



TWO NEW PARASTENOCARIDID GENERA
(COPEPODA, HARPACTICOIDA) FROM SOUTH AMERICA,
INCLUDING A REVISION OF NOODT'S *COLUMBIENSIS*-GROUP AND
THE REDESCRIPTION OF *PARASTENOCARIS TAPAJOSENSIS* NOODT, 1963

BY

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ABSTRACT

The genus *Colombocaris* is proposed for a new species discovered on submerged mosses of a high Andean lake in Colombia. The diagnostic characters of the genus mainly concern the morphology of legs, particularly the endopod of leg 2, leg 3, the endopodite of leg 4 and the peculiar leg 5, the cuticular windows of body segments and the morphology of the furca. The new genus *Noodtcaris* is proposed for three species of the *Parastenocaris columbiensis*-group, viz., *P. columbiensis*, *P. kubitzkii* and *P. roettgeri*, described from the Colombian Llanos Orientales, and for *P. tapajosensis* from the Brazilian Amazonas. This genus is well defined by the ornamentation of the caudal rami and the morphology of legs 2 to 5. The absence of endopod on female leg 3 is a diagnostic character at least for the Colombian species. A key for the identification of the species composing the new genera is provided.

Key words. — Taxonomy, phylogeny, biodiversity, meiofauna, Neotropical region

RESUMEN

Se propone el establecimiento del género *Colombocaris* para una nueva especie descubierta en musgos sumergidos de una laguna altoandina de Colombia. Los caracteres diagnósticos del género están relacionados con la morfología de las patas, en particular el endopodo de la pata 2, la pata 3, la peculiar pata 5, las ventanas cuticulares de los segmentos corporales y la furca. Se propone la creación del nuevo género *Noodtcaris* para las tres especies del grupo *Parastenocaris colombiensis* viz. *P. columbiensis*, *P. kubitzkii* y *P. roettgeri*, descritas de los Llanos Orientales de Colombia, y para

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P. tapajosensis del Amazonas Brasileiro. Este género está bien definido por la ornamentación de las ramas caudales y la morfología de las patas 2 a 5. La ausencia de un endopodo en la pata 3 de la hembras es un caracter diagnóstico para por lo menos las especies de Colombia. Se suministra una clave de identificación de las especies de los nuevos géneros.

INTRODUCTION

Copepods of the family Parastenocarididae Chappuis, 1940 (about 300 species and subspecies) (Defaye & Dussart, 2011; Gaviria-Melo et al., 2017) constitute a species-rich family of harpacticoid copepods with most species inhabiting continental water-bodies (Galassi & De Laurentis, 2004) or semi-terrestrial habitats (Reid, 1994).

Almost all members of the Parastenocarididae dwell in the hyporheic zone of rivers and lakes, phreatic waters and caves (Defaye & Dussart, 2011). A few species inhabit mosses (Boxshall & Hasley, 2004), aquatic plants (Noodt, 1962) and wet soils (Reid, 1994) in semi-terrestrial environments.

In the past, all species belonged to a single genus, *Parastenocaris* Kessler, 1913. A second genus, *Forficatocaris* Jakobi, 1969, was established by Jakobi (1969). Lang (1948) had already recognized eight different groups within the genus *Parastenocaris*. In 1972, Jakobi proposed 24 genera and accommodated therein 98 of the 155 species known worldwide at that time (Jakobi, 1972). Several years later, other genera were established, i.e., *Potamocaris* Dussart, 1979 and *Murunducaris* Reid, 1994 in South America, *Simplicaris* Galassi & De Laurentis, 2004 in Italy, *Cottarellicaris* Schminke, 2013 for several species living around the Mediterranean, *Monodicaris* Schminke, 2009 in West Africa, *Asiacaris* Cottarelli, Bruno & Berera, 2010 in Thailand and *Dussartstenocaris* Karanovic & Cooper, 2011 in Australia. Then, *Horstkutcaris* Karanovic & Lee, 2012 was proposed to include certain species from Germany, the Philippines and the Canary Islands. Finally, *Himalayacaris* Ranga Reddy, Totakura & Corgosinho, 2014 was established for one species from northern India and *Indocaris* Ranga Reddy, Totakura & Shaik, 2016 for 3 species from southeastern India.

During the first 25 years after their establishment, the genera proposed by Jakobi (1972) were not accepted as valid because he applied a very unorthodox model of orbitals based mainly on the morphology of male fourth leg (Reid, 1994). The taxonomic confusion within the family was pointed out by Schminke (1986). In the first decade of the 21st century, Corgosinho & Martínez Arbizu (2005) and Corgosinho et al. (2007) proposed to recognize Jakobi's genera, arguing that they fulfilled the requirements of the ICZN (1999). Subsequently, some genera were redefined. In the Neotropical region, Corgosinho & Martínez Arbizu (2005) re-described *Remaneicaris* Jakobi, 1972, Corgosinho et al. (2010) the genus *Brasilibathynellocaris* Jakobi, 1972 and Corgosinho et al. (2012b) the genus *Siolicaris*

Jakobi, 1972. *Paraforficatocaris* Jakobi, 1972 and *Pararemaneicaris* Jakobi, 1972 were relegated to junior synonyms of *Brasilibathynellocaris* (Corgosinho et al., 2010). Recently, the new genus *Iticocaris* Corgosinho, Martínez Arbizu & Previatelli, 2012 (cf. Corgosinho et al., 2012a) was established to accommodate *Parastenocaris itica* Noodt, 1962 from Central America, previously included by Jakobi (1972) within *Remaneicaris*.

Outside the Neotropical region, other genera proposed by Jakobi (1972) have also been redefined, including *Stammericaris* Jakobi, 1972 (cf. Schminke, 2013) and *Proserpinicaris* Jakobi, 1972 (cf. Karanovic et al., 2012; Karanovic & Lee, 2012) in the Palearctic region.

Species of *Parastenocaris* closely related to *Parastenocaris brevipes* Kessler, 1913 will probably remain the only representatives of the genus *Parastenocaris* (Reid, 1995; Galassi & De Laurentis, 2004; Corgosinho & Martínez Arbizu, 2005; Schminke, 2010), while the other species of the genus will be properly placed in different genera (Karanovic & Lee, 2012). The *P. brevipes*-group has no described representatives in the Neotropical region, although 2 specimens closely related to *Parastenocaris brevipes* were recently found in Brazil (Corgosinho, pers. obs.).

In 2010, Schminke proposed the establishment of two subfamilies, i.e., Parastenocaridinae Chappuis, 1940 and Fontinalicaridinae Schminke, 2010, within the family Parastenocarididae. Within the former one, he accommodated 170 species, and 82 species within the latter (see also Defaye & Dussart, 2011). After Schminke (2010), 17 species were described, 11 belonging to the Parastenocaridinae, 5 to the Fontinalicaridinae and one — *Dussartstenocaris idioxenos* Karanovic & Cooper, 2011 — could not be accommodated in any of both subfamilies.

