 as in normally developed male. A1 (Fig. 18A) eight-segmented, as in male, but weakly geniculate; without the normal development of the fifth segment that can be seen in the male. Praecoxa of legs 2 and 4 is a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Fig. 18C, D; not observed for leg 3). Leg 2 (Fig. 18D) as in male, but with a row of spinules on distal inner corner of exp-2 not transformed into hair-like spinules. Leg 3 (Fig. 18B) basis with a long outer seta, a strong curved spinule, and endopod represented by a seta; exopod two-segmented; exp-1 with a strong outer spine homologous to the thumb and an inner hyaline cushion; exp-2 with a distal spine; thumb and exp-2 spine with a hyaline border. Leg 4 (Fig. 18C) with three-segmented exopod; exp-1 not transformed as in normally developed male, with the proximal invagination on proximal inner corner, without an anterior row of strong spinules; in this case, the plesiomorphic condition is expressed in the neotenic male as a distal row of spinules on distal inner corner of the segment.

Description of copepodid V of B. salvadorensis

Male copepodid with four urosomites and telson. Furca with seven setae (Fig. 19A); seta II not extremely reduced. A1 seven-segmented (Fig. 19B), with aesthetascs present on segments 4 and 7. Praecoxa as a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa of legs 3 and 4 (Fig. 19C, D). Leg 3 (Fig. 19C) with lamelliform endopod; exopod two-segmented, exp-1 without inner hyaline cushion and with a distal inner tube pore, exp-2 without distal hyaline frill; basis with a long outer seta and without strong curved proximal spinule; thumb and exp-2 spines without hyaline margins; structures that appear only in the adult, such as the exp-1 hyaline cushion and the basal hook-like spinule (indicated by dark arrows) can be seen inside the copepodid V limb. Leg 4 coxa without the two anterior modified spinules (Fig. 19D); endopod lamelliform, triangular, with a transverse row of spinules inserted at the midlength of the segment and without hyaline distal margin; exp-1 without invagination on proximal inner corner, rectangular and with distal hyaline frill on inner corner; the strong row of anterior spinules of exp-1, the two modified basal spinules and the outer serrated endopod margin that appear in the adult can be seen inside the copepodid V limb and are indicated by dark arrows. Leg 5 (Fig. 19E) with an inner process, an intercoxal plate, an outer basal seta, and three setae inserted on outer margin; proximal exopodal seta adjacent to outer basal seta very reduced.

BRASILIBATHYNELLOCARIS CUSCATLANENSIS

(NOODT, 1962) **COMB. NOV.** (FIGS 20–22)

Parastenocaris cuscatlanensis Noodt – Noodt (1962: 237); Rouch (1986), Dussart & Defaye (1990).

Pararemaneicaris cuscatlensis (Noodt) – Jakobi (1972a), incorrect subsequent spelling.

Material examined: Syntypes from sample S127 (Noodt, 1962); from this sample, Noodt prepared seven slides now at DZMB (Noodt collection, box 6, nos. 21–27); only slides 21–24 and 26 carry members of *B. cuscatlanensis* comb. nov., as follows: three males (slide no. 21), two males (22), three females (23), three females (24), three females (26).

Collecting locality: El Salvador, on border with Honduras, groundwater from gravel bar of Rio Lempa at Citalá. See note in ‘Collecting locality’ section under *B. panamericana*.

Description

Male: Length as in Noodt (1962). Cephalothorax with dorsal integumental window, second to fifth urosomite with one dorsal integumental window each. Telson smooth, anal operculum smooth (Fig. 20A) and slightly concave (Noodt, 1962: 238, fig. 48). Furca (Fig. 20A) with seven setae; setae I–III inserted proximally to the middle of furca, anterior to seta VII; seta II very reduced, not visible in some animals; seta IV subdistal, inserting dorsally, on outer margin of furca; setae V very long, inserting on distal margin of furca. A1 (Fig. 20B, C) eight-segmented and prehensile; armature beginning with proximal segment: 0/6/4/2/5 + Ae/3/2/9 + Ae. A2, Md, Mx1, and Mxp as in *B. brasilibathynellae*. Praecoxa of legs 1–4 is a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Fig. 21A–D). Leg 1 (Fig. 21A) coxa unarmed; basis with outer seta and one pore on anterior outer margin, four spinules on outer margin, and a distal row of five small spinules between endopod and exopod. Endopod two-segmented, enp-1 as long as the combined length of first two exopod segments, with a proximal row of small transverse spinules and a longitudinal row of larger spinules on outer margin, enp-2 with one subapical outer spine, one geniculate apical seta; exopod three-segmented, exp-1 with outer spine, exp-2 unarmed, exp-3 with two outer spines and two apical geniculate setae of different lengths. Leg 2 (Fig. 21B) coxa unarmed, with one row of small spinules at posterior margin; basis without outer seta and ornamented with one row of spinules and a pore on outer margin; exopod three-segmented, exp-1 with a long outer spine and a hyaline frill on distal inner corner;

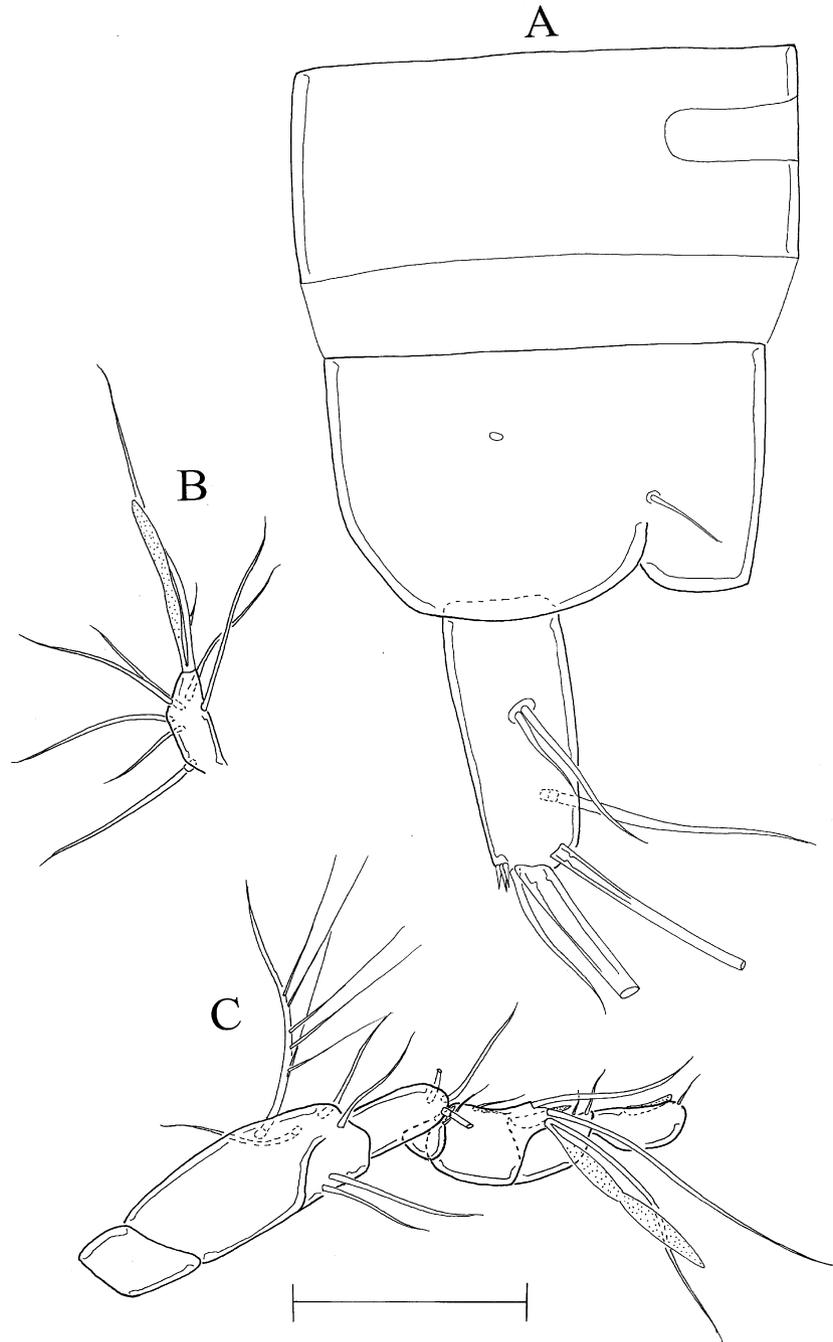


Figure 20. *Brasilibathynellocares cuscatlanensis* **comb. nov.**, male. A, male telson, lateral. B, last segment of right antennule. C, first to seventh segments of left antennule. Scale bar = 20 μ m.

exp-2 without armature and with two divergent rows of long spinules distally inserted (hair-like spinules on distal inner corner); exp-3 with three setae, distal hyaline frill at inner corner and row of long spinules on outer margin; endopod one-segmented, smaller than exp-1, with an inner row of spinules along distal third, a short distal seta, a row of four spinules on distal outer corner, and two proximal spinules on

same side. Leg 3 (Fig. 21C) coxa unarmed; basis with an outer seta (broken in the illustration), an inner strong and curved spinule on proximal portion, and a row of short spinules near insertion of endopod; endopod represented by a slender seta; exopod inwardly curved, strong, ending in a long forceps formed by apophysis and thumb (both with a hyaline margin), proximally with a small hyaline cushion.

