

First record of the taxon *Echinopsyllus* (Copepoda, Harpacticoida, Ancorabolidae) from the deep sea of Campos Basin, Brazil, with the description of three new species and their contribution to phylogenetic analysis

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Received 19 March 2008; accepted for publication 21 May 2008

New species assignable to the formerly monotypic genus *Echinopsyllus* (Copepoda, Harpacticoida, Ancorabolidae) are described from the continental slope of Campos Basin off Brazil in the south-western Atlantic. *Echinopsyllus brasiliensis* sp. nov., *Echinopsyllus nogueirae* sp. nov., and *Echinopsyllus grohmannae* sp. nov. differ from *Echinopsyllus normani* Sars, 1909 in the cephalothorax having two instead of three pairs of lateral processes, first pair of dorsal cephalothoracic processes being smaller than second pair, second pair of dorsal cephalothoracic processes branched, and segmentation and setation of the swimming legs. The discovery of new species of *Echinopsyllus* extends the distributional range of the genus to the southern hemisphere and is further evidence for the formerly unexpected wide genus-level distribution of Ancorabolidae in the world's oceans. The phylogenetic position of *Echinopsyllus* within Ancorabolinae is discussed. © 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, **156**, 52–78.

ADDITIONAL KEYWORDS: Ancorabolinae – *Ceratonus* group – Crustacea – South Atlantic – taxonomy.

INTRODUCTION

Samples from the continental slope of Campos Basin off south-eastern Brazil recently provided important results that increased our knowledge of the biodiversity of meiofauna along the Brazilian coast, which is currently the object of intensive taxonomic and faunistic research (e.g. Botelho *et al.*, 2007). The present report is part of a multidisciplinary environmental research project sponsored by PETROBRAS, 'Campos Basin Deep-sea Environmental Program', in the deep-water oil exploration and production area of the basin.

In this area, nematodes are the most abundant meiofaunal organisms, followed by harpacticoid copepods (Netto, Gallucci & Fonseca, 2005; Botelho *et al.*, 2007). Preliminary examination of meiofauna from

the continental slope of the Campos Basin revealed a large number of new species, including animals of the family Ancorabolidae Sars, 1909.

The family Ancorabolidae was established by Sars (1909) to encompass four monotypic genera: *Ancorabolutus* Norman, 1903; *Arthropysyllus* Sars, 1909; *Ceratonotus* Sars, 1909; and *Echinopsyllus* Sars, 1909. Lang (1944) introduced the subfamilies Ancorabolinae Sars, 1909 and Laophontodinae Lang, 1944. The small taxon Ancorabolidae has grown considerably since that work, and the number of species has almost quadrupled since Lang's (1948) review of the family. Several new ancorabolid taxa were described, revealing an unexpectedly wide distribution in both the northern and southern hemispheres (Conroy-Dalton & Huys, 2000). Recently, several attempts have been made to elucidate systematic questions within this taxon (George, 1998, 2001, 2006a, b, c; George & Schminke, 1998; Conroy-Dalton & Huys, 2000; Conroy-Dalton, 2001, 2003a,b).

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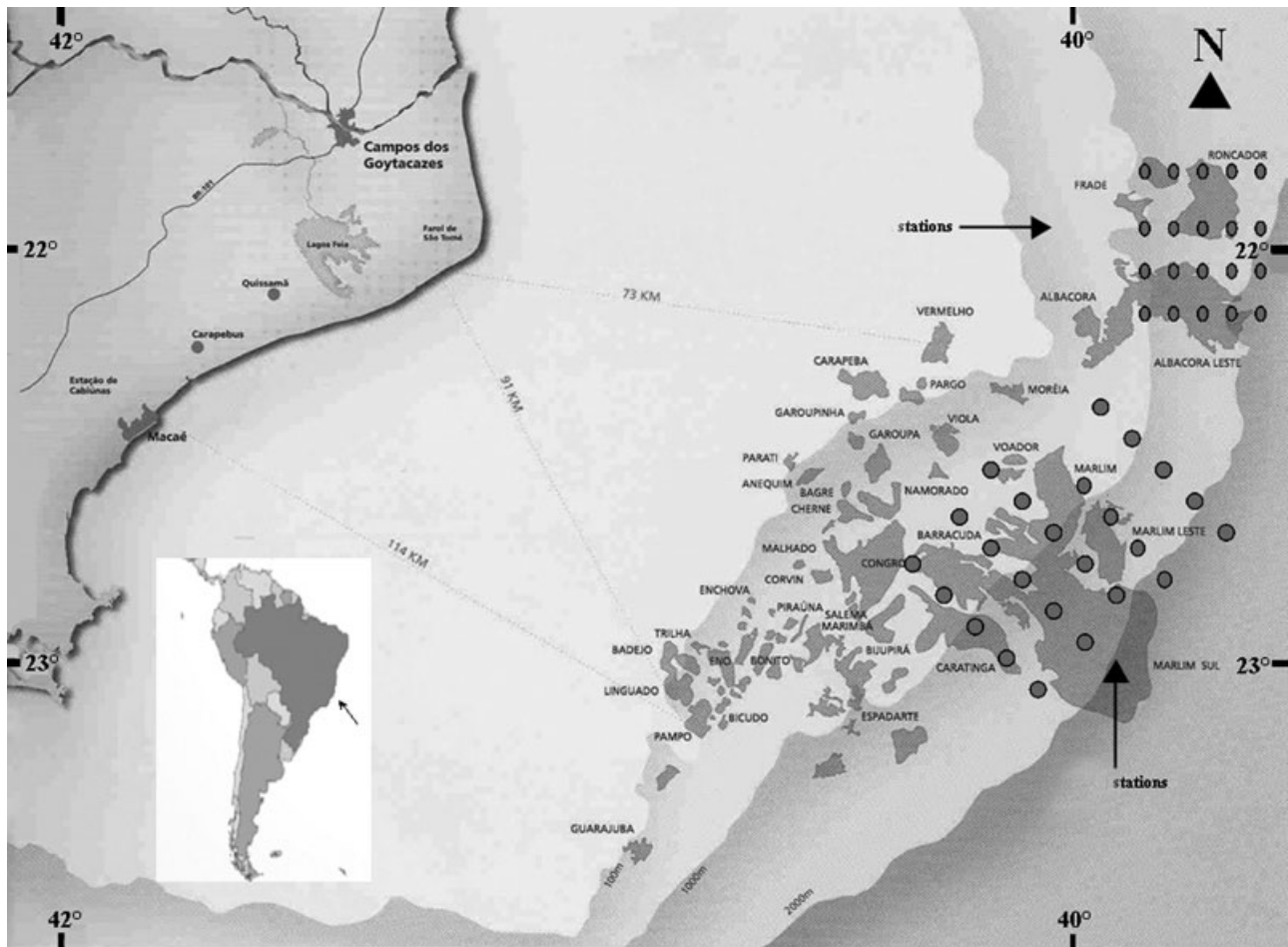


Figure 1. Map of Campos Basin showing the sampling stations (modified from Botelho *et al.* 2007).

The discovery and description of new members of Acorabolinae is of great taxonomic value, because specimens are generally collected in very small numbers (George, 2006a), with males being scarcer than females (Conroy-Dalton, 2001). The relatively high number of descriptions based on single specimens (George, 2006a) means that only one sex is described for most species. Moreover, the large number of monotypic genera found in members of Acorabolinae reflects the inadequate taxonomic knowledge; as research on the group continues, more related species will eventually be found. The present study adds three new species to the formerly monotypic genus *Echinopsyllus*.

MATERIAL AND METHODS

The Campos Basin is located on the south-western margin of the South Atlantic, between latitudes 21°30' and 23°30' S. The continental slope of Campos Basin is 40 km wide, with depths up to

3000 m. It is covered by fine continental sediment and a sandy fraction that is composed mainly of foraminiferan tests (Soares-Gomes *et al.*, 1999). The Campos Basin is the region of highest petroleum production in Brazil; the platforms scattered over the area account for 84% of the offshore oil production of the country.

Sampling was carried out during the cruises OCEANPROF I (November/December 2002) and OCEANPROF II (June/July 2003) on board R/V Astro Garoupa. A total of 44 stations arranged in nine transects along the 750, 1050, 1350, 1650, and 1950-m isobaths were sampled (Fig. 1) using an Unsel spade corer modified to collect 0.25 m² of sediment subdivided into 25 subsamples. From each drop, three subsamples were used for meiofauna, stratifying the subsamples into 0–2 and 2–5 cm layers. In each layer, meiofauna subsamples were taken with a plastic syringe of 2 cm internal diameter. Each sample was transferred to a 100 ml plastic flask and fixed in 10% formalin buffered with borax.

The harpacticoid copepods found in the samples were picked out and preserved in alcohol for later identification to species level. Dissected specimens were mounted on several slides with glycerine. The preparations were sealed with transparent nail varnish.

All drawings were made using a camera lucida on a Leica DMR microscope equipped with differential interference contrast.

Phylogenetic analysis was carried out according to Henning (1982) and Ax (1984).

Descriptive terminology for body and appendage morphology was adopted from Lang (1948), Schminke (1976), and Huys & Boxshall (1991). Abbreviations used in the text and figures are: cphth, cephalothorax; R, rostrum; A1, antennule; A2, antenna; aes, aesthetasc; md, mandible; mxl, maxillule; mx, maxilla; mxp, maxilliped; exp (enp) -1(2, 3) to denote the proximal (middle, distal) segment of a ramus; FR, furcal ramus/rami; P1–P6, swimming legs 1–6; benp, baseoendopod; GF, genital field; LI, first pair of lateral cephalothoracic processes; LII, second pair of lateral cephalothoracic processes; LIII, third pair of lateral cephalothoracic processes; DI, first pair of dorsal cephalothoracic processes; DII, second pair of dorsal cephalothoracic processes. The type specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), Brazil. Scale bars in the figures are indicated in μm .

RESULTS

SYSTEMATICS

HARPACTICOIDA SARS, 1903

ANCORABOLIDAE SARS, 1909

ANCORABOLINAE SARS, 1909

ECHINOPSYLLUS SARS, 1909

Diagnosis: Body cylindrical, tapering slightly posteriorly, without clear demarcation between prosome and urosome; body ornate with series of produced conical processes, each bearing unmodified sensilla apically. Cephalothorax with two to three pairs of lateral and two pairs of dorsal conical processes. Second pair of dorsal cephalothoracic processes branched. Thoracic somites bearing P2–P5 each with paired dorsal conical processes; P6-bearing somite (genital half of double-somite in female) without produced processes. First abdominal somite (abdominal half of double-somite in female) and second abdominal somite with basally fused pair of divergent, conical processes. Remaining integumental sensilla modified, branched. Somatic hyaline frills weakly developed and smooth. Body somites,

swimming legs, P5 and furcal rami with conspicuous tube-pores. Anal operculum rounded with fine setules. Furcal rami elongate and divergent, with seven setae; setae I and II inserted in median third of ramus, seta III sub-distal; seta IV reduced, fused basally to seta V; seta V well developed, pinnate; seta VI reduced; seta VII inserted in median third of ramus, triarticulate at base. Sexual dimorphism in body size, degree of development of cephalothoracic posterodorsal processes and dorsal processes of P2–P3 bearing somites, rostrum size, antennule, P3 endopod, P5, P6, genital segmentation and abdominal ornamentation.

Rostrum moderate in size, discernible in dorsal aspect; fused to cephalic shield; with paired bulbous membranous projections proximal to sensilla; with long distinctive midventral tube-pore subdistally. Antennule four-segmented in female, eight-segmented and subchirocer in male (with three segments distal to geniculation); aesthetasc arising from segments 3 and 4 in female, segments 5 and 8 in male; segment 2 (both sexes) with one subapical anterior seta arising from distinctive spinous projection. Antenna with allobasis showing partial suture along exopodal margin, abexopodal margin with two setae of which endopodal one reduced; exopod entirely absent; endopod with three lateral and six distal elements (two spines and three geniculate setae, longest one fused basally to tiny naked seta). Mandible with robust coxa bearing short pinnate dorsal seta; palp one-segmented, uniramous with two to four setae. Maxillule with one element on coxal endite; basis with three elements on proximal endite; exopod and endopod completely incorporated into basis, each represented by one seta. Maxillary syncoxa with two well-developed endites, each with one to two elements; allobasis drawn out into claw with three accessory elements; endopod minute with two setae. Maxilliped subchelate, slender; syncoxa without armature; endopod drawn out into long narrow, curved claw with one reduced accessory seta.

P1–P4. Intercoxal sclerites wide and narrow; prae-coxae moderately developed; coxa small, quadrangular, bases extremely transversely elongate. P1 exopod three-segmented; exp 3 with three to five geniculate setae; endopod absent, original position indicated by slightly membranous area. P2–P4 exopods three-segmented; endopods absent (P2), one to two-segmented (P3 female and P4 male); P2–P4 exp 2 with or without inner seta. P3 endopod male three-segmented; enp 2 elongate, dorsal surface produced distally into recurved apophysis; enp 3 with two apical setae. Armature formula (based on *Echinopsyllus normani*):

	Exopod 1	Exopod 2	Exopod 3	Endopod 1	Endopod 2	Endopod 3
P1	I:0	I:0	II:2:0	—	—	—
P2	I:0	I:1	II:2:0	—	—	—
P3	I:0	I:1	II:2:0	0	Apophysis	2 (male)
	I:0	I:1	II:2:0	0	2 (female)	
P4	I:0	I:1	II:2:0	1	—	—

P5 biramous in both sexes; basal setophore elongate; endopodal lobe of variable shape and ornamentation, with enp being fused or not to basis. Female genital field located dorsally; gonopores covered by common, unarmed genital operculum derived from medially fused P6, with one seta on either side. Male P6 asymmetrical; without armature; functional member represented by small membranous flap.

Type species: Echinopsyllus normani Sars, 1909.

Locus typicus: Korshaven, Norway (Conroy-Dalton, 2003a).

Additional species: Echinopsyllus brasiliensis sp. nov., *Echinopsyllus nogueirae* sp. nov., *Echinopsyllus grohmannae* sp. nov.

ECHINOPSYLLUS BRASILIENSIS SP. NOV.

Type locality: Station 49K, 22°04'33.9"S 39°52'04.9"W, depth 750 m, layer 0–2 cm, 9.4 °C, 34.6 psu, Campos Basin (Rio de Janeiro, Brazil) in silt-clay sediments.

Type material: one male (holotype), dissected on 15 slides, MZUSP collection no. 18827.

Etymology: The specific name refers to the country where the species was collected.