Today, within the 31 genera of the family Parastenocarididae (Parastenocaridinae with 21 genera, Fontinalicaridinae with 10 genera) listed by Gaviria-Melo & Walter (2017), nine should be redefined or synonymized (Schminke, 2013), eight of them belonging to Parastenocaridinae (*Clujensicaris* Jakobi, 1972, *Entzicaris* Jakobi, 1972, *Italicocaris* Jakobi, 1972, *Lacustricaris* Jakobi, 1972, *Macacocaris* Jakobi, 1972, *Michellicaris* Jakobi, 1972, *Minutacaris* Jakobi, 1972 and *Nanacaris* Jakobi, 1972) and one to Fontinalicaridinae (*Fontinalicaris* Jakobi, 1972).

In the Neotropical region, the genera of the subfamily Fontinalicaridinae, *Forficatocaris*, *Potamocaris*, *Murunducaris* and *Brasilibathynellocaris*, and the species of the *Parastenocaris columbiensis*-group (Noodt, 1972) are monophyletic and endemic to the region. Other species not belonging to these genera are still placed in the genus *Parastenocaris*, waiting for their redefinition. Until today, only one Neotropical genus, i.e., *Siolicaris*, is known to be distributed also outside the region, with one species in the Indian subcontinent (Corgosinho et al., 2012a; Totakura et al., 2014). As already observed by Corgosinho et al. (2012a), the 77 species known from South and Central America are likely to be just a portion of

the highly diversified parastenocaridid fauna of the region. No parastenocaridids have yet been found in the Caribbean Islands.

During a faunal survey of high Andean mountain lakes in Colombia, we discovered a parastenocaridid copepod living in submerged mosses. Only male specimens were found in the sample. This new species shares some characters with *Parastenocaris columbiensis* Noodt, 1972, *P. kubitzkii* Noodt, 1972 and *P. roettgeri* Noodt, 1972, described by Noodt (1972) from the Colombian Llanos Orientales and defined by this author as forming the *P. columbiensis*-group, and *P. tapajosensis* Noodt, 1963 from the Brazilian Amazonas. These characters are particularly the shape of male leg 3, the endopod of male leg 4 and the relative position of the lateral and dorsal setae of the furca. Nevertheless, the new species shows important differences related to the body cuticular window, furca shape and size and structure of leg 5. In the present contribution, we propose the establishment of two genera: one for the Andean species and one for both the *P. columbiensis*-group and *P. tapajosensis*. In addition, we offer a supplementary description for *P. tapajosensis* and an identification key to the species composing the new genera.

MATERIAL AND METHODS

The sample containing harpacticoid copepods from Colombia was collected at the littoral zone of Laguna de Buitrago (for details of the lake, see type locality of the species), using a handnet of 100 μm mesh size. The sample was fixed with 5% formaldehyde (approx. final concentration).

Later, specimens were transferred to lactic acid, measured, dissected in glycerin and mounted on slides with gelatine-glycerin. Specimens were dissected using tungsten needles sharpened in an electrolytic bath consisting of a NaOH solution and a 9 V battery (Camacho & Puch, 1990). Two specimens were mounted in polyvinyl lactophenol in order to study the fine structures with oil immersion. The animals were examined under a Leica DMLB compound microscope. Illustrations were done using a drawing tube mounted on the microscope; final plates were elaborated using the Adobe Photoshop CS3 program after scanning the drawings.

SEM photographs were obtained using a Jeol 840A scanning electron microscope after dehydration in ethanol, critical-point drying with an Emitech K850 and coating with gold with a Jeol JFC-1200 at the Muséum national d'Histoire naturelle in Paris, and with a Philips XL30 Esem microscope and a Jeol JFC-230 HR gold coater at the University of Vienna.

Specimens were deposited at the Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia (ICN-MHN), the Muséum

national d'Histoire naturelle, Paris (MNHN) and the Naturhistorisches Museum Wien, Vienna (NHMW).

The type material on which the redescription of *P. tapajosensis* Noodt, 1963 is based was obtained on loan from the Noodt's Collection deposited in the Deutsches Zentrum für Marine Biodiversitätsforschung, Senckenberg am Meer, Wilhelmshaven (Germany). Drawings were made using a drawing tube on a Leica DMR microscope, equipped with Normarsky interference contrast, at 400× and 1000× magnification. All the characters depicted herein were checked against the literature (Noodt, 1963).

Descriptive terminology follows Huys & Boxshall (1991). However, we used "intercoxal sclerite" (Dussart & Defaye, 2001) to describe the structure connecting the left and right legs of a pair, and "furca" for caudal rami (Schminke, 2010). Names of special structures of parastenocaridids, viz., "apophysis" and "thumb", to describe apical structures of leg 3 of the male exopod follow Noodt (1963).

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 homology of structures, see Glatzel (1991).

Abbreviations used: A1, antennule; A2, antenna; Ae, aesthetasc; enp, endopod; exp, exopod; P1-P6, legs 1 to 6; ur, a somite of the urosome; pers. commun., personal communication; pers. obs., personal observation.

SYSTEMATIC PART

Family PARASTENOCARIDIDAE Chappuis, 1940
Subfamily FONTINALICARIDINAE Schminke, 2010
Genus **Colombocaris** new genus

Generic diagnosis (male).— Small to medium-sized parastenocaridid (363–426 μm) with integumental windows of body segments (if present) only dorsally located. Integumental window on the ur2 strongly reduced. Antennule 8-segmented, second segment armed with 4 setae, geniculated in 2 sections, with last 3 segments coiled, with distal anterior corner of seventh segment not produced into spiniform process. P2-enp almost as long as exp-1, apical margin with elements (setae or spines) of different sizes, one of them as a long seta. P3-enp absent; exp straight, ornamented along the outer margin, apophysis short with apical seta incorporated into the segment, thumb long and thin. P4 coxa without spines on anterior surface; basis without row of spinules between the insertions of the exp and the enp; enp long and unornamented, curved inwards with tips almost touching each other like a forceps, lamelliform in lateral view. Fifth legs without intercoxal sclerite, bilobate, long, reaching far beyond the middle of the urosomite-2, carrying 4 outer setae inserted proximally, distal lobe hypertrophied, extending backwards

like a long tongue. Furcal elements I-III and VII generally inserted opposite to each other at the distal third.

Type species.— *Colombocaris isabellae* Gaviria, Defaye & Corgosinho, 2017.

Etymology.— The prefix of the genus name “Colombo” refers to Cristoforo Colombo, the Italian name of the discoverer of the American continent where the species was collected. The suffix “caris” is the ancient Greek word for a schrimp (gender: feminine, whence the gender of the new name as a whole is also feminine).