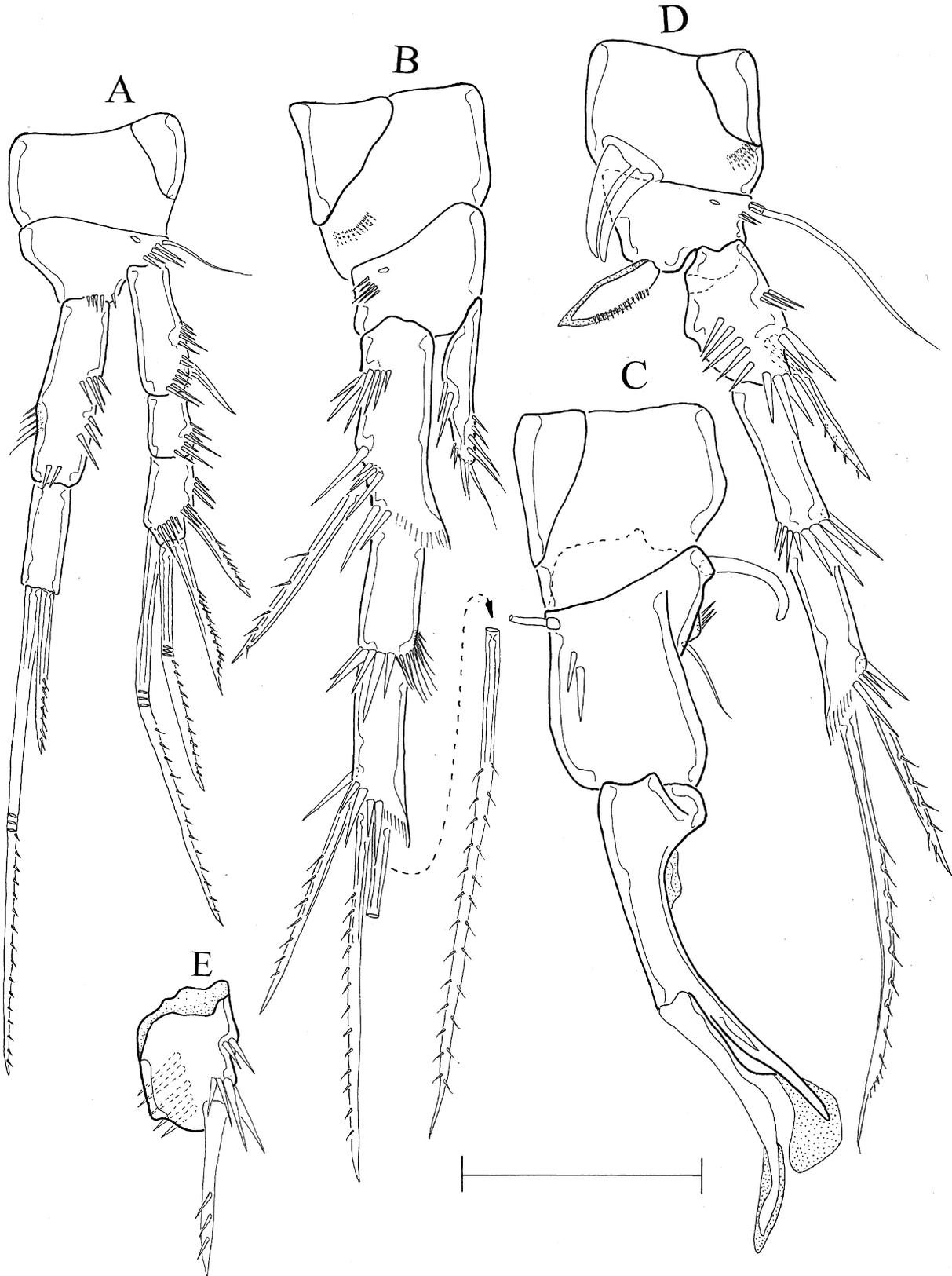


Figure 21. *Brasilibathynellocares cuscatlanensis* **comb. nov.**, male. A, leg 1. B, leg 2. C, leg 3. D, leg 4. E, leg 4 exopod 1, posterior view. Scale bar = 20 μ m.

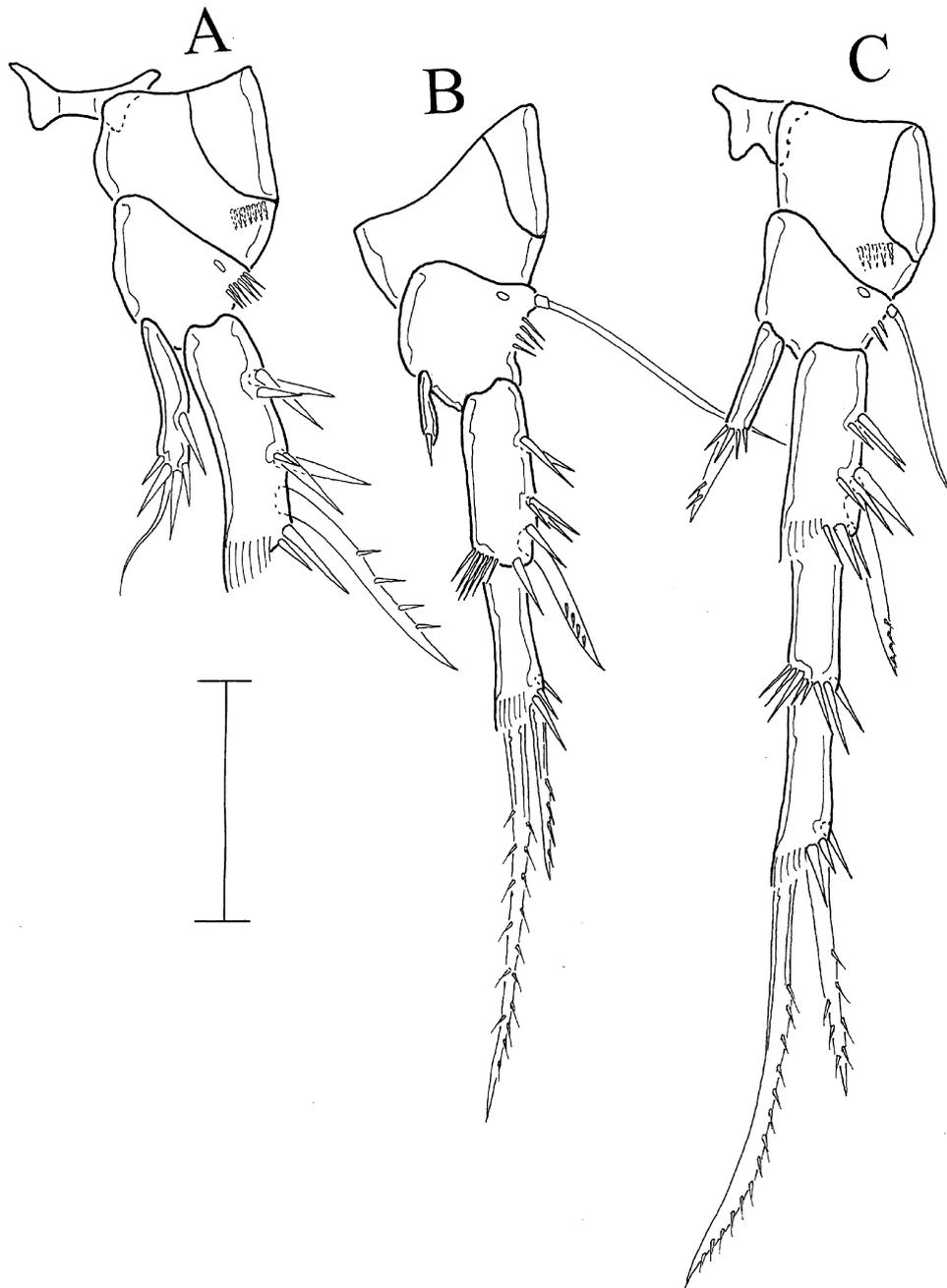


Figure 22. *Brasilibathynellocaris cuscatlanensis* **comb. nov.**, female. A, coxa, basis, endopod, and exopod 1 of leg 2. B, leg 3. C, leg 4. Scale bar = 20 μ m.

Leg 4 (Fig. 21D, E) coxa with two long and strong spinules on anterior margin and a posterior row of small spinules; basis rectangular with an outer seta, two spinules between outer seta and exopod and an outer pore; exp-1 reduced in length and with a proximal invagination on posterior margin (Fig. 21D, dashed area; E), anteriorly with a row of five spinules, outer margin strongly ornamented and with an outer spine; exp-2 unarmed, with a distal row of long

spinules on outer corner and a row of small spinules on inner corner; exp-3 with two distal setae and four spinules distally inserted on outer margin; endopod horizontally displaced, with a row of spinules along outer margin and a hyaline lamella running around segment. Leg 5 trapezoidal, with an inner process, an intercoxal plate, an outer basal seta and two distal setae inserted on outer margin (Noodt, 1962: 238, fig. 55). Leg 6 not observed.

Female: Length as in Noodt (1962). Integumental windows as in *B. brasilibathynellae*. Telson smooth, anal operculum smooth and slightly concave (Noodt, 1962: 238, fig. 47). Furca as in male, with seven setae; setae I–III inserted proximally to the middle of furca, anterior to seta VII; setae 2 reduced, not visible in some animals. A1 as in female of *B. panamericana* (Fig. 13D). A2 and mouthparts as in male. Praecoxa of legs 2–4 is a distinct and relatively large triangular section adjacent to the outer proximal corner of coxa (Fig. 22A–C). Leg 1 as in male. Leg 2 (Fig. 22A) coxa unarmed, with one row of small spinules at posterior margin; basis without outer seta and ornamented with one row of spinules and a pore on outer margin; exopod three-segmented, exp-1 with long outer spine and with a hyaline frill on distal inner corner, exp-2 and exp-3 as in male; endopod one-segmented, less ornamented than in male. Leg 3 (Fig. 22B) coxa unarmed; basis with a long outer seta, an outer pore, and a row of spinules between outer seta and exp-1; endopod represented by a short segment with a subdistal spinule; exopod two-segmented; exp-1 with an outer spine and one row of spinules on distal inner corner; exp-2 with two setae, hyaline frill on distal inner corner, and three spinules on outer distal corner. Leg 4 (Fig. 22C) coxa unarmed, with a posterior row of spinules; basis with an outer seta, an outer pore and two spinules between outer seta and exopod; endopod one-segmented, as long as exp-1, with a transverse row of spinules, probably delineating original separation between endopod and slightly pinnate distal seta, now incorporated in segment; exopod three-segmented, exp-1 normally developed, with an outer spine and a hyaline frill on distal inner corner; exp-2 and exp-3 as in males. Leg 5 trapezoidal, with an inner process, an intercoxal plate, a basal seta, and two distal setae inserted on outer margin (Noodt, 1962: 238, fig. 54). Genital field like in *B. panamericana*. Genital operculum formed by two lateral and unarmed plates covering the gonopores. Single medially located copulatory pore.