Description: Male: Habitus (Fig. 2A) long and slender, without clear demarcation between prosome and urosome. Body length measured from tip of R to posterior margin of FR approximately 720 µm. Integument moderately chitinized and ornate, with series of conical processes bearing unmodified sensilla arrowed in Figure 2A. All remaining sensilla on body somites branched. Cephalothorax (Fig. 2A) with two pairs of lateral and two pairs of dorsal processes. All processes apically with sensilla, each lateral process with one long tube-pore subdistally. Dorsal processes backwardly directed and armed with long spinules. Second pair of dorsal processes longer than first pair, each process protruded at its base and bearing additional sensilla proximally. Rostrum (Fig. 2A) small, rectangular, fused to cphth, with very long tube-pore at its tip, two sensilla, and with membranous bulbs laterally. Body somites bearing P3–P5 dorsally with tube-pores. All somites except for free abdominal somites third and fourth bearing dorsal cuticular processes, accompanied by sensilla apically. First and second abdominal somites dorsally with basally fused pair of divergent processes. Telson (Fig. 3A) smaller

than preceding body somites, broader than long, anal operculum with small teeth.

FR (Fig. 3A) long and slender, about 11 times as long as broad, with seven setae: I and II of nearly same length, inserted close together in the middle of FR. III as long as I and II, inserted in distal quarter of FR. IV, V and VI inserted distally; seta V longest, seta IV much smaller, VI shorter than IV. Seta VII articulated at its base, inserted dorsally in the middle of FR, close to setae I and II.

A1 (Fig. 4A and A') eight-segmented, subchirocer. First segment longest, with several long spinules, and with one bipinnate distal seta. Second segment smaller than first one, with six bare setae and several long spinules posteriorly. Third segment much smaller than preceding segments, with five bare setae. Fourth segment smallest, with two bare setae. Fifth segment slightly swollen, covered with long hairy spinules, and bearing seven very small spiniform setae, one longer seta proximally, three long setae distally, and one seta plus one aes arising subterminally from long protrusion. Sixth segment slender, with three modified spines, arrowed in Figure 4A', on its dorsal margin. Seventh segment small, with one bare seta; eighth segment enlarged, distally acute, with eight bare setae and one aes fused with one additional seta. Setal formula: I-1; II-6; III-5; IV-2; V-12 + aes; VI-3; VII-1; VIII-9 + aes.

A2 (Fig. 4B) with allobasis covered with spinules, with two abexopodal setae (the distal one bare and smaller than the first, bipinnate seta). Without exp. Enp with several spinules, medially with two (one unipinnate and one bare) spines and one bare seta smaller than preceding spines. Terminally with six setae, three of which long, dentate, and geniculate, two unipinnate setae, and one small bare seta. Subterminally on anterior margin there is a strong cuticular dentate frill.

Md (Fig. 2B and B') gnathobase badly damaged. Mandibular palp one-segmented, long and slender, covered with spinules, with two apical setae.

Mxl (Fig. 2C) praecoxal arthrite apically with seven strong spines, subapically with two surface setae. Additionally with surface row of long spinules. Coxa with one single bare seta. Basis, enp, and exp fused, bearing four setae.

Mx (Fig. 2D) badly damaged, proximal endite with one seta.

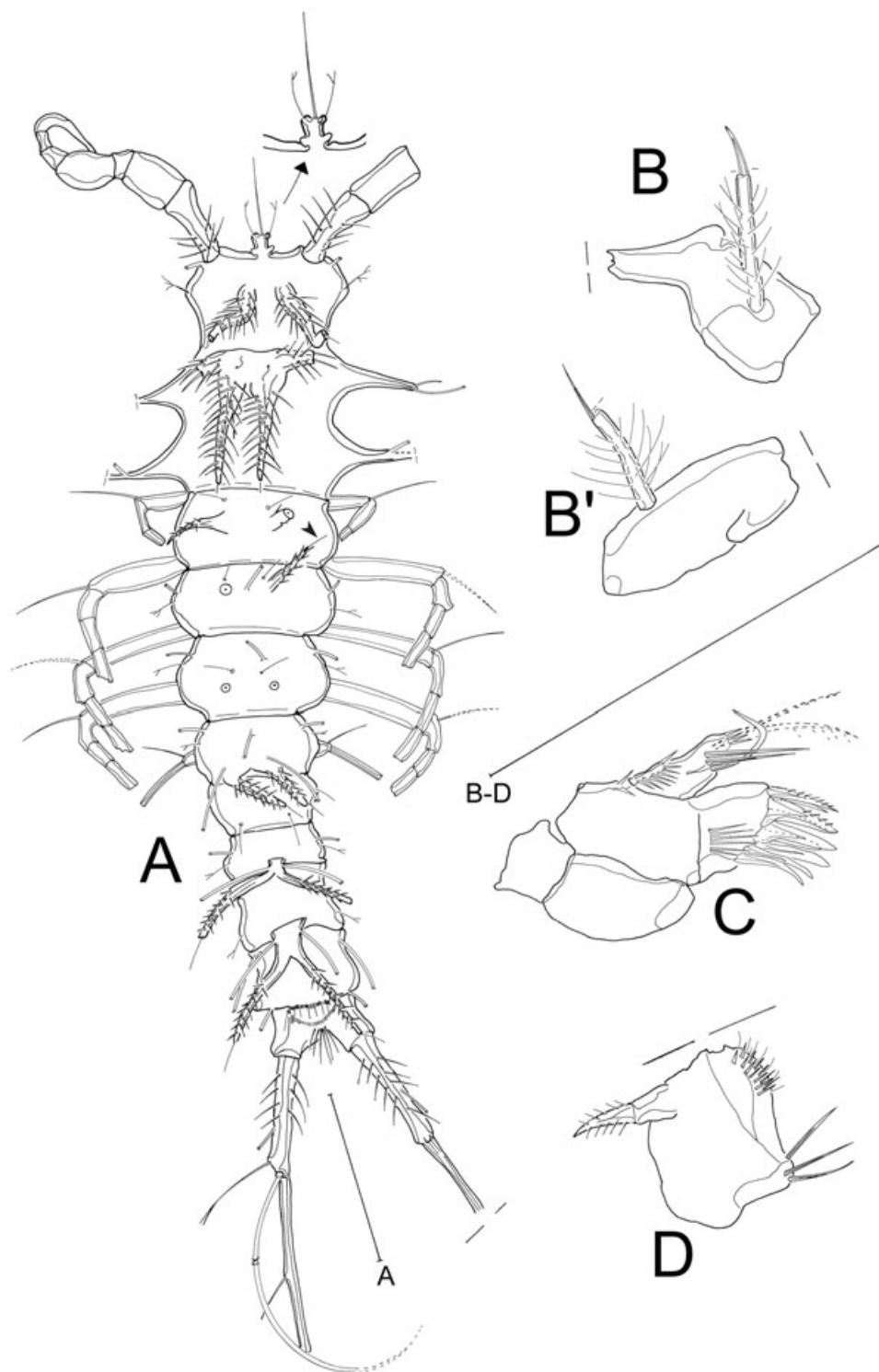


Figure 2. *Echinopsyllus brasiliensis* sp. nov., male. A, habitus dorsal view (unmodified sensillum arrowed); B, B', md; C, mxl; D, mx. Scale bars = 100 µm.

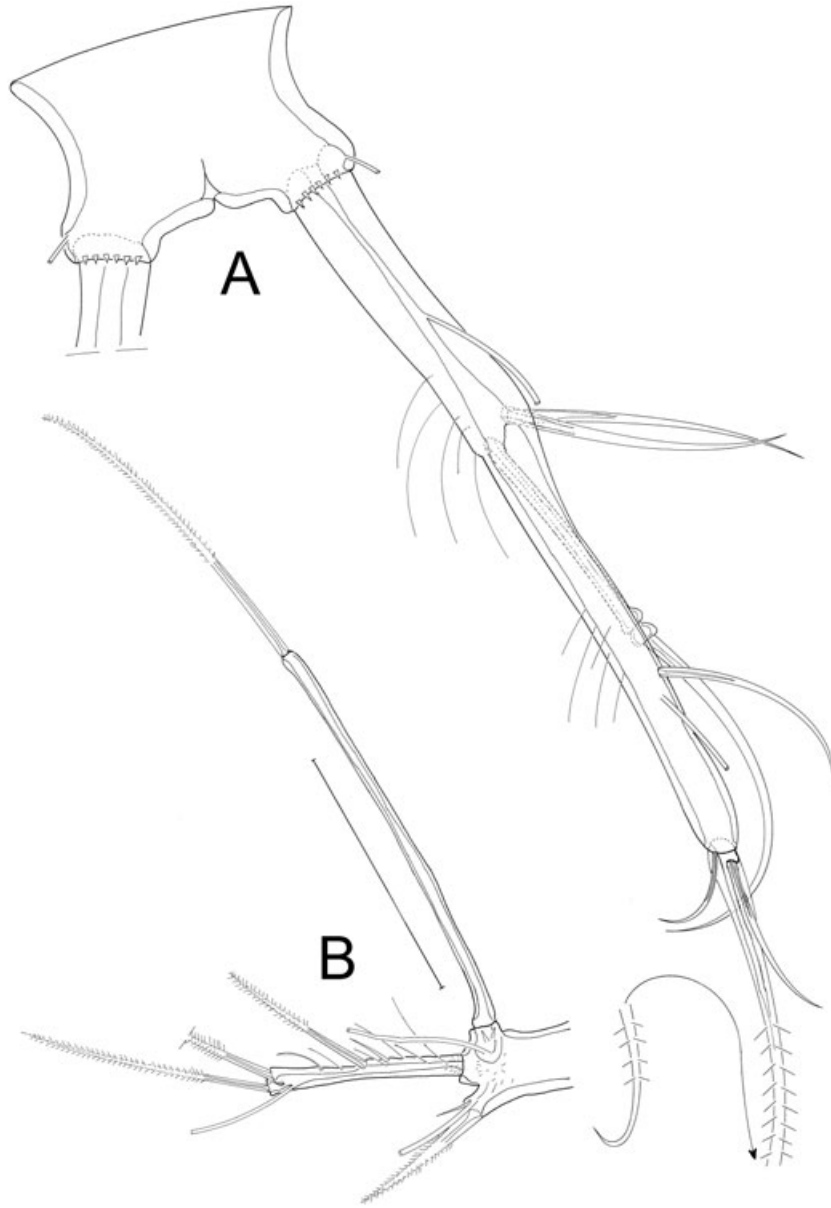


Figure 3. *Echinopsyllus brasiliensis* sp. nov., male. A, telson and FR, dorsal view; B, P5. Scale bar = 50 µm.

Mxp broken, not described.

P1 (Fig. 5A) with three-segmented exp, without enp. Basis transversely prolonged, with bare inner and bipinnate outer seta. Exp1 with outer spine, exp2 with one outer geniculate seta. Exp3 with two outer and two apical geniculate setae.

P2–P4 (Figs 5B, 6A, B) with transversely prolonged bases ornamented with long spinules and one tubepore at their dorsal margins (arrowed in Figs 5B, 6A).

Exps three-segmented, exp2 without inner seta. P2 without enp. P3 with three-segmented enp, enp1 small, without setae; enp2 longest, with a strongly and outwardly curved apophysis; enp3 as long as enp1, with two small bare apical setae. Enp P4 two-segmented, segments small, of nearly the same size. Enp1 without armature, enp2 with two small and bare apical setae and one longer bipinnate seta. Armature formula as follows:

	Exopod 1	Exopod 2	Exopod 3	Endopod 1	Endopod 2	Endopod 3
P2	I;0	I;0	II;2;0	–	–	–
P3	I;0	I;0	II;2;0	0	Apophysis	2
P4	I;0	I;0	II;2;0	0	3	–

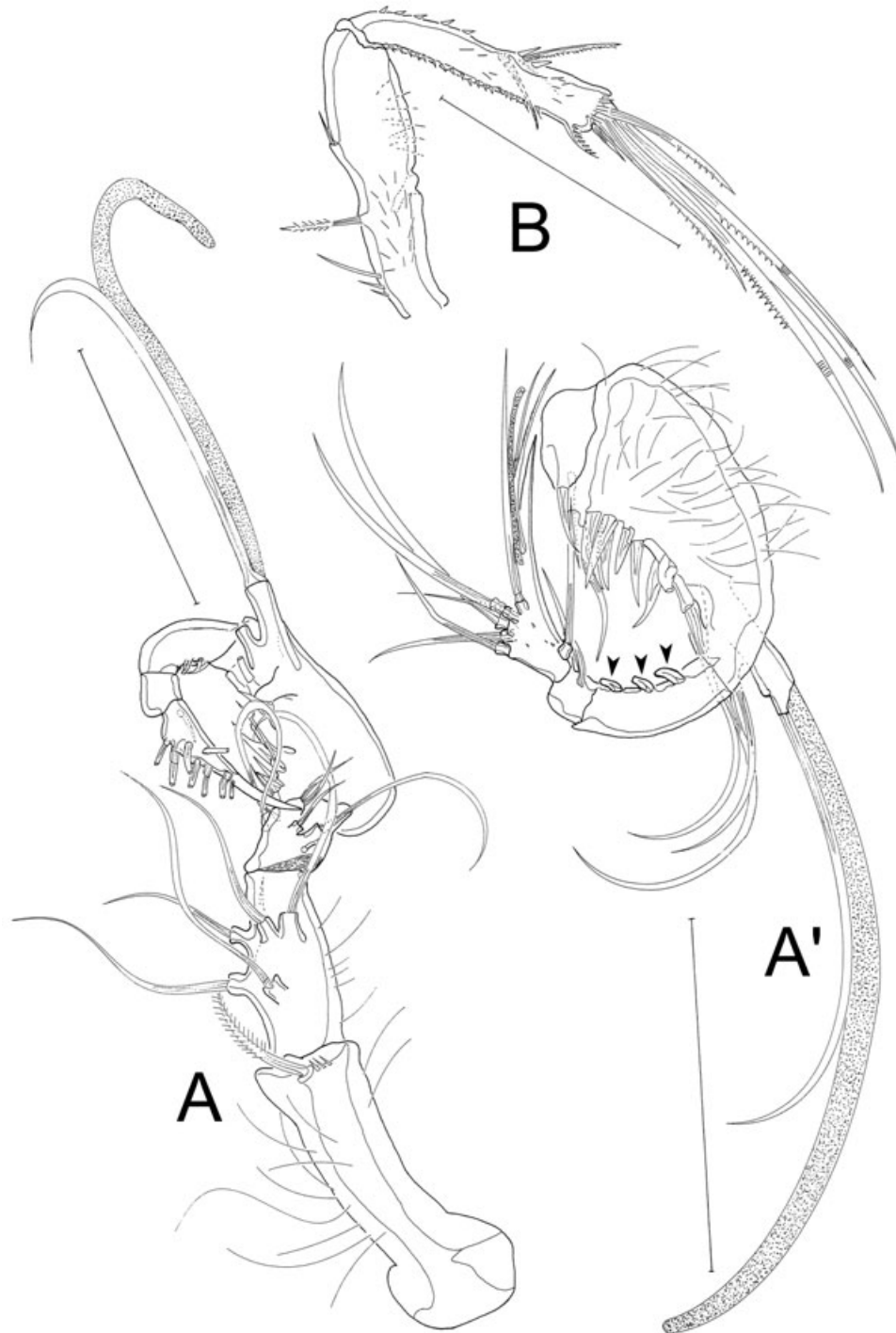


Figure 4. *Echinopsyllus brasiliensis* sp. nov., male. A, A1 ventral view; A', A1 segments 4–8 (modified spines arrowed); B, A2. Scale bar = 50 µm.