***Colombocaris isabellae* new genus, new species**

(figs. 1-6)

Material examined.— Holotype, male ICN-MHN-CR 2719, dissected in 2 slides.

Type locality.— Collected on 13 June 1989 from submerged *Sphagnum*-mosses at the littoral zone, Laguna de Buitrago (4°45'15"N 73°49'44"W), 3000 m altitude, Chingaza Region, Cundinamarca State, Colombia, leg. S. Gaviria.

The following specimens (15) are paratypes, same locality, date and collector as holotype: specimens mounted in glycerin-gelatine: 1 male ICN-MHN-CR 2734, undissected on one slide; 1 male MNHN-IU-2013-8003, dissected on one slide; 1 male NHMW 25498, dissected on 2 slides; 1 male NHMW 25529, dissected on 2 slides. Specimens undissected and mounted in polyvinyl lactophenol: 1 male ICN-MHN-CR 2721 on one slide, 1 male MNHN-IU-2013-8001 on 1 slide. Specimens preserved in ethanol, undissected: 2 males ICN-MHN-CR 2720, 2 males NHMW 25500.

Additionally, 2 male paratypes MNHN-IU-2013-8004 worked up at the Museum in Paris and 3 males paratypes NHMW 25528 worked up at the University of Vienna were used for SEM photographs.

Females were not found in the sample.

Ecology.— *C. isabellae* n. gen., n. sp. was found together with *Elaphoidella paramuna* Gaviria & Defaye, 2015.

Etymology.— Species dedicated to Isabella Gaviria Melo, granddaughter of the first author. The species name consequently is a noun in the genitive singular.

Description of male.— Total length of holotype measured from rostrum to posterior margin of furca (excluding furcal setae) 426 μm , length of longest caudal seta 110 μm . Rostrum small, with demarcation between head and rostrum. Body slender, 6.5 times as long as wide (fig. 3a). Body composed of prosome (consisting of cephalothorax and three somites, first pedigerous somite fused to cephalothorax) and urosome (consisting of fifth pedigerous somite = first urosomite, genital somite, four abdominal somites and furca) (figs. 1a, 3a-b). Prosome/urosome ratio about 0.7. Body somites (except anal one) about 0.7 times as long as broad (fig. 3a). Anal somite longer than other body somites and 1.75 times as long as urosomite 5 (in lateral view). Body somites ornamented with 40 pairs of long sensillae distributed as in figs. 3a and 3b. Urosomite 5 without sensillae.

First urosomite carrying fifth pair of legs. Proximal half of somite with scale-shaped structures ventrally (fig. 5f), paired and apparently located inside the body

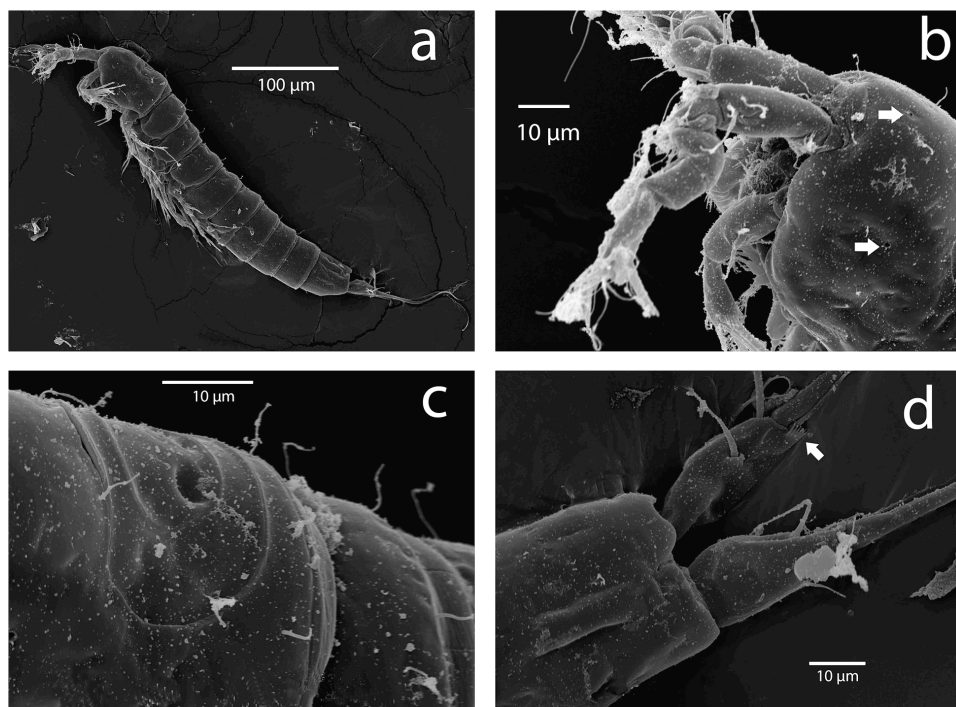


Fig. 1. SEM photographs of *Colombocaris isabellae* n. gen., n. sp., male: a, habitus paratype MNHN-IU-2013-8004, lateral; b, anterior region of cephalothorax, dorsolateral (arrows indicate integumental pores); c, cephalosoma (with integumental window) and first free thorax somite, lateral; d, anal somite and furca (arrow indicates multispinous process), laterodorsal.

as they are not visible in the SEM photograph. Genital somite, third, fourth and fifth urosomites with dorsal integumental windows located on anterior part of somites. Window of cephalosoma consisting of two rings, integumental surface inside inner ring with 2 crater-like concavities, no concavities between inner and outer ring, dorsal surface of cephalosoma with 3 anterior pores (2 of them indicated by arrows on SEM photograph, fig. 1b). Window of genital somite small and oval, windows of urosomites III to V of similar size, quadrate, large and narrow, extending partially below the preceding somite. Lateral windows absent. Anal operculum sub-quadrate (fig. 4b).