PHYLOGENY RECONSTRUCTION

Figures 24 and 25A–B show the hypothesis of phylogenetic relationships within the genus *Brasilibathynellocaaris* for both the manual and computer-derived methods, applying both Wagner and Camin–Sokal algorithms. Results, using the classical Hennigian procedures as well as the computer-based cladistic approach, were three most parsimonious trees (length = 19) with two different topologies and different optimization of characters. The same topology, but with different character distributions (see Characters 4 and 7 below), was obtained when applying the manual method (Fig. 24) and the computer method for the Camin–Sokal algorithm (Fig. 25A),

respectively. Characters 4 and 7 are considered as autapomorphic for the genus *Brasilibathynellocaaris* in the phylogeny inferred manually, with the loss of character 7 occurring in the stem line of *B. salvadorensis*–*B. cuscatlanensis* comb. nov. and the loss of character 4 in *B. brasilibathynellae*. In the result obtained by the application of the purely cladistic method supporting parsimony for Camin–Sokal (Fig. 25A), characters 4 and 7 are homoplastic. An alternative topology was also obtained by the application of the Wagner algorithm (Fig. 25B); its biological implications are discussed in the text. Other character distributions remained the same when applying both methods. A character state matrix is given in Table 1. We endorse the hypothesis presented in Figure 24. The characters and polarizations are as follows:

1. Leg 4 exp-1 of male with normal development (0, pl); reduced in length, with an invagination on the proximal inner corner (1, ap).
2. Leg 4 coxa of male without strong ornamentation (0, pl); with two strong spinules on anterior margin (1, ap).
3. Leg 3 apophysis of male as long as broad, or shorter than broad (0, pl); much longer than broad, inwardly curved, forming a pincer with the thumb, and with hyaline margin (1, ap).
4. Leg 3 exp-1 of male without an inner hyaline cushion (0, pl); with an inner hyaline cushion (1, ap).
5. Leg 4 exp-1 of male with a normal hyaline frill on distal inner corner or modified as an row of spinules on distal inner corner (0, pl); strong row of spinules on anterior margin (1, ap).
6. Leg 4 exp-1 of male with a strong row of spinules on anterior margin (0, pl); without such a row (1, ap).
7. Endopod of leg 4 of male not transformed into a grasping organ (0, pl); modified, forming a grasping organ (1, ap).
8. Leg 4 endopod of male without hyaline lamella (0, pl); with hyaline lamella (1, ap).
9. Distal inner corner of leg 2 exp-2 of male with strong spinules (0, pl); with hair-like spinules (1, ap).
10. Basis of leg 4 of male without ornamentation on outer margin (0, pl); with row of spinules between outer seta and exp-1 (1, ap).
11. Leg 2 endopod of male short (0, pl); longer than exp-1 (1, ap).
12. Last urosomite without well-developed serrated hyaline frill (0, pl); with well-developed serrated hyaline frill (1, ap).
13. Leg 5 of male without any ornamentation on distal inner margin (0, pl); with row of spinules on distal inner margin (1, ap).

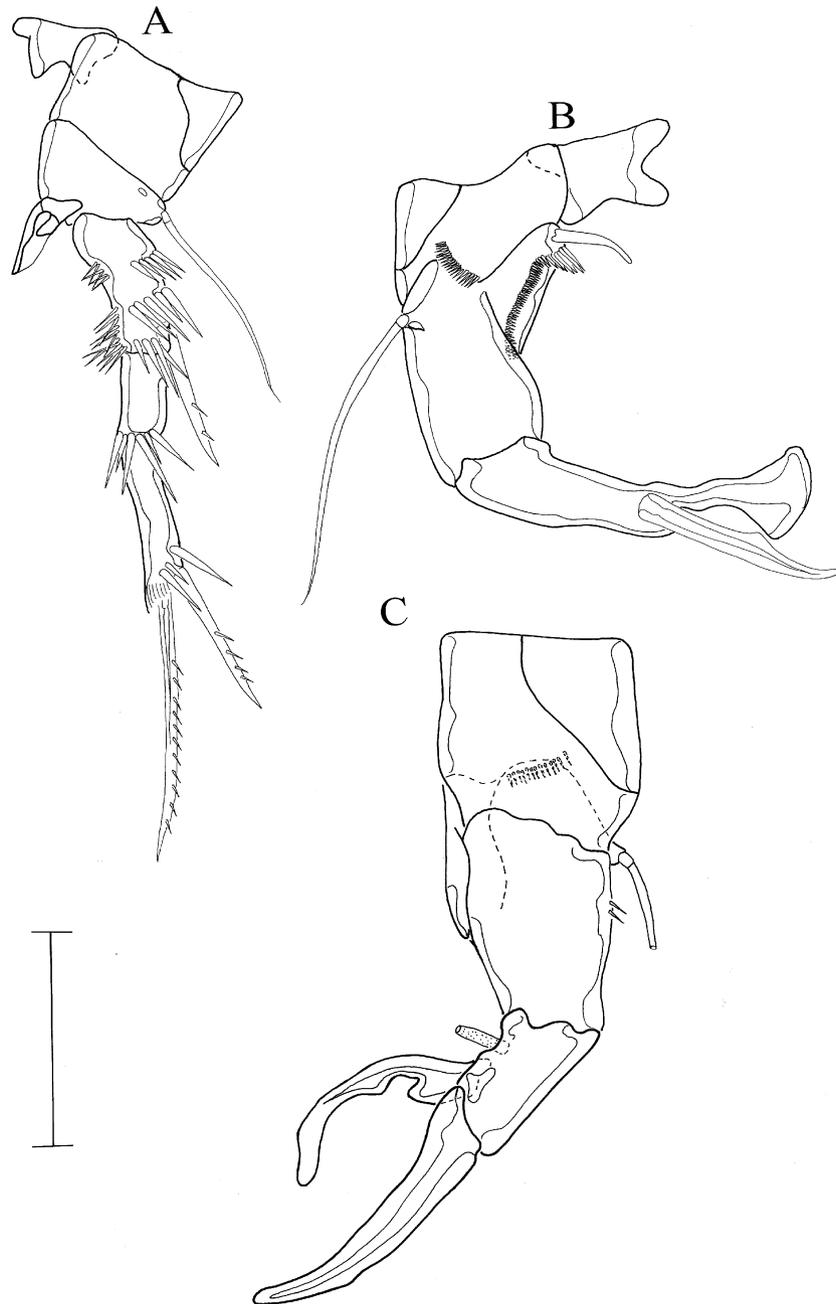


Figure 23. Males of *Parastenocaris* species. A, *Parastenocaris santarensis*, leg 4. B, *Parastenocaris santarensis*, leg 3. C, *Parastenocaris itica*, leg 3. Scale bar = 20 μ m.

14. Endopod of leg 4 of male longer than broad (0, pl); as long as broad in its proximal half (1, ap).
15. Endopod of leg 4 of male with hyaline membrane on distal margin only (0, pl); with hyaline membrane along entire surface (1, ap).
16. Endopod of leg 4 of male without proximal ornamentation (0, pl); with serrated proximal membrane (1, ap).

DISCUSSION

The genus *Brasilibathynellocaris* was proposed by Jakobi (1972a) to accommodate the species *B. pan-americana*, *B. salvadorensis*, and *B. brasilibathynellae*. The latter was validly fixed as the type species, and the genus was properly diagnosed. Therefore, the name *Brasilibathynellocaris* is nomenclaturally available and can be used as valid.

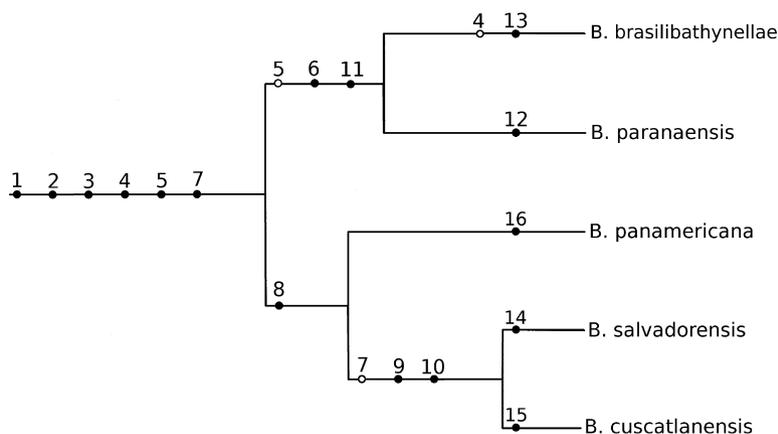


Figure 24. Phylogeny of *Brasilibathynellocaris* reconstructed by hand, applying Hennigian principles and criterion of putative parsimony. Characters as explained in the text; characters binary, polarized a priori; length of cladogram = 19. Circles represent autapomorphies, open circles represent autapomorphies by reversion of character state.