P5 (Fig. 3B) baseoendopod with one bipinnate seta accompanied by one tube-pore and one spinule. One additional very long tube-pore inserts on the outer margin close to the setophore. Setophore very long,

much longer than terminally arising bipinnate seta. Exp distinct, with three bipinnate setae, several long spinules, and one subapical tube-pore.

Female unknown.

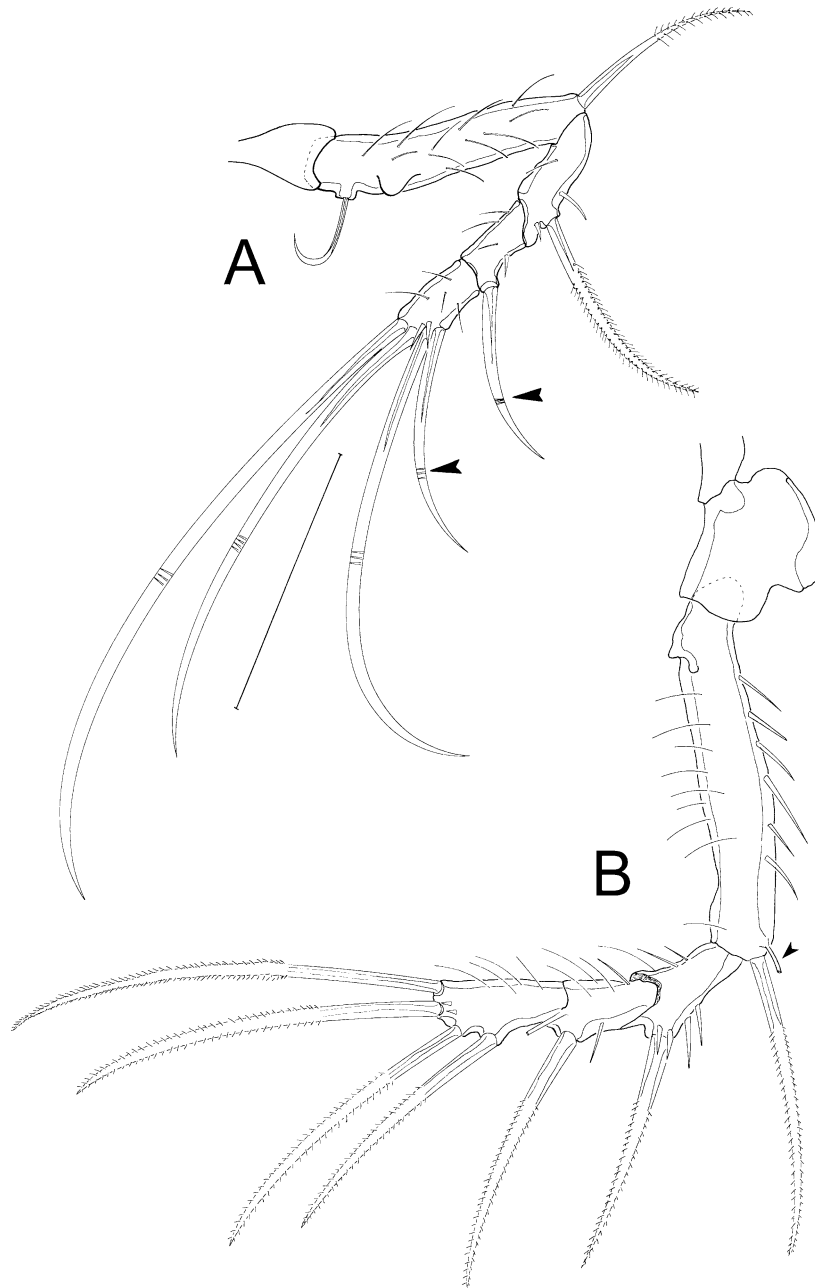


Figure 5. *Echinopsyllus brasiliensis* sp. nov., male. A, P1 (geniculate outer setae arrowed); B, P2 (tube-pore arrowed). Scale bar = 50 μ m.

***ECHINOPSYLLUS NOGUEIRAE* SP. NOV.**

Type locality: Station 75P, 22°31'28.3"S 40°03'50.4"W, depth 1050 m, layer 0–2 cm, 4 °C, 34.3 psu, Campos Basin (Rio de Janeiro, Brazil) in silt-clay sediments.

Type material: one female (holotype), dissected on 12 slides, MZUSP collection no. 18828.

Etymology: the species is dedicated in fond appreciation of the late Professor Catarina R. Nogueira, who

introduced the first author to the taxonomic study of copepods.

Description: Female. Habitus (Fig. 7A) body length measured from tip of R to posterior margin of FR of approximately 673 μ m. Pattern of body processes and sensilla as in *E. brasiliensis* sp. nov. Telson (Fig. 10A) smaller than preceding body somites, broader than long, anal operculum with small teeth. FR (Fig. 10A) long and slender, about 11 times as long as broad,

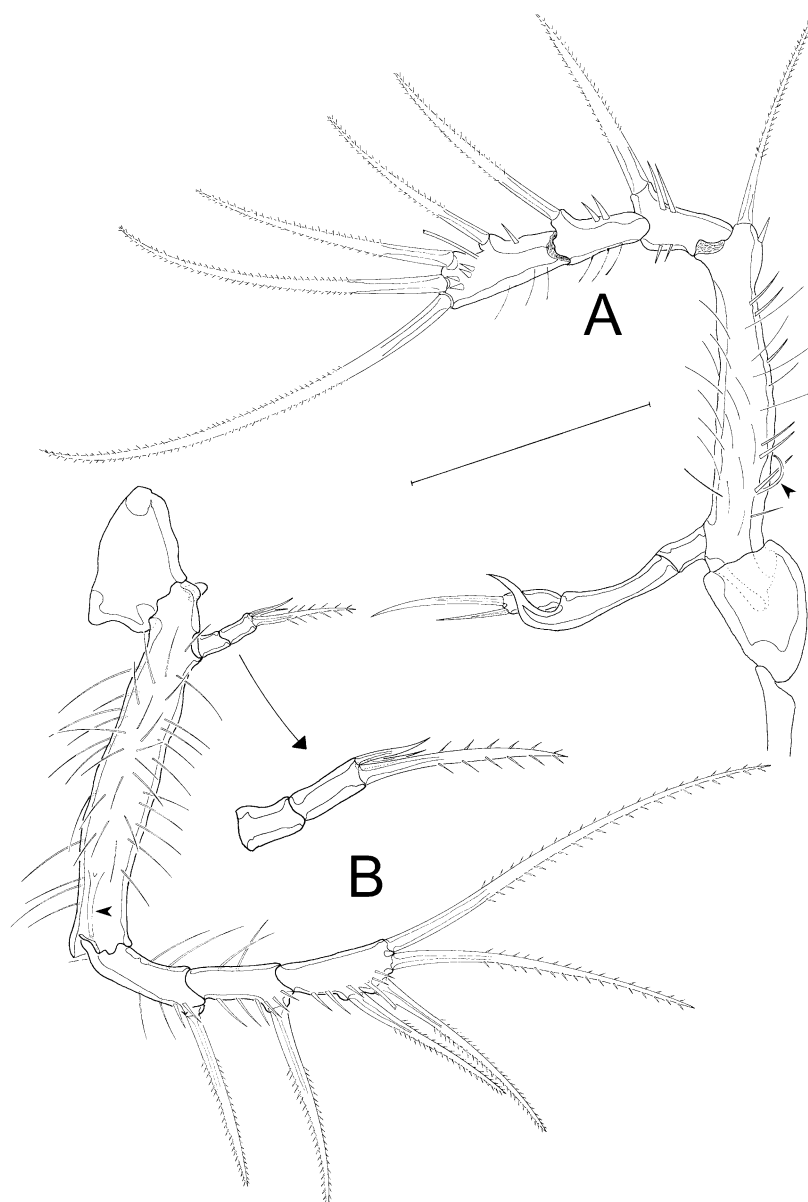


Figure 6. *Echinopsyllus brasiliensis* sp. nov., male. A, P3 (tube-pore arrowed); B, P4. Scale bar = 50 μ m.

with seven setae. Setae I and II of different length, seta I smaller and bare, seta II bipinnate, close to proximal quarter of FR. Seta III bare, inserted in distal quarter of FR. Setae IV, V, and VI inserting distally. Setae IV and V lost during processing, seta VI bare. Seta VII articulated at its base, inserted dorsally in the middle of FR.

A1 (Fig. 8A) four-segmented. Segments 1, 3, and 4 elongate. First segment with several long spinules, with one bipinnate seta. Second segment shortest, with five setae. Third segment with seven setae and apical acrothek consisting of aesthetasc and one bare seta. Fourth segment with nine bare setae (one broken) and apical acrothek enclosing two setae

and aes. Setal formula: I-1; II-5; III-8 + aes; IV-11 + aes.

A2 (Fig. 9A). Allobasis ornamented with spinules with two abexopodal setae (distal one bare and smaller than the proximal, pinnate seta), without exp. Enp with several spinules, medially with two (one unipinnate and one bare) spines and one bare seta smaller than preceding spines. Apically with six setae, four of which geniculate and one small bare seta.

Md (Fig. 7B). Mandibular palp one-segmented, long and slender; covered with spinules, with one inner and three apical setae.

Mxl (Fig. 7D). Praecoxal arthrite with two surface setae subapically and seven distal spines. Coxa with

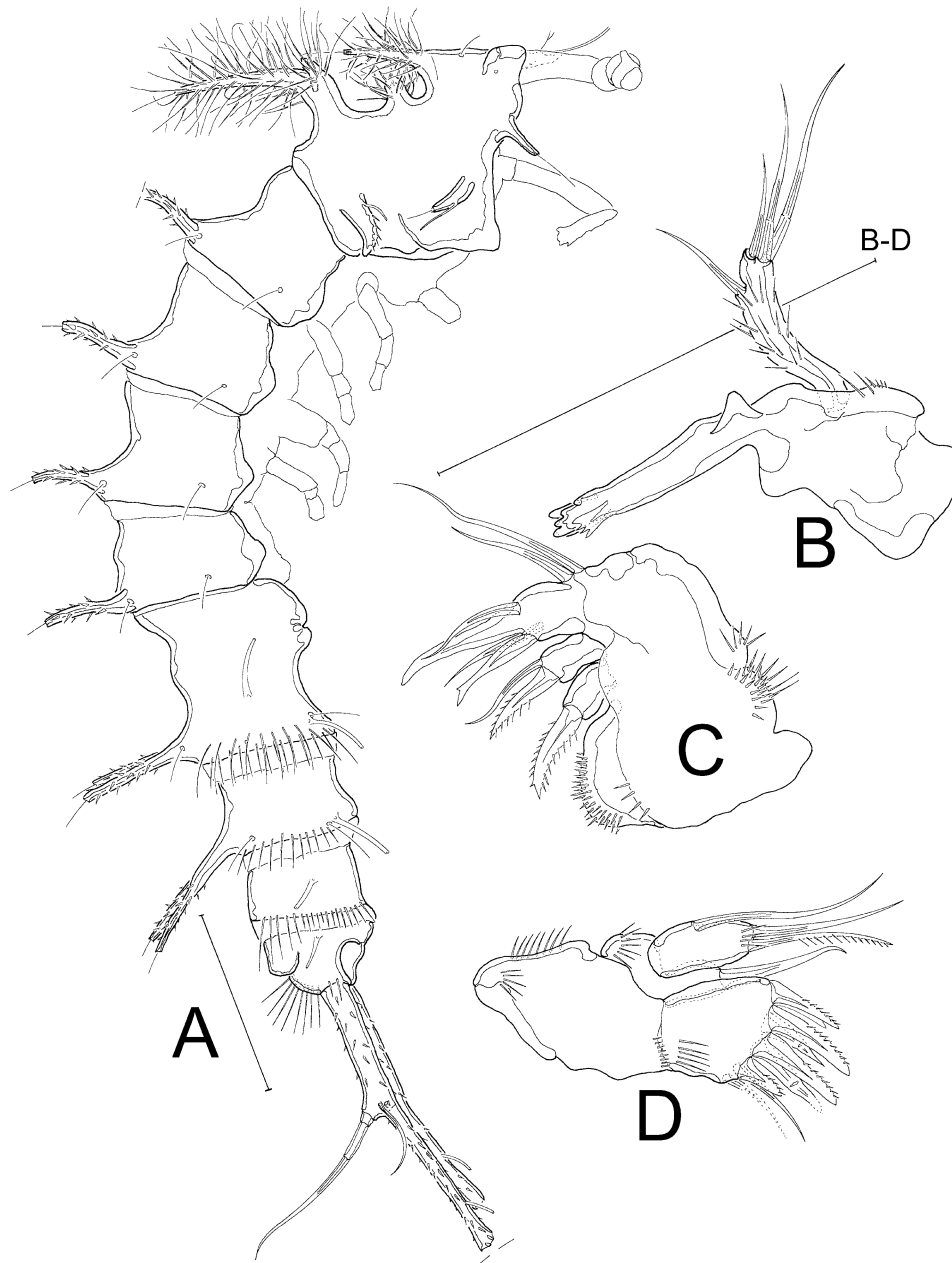


Figure 7. *Echinopsyllus nogueirae* sp. nov., female. A, habitus, lateral view; B, md; C, mx; D, mxl. Scale bars: A = 100 μ m, B–D = 50 μ m.

one single bare seta. Basis, enp, and exp fused, bearing three setae (two bare and one unipinnate).

Mx (Fig. 7C). Syncoxa with spinule patches. With two coxal endites; proximal endite with one bipinnate spine and second endite with one bipinnate spine and one bare seta. Allobasal endite with one fused spine and an accessory armature consisting of three bare setae, one apically bifid spine, and one spine. Enp represented by two bare setae.

Mxp (Fig. 8B) Subchelate and slender. Syncoxa with spinule patches. Enp with curved claw bearing one accessory seta.

P1 (Fig. 10B) with three-segmented exp, without enp. Basis transversely prolonged, with bare inner and outer bipinnate seta. Exps 1 and 2 with outer bipinnate spine, exp3 with one bipinnate spine and one geniculate seta on outer margin and two geniculate setae on distal margin.

P2 as in *E. brasiliensis* sp. nov.