Furca (figs. 1d, 3a-b, 4a-b) 3 times as long as broad (maximal length considers inner terminal structure) and about 0.7 times as long as anal somite, with space between rami smaller than one ramus width, dorsally inflated, with inner posterior corner transformed into a multispinose process (indicated by arrow on fig. 1d). Multispinous process consisting of a comb-like structure with 9 spinules (spinules visible only on SEM photograph, fig. 1d). Furca with 7 smooth setae: setae I, II and III (lateral setae) inserted close to each other, at same distance from the base of the

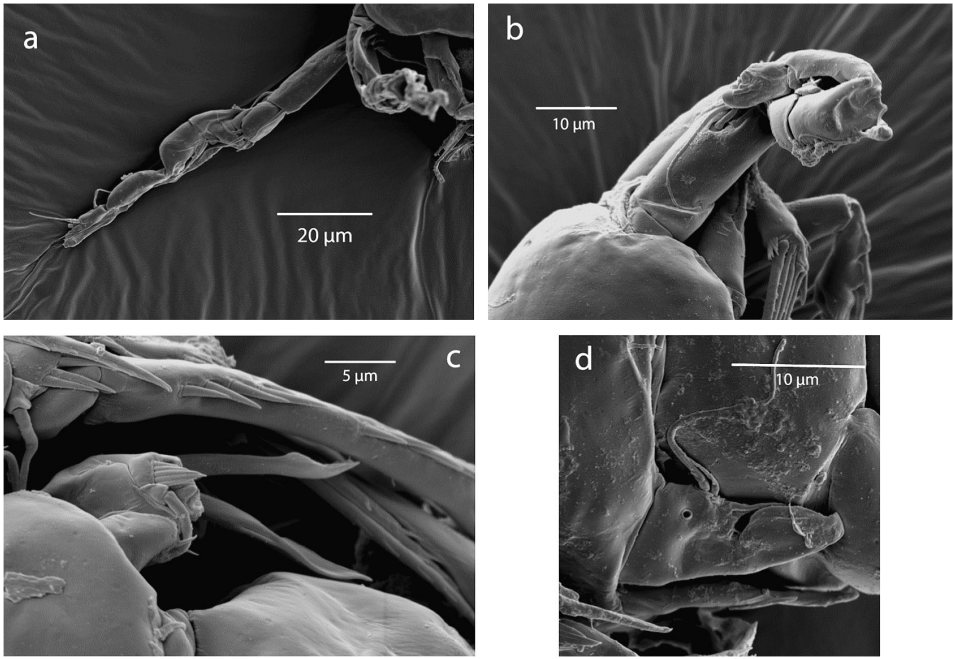


Fig. 2. SEM photographs of *Colombocaris isabellae* n. gen., n. sp., paratypes NHMW 25528, males: a, A1 extended position; b, A1 coiled position, another paratype; c, P2, endopods; d, P5, latero-ventral view.

ramus as seta VII (dorsal seta); seta VII, somewhat shorter than seta IV, inserted near the inner edge of the furca opposite to lateral seta; lateral setae inserted at about 2/3 of ramus length, proximalmost seta (I) shortest, seta II longest, inserted close to seta I and 0.6 times as long as furca, about 5 times as long as seta I; seta III inserted more dorsally than seta I and II, about 0.9 times as long as seta II; seta IV about as long as furca, inserted on dorsal surface subterminally; setae V and VI inserted terminally, seta V, strongest seta and 3.5 times as long as furca, seta VI about 0.5 times as long as furca and inserted slightly ventral to seta V.

A1 (figs. 1b, 2a-b, 5a-b) 8-segmented, prehensile and digeniculate between third and fourth, and between sixth and seventh segments (in geniculate position, last three segments forming a dorsal coil) (as shown in one of the 3 paratypes NHMW 25528 used for SEM photographs, fig. 2b and in fig. 5b). Distal anterior corner of seventh segment not produced into spiniform process. Setal formula: 0 / 4 / 3 / 0 / 1 + Ae (with conjoined basis) + 1 / 0 / 0 / 2 + Ae (= trithek; two subequal setae and Ae with conjoined basis) + 6.

A2 (fig. 5c) composed of coxa, allobasis, 1-segmented enp and 1-segmented exp. Coxa short, distal margin ornamented anteriorly with spinules. Allobasis 2.5 times longer than wide, with exp inserted on middle of outer margin. Exp minute

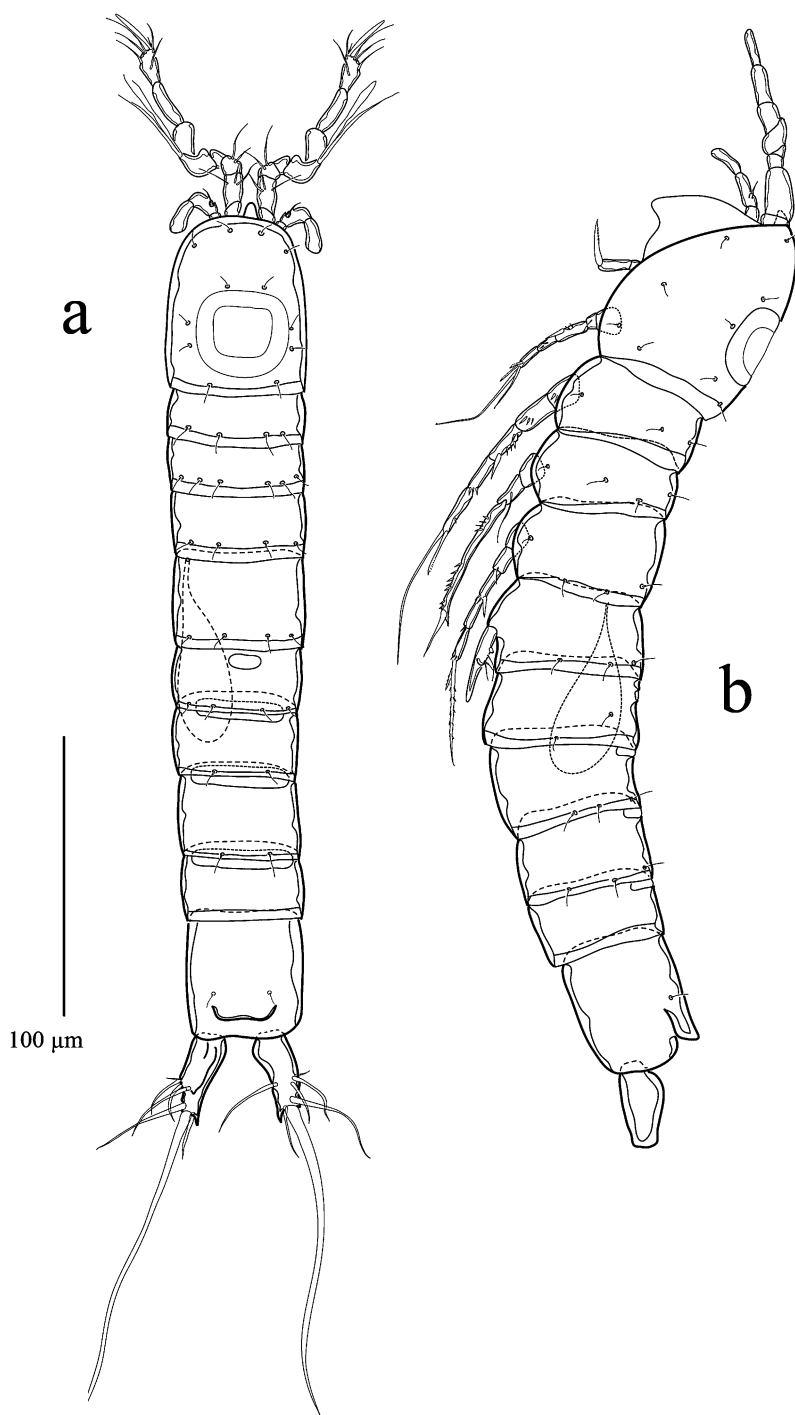


Fig. 3. *Colombocaris isabellae* n. gen., n. sp., male: a, habitus, dorsal; b, habitus, lateral.