Probably because of the ‘Schalenmodell’ system developed by Jakobi (1972a), this author did not follow Noodt’s (1962) classification, thus removed *Parastenocaris cuscatlanensis* from Noodt’s (1962) *Parastenocaris panamericana* group and placed it, together with *Pararemaneicaris membranacea* Noodt (1965) and *Pararemaneicaris santaremensis* Noodt (1963), in the genus *Pararemaneicaris* Jakobi, 1972. This genus name is available for use as valid for the same reasons as given for *Brasilibathynellocaris* above. However, *Pararemaneicaris* in Jakobi’s interpretation is clearly polyphyletic, containing different evolutionary lineages within the Parastenocarididae. We consider *Pararemaneicaris cuscatlanensis*, the type species of *Pararemaneicaris*, to fall well within our taxonomic concept of *Brasilibathynellocaris*, and thus treat the two genus names as synonymous and select *Brasilibathynellocaris* as the valid senior synonym by First Reviser action (ICZN, 1999: Art. 24.2). *Parastenocaris santaremensis* seems to be closely related to the genus *Murunducaris*, sharing the presence of an inner dimorphic spinule on the inner margin of leg 1 basis, a proximal row of spinules on the inner margin of leg 4 exp-1, a large intercoxal sclerite with medial process on leg 5, and maybe the hypertrophy of the distal spine of leg 5 (Corgosinho, Martínez Arbizu & Reid, 2008). *Remaneicaris membranacea* is a typical *Remaneicaris* species, sharing with other members of this genus the retention of several plesiomorphic characters within the family as well as the subdistal position of the outer seta on the leg 4 exp-3 (Corgosinho & Martínez Arbizu, 2005).

As a result of his ‘Schalenmodell’, Jakobi (1972a) also proposed the genus *Paraforficatocaris*, the name of which is as available nomenclaturally as the names *Brasilibathynellocaris* and *Pararemaneicaris*. Our analysis, however, shows clearly that *Paraforficato-*

caris paranaensis, the type species of *Paraforficatocaris*, is a derived *Brasilibathynellocaris* species. Consequently the name *Paraforficatocaris*, established six months later than *Brasilibathynellocaris* – see the publication dates of Jakobi (1972a, b) given in the References section – becomes invalid as a junior synonym.

The species redescribed here differ from each other in size and ornamentation of the male leg 2 endopod; in ornamentation of the leg 2 exp-2; shape and size of the inner hyaline cushion on male leg 3; shape and ornamentation of the male leg 4 endopod and exp-1; and in absence/presence or extension of the hyaline margin on the male leg 4 endopod.

We propose to assign the species *B. cuscatlanensis* comb. nov. and *B. paranaensis* comb. nov. to the genus *Brasilibathynellocaris* based on the following character states, which we consider as autapomorphic for the genus:

- A. short exp-1 present on male leg 4, with inner invagination in proximal region;
- B. presence of 2 long spinules on coxa of male leg 4;
- C. long apophysis of male leg 3 inwardly curved and with a hyaline margin;
- D. exp-1 of male leg 3 with hyaline cushion on inner margin;
- E. exp-1 of male leg 4 with strong row of spinules on anterior margin;
- F. endopod of leg 4 of male forming a grasping organ against exp-1.

Character (E; 5 in the phylogeny) is present only in the *B. salvadorensis* group, whereas character (F; 7 in the phylogeny) is absent in *B. cuscatlanensis* comb. nov. and *B. salvadorensis*. However, we hypothesize their presence in the groundpattern of the genus (Fig. 24; see discussion below).

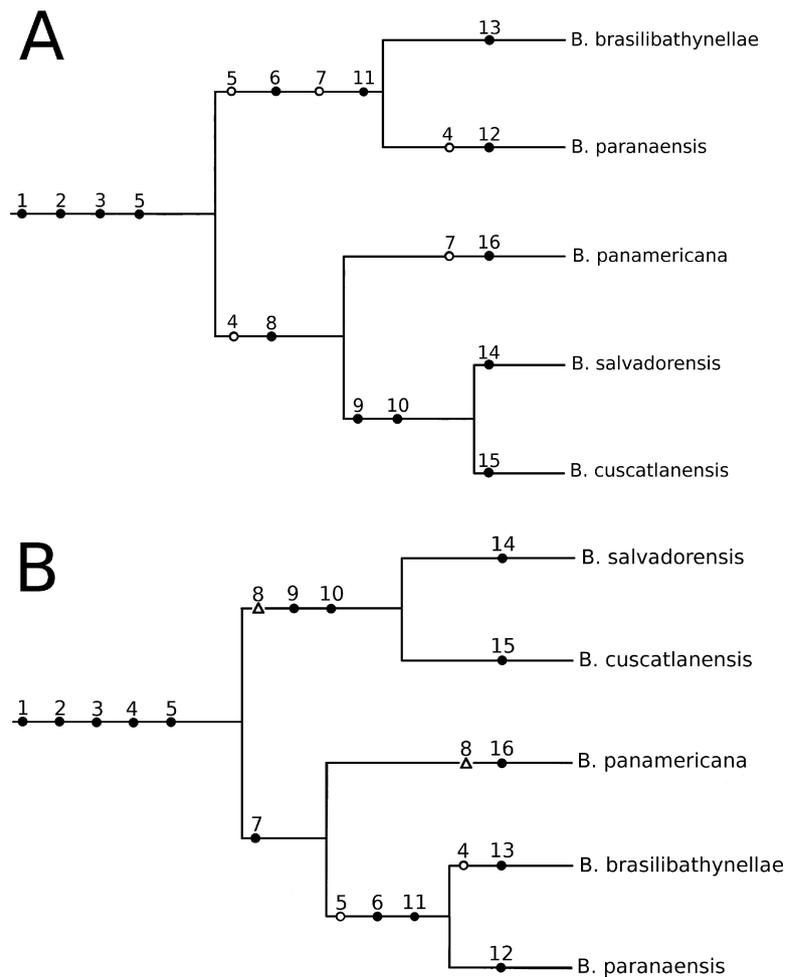


Figure 25. Alternative phylogenies of *Brasilibathynellocaris* reconstructed by cladistic parsimony. A, cladogram resulting from application of the Camin–Sokal algorithm (a single most parsimonious tree, length = 19), and one of two equally parsimonious cladograms resulting from application of the Wagner algorithm (tree length = 19). B, second of two equally parsimonious cladograms resulting from application of Wagner algorithm (tree length = 18). Characters as explained in the text; characters binary, polarized a priori. Circles represent autapomorphies; open circles represent homoplasies in (A), reversion of character state in (B); open triangles represent homoplasies in (B).

REMARKS ON THE NEOTENIC MALE OF *B. SALVADORENSIS*

Considering the aberrant morphology of the neotenic male of *B. salvadorensis*, it might be considered a juvenile rather than a sexually mature male. Even Noodt, when labelling the slide containing this specimen, supposed that it was a juvenile, probably because of the two-segmented condition of the exopod of leg 3 and the antennule morphology. However, some indirect as well as direct evidence, derived from comparison of the neotenic male with a copepodid V of *B. salvadorensis*, strengthens support for an hypothesis of neoteny. First, the neotenic male has a five-segmented urosomite before the telson. In the copepodid V of *B. salvadorensis* as well as in other

species within the family (see, e.g. Glatzel, 1991: 390, fig. 12E on *Parastenocaris phyllura* Kiefer, 1938), parastenocaridid males have only four urosomites before the telson. The presence of a five-segmented urosomite before the telson is a clear adult character, present in the groundpattern of Harpacticoida. Copepodid V males of *Parastenocaris phyllura* and *Parastenocaris hispanica* Martínez Arbizu (1997) have a two-segmented leg 3 with two setae on exp-2 and a one-segmented short endopod (Glatzel, 1991; Martínez Arbizu, 1997). In the case of *Parastenocaris hispanica*, the moult from copepodid V to adult involves the loss of one seta of exp-2 and the endopod, whereas two setae are retained in *Parastenocaris phyllura*. An alternative condition can be seen in the copepodid V of *B. salvadorensis*. In this species, leg 3

has a lamelliform short endopod, whereas its exp-2 has only one strong spine. In the neotenic male, the endopod (arrowed in Fig. 19C) is lost. Additionally, in the copepodid V of *B. salvadorensis* there is no trace of the strong curved spinule on the inner margin of the basis of leg 3, and the exp-1 has no inner cushion. In fact, these characters can be observed inside the limb, both appearing after the moult between copepodid V and adult. An additional character supporting our hypothesis concerns the structure of leg 4. In both *Parastenocaris phyllura* and *Parastenocaris hispanica*, copepodid V still has an endopod that does not differ significantly from the female endopod, whereas the most apparent sexual dimorphism appears after the moult between copepodid V and adult. The condition present in the copepodid V of *B. salvadorensis* is somehow modified, already showing a lamelliform triangular morphology. However, it still retains a medial transverse row of spinules as in the female, and the distal hyaline margin present in the adults is absent. Additionally, it does not have the outer serrated margin, although the latter can be seen inside the endopod as a developing adult character. The neotenic male of *B. salvadorensis* has a leg 4 endopod quite similar to in the one of the typical male, with an outer row of spinules and the distal hyaline margin. It is worth mentioning here that, similar to the copepodid V, the neotenic male also does not have the modified spinules on the anterior margin of the basis of leg 4. Completely developed adults males of *Brasilibathynelloccaris* share the loss of the proximal outer setae of the leg 5 exopod. This character is also present in the neotenic male of *B. salvadorensis*, and in copepodid V a very reduced seta appears near the insertion of the outer basal seta. Finally, we can mention the presence of a weakly geniculate eight-segmented antennule without the normal development of the fifth segment in the neotenic male of *B. salvadorensis*. In accordance with Glatzel (1991), male antennules of the copepodid V are six-segmented (or probably seven-segmented, considering that the third segment illustrated below the proximal aesthetasc-bearing segment was not counted). In *B. salvadorensis* a seven-segmented antennule occurs in the copepodid V instar.