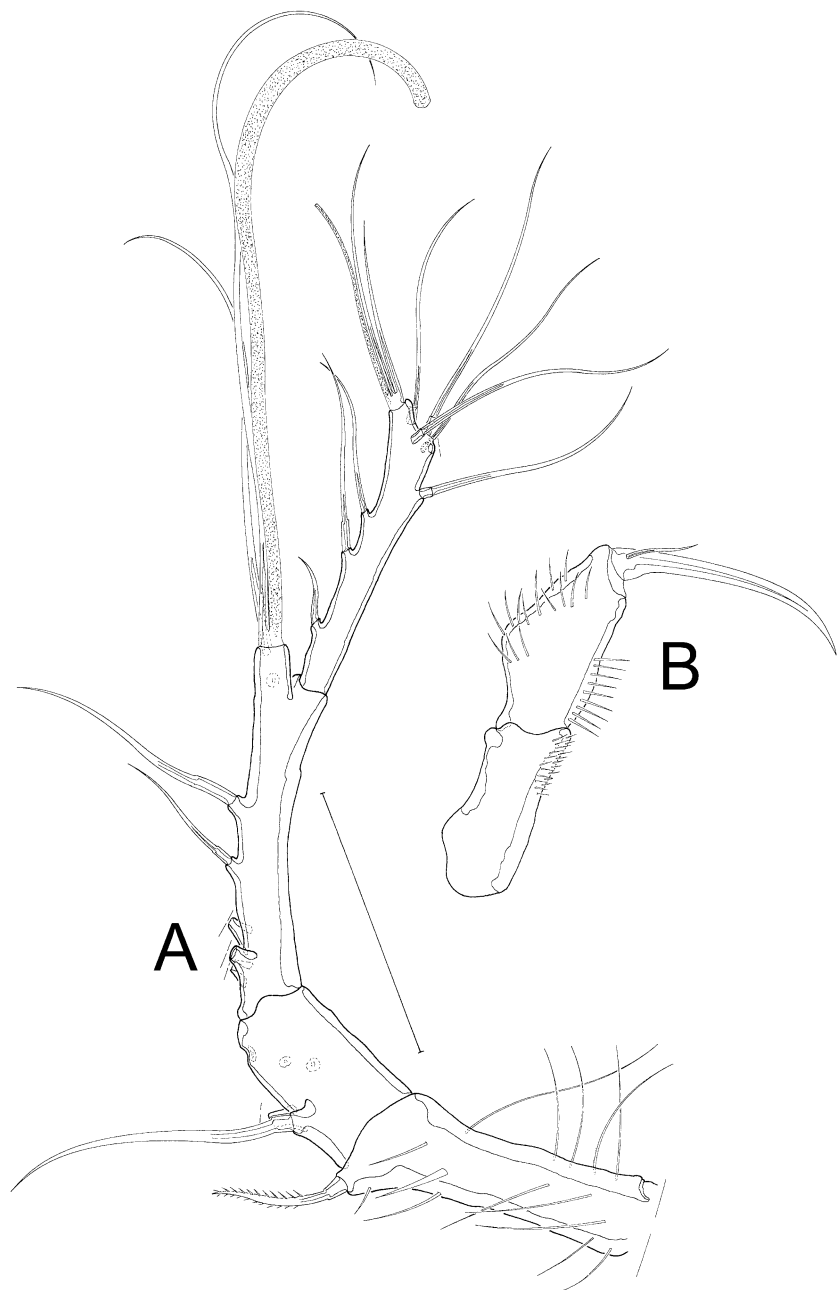


Figure 8. *Echinopsyllus nogueirae* sp. nov., female. A, A1, ventral view; B, mxp. Scale bar = 50 µm.

P3–P4 (Fig. 11A, B) with transversely prolonged bases ornamented with long spinules and one tube-pore on their dorsal margins. Exps three-segmented, exp2 without inner seta. P3 with one-segmented enp armed with one small and one long bipinnate seta. Enp P4 one-segmented, with one bipinnate seta. Armature formula as follows:

	Exopod 1	Exopod 2	Exopod 3	Endopod 1	Endopod 2	Endopod 3
P2	I;0	I;0	II;2;0	–	–	–
P3	I;0	I;0	II;2;0	2	–	–
P4	I;0	I;0	II;2;0	1	–	–

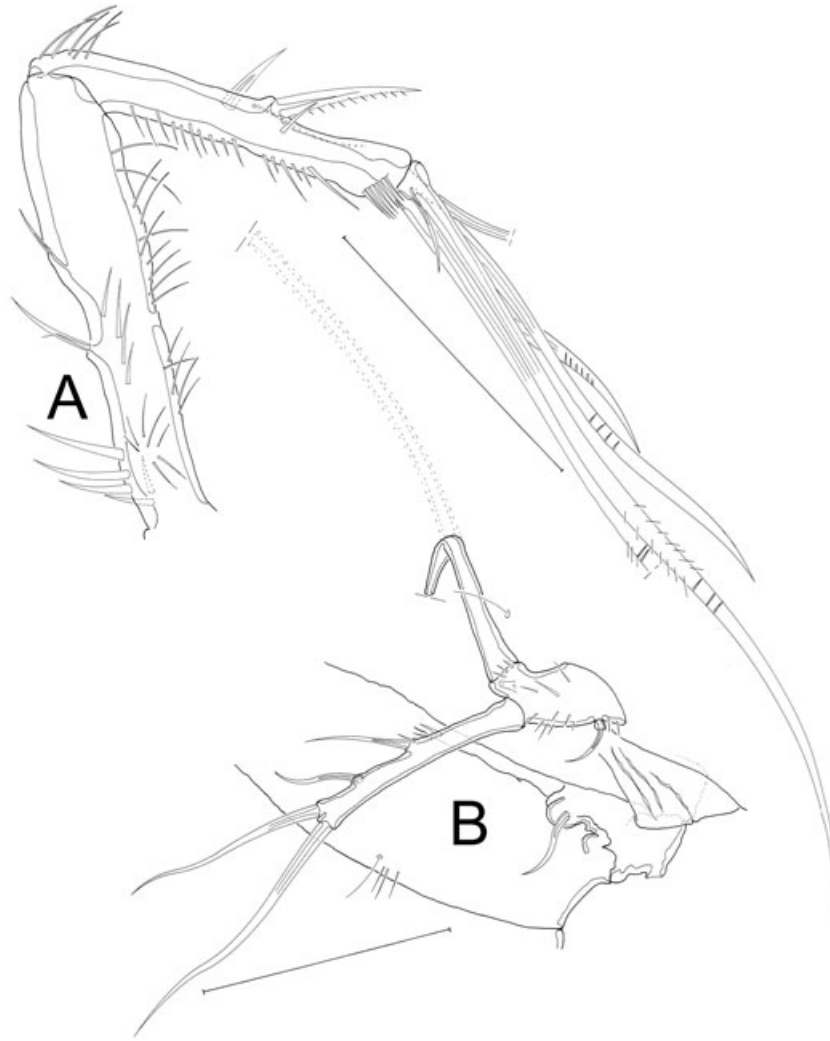


Figure 9. *Echinopsyllus nogueirae* sp. nov., female. A, A2; B, P5 with P6. Scale bar = 50 µm.

P5 (Fig. 9B). Baseoendopodal lobe represented by one small bare seta; with tube-pore at base of setophore. Exp distinct, with four bare setae.

GF (Fig. 9B) gonopores covered by P6 with one bare seta.

Male unknown.

***ECHINOPSYLLUS GROHMANNAE* SP. NOV.**

Type locality: Station 75F, 22°31'28.3"S 40°03'50.4"W, depth 1050 m, layer 0–2 cm, 4 °C, 34.3 psu, Campos Basin (Rio de Janeiro, Brazil) in silt-clay sediments.

Type material: two females, dissected on 14 slides, MZUSP collection no. 18829.

Etymology: the species name is given in grateful dedication to Dr. Priscila A. Grohmann (Universidade Federal do Rio de Janeiro, Brazil), in recognition of

her contribution to the scientific formation of the first author.

Description: Female: Habitus (Fig. 12A) body length measured from tip of R to posterior margin of FR of approximately 670 µm. Pattern of body processes and sensilla as in *E. brasiliensis* sp. nov. Telson (Fig. 12A) smaller than preceding body somites, broader than long, anal operculum with small teeth. FR (Fig. 13A) long and slender, about 11 times as long as broad, with seven setae: I and II bipinnate of nearly same length, inserted close together in the middle of FR. Seta III bipinnate as long as I and II, inserted in distal quarter of FR. Setae IV, V, and VI inserted distally; seta V longest, seta IV much smaller, seta VI shorter than seta IV. Seta VII inserted dorsally in the middle of FR, close to setae I and II.

A1 (Fig. 14A) four-segmented. Segments 1, 3, and 4 elongate. First segment with several long spinules

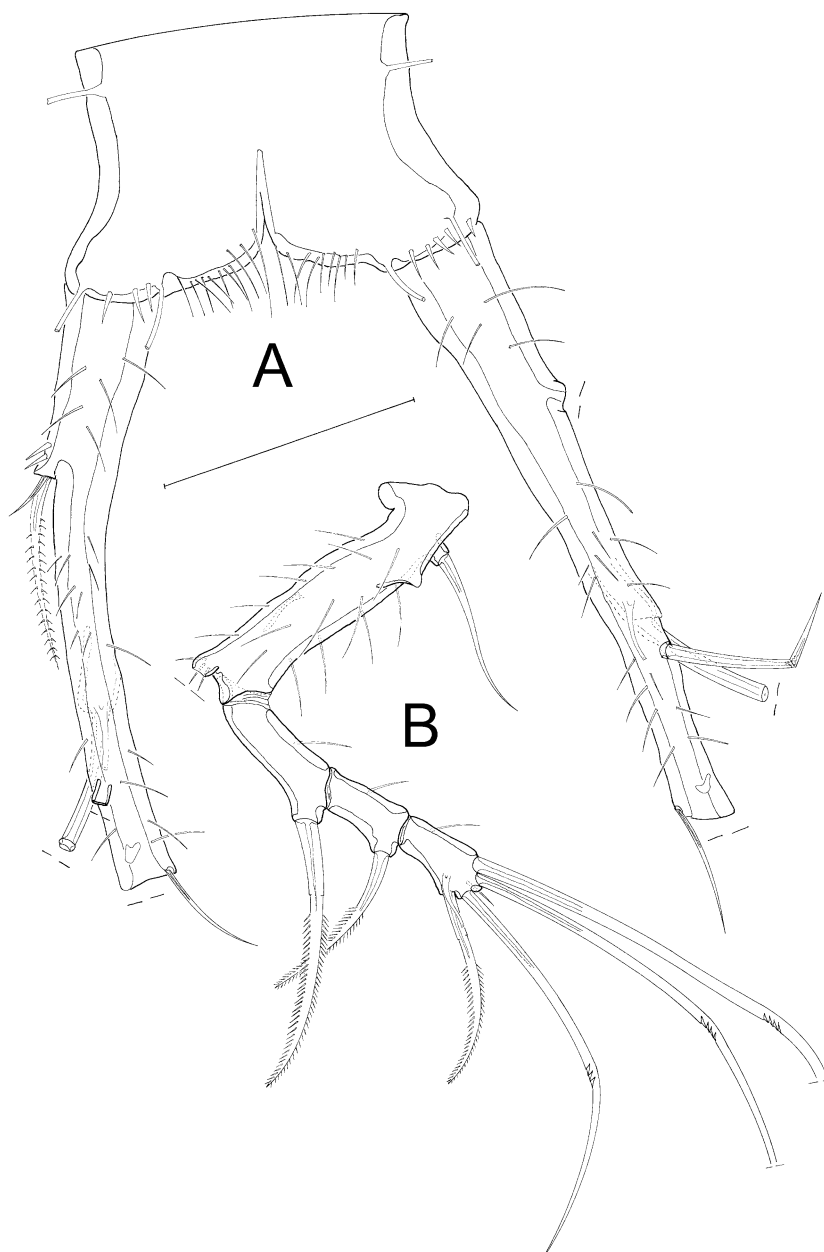


Figure 10. *Echinopsyllus nogueirae* sp. nov., female. A, telson and FR, dorsal view; B, P1. Scale bar = 50 µm.

and distally with one seta. Second segment shortest, with five setae. Third segment with seven setae and apical acrothek consisting of aesthetasc and one bare seta. Fourth segment with nine setae and apical acrothek consisting of two setae and aes. Setal formula: I-1; II-5; III-8 + aes; IV-11 + aes.

A2 (Fig. 14B) with allobasis ornamented with spinules, with two abexopodal setae (distal one bare, arrowed in Fig. 14B, and smaller than the proximal, pinnate seta), without exp. Enp with several spinules, medially with two (one unipinnate and one bare) spines and one bare seta smaller than preceding spines. Terminally with six setae, three of which

geniculate, two unipinnate, and one small bare seta.

Md (Fig. 13B and B'). Mandibular palp one-segmented, long and slender; covered with spinules, with two bare terminal setae.

Mxl (Fig. 12B). Praecoxal arthrite with two surface setae subapically and seven distal spines. Coxa with one single pinnate seta. Basis, enp, and exp fused, bearing four setae (three bare and one unipinnate).