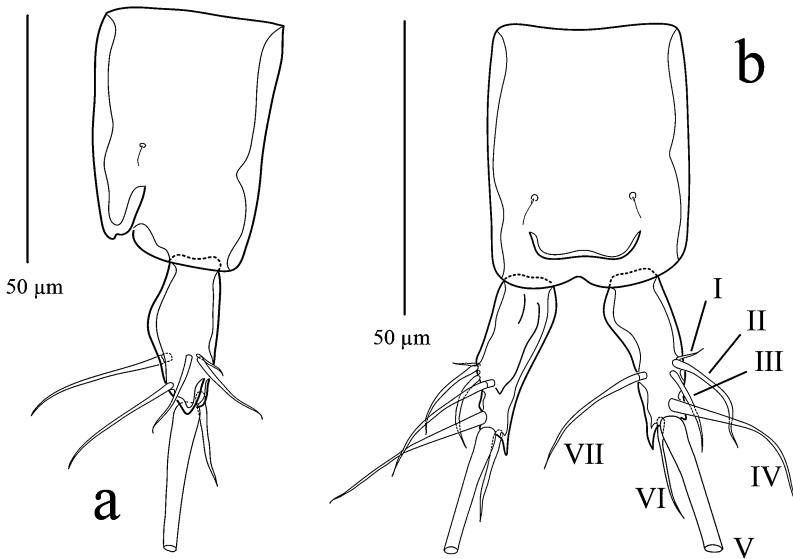


Fig. 4. *Colobocaris isabellae* n. gen., n. sp., male: a, anal somite and furca, lateral; b, same, dorsal. Roman numbers, see text.

(fig. 5d), segment about 3 times as long as wide, armed with naked apical seta, about 2.5 times as long as segment. Enp 1-segmented, as long as allobasis, outer margin armed with 3 spines (both distal spines unipinnate) and ornamented with row of minute spinules proximally, anterior surface ornamented with few distal minute spinules. Inner margin of enp ornamented with spinules (probably 5) near the base of innermost seta of distal margin. Distal margin armed with 5 unipinnate setae, third and fourth geniculate.

Mandible, maxillule and maxilla not observed. Maxilliped (fig. 5e) well developed comprising syncoxa, basis and enp. Syncoxa and basis cylindrical, both unarmed and unornamented (no accessory seta present on basis). Syncoxa short, wider than long. Basis about 2 times as long as broad. Enp drawn out into a long prehensile claw, 2.7 times as long as basis, with swollen basis as indication of ancestral one-segmented enp, anterior margin armed distally with 4 spinules.

P1 (fig. 6a): coxa and intercoxal sclerite unarmed. Intercoxal sclerite very small, quadrate. Basis with seta on outer margin and spinule on anterior surface near inner margin. Exp 3-segmented, inner margin of first and second segments unarmed; first segment armed with unipinnate spine and ornamented with spinules on outer margin; second segment unarmed but ornamented with spinules on outer margin; third segment armed with 1 unipinnate spine and ornamented with spinules on outer margin, apical margin armed with 1 unipinnate outer spine and 1 geniculate inner seta, inner margin armed with long geniculate seta, inserted subapically. Enp 2-segmented, about as long as exp, first segment as long as two first segments of

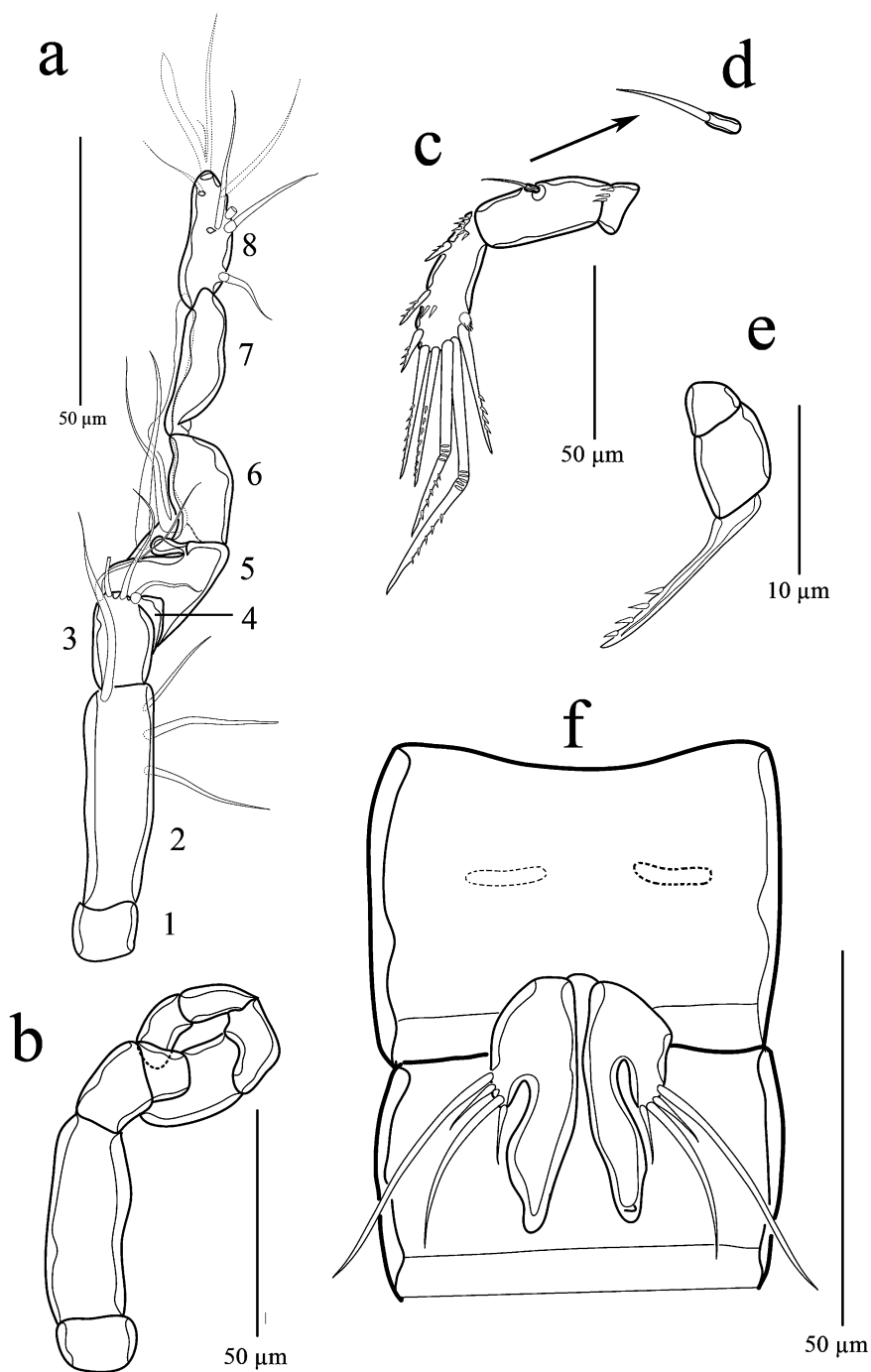


Fig. 5. *Colombocaris isabellae* n. gen., n. sp., male: a, A1 extended; b, A1 coiled (without setae and aethetascs); c, A2; d, A2, exopod; e, maxilliped; f, first and second urosomites with P5, ventral.