DISCUSSION OF CHARACTERS

CHARACTER 1 – TRANSFORMATION OF LEG 4 EXP-1 OF MALE

The first character concerns the strong modification undergone by the exp-1 of the male leg 4, which is reduced in length, having an invagination on the proximal inner corner. Besides *Brasilibathynelloccaris*, only *Parastenocaris delamarei* Chappuis, 1958

shows a reduction in length of the exp-1 of male leg 4. However, this should not be considered as a synapomorphy uniting these taxa in a monophyletic group. *Parastenocaris delamarei* is a typical member of the *Parastenocaris minuta* group (Lang, 1948) and belongs to a group of species characterized by the transformation of the penultimate segment of the male A1. In contrast, members of *Brasilibathynelloccaris* do not exhibit this character and belong to a monophyletic group around Lang's (1948) *Parastenocaris fontinalis* group (*sensu* Martínez Arbizu, 1997) that is not closely related to the *Parastenocaris minuta* group. No other member of Parastenocarididae shows such a transformation on the male leg 4 exp-1, making this character what we consider to be the most important autapomorphy for *Brasilibathynelloccaris*.

CHARACTER 2 – LEG 4 COXA OF MALE

The second most important autapomorphy is the presence of two strong spinules on the anterior margin of the coxa of the male leg 4. Noodt (1962) described this structure as belonging to the basis. A similar structure has appeared only in *Siolicaris jakobi* (Noodt, 1963), *Siolicaris sioli* (Noodt, 1963), *Murunducaris dactyloides* (Kiefer, 1967), and perhaps also in *Parastenocaris psammica* Songeur, 1961. However, none of these species has these spinules as strongly developed as in the *Brasilibathynelloccaris* species. Therefore, we cannot ascertain whether the presence of long spinules on the anterior margin of the coxa of male leg 4 is an autapomorphy for a larger group or if it appears as a homoplasy within different evolutionary lineages more related to the *Parastenocaris fontinalis* group. Nevertheless, we can confirm that the condition found in *Brasilibathynelloccaris*, with two strong spinules, with a blunt tip, and surrounded by a hyaline region, is an autapomorphy for the genus.

CHARACTER 3 – LEG 3 APOPHYSIS OF MALE

Another very characteristic autapomorphy for the genus *Brasilibathynelloccaris* is the shape of the apophysis and thumb. In all the species that compose the genus the apophysis is very long and inwardly curved, ending in a sharp tip with a hyaline structure around it. The thumb is also very long, a little larger than the apophysis, forming a kind of 'forceps' with this structure and with a more or less developed hyaline margin. This kind of leg 3 structure is very uncommon within the Parastenocarididae. Apart from *Brasilibathynelloccaris* species, a similar leg 3 can be observed only in *Parastenocaris itica* Noodt (1962) (Fig. 23C). However, in *Parastenocaris itica* the male leg 3 exopod is two-segmented, a character observed

only in some *Forficatocaris* species (see Ahnert, 1994) and in a neotenic specimen of *B. salvadorensis* (Fig. 18B). Besides, males of *Parastenocaris itica* do not have any hyaline structure on leg 3 (contrary to the original description, in which the apophysis is illustrated with an underlying irregular hyaline region) and, as already observed by Noodt (1962), this species does not have the typical characters (synapomorphies) observed for the *Brasilibathynellocaris* species, such as the aberrant transformations of the endopod and exp-1 of male leg 4. In view of these facts, and in the absence of a good synapomorphy for a taxon formed by *Parastenocaris itica* and the *Potamocaris-Forficatocaris* complex, we hypothesize that *Parastenocaris itica* is a sister group of *Brasilibathynellocaris*, sharing with the latter the transformed, pincer-like male leg 3 exopod. Additionally, because it does not share any of the other synapomorphies with the *Brasilibathynellocaris* species, we hypothesize also that it is a representative of an undescribed neotropical genus, until now recorded only in Central America and defined by the retention of some neotenic characters, such as the two-segmented exopod of the male leg 3 (Fig. 23C).

Another possible interpretation would be that what we call exp-2 in *Parastenocaris itica* is the much-enlarged terminal spine of the apophysis, present as a short claw-like spine in the *Parastenocaris fontinalis* group. In this sense, a pincer-like leg 3 would have appeared independently within *Parastenocaris itica* and *Brasilibathynellocaris* species. However, the articulated condition observed between this *Parastenocaris itica* structure and the previous segment is an indication that it is not a spine but an apophysis. Pending a future revision, *Parastenocaris itica* is, therefore, considered as a *Parastenocaris incertae sedis* here.

The apparent two-segmented condition of the male leg 3 exopod, which can be seen in the original description of *B. paranaensis* comb. nov., was not confirmed in this study.

CHARACTER 4 – LEG 3 EXP-1 OF MALE

The presence of a hyaline cushion on the inner margin of the male leg 3 exp-1 is considered as another autapomorphy for the genus. The cushion is absent in *B. brasilibathynellae* only, and is perhaps related to the development of a strong cuticular process on the inner margin of the male leg 3 in this species. A similar structure was described for *Parastenocaris orcina* Chappuis, 1938, but it is not figured in the drawings of Cottarelli & Drigo (1972). However, this seems to be a clear case of convergent evolution. When applying the computer-derived phylogenetic reconstruction (Fig. 25A), this character appears con-

vergently in the stem line of the *B. salvadorensis* group and in *B. paranaensis* comb. nov. The rarity of appearance of this structure within the family Parastenocarididae, and its absence only in *B. brasilibathynellae* within *Brasilibathynellocaris*, lets us assume that such an unusual structure may have appeared only once within the genus, constituting part of its groundpattern.

CHARACTERS 5, 6 – LEG 4 EXP-1 OF MALE

An interesting character in some species of *Brasilibathynellocaris* is the presence of an anterior row of strong spinules on the male leg 4 exp-1. The presence of this structure has raised some questions about the identity and homology of this character that could be resolved only after observation of the patterns of frill and spinule ornamentation on the distal inner corner of the leg 4 exp-1 in other species within the family, and of its ontogeny within *B. salvadorensis*. For example, in some species of *Murunducaris*, the exp-1 of the male leg 4 does not have a hyaline frill, and an inner row of short spinules appears on the proximal region (Corgosinho *et al.*, 2008). In *Murunducaris juneae* Reid, 1994, however, the presence of a hyaline frill on the distal inner corner, distal to the proximal row of short spinules, is clear, highlighting that they are not homologous to the frill (Corgosinho *et al.*, 2008). It seems that at least in some groups more related to the *Parastenocaris fontinalis* group, the hyaline frill undergoes a modification, appearing as an inner row of spinules. We can see this, for example, in *Parastenocaris santaremensis*, where a proximal row of strong spinules on the inner margin of the male leg 4 exp-1 (homologous to the proximal row of short spinules in *Murunducaris*) is proximal to the modified 'hyaline frill' (Fig. 23A). The modification of the hyaline frill can be seen also in other parastenocaridids. For example, Martínez Arbizu (1997) has shown that a subdistal row of strong spinules (modified frill) occurs in the *Parastenocaris fontinalis* group, and a distal row of spinules can be seen also in the group around *Parastenocaris kabyloides* Enckel, 1969 and *Parastenocaris aquaeductus* Chappuis, 1925.

The condition observed for *Brasilibathynellocaris* is a modification of a previously unmodified hyaline frill, as evidenced by the observation of both the copepodid V (Fig. 19D) and the neotenic specimen of *B. salvadorensis* (Fig. 18C). In this species, both the copepodid V and the neotenic male leg 4 exp-1 have a distal row of spinules on the distal inner corner, occupying the same position as the hyaline frill, and no trace of the anterior row of strong spinules (although they already appear inside the copepodid V leg 4 exp-1 as a developing adult character).

In our view, the presence of an anterior row of strong spinules on the male leg 4 exp-1 is an autapomorphy for the genus *Brasilibathynellocaris* (character 5) that has disappeared in the *B. brasilibathynellae* group (character 6). To assume that presence of the anterior row of strong spinules is an autapomorphy for the *B. salvadorensis* group would imply considering the presence of a distal row of spinules on the inner corner of the leg 4 exp-1 as its plesiomorphic state within the genus. This is a character present at least in the neotenic specimen of *B. salvadorensis* (Fig. 18C), and probably also in the copepodid V of all species of this genus, but absent in the adults of the *B. brasilibathynellae* group. This reveals that the species in the latter group share the loss of this character as a synapomorphy. In other words, following the Hennigian rule of character heterobathmy (Hennig, 1984), the presence of an autapomorphy in one group is followed by the expression of its plesiomorphic state in the sister group. Thus, if we consider the presence of the anterior row of strong spinules (character 5) as autapomorphic for the *B. salvadorensis* group, we cannot consider the loss of this ornamentation as a synapomorphy for the *B. brasilibathynellae* group. That refutes the hypothesis that presence of the row is an autapomorphy for the *B. salvadorensis* group only.