Mx (Fig. 13C). Syncoxa with spinular patches, with two coxal endites; proximal endite with one bipinnate, apically bifid spine, and distal endite with one bipinnate, apically bifid spine and one bare seta. Allobasal

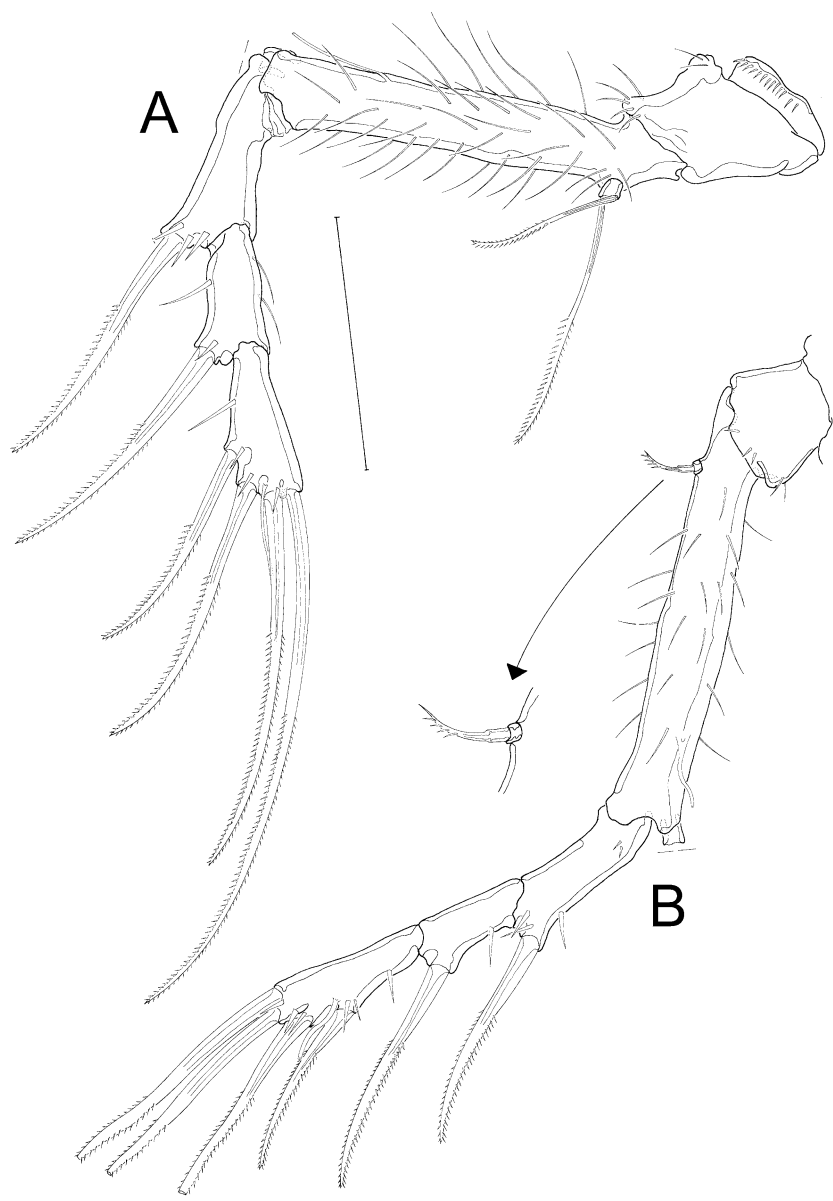


Figure 11. *Echinopsyllus nogueirae* sp. nov., female. A, P3; B, P4. Scale bar = 50 µm.

endite with one fused spine and an accessory armature consisting of two bare setae, one apically bifid spine, and one spine. Enp with two bare setae.

Mxp (Fig. 12C). Subchelate and slender. Syncoxa with spinule patches. Enp with curved claw bearing one accessory seta.

P1 (Fig. 15A) with three-segmented exp, without enp. Basis transversely prolonged, with bare inner and outer bipinnate seta. Exps 1 and 2 with outer

bipinnate spine, exp3 with two outer and two apical geniculate setae.

P2 as in *E. brasiliensis* sp. nov.

P3–P4 (Figs 15B, B' and 16A, A') with transversely prolonged bases, with long spinules on their dorsal margins. Exp three-segmented, exp2 without inner seta. P3 with one-segmented enp, with two small bare setae. Enp P4 one-segmented, with one small bare seta and one longer bipinnate seta. Armature formula as follows:

	Exopod 1	Exopod 2	Exopod 3	Endopod 1	Endopod 2	Endopod 3
P2	I;0	I;0	II;2;0	—	—	—
P3	I;0	I;0	II;2;0	2	—	—
P4	I;0	I;0	II;2;0	2	—	—

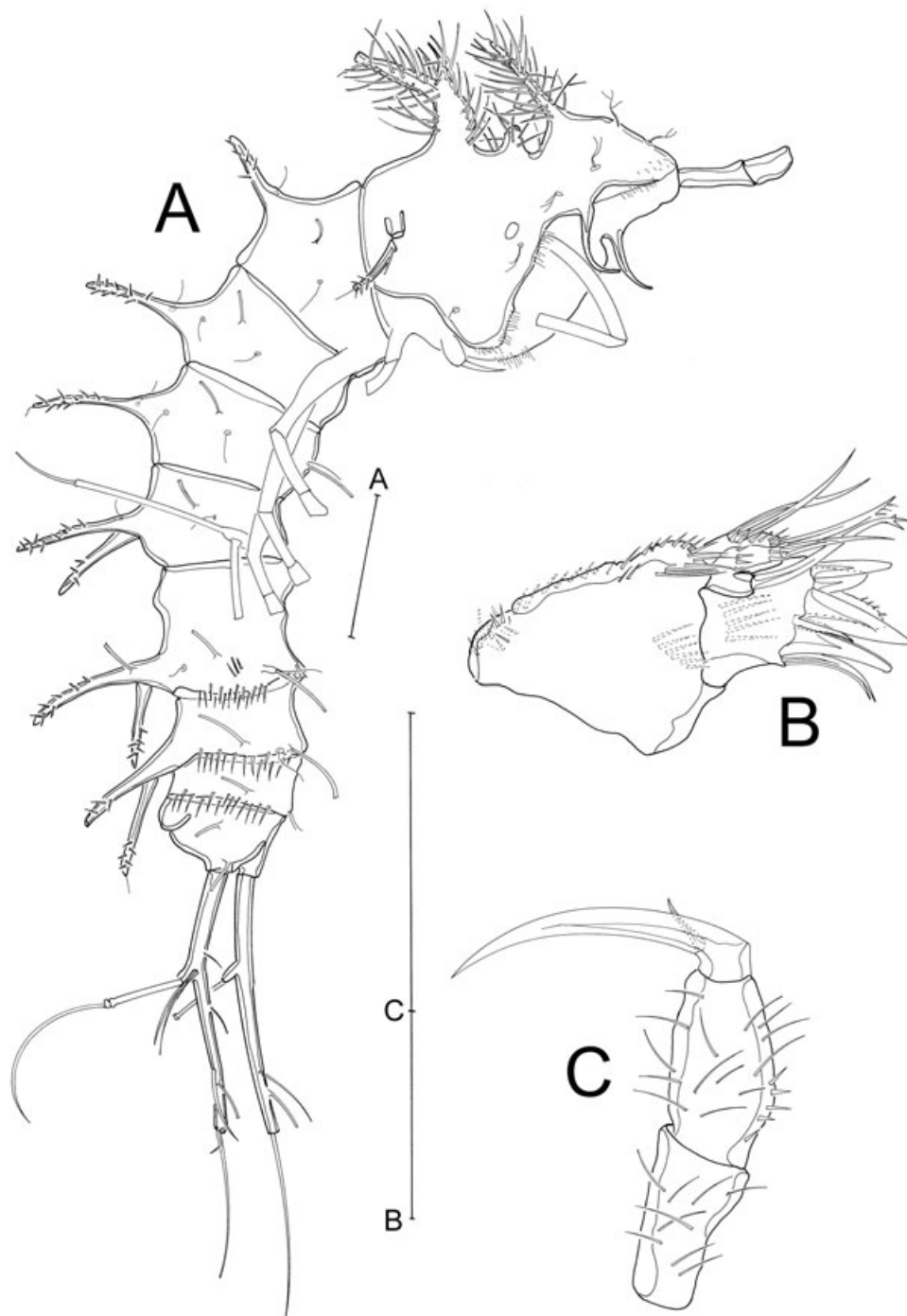


Figure 12. *Echinopsyllus grohmannae* sp. nov., female. A, habitus, lateral view; B, mxl; C, mxp. Scale bars: A = 100 µm, B, C = 50 µm.

P5 (Fig. 16B) baseoendopod bearing two small bare setae accompanied by one tube-pore. Setophore long, articulated. One additional very long tube-pore present on the outer margin near the setophore. Exp distinct, with four setae and one long tube-pore.

GF (Fig. 16C) gonopores covered by fused P6 bearing one pair of bare setae.

Male unknown.

With the addition of three new species to the genus *Echinopsyllus*, a key to the species is presented.

- | | |
|---|---------------------------------|
| 1. Cephalothorax with pair of anterolateral conical processes; P2–P4 exp2 with inner seta... | <i>E. normani</i> Sars, 1909 |
| Cephalothorax without pair of anterolateral conical processes; P2 exp2 without inner seta..... | 2 |
| 2. P4 enp two-segmented..... | <i>E. brasiliensis</i> sp. nov. |
| P4 enp one-segmented..... | 3 |
| 3. P4 enp with one unipinnate seta; P5 benp minute and distinct, with one small bare seta, exp with four bare setae | <i>E. nogueirae</i> sp. nov. |
| P4 enp with two setae; P5 baseoendopodal lobe elongate with two small bare setae and one tube-pore, exp with four bare setae and one tube-pore..... | <i>E. grohmannae</i> sp. nov. |

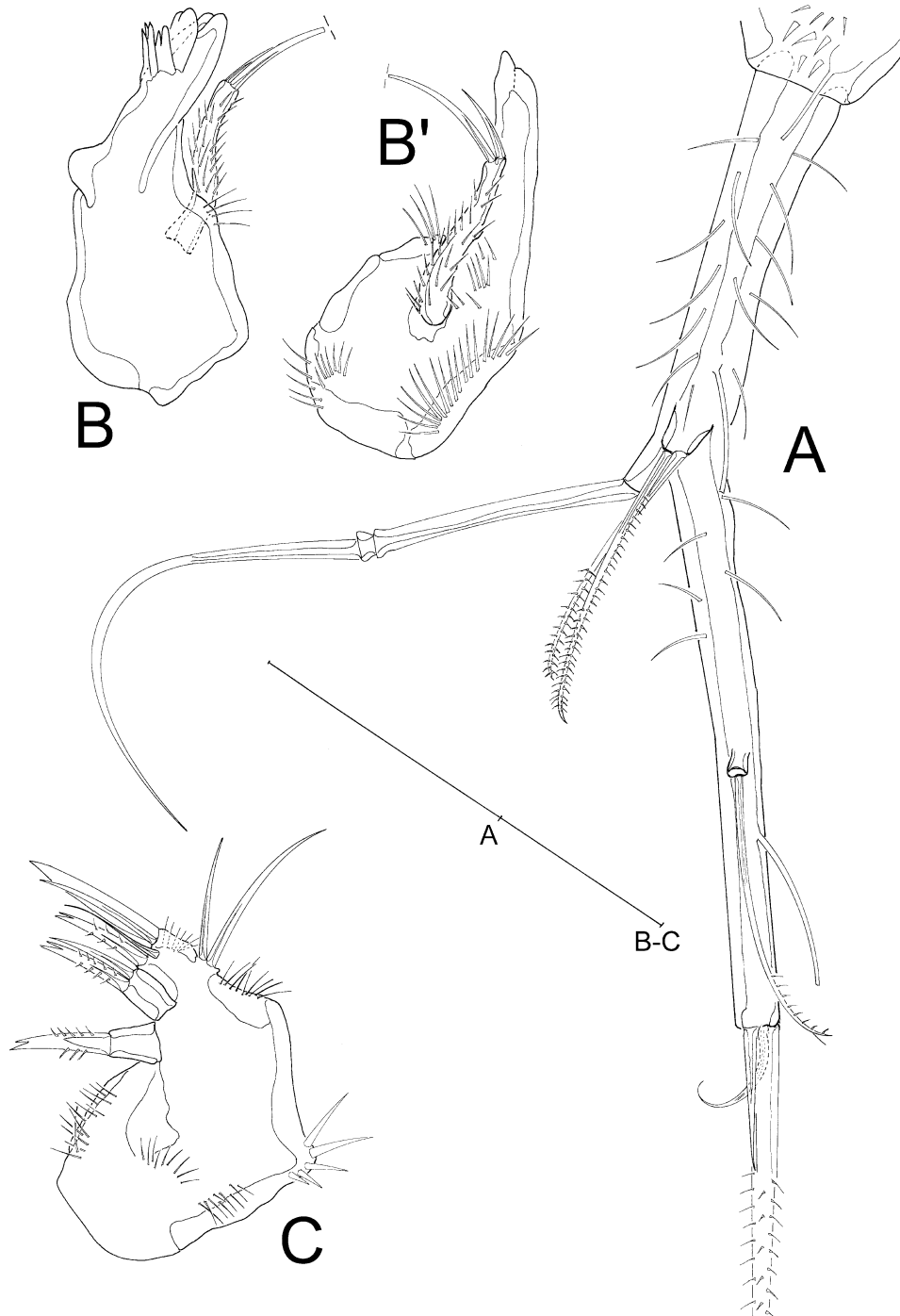


Figure 13. *Echinopsyllus grohmannae* sp. nov., female. A, FR, lateral view; B, B', md; C, mx. Scale bar = 50 µm.

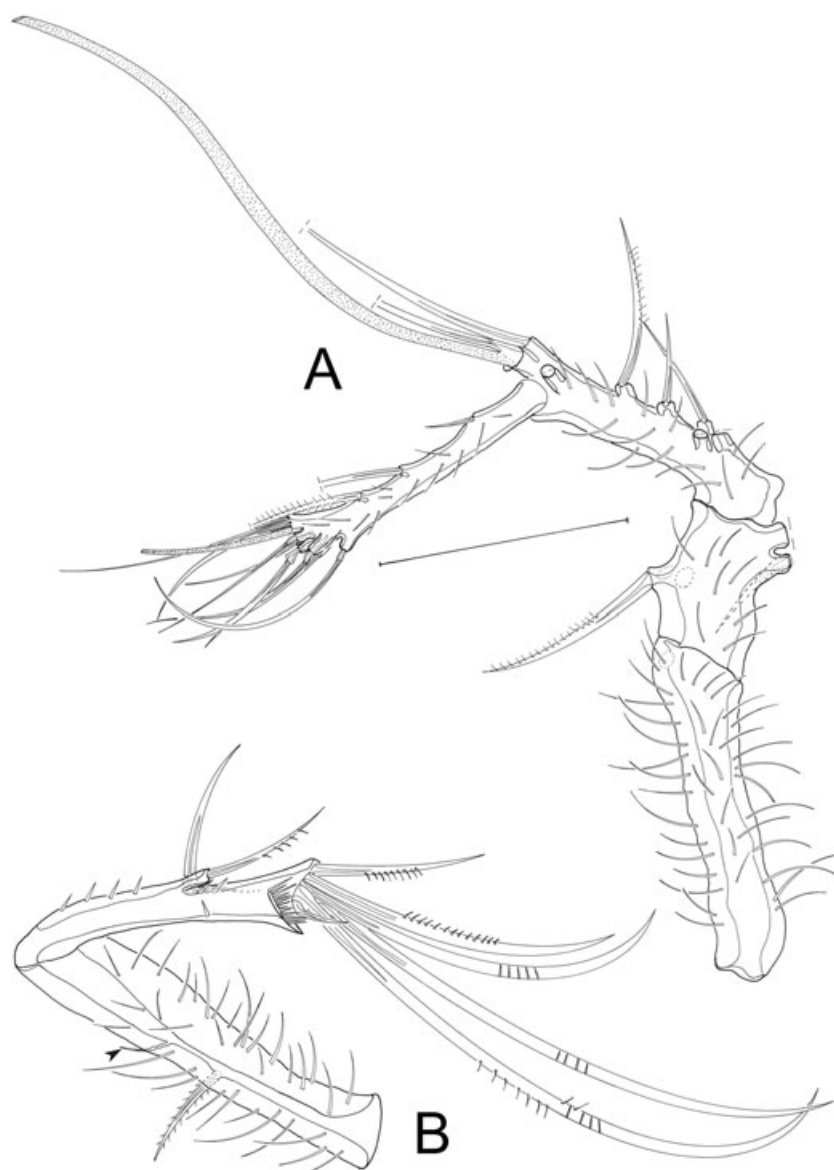


Figure 14. *Echinopsyllus grohmannae* sp. nov., female. A, A1; B, A2 (distal minute seta on the allobasis arrowed). Scale bar = 50 μ m.