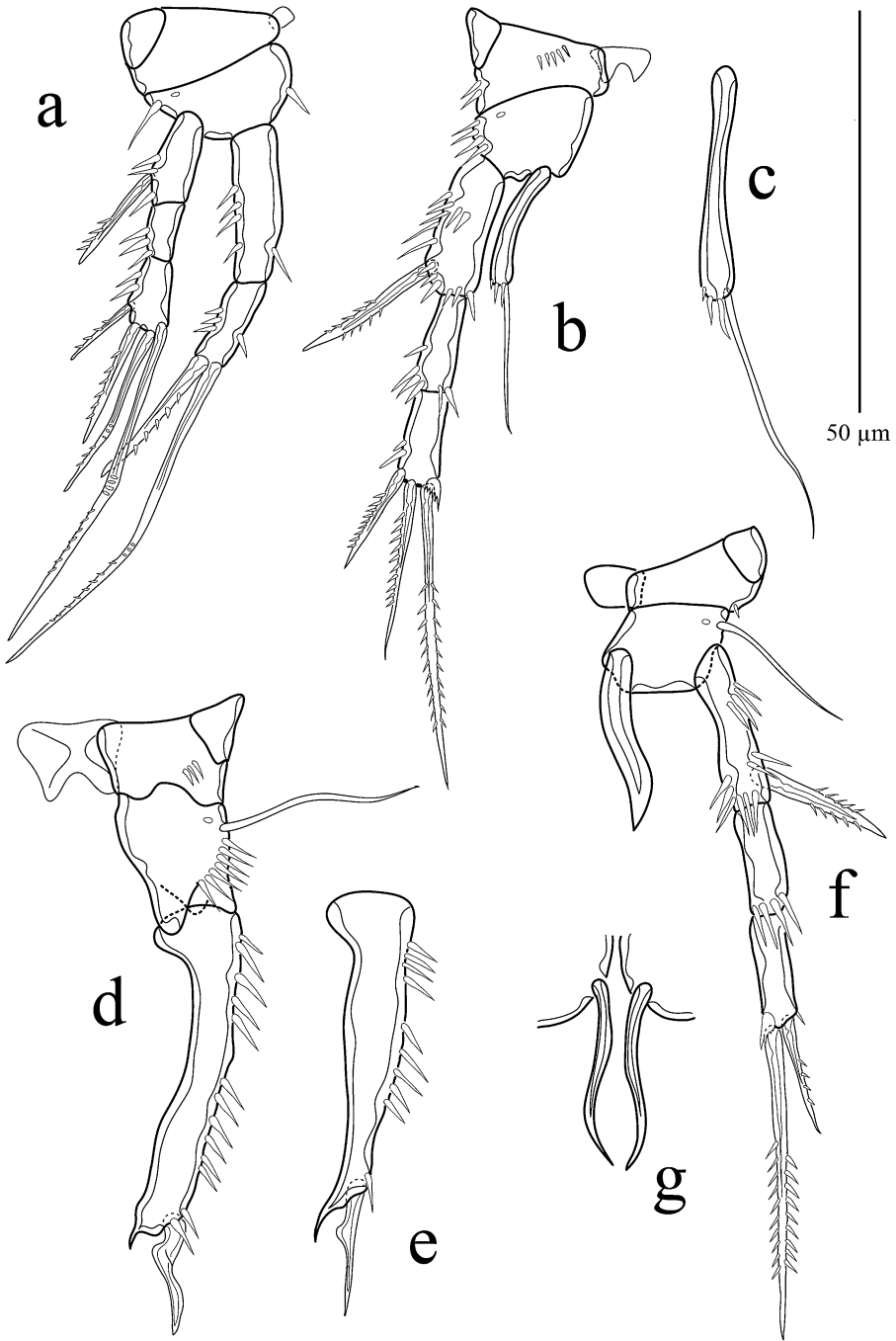


Fig. 6. *Colombocaris isabellae* n. gen., n. sp., male: a, P1, anterior view; b, P2, anterior; c, P2, endopod enlarged; d, P3, anterior; e, P3, exopod inner view (paratype NHMW 25499); f, P4, anterior (endopod turned, lateral view); g, P4, endopods, anterior view (paratype NHMW 25499).

exp, ornamented with 1 spinule on inner margin and spinule row on outer margin; second segment ornamented with 1 spinule on inner margin and 3 spinules on outer margin, apical margin armed with 1 outer unipinnate spine and 1 inner geniculate seta, endopodal geniculate seta 2.6 times as long as first segment, 1.6 times as long as entire enp and slightly longer than large exopodal geniculate seta.

P2 (fig. 6b-c): intercoxal sclerite unarmed, distal margin strongly concave. Coxa, anterior surface with row of spinules, outer distal margin with spinules. Basis, outer margin with row of spinules. Exp 3-segmented; first segment, outer margin armed with bipinnate spine and ornamented with spinules, anterior surface ornamented with spinule row inserted at about 1/3 of segment length and spinule row near distal margin; second segment unarmed but ornamented with 1 spinule on outer margin and spinules near outer and inner distal corners of segment; third segment, outer margin armed with 1 unipinnate spine inserted subapically and ornamented with distal spinules, apical margin armed with outer unipinnate spine and inner bipinnate seta, inner margin with 1 spinule on distal corner. Enp 1-segmented, long, consisting of 1 slender article slightly curved outwards and slightly narrower in the middle, almost as long as exp-1, armed apically with 1 long naked inner seta and 3 curved spinules of different size (fig. 6c), outermost spinule the shortest, naked seta longer than article and longer than exp-2.