CHARACTERS 7, 8 – LEG 4 ENDOPOD OF MALE

It seems that there are some relationships between the degree of transformation of the exp-1 of the male leg 4 and the modification of the endopod as a grasping organ. Here we consider the presence of this grasping endopod (character 7) as an autapomorphy for the whole genus (Fig. 24), being reversed in *B. salvadorensis* and *B. cuscatlanensis* comb. nov. In the latter species the endopod is not transformed into a grasping organ and the exp-1 is not as modified as in the other species (Fig. 21D, E), showing an invagination on the posterior margin of the segment. In contrast, in *B. paranaensis* comb. nov. the endopod is strongly modified and the exp-1 shows the highest degree of transformation (Fig. 10C–E). It is currently impossible to say which mechanisms are involved in the development of these structures, or which evolutionary pressure has driven their evolution. A possibility is that the leg 4 of males in *Brasilibathynellocaris* is important during copula, helping leg 3 during mating; this could help explain the modification this limb has undergone. A grasping endopod can also be seen in *Forficatocaris*. However, in this genus no similar transformation occurs on the exp-1 of leg 4. In this case, the grasping endopod works against a more or less strongly developed row of spinules on the proximal inner margin of exp-1.

This is also a possible adaptation to grasping. However, these grasping adaptations are very different, involving different structures (i.e. spinules and invagination of the inner margin of exp-1) and probably cannot be considered as part of the same series of transformation; they are not homologous structures. In addition, it has been shown that *Forficatocaris* and *Potamocaris* compose a monophyletic group that shares, as a synapomorphy, the transformation of one or more spinules on the inner margin of the male leg 1 enp-1 (Ahnert, 1994). In view of these facts, we consider that the presence of a grasping endopod is the result of independent evolution in both genera and that the lack of synapomorphies allows us to assume that *Forficatocaris* and *Brasilibathynellocaris* belong to different evolutionary lineages within the South American Parastenocarididae.

Within the genus *Brasilibathynellocaris* an alternative phylogeny (Fig. 25B), equally parsimonious as the one proposed here, could be derived if we consider the presence of a grasping endopod (character 7) on the male leg 4 of as a synapomorphy for a taxon formed by the species *B. panamericana*, *B. paranaensis* comb. nov., and *B. brasilibathynellae*. In the phylogeny endorsed by us (Fig. 24), *B. panamericana* grouped with *B. cuscatlanensis* comb. nov. and *B. salvadorensis* (both from Central America), this monophyletic group being supported by the presence of a hyaline region on the male leg 4 endopod (character 8).

The consideration of a transformed leg 4 endopod as a synapomorphy for a taxon formed by *B. panamericana* and the Brazilian species (Fig. 25B) has some serious biogeographical consequences, which would necessitate an increase in ad hoc hypotheses in order to explain the actual knowledge of the geographical distribution of the studied species. Besides, as already mentioned, it seems that there is some degree of interdependence between the shape of the male leg 4 endopod and the degree of modification of the exp-1 of the same leg, and that this modification can be associated with some kind of grasping behaviour during copula. A reproductive pressure could give some direction to the appearance of a grasping endopod on male leg 4. This may have occurred independently in some genera such as *Forficatocaris* and *Brasilibathynellocaris*. The same does not seem to occur in relation to the presence of a hyaline margin on the male leg 4 endopod in *Brasilibathynellocaris*. In fact, in the *B. salvadorensis* group, in species with different levels of transformation of leg 4 endopod and exp-1, we can see a hyaline region of unknown function, more developed in those species with a more or less transformed endopod (viz. *B. salvadorensis* and *B. cuscatlanensis* comb. nov.). No species from the *B. brasilibathynellae* group (both with a

very transformed exp-1 of leg 4 and a grasping endopod) has a hyaline margin on the endopod of the male leg 4. Thus, it seems that the grasping endopod of the male leg 4 arose only once in the stem line of *Brasilibathynellocaris*, later suffering a reversion in the stem line of *B. salvadorensis* and *B. cuscatlanensis* comb. nov. (Fig. 24) because of retardation of development of the grasping structure, perhaps as the result of decreased reproductive pressure. To consider its appearance independently (Fig. 25A), we would need to accept that the transformation undergone by the exp-1 of leg 4 (character 1) also appeared independently within both lineages of *Brasilibathynellocaris*.

CHARACTER 9 – LEG 2 EXP-2 OF MALE

The ornamentation of the distal inner corner of the male leg 2 exp-2 is an interesting character for phylogenetic reconstruction in the genus. The presence of a strong row of spinules more developed in the *B. brasilibathynellae* group, but also present in *B. panamericana*, could be seen as indicative of a closer relationship between *B. panamericana* and the Brazilian species. However, the observation of the neotenic male of *B. salvadorensis* (Fig. 18D) revealed that the plesiomorphic condition of this character is the presence of such strong spinules, more similar to what can be seen in *B. panamericana*. Thus, here we interpret the presence of hair-like spinules on the distal inner corner of leg 2 exp-2 as a synapomorphy for the species *B. salvadorensis* and *B. cuscatlanensis* comb. nov., this condition being derived from the presence of strong spinules on the distal inner corner of the leg 2 exp-2. An alternative would be to consider the condition present in *B. panamericana* and also in the neotenic male of *B. salvadorensis* as the plesiomorphic condition of the character, whereas the strongest condition observed in the *B. brasilibathynellae* group and the bristle-like condition present in *B. cuscatlanensis* comb. nov. and *B. salvadorensis* would have appeared independently. This does not change the topology of the cladogram, but adds one more step to it. Until now, there are no data supporting this hypothesis, and because this kind of character, defined by some controversial limits such as ‘more or less developed’, can be interpreted as a very personal perception of a given structure, here we hypothesize the presence of a strong row of spinules on the distal inner margin in the *B. brasilibathynellae* group as plesiomorphic within the genus.

CHARACTER 10 – LEG 4 BASIS OF MALE

A row of spinules between the outer seta of the base and the endopod of the male leg 4 is present in *B.*

salvadorensis and *B. cuscatlanensis* comb. nov. only. This is a very unusual character within the family and does not form part of the groundpattern of *Brasilibathynellocaris*. Hence, here we interpret it as a synapomorphy for these two species within the *B. salvadorensis* group.

CHARACTER 11 – LEG 2 ENDOPOD OF MALE

The *B. brasilibathynellae* group is well characterized by the presence of a long endopod on the male leg 2, of the same size of exp-1. Although we have not found the female of *B. paranaensis* comb. nov., the observation of the equivalent structure in *B. brasilibathynellae* leads us to assume that, in this group, the leg 2 endopod is probably sexually dimorphic in length. It seems that no other species of Parastenocarididae has this endopod developed as much as it appears to be in *B. brasilibathynellae* and *B. paranaensis*.

CHARACTER 13 – INNER MARGIN OF LEG 5 OF MALE

The ornamentation of the inner margin of leg 5 is a frequent character within parastenocaridids. For example, it is present in *Parastenocaris fossoris* Fryer, 1955 and in *Parastenocaris crassicaudis* Chapuis, 1955 (after Fischer, 1998). It has also been observed in *Parastenocaris santaremensis* (P.H.C. Corgosinho), in *Parastenocaris hispanica* Martínez Arbizu (1997), as well as in other apparently not closely related species. Within *Brasilibathynellocaris*, this character is observed only in *B. brasilibathynellae*. Therefore, we consider it as an autapomorphy for this species.

CHARACTERS 14–16 – LEG 4 ENDOPOD OF MALE

The structure of the endopod of the male leg 4 has been commented on above (characters 7, 8), where the presence of hyaline structures on it was discussed. It remains very difficult to understand the role played by the male leg 4 endopod and associated structures in the biology of the studied species, although a possible connection with a sexual behaviour can be inferred on the basis of the grasping structure of the endopod in some species and the invagination on the proximal inner corner of the leg 4 exp-1 in *Brasilibathynellocaris* males.

To our knowledge, no parastenocaridid species outside of *Brasilibathynellocaris* has a hyaline structure on the endopod of the male leg 4. The structure shows varying morphology within the *B. salvadorensis* group, being most developed in *B. cuscatlanensis* comb. nov., where it covers the whole endopod margin (character 15).

With the exception of *B. salvadorensis*, no species of *Brasilibathynellocaris* has the proximal half of the endopod of the male leg 4 as broad as long (character 14). This is a character neither present in the ground-pattern of the genus *Brasilibathynellocaris*, nor outside of this genus; it does not seem to be shared by any member of the family Parastenocarididae. The same applies to the presence of a serrated hyaline membrane (character 16) on the outer margin of the male leg 4 endopod in *B. panamericana*. Therefore, it is here considered as autapomorphic for this species.

OTHER CHARACTERS OF POTENTIAL PHYLOGENETIC VALUE

SIZE OF OUTER SPINE OF LEG 2 EXP-1

The size of the outer spine of the leg 2 exp-1 is another very distinctive character for the genus *Brasilibathynellocaris*. In all member species, this spine is longer than usually seen in other parastenocaridids. A longer spine was described by Noodt (1963) for *Parastenocaris tapajoensis* Noodt, 1963. It seems that this species belongs to Noodt's *Parastenocaris columbiensis* group, as mentioned by Noodt (1972a), but despite this character there is not a single synapomorphy indicating a close relationship between the *Parastenocaris columbiensis* group and *Brasilibathynellocaris*. Therefore, pending a more general revision of the family, at least for the neotropical region, we have opted for a more conservative approach, rejecting a close relationship between the above-mentioned taxa.

STRONG AND CURVED SPINULE ON INNER MARGIN OF LEG 3 BASIS

With the exception of *B. paranaensis* comb. nov., all *Brasilibathynellocaris* have this character. Nevertheless, it is difficult to polarize it because it is also present in *Parastenocaris santaremensis* (Fig. 23B), a species that has some interesting synapomorphies with *Murunducaris*. As we are not sure about the exact position of the genus *Brasilibathynellocaris* within the South American Parastenocarididae, we have also opted for the exclusion of this character from being a synapomorphy here.

THE PROBLEM AROUND *B. PARANAENSIS* COMB. NOV.