DISCUSSION

The diagnosis of monotypic genera is inevitably the same as that of the single species they enclose. Therefore, the detailed diagnosis of *Echinopsyllus* given by Conroy-Dalton (2003a) is identical to the specific diagnosis of *E. normani*. This may lead, however, to certain problems when new species are found to be closely related to a species of a monotypic genus. Are the differences between a new species and a known species merely specific differences, or these would be enough to justify the erection of another new (and probably) monotypic genus? We had to face this

problem when describing the species collected in Campos Basin, which share many derived characters with *E. normani*, but at the same time present several unique features. We had also to face that problem when analysing the phylogenetic status of *Echinopsyllus*, particularly with its supposed sister-taxon, the monotypic genus *Pseudechinopsyllus* George, 2006a. Providing the reasons for our actions below, we allocate the newly described species *E. brasiliensis* sp. nov., *E. nogueirae* sp. nov., and *E. grohmannae* sp. nov. into the formerly monotypic genus *Echinopsyllus*. They share a series of strong synapomorphies with *E. normani*, justifying their

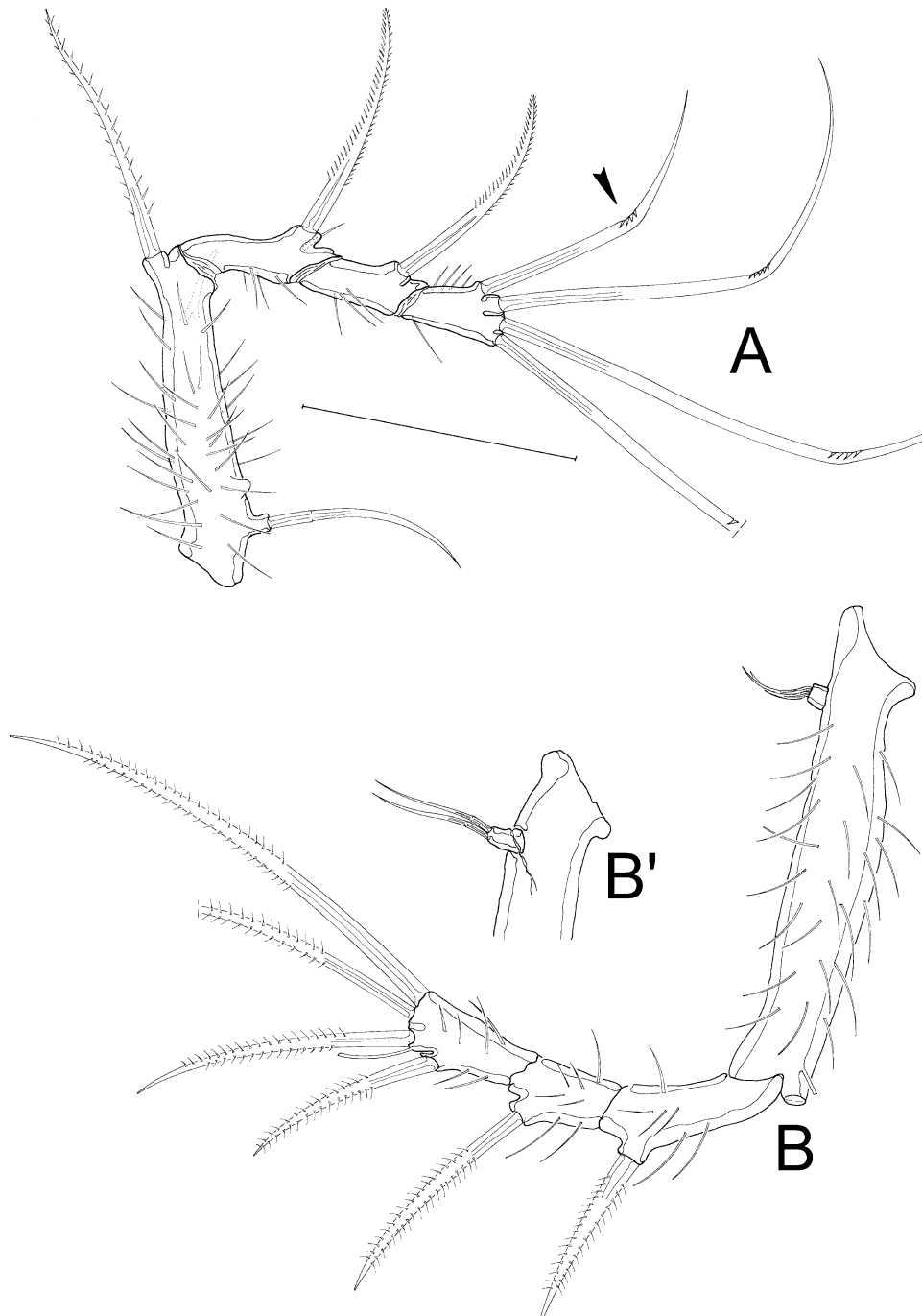


Figure 15. *Echinopsyllus grohmannae* sp. nov., female. A, P1 (geniculate outer setae arrowed); B, P4; B', P4, enp. Scale bar = 50 μ m.

assignment to *Echinopsyllus*. This genus shows several peculiar features, which are unique within Ancorabolinae. Conroy-Dalton (2003a: 167) even stated that '*Echinopsyllus* occupies an isolated position in the Ancorabolinae', and she felt unable to allocate *E. normani* either to the *Ancorabolus*- or to the *Ceratonotus*-group (Conroy-Dalton, 2003a). Thus,

to clarify the systematic position of *Echinopsyllus* within Ancorabolinae, discoveries of new species were necessary. While George (2006a) was able to allocate *E. normani* to the *Ceratonotus*-group, based on new information obtained by description of and comparison with *Pseudechinopsyllus sindemarkae* George, 2006a, the new Brazilian *Echinopsyllus* species

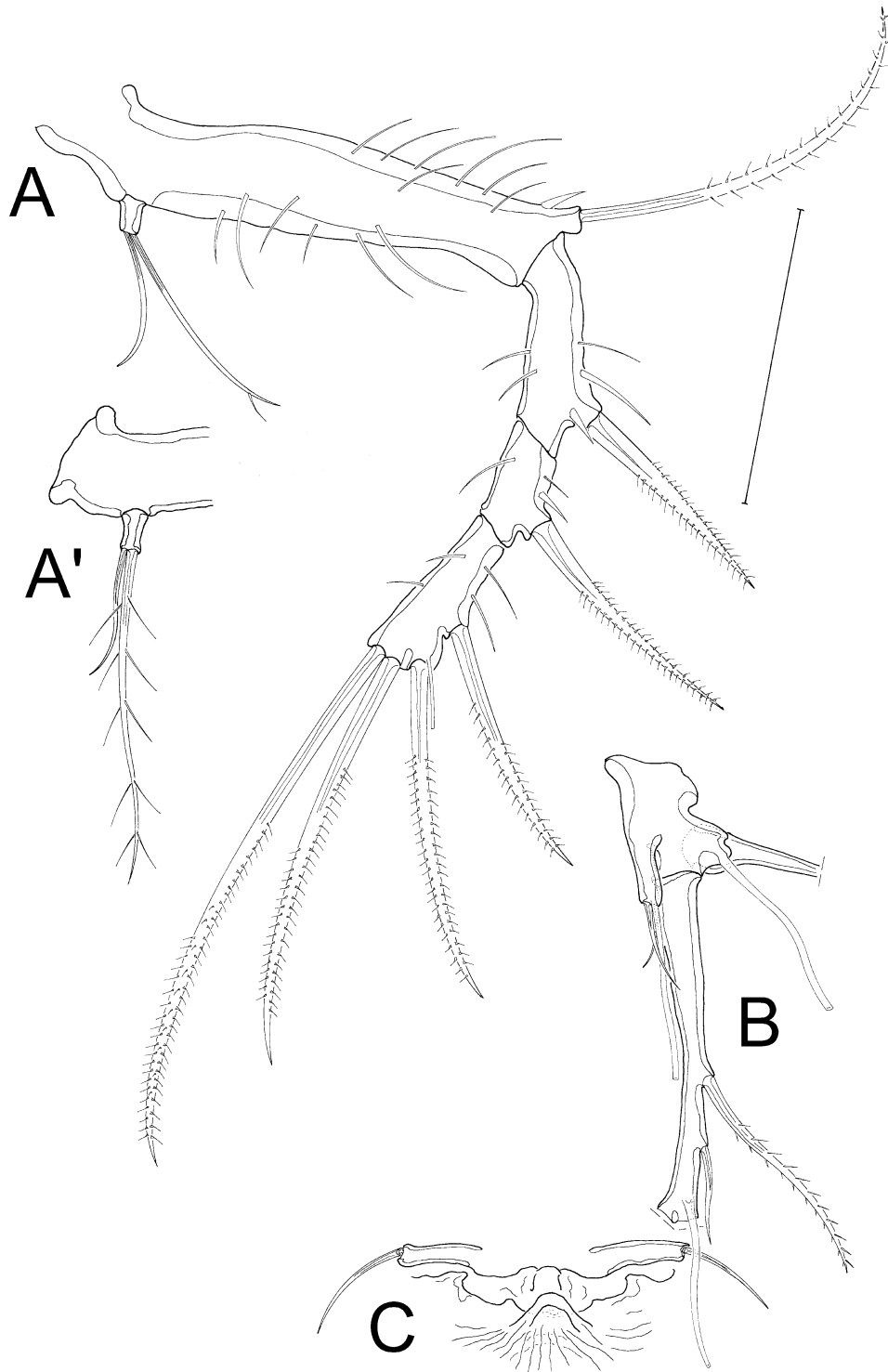


Figure 16. *Echinopsyllus grohmannae* sp. nov., female. A, P4; A', P4 enp; B, P5; C, GF with P6. Scale bar = 50 µm.

enable us to sharpen the characteristics of the taxon *Echinopsyllus*, which is no longer monotypic but becomes a monophylum.

The 46 characters used for the phylogenetic analysis are listed below. Their phylogenetic states

(Plesiomorphic/apomorphic) are presented in the Appendix. Characters 41–46 remain incongruent (Appendix).

Echinopsyllus shows eight autapomorphies, compared not only with the remaining members of the

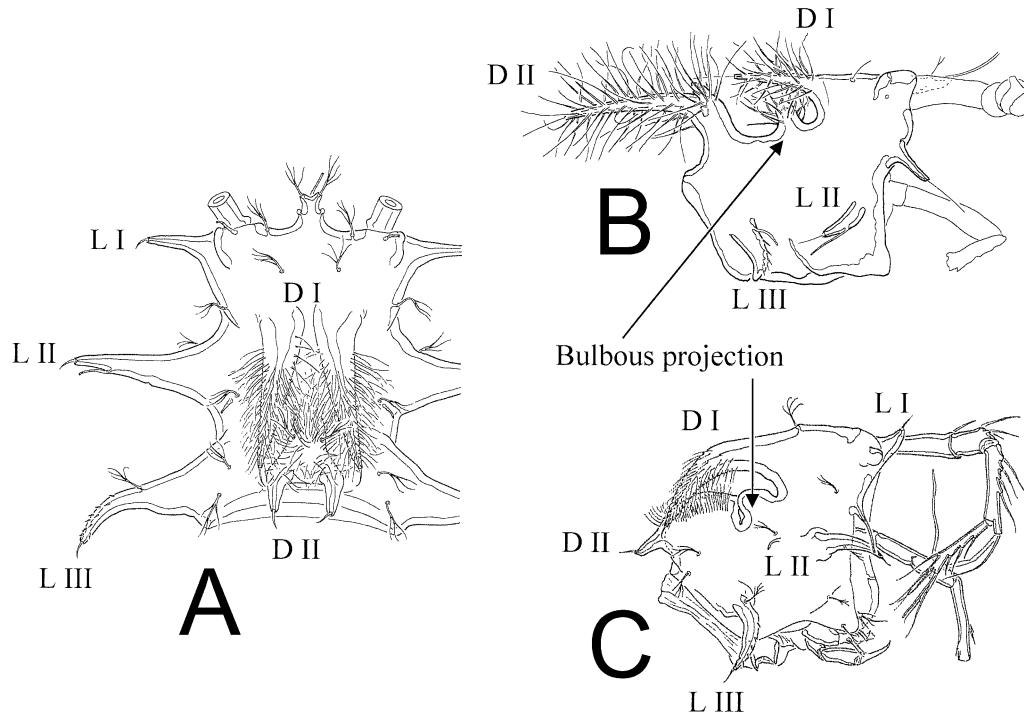


Figure 17. Cephalothorax with dorsal (D I, D II, and D III) and lateral (L I, L II, and L III) processes. A, C, *E. normani* (after Conroy-Dalton, 2003a); B, *E. nogueirae* sp. nov.

Ceratonotus-group, but also with most Ancorabolidae [plesiomorphies in square brackets]:

1. Cphth with dorsal process DI [process not developed]
2. Cphth with dorsal bulbous projection between D I and D II [without bulbous projection]
3. Cphth DI and DII with long hair-like spinules [hair-like spinules not developed]
4. Sensilla on body branched [sensilla not branched]
5. P5 exp inner seta lost [P5 exp with inner seta]
6. First abdominal somite dorsally with fused, V-like processes [such processes absent]
7. Second abdominal somite dorsally with fused, V-like processes [such processes absent]
8. FR elongate between setae III and VII [not elongate]

Character 1: Cphth with dorsal processes D I: Although distal processes (D II; cf. Fig. 17) are common in the *Ceratonotus*-group, no other species of this taxon shows proximal processes (D I, Fig. 17). Their development is regarded as derived and therefore as apomorphic for *Echinopsyllus*.

Character 2: Cphth with bulbous projection between D I and D II: Like the D I, the bulbous projection on the cphth (Fig. 17B, C) is also unique to *Echinopsyllus*. Thus, it is considered as apomorphic for the genus.

Character 3: Cephalothoracic D I and D II covered with long hair-like spinules: The same applies for this character (Fig. 17B, C) as for characters 1 and 2: it is an exclusive and derived feature in *Echinopsyllus* and therefore interpreted as an apomorphy.