P3 (fig. 6d-e): intercoxal sclerite with strong concave distal margin. Coxa, anterior surface with spinule row near distal outer corner. Basis robust, outer margin with long slender naked seta, inner distal corner of anterior and posterior surfaces extended, forming protrusions, anterior protrusion bigger than posterior and ornamented with diagonal row of spinules inserted near outer margin. Exp with both segments fused; proximal ancestral segment, inner margin with proximal protrusion, 3.6 times as long as wide (maximal width corresponds to section on inner protrusion), outer margin ornamented with 2 groups of large spinules, proximal row with 5, distal row with 6 spinules; inner margin concave, with slight distal expansion; ancestral second segment transformed into apophysis, apophysis small, ending with sharp tip and with proximomedial outer process, apophysis ornamented with 2 proximal spinules; lateral thumb 1.6 times as long as apophysis (base of apophysis corresponds to insertion of proximalmost outer spine), thumb curved with strong inner protrusion. Apophysis and thumb without hyaline membrane. Enp absent.

P4 (figs. 2c, 6f-g): intercoxal sclerite without ornamentation. Coxa unarmed and ornamented with only 1 minute spinule on outer margin. Basis robust, with long slender naked seta on outer margin. Exp 3-segmented; first segment with inner margin concave (reception surface for contact of enp), posterior surface with 1 strong bipinnate spine inserted near outer distal corner and spinules near its base, anterior surface ornamented with 1 row of spinules on proximal half of

segment near outer margin and with 1 row of spinules near inner distal corner; second segment unarmed, anterior surface ornamented with spinule row near distal margin; third segment, inner margin with 1 spinule distally, outer margin armed with 1 short unipinnate spine inserted subdistally (ancestral inner spine of apical margin) and with 1 spinule at its base, apical margin armed with 1 large bipinnate seta. Enp consisting of 1 curved simple article with tip directed inwards, reaching in length the last quarter of first exp segment (fig. 6f), article leaf-like in lateral view (figs. 2c, 6f), proximal and medial sections with the same width, tapering distally, article unarmed and unornamented. Right and left enps turned inwards so that proximal margins and tip of articles are close to each other, reminiscent of a forceps (fig. 6g).

P5 (figs. 2d, 5f): legs well developed, without intercoxal sclerite, each leg consisting of an outer short lobe and an inner long lobe; outer lobe armed with 4 smooth setae, outermost seta (ancestral basal one) longest, about 0.9 times as long as entire leg, second seta (ancestral exopodal one) much smaller, about 0.2 times as long as outermost seta and inserted close to it, third seta (ancestral outer endopodal one) about 0.7 times longer than outermost seta, fourth seta (ancestral inner endopodal one) about 0.9 times as long as second seta; inner lobe, proximal section consisting of basal neck, outer margin of lobe with strong middle expansion, distal section of lobe narrow and turned slightly outwards. Leg surface with large pore located ventrolaterally on outer lobe, visible only with SEM microscopy.

P6 (not figured) represented by caudally directed, small, unarmed and unornamented operculum, covering opening of vasa deferentia.

Family PARASTENOCARIDIDAE Chappuis, 1940
Subfamily FONTINALICARIDINAE Schminke, 2010
Genus **Noodtcaris** new genus

Generic diagnosis (male).— Small to medium-sized parastenocaridid (363–454 μm) with integumental windows of body segments (if present) located only dorsally. Antennule 8-segmented, geniculate in 2 sections with last 3 segments coiled, with distal anterior corner of seventh segment not produced into spiniform process. Small P2-enp, shorter than exp-1. P3-exp long and slim, slightly curved inwards, without ornamentation on outer margin, apophysis much longer than wide, with distal seta incorporated into the segment or transformed into a hyaline spine, thumb shorter or as long as apophysis. The absence of the enp on female leg 3 is a diagnostic character, at least for the Colombian species of *Noodtcaris* n. gen. P4 coxa without spines on anterior surface; basis with row of spinules between insertions of exp and enp; enp of male generally longer than exp-1, thin and unornamented, curved inwards with tips almost touching each other like a

forceps, except for *N. tapajosensis* gen. et comb. nov. in which the enp is short and spiniform. Exp-2 and exp-3 of male P4 reaching the same size as exp-1 or becoming larger than exp-1. P5 well developed, long, reaching beyond middle of urosomite-2, triangular or trapezoidal, with setae inserted along outer margin. Furcal elements I-III and VII generally inserted opposite to each other at the distal third.

Type species.— *Parastenocaris columbiensis* Noodt, 1972.

Other species.— *Noodtcaris kubitzkii* (Noodt, 1972) n. gen., n. comb., *Noodtcaris roettgeri* (Noodt, 1972) n. gen., n. comb., and *Noodtcaris tapajosensis* (Noodt, 1963) n. gen., n. comb.

Etymology.— The generic name is in honour of the German copepodologist Wolfram Noodt, who enormously contributed to the knowledge of the Parastenocarididae diversity in the Neotropical region, and combining his family name with the ancient Greek substantive for shrimp, *καρίς* (caris). The gender of the new name is feminine.

¹⁹⁶³
Noodtcaris tapajosensis (Noodt, ~~1972~~) new genus, new combination
(figs. 7-8)

Parastenocaris tapajosensis Noodt, ~~1972~~ 1963

Material examined.— One slide with one dissected male stored on a microscope slide storage map (Map2, side 7; identification: *Parastenocaris tapajosensis* n. sp., T, 1mp, Brasilien); Noodt collection, Deutsches Zentrum für Marine Biodiversitätsforschung, Senckenberg am Meer, Wilhelmshaven (Germany).

Type locality.— Groundwater of the ^{Amazonas}~~Tapajós~~ River at Santarém-AM (Brazil).

Description of male.— Rostrum, integumental windows, sensilla, antenna, mandible, maxilla, maxillula, maxilliped, and body habitus cannot be described from Noodt preparations. Total length as described by Noodt. Anal somite (fig. 7a) smooth, about as long as the previous urosomite, twice as long as furca. Anal operculum smooth and slightly concave (fig. 7a).

Furca (fig. 7a) as described by Noodt, smooth, slightly enlarged posteriorly, 2.75 times as long as wide at its widest region and 3.7 times as long as wide at the slimmest proximal region, with all elements distally inserted, lateral setae inserted opposite to dorsal seta VII, seta II missing, ¹⁹⁶³setae I much shorter (1/4) than seta III, differently than described by Noodt (~~1972~~), who depicted seta I and III of approximately the same length, seta III, IV, and VI and VII approximately of the same length, seta V the longest, proximally enlarged, rat-tail-like, about 4 times as long as furca.