The synapomorphies mentioned above clarify the monophyletic status of the genus *Brasilibathynellocaris* and support our decision to include *B. paranaensis* comb. nov. and *B. cuscatlanensis* comb. nov. and synonymize *Paraforficatocaris* and *Pararemaneicaris*. However, if one considers only Jakobi's (1972b)

original description, without a detailed observation of the specimen, it is conceivable to see *B. paranaensis* comb. nov. as a member of a different genus than *Brasilibathynellocaris*.

The most intriguing structures that probably influenced Jakobi's decision are the strongly reduced and quadratic exp-1 on the male leg 4, the last urosomite cuticular support for the serrated hyaline frill, that in dorsal and ventral view is superficially similar to a lateral process (at first sight seemingly analogous to a spinulous cuticular process, like the one present on the distolateral margin of the telson in *Forficatocaris*), and the long, grasping and downward-curved endopod of the male leg 4 (character 12). Additionally, Jakobi (1972b) mentioned strong sexual dimorphism of leg 5, which in the male is constructed like a penis, and leg 6 having three setae.

Sexual dimorphism of leg 5 is very common in Parastenocarididae. For example, it is weakly expressed in some species of *Remaneicaris*, and more pronounced in the *Parastenocaris brevipes* group (H. K. Schminke pers. comm.) and in the neotropical genera *Murunducaris* and *Forficatocaris*. However, observations of other species in *Brasilibathynellocaris* shows that no male in the genus has sexual dimorphism as pronounced as described by Jakobi (1972b). Additionally, examination of the original description offers some evidence that Jakobi erroneously illustrated the male leg 4 endopod as leg 5 (see Jakobi, 1972b: 246, fig. 2i and Fig. 10C in this work), and probably described leg 5 as leg 6.

These conclusions are further supported by the structure of leg 6 of males within the genus *Brasilibathynellocaris*, appearing in all the included species as an unarmed plate covering the genital aperture. An armed leg 6 was until now observed only for some derived species of *Remaneicaris* (Corgosinho, 2007), such as *Remaneicaris hecate* (Noodt, 1965), *Remaneicaris persephone* (Noodt, 1965), *Remaneicaris ciliata* (Noodt, 1965), and *Remaneicaris cordobaensis* (Noodt, 1965). However, in these species, leg 6 appears as an opercular plate armed with two diminutive setae.

Finally, we believe that the most problematic characters concern the interpretation of the structure of the male leg 4 in the different species now assigned to *Brasilibathynellocaris*. This appendix was misinterpreted by different authors in the past. Jakobi & Loyola e Silva (1962) described the endopod of the male leg 4 of *Parastenocaris brasilibathynellae* as part of the exp-1, and the two coxal spinules as the endopod ('P4 with grasping surface on inside of basal article of exopod, forming pincers. Endopod clamplike, very different from that of female'; Jakobi & Loyola e Silva, 1962). Noodt (1962) when describing *Parastenocaris panamericana*, *Parastenocaris salvadorensis*, and *Parastenocaris cuscatlanensis*, correctly

described the structure of the male leg 4 endopod and exp-1, but wrongly interpreted the two strong spinules that can be seen on the coxa of all *Brasilibathynellocaris* as inserted in the basis. Jakobi (1972a), when creating the genus *Brasilibathynellocaris*, basically used the description by Noodt (1962) for leg 4 in his *Parastenocaris panamericana* group. Finally, when proposing the genus *Paraforficatocaris*, Jakobi (1972b) correctly described the male leg 4 endopod of the type species of the genus (now *B. paranaensis* comb. nov.) as forming pincers, but wrongly described the exp-1 as lacking an invagination. Also, in the description of this limb Jakobi (1972b) did not make any mention of the presence of two strong spinules on the coxa.

Thus, the wrong interpretation of these structures, in combination with the absence of a strong spinule on the basis of the male leg 3, a character present only in *B. paranaensis* comb. nov., and with the peculiar last urosomite, probably were a starting point for the creation of a separate genus.

PHYLOGENETIC POSITION OF THE GENUS *BRASILIBATHYNELLOCARIS*

The exact phylogenetic position of the genus *Brasilibathynellocaris* within the family Parastenocarididae is unclear. However, the presence in South America of a group of species that have lost the proximal exopodal seta adjacent to the outer basal seta of the male leg 5 and that have the furca seta II extremely reduced (not seen in some specimens) is very interesting. For the moment we cannot be sure whether these transformations are autapomorphies for a South American group or for a larger group of species more closely related to the *Parastenocaris fontinalis* group, or whether they have developed independently in different lineages. Looking forward to the construction of a comprehensive hypothesis on the evolution of all South American Parastenocarididae, we recommend further examination of the relationships between the genera *Brasilibathynellocaris* and *Siolicaris*, as well as with *Parastenocaris itica*, *Parastenocaris santaremensis*, *Murunducaris*, and the two African species *Parastenocaris fossoris* Fryer, 1956 and *Parastenocaris crassicaudis* Chappuis, 1955.

BIOGEOGRAPHY

Brasilibathynellocaris probably is an endemic neotropical group (Noodt, 1962) of groundwater parastenocaridids. Member species occur in Central and South America, in the Atlantic and Pacific domains. *B. cuscatlanensis* comb. nov., *B. panamericana*, and *B. salvadorensis* are the most northern species, occurring

in El Salvador, with *B. panamericana* having a widespread distribution, including populations in Peru. *Brasilibathynellocaris brasilibathynellae* and *B. paranaensis* comb. nov. are the most austral species, with members known only from the south of Brazil (states of Paraná and Santa Catarina). None of these species has been found in other areas in South America, but we found a single damaged male on a Noodt slide from a sample taken in groundwaters in southern California, which can be considered as another example of faunal exchanges between the Neotropical and Nearctic regions.

The lack of records in intermediate areas is probably because of the lack of sampling, but here it is interesting to mention that no species have been found in black or white waters of the Amazon river and its tributaries, although only a few samples have been taken from white waters (Solimões river, Noodt, 1963; Kiefer, 1967a). This pattern is very similar for the genus *Remaneicaris* (P. H. C. Corgosinho, unpubl. data).

Despite this lack of records, the complete absence of *Brasilibathynellocaris* species in samples taken from other South American localities such as the São Francisco and Jequitinhonha river basins in Minas Gerais state, Brazil, as well as from rivers in the states of São Paulo and Paraná (P. H. C. Corgosinho, unpubl. data) is intriguing. Other workers (viz. Menzel, 1916; Delachaux, 1924; Kiefer, 1936a, b, 1967a, b, 1968; Noodt, 1955, 1963, 1965, 1972a, b; Rouch, 1962; Jakobi, 1969, 1972b; Dussart, 1979, 1981, 1983; Reid, 1982, 1991, 1994; Rocha, Torres & Maia-Barbosa, 1998) did not find representatives of *Brasilibathynellocaris* in other South American groundwater habitats, this being indicative of the scarcity of species of this genus in South America.

The phylogeny depicted in Figure 24 shows a separation between the Central American and the South American species.

Our hypothesis is that the genus originated in South America. Following this line of thought, we speculate that *Brasilibathynellocaris* may have evolved outside the Brazilian craton shield, on the areas of influence of the palaeo-Amazon-Orinoco or the Paraná rivers (approximately between 83 and 30 Mya; Lundberg *et al.*, 1998), and dispersed northward, before the formation of the northern Andes, via the palaeo-Amazon-Orinoco or following the successive marine invasions (see Noodt, 1962 for a discussion of the brackish water tolerance of *B. panamericana*; and Lundberg *et al.*, 1998 for history of South America's drainage patterns). After the formation of the isthmus, the colonization of Central America became possible. This pattern would explain the presence of *B. panamericana* in both Central America and Peru.