Character 4: Sensilla on body branched: Although not discernible in all body parts of the new *Echinopsyllus* species, mainly because of the extensive coverage of the body with detritus, branched sensilla were detected in all three species. They are absent in all remaining Ancorabolinae and therefore considered as apomorphic for *Echinopsyllus*.

Character 5: Inner seta of Exp P5 lost: All remaining members of the *Ceratonotus*-group show an inner seta on P5 exp. Its reduction in *Echinopsyllus* is regarded as apomorphic.

Characters 6 and 7: First and second abdominal somites dorsally with pair of V-shaped processes fused at their bases: This kind of cuticular process is again unique within the entire family Ancorabolidae and apomorphic for the genus.

Character 8: Elongation of FR between seta III and seta VII: Seta VII is commonly located at the distal margin of the FR, set close to ventrolateral seta III, which is located subterminally. In all *Echinopsyllus*

species, seta VII is located dorsally in the median half of the FR, whereas seta III still inserts subterminally at the outer lateral margin. This is in our opinion because of an elongation of the FR between setae VII and III. Such an elongation occurs exclusively in *Echinopsyllus* and is therefore regarded as apomorphic.

Together with *E. normani*, *E. brasiliensis* sp. nov., *E. nogueirae* sp. nov., and *E. grohmannae* sp. nov. present the set of characters 1–8, which are therefore considered as synapomorphies for these species, confirming their monophyletic status. However, all *Echinopsyllus* species obviously show unique apomorphies confirming their status as distinct species. *Echinopsyllus normani* is characterized by the following apomorphies (9–11) [plesiomorphies in square brackets]:

9. Cphth DII with swollen base [base not swollen]
10. A2 enp with third lateral seta very small [seta of moderate length]
11. P4 endopodal seta minute [seta of moderate length]

Character 9: Cphth D II with swollen base: As shown in Figure 17C, the base of D II is remarkably thickened in *E. normani*, which is not the case in any other Ancorabolinae. This character is considered to be an apomorphy for *E. normani*.

Character 10: A2 enp with third lateral seta very small: Comparison with the Brazilian *Echinopsyllus* species reveals that the latter shows a remarkably longer third seta. Because the reduction in size of a usually long seta is generally considered as derived (rather than its elongation), the small seta in *E. normani* is regarded as apomorphic. This assumption is supported by the fact that other and perhaps more basal members of the *Ceratonotus*-group, i.e. *Dorsiceratus* Drzycimski, 1967 and *Pseudechinopsyllus* also have a long third seta.

Character 11: P4 endopodal seta minute: *Echinopsyllus normani* and *E. nogueirae* sp. nov. bear a vestigial P4 enp carrying only a single seta. That seta is of moderate length in *E. nogueirae* sp. nov., but strongly reduced in size in *E. normani*, and is considered therefore as apomorphic for this species.

As expected, the three Brazilian species have characters in common, the derived states confirming a closer phylogenetic relationship to each other than to *E. normani*, which has so far been collected only from northern boreal and subpolar localities. Six synapomorphies (12–17) support the monophyletic status of *E. brasiliensis* sp. nov., *E. nogueirae* sp. nov. and *E. grohmannae* sp. nov. [plesiomorphies in square brackets]:

12. Cphth DII with lateral projection at its base [lateral projection not developed]
13. P2 exp2 without inner seta [inner seta present]
14. P3 exp2 without inner seta [inner seta present]
15. P4 exp2 without inner seta [inner seta present]
16. Mx proximal endite with one seta [with two setae]
17. Cphth LI secondarily lost [present]

Character 12: Cephalothoracic processes D II with lateral projection at their bases: All Brazilian species bear basally branched processes D II (cf. Figs 2A, 7A, 12A, 17B), whereas *E. normani* lacks such branched processes. This is interpreted as a synapomorphy for a 'Brazilian *Echinopsyllus*-group'.

Characters 13–15: P2–P4 exp2 inner seta lost: Whereas *E. normani* bears an inner seta on P2–P4 exp2, the Brazilian species do not. Although we are aware of a certain weakness of the quality of such characters – loss of setae may occur often and independently – in our opinion, the combination of the loss on all three natatory legs 2–4 in the Brazilian species does support their close phylogenetic relationship.

Character 16: Maxillar proximal endite with only one seta: Members of the *Ceratonotus*-group commonly bear three setae on the proximal maxillar endite. Exceptions are observed in *Ceratonotus vareschii* George, 2006a, *Pseudechinopsyllus sindemarkae*, and *E. normani*, which possess only two setae (cf. character 36). Although a closer relation to *C. vareschii* appears to be rather implausible – *Ceratonotus* Sars, 1909 is a well-founded monophyletic taxon with clear autapomorphies (George, 2006b) – the loss of one seta in both *E. normani* and *P. sindemarkae* may indicate a closer relationship between these taxa, as previously suggested by George (2006a). The Brazilian species present a second loss on the maxillar proximal endite, retaining only one bipinnate seta. This is considered as a synapomorphy for *E. brasiliensis* sp. nov., *E. nogueirae* sp. nov., and *E. grohmannae* sp. nov.

Character 17: Cephalothoracic first lateral process L I secondarily lost: Members of Ancorabolinae often show frontolateral processes on cphth (*Ancorabolutus*, *Arthricornua* Conroy-Dalton, 2001, *Ceratonotus*, *Dendropsyllus* Conroy-Dalton, 2001, *Echinopsyllus normani*, *Pseudechinopsyllus*, *Polyascophorus* George, 1998). Such processes are missing only in *Dorsiceratus* and *Touphapleura*. Whether the lack of these 'frontolateral horns' (L I) occurs secondarily in certain taxa of the *Ceratonotus*-group is the object of recent discussion (Conroy-Dalton, 2001; George, 2006a). For

both *Touphapleura* and *Dorsiceratus*, George (2006a) assumed that the lack of L I would be the ancestral condition. Nevertheless, this may perhaps not apply to *Echinopsyllus*. As mentioned above, L I are common within the *Ceratonotus*-group. To explain the lack of L I in *E. brasiliensis* sp. nov., *E. nogueirae* sp. nov., and *E. grohmannae* sp. nov., two possibilities exist: (1) their absence represents the ancestral state as assumed by George (2006a) for *Touphapleura* and *Dorsiceratus*. That would, however, mean that *E. normani* shared the development of L I as a synapomorphy with quite different taxa such as *Arthricornua*, *Ceratonotus*, and *Polyascophorus*, ignoring at the same time its here-demonstrated close affiliation to the Brazilian species and considering characters 1–8 as homoplastic instead of synapomorphic; (2) the absence of L I in the Brazilian species is the result of a secondary loss. Then, their presence in *E. normani* would have to be regarded as the plesiomorphic state, shared with other members of the *Ceratonotus*-group, whereas their loss would be synapomorphic for *E. brasiliensis* sp. nov., *E. nogueirae* sp. nov., and *E. grohmannae* sp. nov. We follow the second alternative.

The Brazilian species show perhaps even more synapomorphies [plesiomorphies in square brackets]:

18. Cphth anterolateral tube pore arising from long projection [projection moderate]
19. Cphth bulbous projection with long hairy spinules [projection bare]
20. Mx enp incorporated into basis [enp distinct]
21. Female P3 enp one-segmented [enp two-segmented]

However, the phylogenetic meaningfulness of these characters cannot yet be confirmed. Description of *E. brasiliensis* sp. nov., *E. nogueirae* sp. nov., and *E. grohmannae* sp. nov. is based on single specimens only, which are partly damaged and of different sexes (*E. brasiliensis* sp. nov., male; *E. nogueirae* sp. nov. and *E. grohmannae* sp. nov., females only). Future re-examination of these characters in additional material will reveal if they are sexually dimorphic or specific. In the latter case, they would support a close relationship between *E. nogueirae* sp. nov. and *E. grohmannae* sp. nov. In the present discussion, characters 18–21 are not taken into account.

PHYLOGENETIC CHARACTERIZATION OF THE BRAZILIAN SPECIES

Echinopsyllus brasiliensis sp. nov.

Only one collected male specimen represents this species. It differs from the remaining Brazilian species in the plesiomorphic retention of a two-segmented P4 enp, but at the same time shows one unique apomorphy:

22. P1 exp2 outer seta geniculate [outer spine]

All remaining *Echinopsyllus* species show as ancestral condition an outer spine on P1 exp2. Thus, its transformation into a geniculate seta is considered as autapomorphic for this species.

Echinopsyllus nogueirae sp. nov.

This species shows the highest number of autapomorphies among the Brazilian species:

23. P5 endopodal lobe without tube pore [tube pore present]
24. FR seta I minute [seta I long]
25. FR elongate between seta III and terminal setae IV–VI [not elongate]
26. A2 enp with four geniculate terminal setae [with three geniculate setae]
27. Abdominal somites laterally with long spinules [spinules of moderate size]

The tube pore is present in almost all Ancorabolinae, so its absence (character 23) is regarded to be a secondary loss. In the remaining *Echinopsyllus* species, furcal setae II and I are of the same considerable length. Reduction in size of seta I (character 24) is therefore considered to be apomorphic. It must be noted that *Pseudechinopsyllus sindemarkae* also shows a reduced furcal seta I. However, as demonstrated below, these species do not show a close relationship to each other, so the presence of this character in both species is regarded as convergent. Additionally to the furcal elongation between setae VII and III (cf. character 8), in *E. nogueirae* sp. nov. the FR are elongate also between seta III and the terminal setae IV–VI (character 25), which is interpreted as apomorphic. Similar reasoning applies to character 26: all remaining *Echinopsyllus* species show three geniculate terminal setae on A2 enp only. The derived presence of a fourth geniculate seta in *E. nogueirae* sp. nov. is therefore regarded as an apomorphy. Additionally, this species shows as a unique and derived feature, long and slender spinules laterally on the abdominal somites (character 27), which does not occur in any other *Echinopsyllus* species and is therefore considered as an apomorphic character.

Echinopsyllus grohmannae sp. nov. seems to be closer to *E. brasiliensis* sp. nov. than to *E. nogueirae* sp. nov. This assumption is based on one derived character shared with *E. brasiliensis*:

28. Md palp with two setae [with four setae]

All remaining *Echinopsyllus* species possess four setae on the mandibular palp, consisting of one basal and three endopodal setae (Conroy-Dalton, 2003a). In both *E. grohmannae* sp. nov. and *E. brasiliensis* sp. nov., the basal seta and one endopodal seta are also

lost (cf. Figs 2B, B', 13B, B'). This is considered to be synapomorphic for both species (but cf. discussion of characters 18–21).

Systematic position of Echinopsyllus within the Ceratonotus-group

Within the *Ceratonotus*-group, *Echinopsyllus* seems to be closely related to *Pseudechinopsyllus*. George (2006a) observed some similarities without analysing their phylogenetic significance. Some features show a derived condition and are re-evaluated here. Thus, nine characters arose (30–38), supporting a close phylogenetic relationship of both *Echinopsyllus* and *Pseudechinopsyllus* [plesiomorphies in square brackets]:

29. Cphth lateral process L II present [process not developed]
30. Cphth L II subterminally with tube pore [tube pore absent]
31. Cphth lateral process L III present [process not developed]
32. Rostrum elongate in its proximal half [rostrum small, constricted]
33. Loss of exopodal seta on Md palp [exopodal seta present]
34. MxI coxa with one seta [two setae]
35. Mx proximal endite with at most two setae [endite with three setae]
36. P1 enp lost [P1 enp at least one-segmented]
37. P2 enp lost [P2 enp at least one-segmented]

Character 29: Cphth laterally with process L II: Within the *Ceratonotus*-group and apart from *Echinopsyllus* and *Pseudechinopsyllus*, only *Ceratonotus* and *Dendropsyllus* possess lateral projections on cphth. However, as observable in the corresponding species descriptions (George & Schminke, 1998; Conroy-Dalton, 2001; George, 2006b), the shape of L II differs considerably, being less chitinized and lacking a tube pore (cf. character 30) in *Ceratonotus* and *Dendropsyllus*. Therefore, the development of L II in *Echinopsyllus* and *Pseudechinopsyllus* is regarded as synapomorphic for both. Future investigations may reveal whether this synapomorphy extends to more taxa.

Character 30: L II subterminally with tube pore: Only *Echinopsyllus* and *Pseudechinopsyllus* bear a subterminal tube pore on L II. It is considered as synapomorphic.

Character 31: Cphth laterally with process L III: A laterodistal process on cphth is observable in several ancoraboline taxa (*Ancorabolina* George, 2006a, *Ancorabolus*, *Juxtaramia* Conroy-Dalton & Huys,

2000, *Uptionyx* Conroy-Dalton & Huys, 2000, *Echinopsyllus*, *Polyascophorus*, *Pseudechinopsyllus*). For both the *Ancorabolus*- and the *Ceratonotus*-groups, convergent development of L III can be concluded, as each group can doubtlessly be distinguished by several autapomorphies (Conroy-Dalton & Huys, 2000; Conroy-Dalton, 2001; George, 2006a), and because both groups enclose species lacking L III, which indicates their independent evolution in each group. Nevertheless, the phylogenetic status of L III remains uncertain, as even *Ancorabolina chimaera* George, 2006a, which cannot be placed either into the *Ancorabolus*- or the *Ceratonotus*-group, and even some species in 'Laophontodinae' also possess such L III. The reason for using this uncertain character is that the L III of both *Echinopsyllus* and *Pseudechinopsyllus* are of similar derived shape, being strongly chitinized and covered with spinules. Thus, L III is regarded as a synapomorphic structure for both taxa.

Character 32: Rostrum enlarged in its proximal half: Within the *Ceratonotus*-group, at least two different lineages may exist concerning the rostral shape and size. *Arthuricornua*, *Dorsiceratus*, *Polyascophorus*, and *Touphapleura* have a small and constricted rostrum, becoming virtually absent in *Ceratonotus* and *Dendropsyllus*, but enlarged in its proximal half in *Echinopsyllus* and *Pseudechinopsyllus*. George (2006a) felt unable to decide which of the conditions might be ancestral or derived. However, the record of *Ancorabolina chimaera* George, 2006a may provide more information. This species, which is considered a basal taxon within Ancorabolinae (George, 2006c), shows a small and constricted rostrum, generally resembling that of the corresponding species named above. Thus, a small rostrum as present in *Ancorabolina* George, 2006a, *Arthuricornua*, *Dorsiceratus*, *Polyascophorus*, and *Touphapleura* may represent the ancestral state. This leads to the conclusion that within the *Ceratonotus*-group in fact two lineages evolved: in *Ceratonotus* and *Dendropsyllus* the former small rostrum reduced even more until it nearly disappeared. However, in both *Echinopsyllus* and *Pseudechinopsyllus* the originally small rostrum began to enlarge in its proximal part, which is regarded as a synapomorphy for both taxa.

Character 33: Loss of exopodal seta on mandibular palp: Most members of the *Ceratonotus*-group bear five setae on the mandibular palp (*Arthuricornua*, *Ceratonotus*, *Dendropsyllus*, *Dorsiceratus*, *Polyascophorus*, *Touphapleura*), consisting of one basal and one exopodal seta, and three endopodal setae. In *Echinopsyllus* and *Pseudechinopsyllus* the exopodal seta is lost, which is considered to be a synapomorphy for both taxa.

Character 34: Maxillular coxa with one seta: Most members of the *Ceratonotus*-group possess two elements on the maxillular coxa, with the exception of *Echinopsyllus* and *Pseudechinopsyllus*, which bear one seta only. This reduction is regarded as synapomorphic for both genera.

Character 35: Maxillar proximal endite with at most two setae: Similar condition as in character 26: most species of the *Ceratonotus*-group show three elements on the maxillar proximal endite, but in *Echinopsyllus* and *Pseudechinopsyllus* one seta is lost, which is interpreted as a synapomorphy.

Characters 36–37: P1 and P2 enps lost: Although the loss of single setae may be a relatively common and convergent derivation, the loss of a whole natatory ramus is probably not. Although Ancorabolinae show several peculiar modifications in their natatory endopods, the complete loss of the latter is a rather uncommon event. In fact, it has been observed only in the *Ceratonotus*-group (cf. Conroy-Dalton & Huys, 2000; Conroy-Dalton, 2001; George, 2006a,b). Within this taxon the loss of P1 and/or P2 endopods appears, however, to be quite disjunctive. Loss of P2 enp occurs in *Arthuricornua*, *Dendropsyllus*, *Ceratonotus steingeri* George, 2006a, *Echinopsyllus*, and *Pseudechinopsyllus*; whereas the loss of P1 enp is observed in *Arthuricornua*, *Echinopsyllus*, and *Pseudechinopsyllus* only. At this time it is unclear if the shared derived characters have to be interpreted as a synapomorphy of all corresponding taxa, or if reduction of P1 and/or P2 enps occurred several times within the *Ceratonotus*-group. Future studies on Ancorabolinae will clarify this question. In the meantime and in combination with the other listed synapomorphies, both characters are also considered as synapomorphic (at least) for *Echinopsyllus* and *Pseudechinopsyllus*, supporting their monophyletic status.

Despite the synapomorphies 29–37 confirming the monophyly of *Echinopsyllus* and *Pseudechinopsyllus*, both genera show several differences. Although *Echinopsyllus* is well characterized by autapomorphies 1–8 (see above), *Pseudechinopsyllus* also presents a set of unique characters [plesiomorphies in square brackets]:

- 38. Rostrum remarkably elongate [rostrum moderately elongate]
- 39. Cphth laterally with additional extremely long tube pore [tube pore absent]
- 40. FR seta II reduced in size [seta II long]

Character 38: Rostrum remarkably elongate: Although retaining a moderate length in *Echinopsyllus*, the rostrum continued its elongation in

Pseudechinopsyllus until reaching its recent considerable length. This is considered to be an autapomorphy for *Pseudechinopsyllus*.

Character 39: Cphth laterally with additional extremely long tube pore: Apart from *Pseudechinopsyllus* no other ancoraboline species presents such a pronounced lateral tube pores on cphth, which therefore can clearly be considered as an autapomorphy.

Character 40: FR setae II (and I) reduced in size: The strong reduction of furcal seta II occurs in no Ancorabolinae except for *Pseudechinopsyllus*. Together with the reduction of seta I (cf. discussion of character 24), it is regarded as an autapomorphy of that taxon.

Incongruent characters 41–46: As is common in phylogenetic analyses, some characters do not support the here presented phylogenetic relationships [plesiomorphies in square brackets]:

- 41. P5 basis and enp fused to benp [P5 enp distinct]
- 42. P1 exp3 first outer element transformed into geniculate seta [remaining as outer spine]
- 43. P5 endopodal lobe with one seta [with two setae]
- 44. P4 enp one-segmented [enp two-segmented]
- 45. P4 enp with one seta [with two setae]
- 46. P5 benp with minute seta [seta of moderate length]

In most Ancorabolinae, P5 shows a fusion of its basis and the enp, forming a baseoendopod (character 41). The retention of a distinct enp in *E. nogueirae* sp. nov. is problematic. As only one female specimen was available for examination, future comparison of other individuals of that species may clarify whether this is a specific character or a malformation. Both *E. normani* and *E. nogueirae* sp. nov. retain a spine as the first outer element on P1 exp3, whereas the remaining *Echinopsyllus* species show its transformation into a geniculate seta (character 42). They share this character with other Ancorabolinae such as *Dorsiceratus* and *Pseudechinopsyllus*, being an indication for convergent evolution of this character. Similar reasoning may apply to characters 43 and 45–46: as discussed above, the loss of homologue setae is of relatively weak phylogenetic value, as it is observed several times within harpacticoid taxa that show no closer phylogenetic relationship, indicating that such reduction has a certain homoplastic property. Thus, the loss of single setae in P5 (character 43), shared by *E. normani*, *E. nogueirae* sp. nov., and *E. brasiliensis* sp. nov. is an indication for rather convergent reduction than for any close relationship, which would contradict the above argument. Character 45 would even place *E. normani* close to *P. sindemarkae*, ignoring the synapomorphies

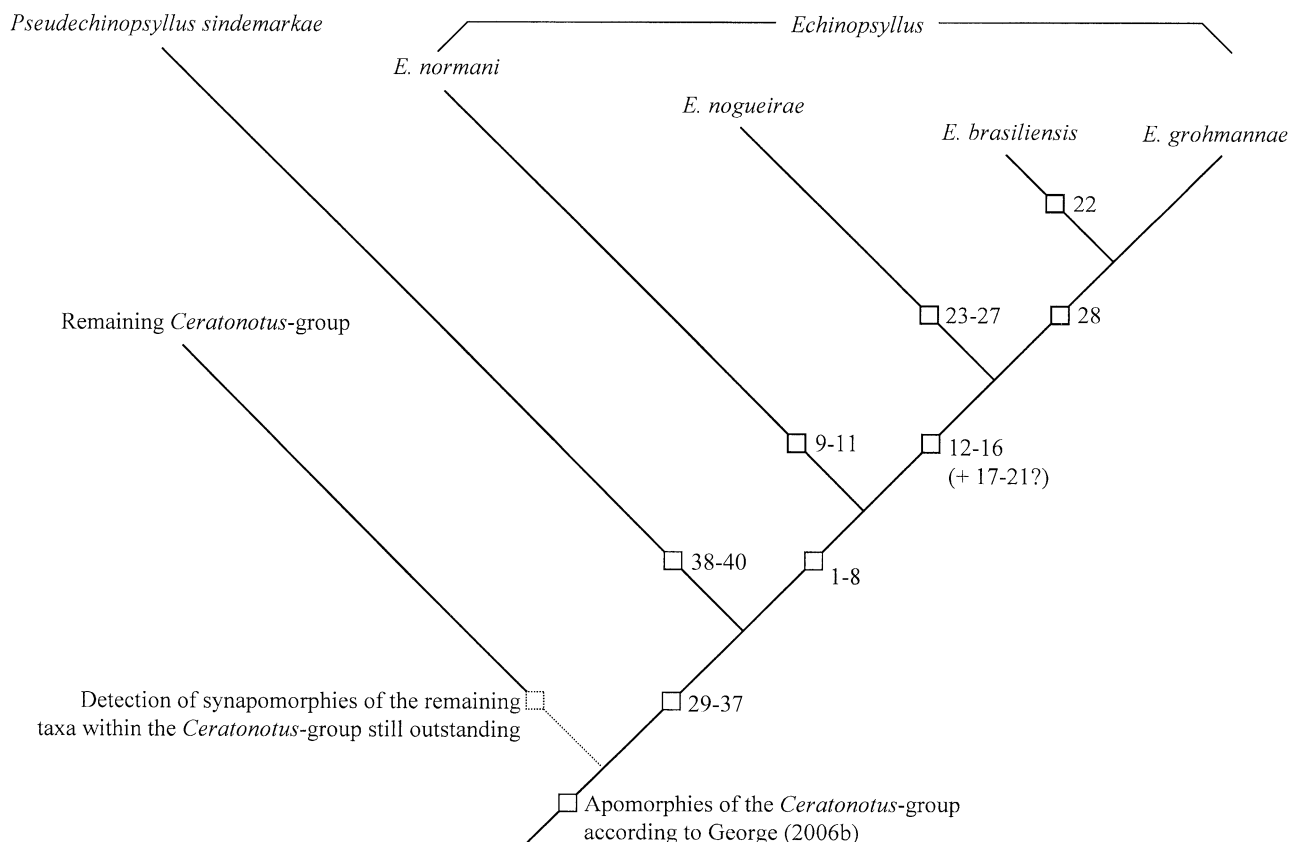


Figure 18. The proposed phylogeny of *Echinopsyllus* based on morphological characters listed in the text.

of the first with the Brazilian species completely. Character 44 suggests a closer relationship of *E. normani*, *E. nogueirae* sp. nov. and *E. grohmannae* sp. nov., with *Pseudechinopsyllus sindemarkae* than it does with *E. brasiliensis*, whereas character 46 excludes Brazilian species *E. grohmannae* sp. nov. and *E. brasiliensis* sp. nov. from that genus. All of these suggestions are based on single incongruent characters and are unable to compete with the argumentation presented above and well founded by characters 1–40.

The discussed phylogenetic relationships concerning *Echinopsyllus* and *Pseudechinopsyllus* within the *Ceratonotus*-group are presented in Figure 18. As a result of the large number of autapomorphies present in *Echinopsyllus*, and because of autapomorphies 38–40 manifested in *Pseudechinopsyllus*, the maintenance of both generic categories appears well justified so far. We are aware, however, that *Pseudechinopsyllus* is a monotypic genus (so far), whose 'generic autapomorphies' may readily turn into specific ones if new species are recorded. Nevertheless, we state that the maintenance of *Pseudechinopsyllus* as a separate genus is at the moment justified because of the large number of strong apomorphies characterizing *Echinopsyllus*, which are not shared by *P. sindemarkae*. At

first sight this may contradict our decision to include the Brazilian species in *Echinopsyllus* instead of assigning them to a new genus. But here, the circumstances are quite different. Whereas *P. sindemarkae* does not fit any of *Echinopsyllus*' autapomorphies, *E. brasiliensis* sp. nov., *E. nogueirae* sp. nov., and *E. grohmannae* sp. nov. do fit them all. Furthermore, erection of a new 'Brazilian' genus would mean that the remaining monotypic genus *Echinopsyllus* would be characterized by just three autapomorphies, which are here regarded as being specific ones of *E. normani*, whereas both genera (*Echinopsyllus* and the 'Brazilian' one) showed the closest phylogenetic relationship based on synapomorphies 1–8. Moreover, erecting a new genus for the Brazilian species would mean that any subsequently detected new species had to show exactly the same three apomorphies of *E. normani* to be assigned to *Echinopsyllus*, which would be senseless, because in that case it would be the same species. Alternatively, if a new species presented a mixture of characters of both *E. normani* and the 'Brazilian genus', it would be impossible to allocate that new species into one of the two genera, and the author would be forced to erect another new genus. The same applies for a new species fitting not all apomorphies of

Echinopsyllus. The result would be an increased number of monotypic genera, all of them showing close relationships to each other, but being separated by several quite narrow 'generic' characters, as recently occurred with groups of taxa such as *Ancorabolus*/*Juxtaramia* and *Ceratonotus*/*Dendropsyllus*. Thus, we prefer instead to assign the Brazilian species to *Echinopsyllus*, expecting that future research may clarify its phylogenetic relationship to the so-far monotypic taxon *Pseudechinopsyllus*.

ACKNOWLEDGEMENTS

This research is part of the Campos Basin Deep-sea Environmental Program. We are grateful to the Brazilian Petroleum Company (PETROBRAS) for granting access to these deep-sea samples. The research was conducted at the Laboratory of Population Dynamics of Benthic Marine Invertebrates, UFPE and the Forschungsinstitut Senckenberg (DZMB). This study was supported by PETROBRAS, CNPq (Research Fellowship 305609/04-1 to PJPS and Post-Graduate Studentship to APW) and Forschungsinstitut Senckenberg (DZMB). We are grateful to the two anonymous reviewers whose valuable comments led to the improvement of this manuscript. The first author is very grateful to Prof. Verônica Genevois (Dept. Zoology- UFPE) for all arrangements to obtain this scientific material and, especially, for her great incentive and friendship. The authors are grateful to Mrs Gisela Moura (Forschungsinstitut Senckenberg) for discussion of some important aspects of this paper. Finally, we would like to express our acknowledgement to the journal editor for his attention and quick and efficient management of submission and evaluation procedures.

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APPENDIX

Data matrix showing characters 1–46 (0 = plesiomorphic state; 1 = apomorphic state; ? = unknown state)

Taxon/ character	<i>Echinopsyllus normani</i>	<i>Echinopsyllus nogueirae</i>	<i>Echinopsyllus grohmannae</i>	<i>Echinopsyllus brasiliensis</i>	<i>Pseudechinopsyllus sindemarkae</i>	<i>Ceratonotus</i> -group
1	1	1	1	1	0	0
2	1	1	1	1	0	0
3	1	1	1	1	0	0
4	1	1	1	1	0	0
5	1	1	1	1	0	0
6	1	1	1	1	0	0
7	1	1	1	1	0	0
8	1	1	1	1	0	0
9	1	0	0	0	0	0
10	1	0	0	0	0	0
11	1	0	0	0	0	0
12	0	1	1	1	0	0
13	0	1	1	1	0	0
14	0	1	1	1	0	0
15	0	1	1	1	0	0
16	0	1	1	1	0	0
17	0	1	1	1	0	0
18	0	1	1	?	0	0
19	0	1	1	?	0	0
20	0	1	1	?	0	0
21	0	1	1	?	0	0
22	0	0	0	1	0	0
23	0	1	0	0	0	0
24	0	1	0	0	0	0
25	0	1	0	0	0	0
26	0	1	0	0	0	0
27	0	1	0	0	0	0
28	0	0	1	1	0	0
29	1	1	1	1	1	0
30	1	1	1	1	1	0
31	1	1	1	1	1	0
32	1	1	1	1	1	0
33	1	1	1	1	1	0
34	1	1	1	1	1	0
35	1	1	1	1	1	0
36	1	1	1	1	1	0
37	1	1	1	1	1	0
38	0	0	0	0	1	0
39	0	0	0	0	1	0
40	0	0	0	0	1	0
41	1	0	1	1	1	1
42	0	0	1	1	1	1
43	1	1	0	1	0	0
44	1	1	1	0	1	0
45	1	0	1	0	1	0
46	1	1	0	0	0	0