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REFERENCES

- Ahnert A. 1994.** Eidonomie, Systematik und Entwicklung von *Potamocaris* Dussart, 1979 und *Forficatocaris* Jakobi, 1969 (Copepoda, Harpacticoida, Parastenocarididae) sowie Verteilung im Lebensraum und Verhalten zweier koexistierender Vertreter beider Gattungen an einem sandigen Flußabschnitt im Küstengebirge von São Paulo (Brasilien). D. Phil. Thesis, Christian-Albrechts-Universität.
- Ax P. 1984.** *Das phylogenetische system*. Stuttgart: Gustav Fischer Verlag.
- Chappuis PA. 1942.** Eine neue Methode zur Untersuchung der Grundwasserfauna. *Acta Scientifica der Mathematisch-Naturwissenschaftlichen Universität Francisco Josephinae Koloszar* **6**: 1–17.
- Corgosinho PHC. 2007.** Phylogenetic systematics of *Remaneicaris* Jakobi (Copepoda, Harpacticoida, Parastenocarididae) from the neotropical region. D. Phil. Thesis, Instituto Nacional de Pesquisas da Amazônia/Universidade Federal do Estado do Amazonas.
- Corgosinho PHC, Martínez Arbizu P. 2005.** Two new interstitial species of *Remaneicaris* Jakobi (Copepoda, Harpacticoida, Parastenocarididae) from the Ribeirão do Ouro river, Brazil, with a redefinition of the genus. *Senckenbergiana Biologica* **85**: 147–162.
- Corgosinho PHC, Martínez Arbizu P, Reid JW. 2008.** Revision of the genus *Murunducaris* (Copepoda: Harpacticoida: Parastenocarididae), with descriptions of two species from South America. *Journal of Crustacean Biology* **28**: 700–720.
- Cottarelli V, Drigo E. 1972.** Sulla presenza di *Parastenocaris orcina* Chappuis (Cop. Harpacticoida) in acque interstiziali del Lago di Bracciano. *Notiziario del Circolo Speleologico Romano* **17**: 51–54.
- Delachaux T. 1924.** Zur Kenntnis der Copepodenfauna von Surinam. II. Harpacticiden. *Zoologischer Anzeiger* **59**: 1–16.
- Dussart BH. 1979.** Algunos Copépodos de America del Sur. *Publicaciones Ocasionales del Museo Nacional de Historia Natural, Santiago de Chile* **30**: 1–13.
- Dussart BH. 1981.** Sobre algunos Copépodos de America del Sur. II. *Comunicaciones Científicas del Centro de Ecología Aplicada del Litoral (CECOAL)* **12**: 1–6.
- Dussart BH. 1983.** Sobre algunos Copépodos de America del Sur. III. *Comunicaciones Científicas del CECOAL* **16**: 1–8.
- Dussart BH, Defaye D. 1990.** Répertoire mondial des crustacés copépodes des eaux intérieures III. Harpacticoides. *Crustaceana Supplement* **16**: 1–384.
- Felsenstein J. 2007.** *PHYLIP (phylogeny inference package), version 3.67*. Distributed by the author. Seattle, WA: Department of Genome Sciences, University of Washington.
- Fischer L. 1998.** Parastenocarididae (Copepoda) aus Stränden des Malawisees (Ostafrika): Taxonomie, Vertikalverteilung und geographische Verbreitung. Master's Thesis, Oldenburg University.
- Galassi DMP, De Laurentiis P. 2004.** Towards a revision of the genus *Parastenocaris* Kessler, 1913: establishment of *Simplicaris* gen. nov. from groundwaters in central Italy and review of the *P. brevipes*-group (Copepoda, Harpacticoida, Parastenocarididae). *Zoological Journal of the Linnean Society* **140**: 417–436.
- Glatzel T. 1991.** Neue morphologische Aspekte und die Copepodid-Stadien von *Parastenocaris phyllura* Kiefer (Copepoda, Harpacticoida). *Zoologica Scripta* **20**: 375–393.
- de Haro JJ. 2002.** PhylEdit: inferencia filogenética con Phylip, versión 2.0.
- Hennig W. 1966.** *Phylogenetic systematics*. Urbana, IL: University of Illinois Press.
- Hennig W. 1984.** Phylogenetic systematics. In: Sober E, ed. *Conceptual issues in evolutionary biology – an anthology*. Cambridge: MIT Press, 257–276.
- ICZN. 1999.** *International code of zoological nomenclature*, 4th ed. London: International Trust for Zoological Nomenclature.
- Jakobi H. 1969.** *Forficatocaris noodti* n. gen., n. sp. (Copepoda Harpacticoida) aus brasilianischem Limnopsammal. *Crustaceana* **17**: 231–238.
- Jakobi H. 1972a.** Trends (Enp. P₄ ♂) innerhalb der Parastenocarididen (Copepoda Harpacticoida). *Crustaceana* **22**: 127–146. [Issue dated 'March 1972']
- Jakobi H. 1972b.** Zur Kenntnis der *Forficatocaris*-Zoonose des Nhundiaquara (Parana – Brasilien). *Studies on the Neotropical Fauna* **7**: 239–251. [Issue dated 'October 1972']
- Jakobi H, Loyola e Silva J. 1962.** Two new species of *Parastenocaris* (Copepoda: Harpacticoida) from Santa Catarina, Brazil. *Proceedings of the United States National Museum* **113**: 389–397.
- Kessler E. 1913.** *Parastenocaris brevipes* nov. gen. et nov. spec., ein neuer Süßwasserharpacticide. *Zoologischer Anzeiger* **42**: 514–520.
- Kiefer F. 1936a.** Eine neue *Parastenocaris*-Art (Crustacea Copepoda) aus Brasilien. *Zoologischer Anzeiger* **116**: 142–144.

- Kiefer F. 1936b.** Brasilianische Ruderfusskrebse (Crustacea Copepoda), gesammelt von Herrn Dr. Otto Schubart, V. Mitteilung. *Zoologischer Anzeiger* **116**: 31–35.
- Kiefer F. 1967a.** Zwei neue *Parastenocaris*-Arten (Copepoda Harpacticoida) aus dem mittleren Amazonas-Gebiet. *Ama-zoniana* **1**: 131–134.
- Kiefer F. 1967b.** Neue Copepoda Harpacticoida aus dem Amazonasgebiet. *Crustaceana* **13**: 114–122.
- Kiefer F. 1968.** Zwei weitere *Parastenocaris*-Arten (Copepoda Harpacticoida) aus dem mittleren Amazonas-Gebiet. *Ama-zoniana* **1**: 257–258.
- Lang K. 1948.** *Monographie der Harpacticiden*. Lund: H. Ohlsson.
- Löffler H. 1981.** Copepoda. In: Hurlbert SH, Rodríguez G, dos Santos ND, eds. *Aquatic biota of tropical South America. Part 1. Arthropoda*. San Diego, CA: San Diego State University Press, 14–19.
- Lundberg JG, Marshall LG, Guerrero J, Horton B, Malabarba MC, Wesselingh F. 1998.** The stage for neotropical fish diversification: a history of tropical south American rivers. In: Malabarba LR, Reis RE, Vari RP, Lucena CAS, Lucena ZMS, eds. *Phylogeny and classification of neotropical fishes*. Porto Alegre: Museu de Ciências e Tecnologia, PUCRS, 13–48.
- Martínez Arbizu P. 1997.** *Parastenocaris hispanica* n. sp. (Copepoda: Harpacticoida: Parastenocarididae) from hyporheic groundwaters in Spain and its phylogenetic position within the *fontinalis*-group of species. *Contributions to Zoology* **66**: 215–226.
- Meier R. 1992.** Der Einsatz von Computern in phylogenetischen Analysen – eine Übersicht. *Zoologischer Anzeiger* **229**: 106–133.
- Menzel R. 1916.** Über das Auftreten der Harpacticiden-Gattungen *Epactophanes* und *Parastenocaris* in Surinam. *Zoologischer Anzeiger* **47**: 149–152.
- Nixon KC. 1999.** *Winclada (BETA), version 0.9.9*. Ithaca: Published by the author.
- Noodt W. 1955.** Eine neue *Parastenocaris* (Copepoda Harpacticoida) als Vertreterin limnischen Mesopsammons aus Südamerika. *Archiv für Hydrobiologie* **50**: 76–81.
- Noodt W. 1962.** Limnisch-subterrane Copepoden der Gattung *Parastenocaris* Kessler aus Mittelamerika. *Beiträge zur Neotropischen Fauna* **2**: 223–248.
- Noodt W. 1963.** Subterrane Crustaceen der zentralen Neotropis. *Zoologischer Anzeiger* **171**: 114–147.
- Noodt W. 1965.** Crustacea subterranea aus Argentinien. *Beiträge zur Neotropischen Fauna* **4**: 84–129.
- Noodt W. 1972a.** Brasilianische Grundwasser-Crustacea, 1: Studien an den Gattungen *Parastenocaris* Kessler und *Forficatocaris* Jakobi aus der Serra do Mar von São Paulo (Copepoda, Harpacticoida). *Crustaceana* **23**: 76–99.
- Noodt W. 1972b.** Drei neue *Parastenocaris* aus Kolumbien (Crustacea Copepoda). 1. Mitteilung über kolumbianische Grundwasser-Crustaceen. *Studies on the Neotropical Fauna* **7**: 101–112.
- Reid JW. 1982.** *Forficatocaris schadeni*, a new copepod (Harpacticoida) from Central Brazil, with keys to the species of the genus. *Journal of Crustacean Biology* **2**: 578–587.
- Reid JW. 1991.** The neotropical genus *Potamocaris* Dussart (Copepoda: Harpacticoida: Parastenocaridae), with descriptions of two new species. *Journal of Crustacean Biology* **11**: 463–472.
- Reid JW. 1994.** *Murunducaris juneeae*, new genus, new species (Copepoda: Harpacticoida: Parastenocarididae) from a wet campo in central Brazil. *Journal of Crustacean Biology* **14**: 771–781.
- Reid JW. 1995.** Redescription of *Parastenocaris brevipes* Kessler and description of a new species of *Parastenocaris* (Copepoda: Harpacticoida: Parastenocarididae) from the U.S.A. *Canadian Journal of Zoology* **73**: 173–187.
- Reid JW. 1998.** Maxillopoda – Copepoda. Harpacticoida. In: Young PS, ed. *Catalogue of Crustacea of Brazil*. Rio de Janeiro: Museu Nacional/UFRJ, 75–127.
- Rocha CEF, Torres IC, Maia-Barbosa PM. 1998.** *Haplocyclops torresi* n. sp. and *Potamocaris estevesi* Reid, 1991 from Brazil, with a proposal for revalidation of the genus *Haplocyclops* Kiefer, 1952 (Copepoda). *Beaufortia* **48**: 1–15.
- Rouch R. 1962.** Harpacticoides (Crustacés Copépodes) d'Amérique du Sud. In: Delamare Deboutville C, Rapoport E, eds. *Biologie de l'Amérique Australe*. Paris: CNRS, 237–280.
- Rouch R. 1986.** Copepoda: Les Harpacticoides souterrains des eaux douces continentales. In: Botosaneanu L, ed. *Stygofauna Mundi, a Faunistic, Distributional, and Ecological Synthesis of the World Fauna Inhabiting Subterranean Waters*. Leiden: EJ Brill/Dr. W Backhuys, 321–355.
- Schminke HK. 1976.** The ubiquitous telson and the deceptive furca. *Crustaceana* **30**: 292–300.
- Wägele J.-W. 2004.** Hennig's phylogenetic systematics brought up to date. In: Williams DM, Forey PL, eds. *Milestones in systematics*. Systematics Association Special Volume **67**: 101–125.
- Wägele J.-W. 2005.** *Foundations of phylogenetic systematics*. Munich: Dr. F. Pfeil.