A1 (fig. 7b) not described by Noodt (¹⁹⁶³~~1972~~), 8-segmented, haplocer, segment 1 short and ornamented with small spinules; segment 2 the longest; armature beginning with proximal segment: 0 / 6 / 4 / 1 / 1 + Ae (with conjoined basis) +

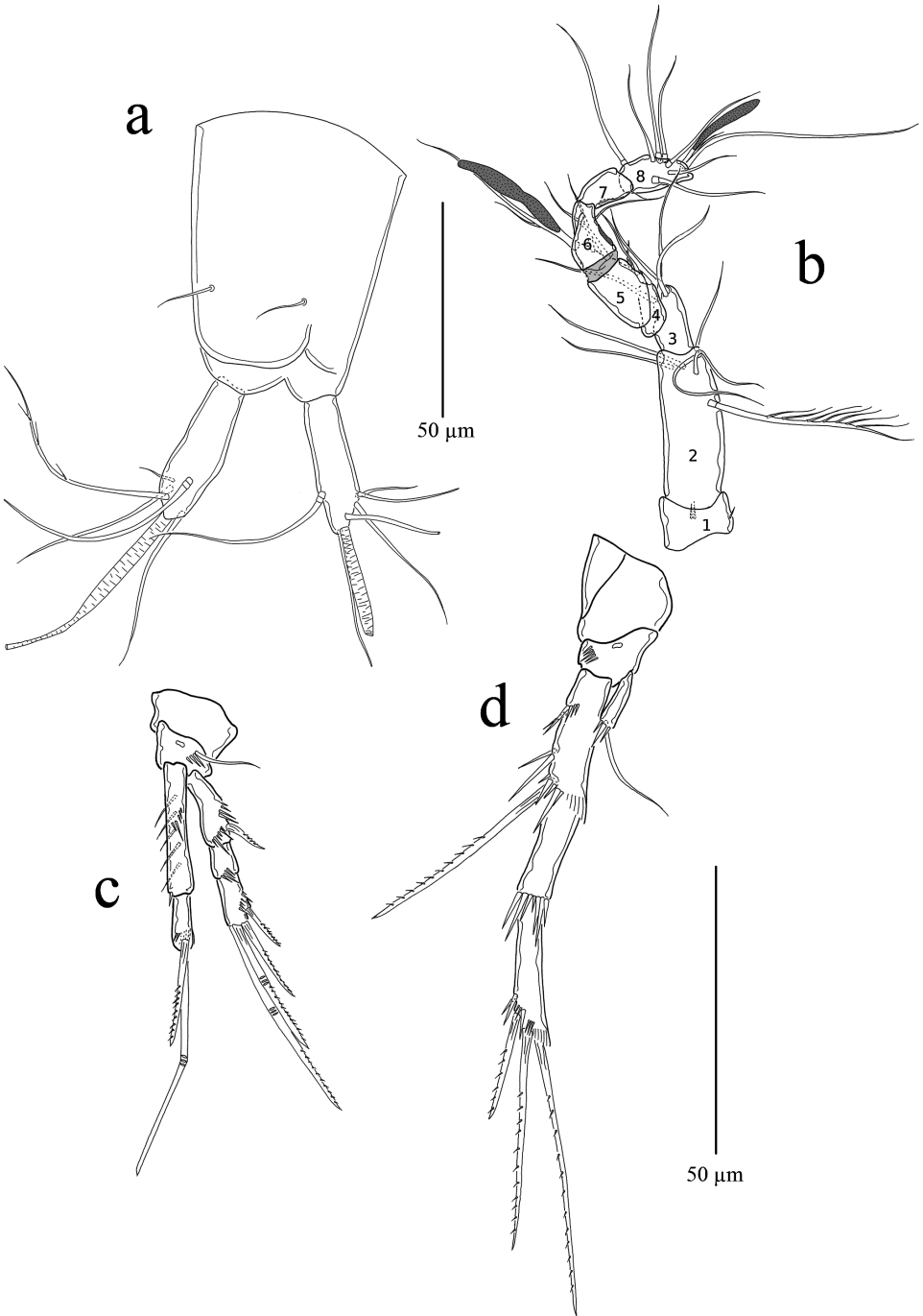


Fig. 7. *Noodtcaris tapajosensis* (Noodt, 1963) n. gen., n. comb., male: a, anal somite and furca, dorsal view; b, A1; c, P1; d, P2.

5 / 1 + modified spine / 1 + modified spine / 2 + aesthetask (trithek; two subequal setae and Ae with conjoined basis) + 7.

P1 (fig. 7c) coxa without ornamentation; basis with outer seta, ornamented with 1 row of spinules on outer margin and 1 pore on anterior surface near distal margin; exp 3-segmented, exp-1 longer than each of the remaining two segments; with spinule row proximal to insertion of outer spine, and spinule row distal to outer spine; exp-2 without armature, with row of distal spinules of unequal sizes at distal margin; exp-3 with spinule row near insertion of outer spine; armed with 1 unipinnate subapical spine, 1 unipinnate distal outer spine and 2 articulate distal setae, distally unipinnate. Enp 2-segmented, enp-1 longer than exp-1 and exp-2 together, with row of long spinules along entire inner margin; outer margin with spinule row at its midlength; enp-2 about 2.5 times shorter than enp-1, with spinule row near outer margin on proximal third of segment and distal hyaline frill; apical edge with 1 unipinnate outer spine and 1 geniculate seta.

P2 (fig. 7d) coxa without ornamentation; basis without outer seta, ornamented with 1 spinule row near outer margin and 1 pore near proximal margin; exp 3-segmented, exp-1 about as long as exp-3 and 1.16 times as long as exp-2, with row of transversal spinules proximally on outer margin; with spinule row located proximal to insertion of outer spine, proximal ones long, a row of spinules of unequal size distal to outer spine and inner hyaline frill, outer spine unipinnated, very long, 1.75 times as long as exp-1, about as long as exp-2 and exp-3 together; exp-2 without armature, with row of spinules of unequal sizes at distal margin; exp-3 with row of spinules of unequal sizes inserted distally to outer spine, row of minute spinules located near insertion of distal outer seta, distal margin with inner hyaline frill, 1 unipinnate subapical spine and 2 unipinnate apical setae, outer seta shorter than inner one; enp subcylindrical, 1-segmented, nearly half the length of exp-1, with 1 smooth distal seta, and three distal spinules.

P3 (fig. 8a): basis rectangular, longer than wide, with outer seta, two long spinules inserted distally to outer seta, and row of minute spinules inserted proximally to enp; enp 1-segmented, spiniform; exp 1-segmented, slender, smooth, slightly curved inwards; thumb distally curved outwards, slightly longer than apophysis; apophysis ventrally enlarged by a continuous hyaline cushion, distal spine blunt, not incorporated into apophysis.

P4 (fig. 8b) coxa with row of spinules on anterior surface inserted near outer margin, basis with outer seta and 1 pore on anterior surface near proximal margin, between exp and enp ornamented with row of long and thin spinules; exp 3-segmented, exp-3 1.14 times as long as each of the previous two segments; exp-1 with row of transversal spinules proximally on outer margin; with row of long spinules located proximally to insertion of outer spine, a row of long spinules distal to outer spine, and inner hyaline frill, outer spine 1.14 times as long as

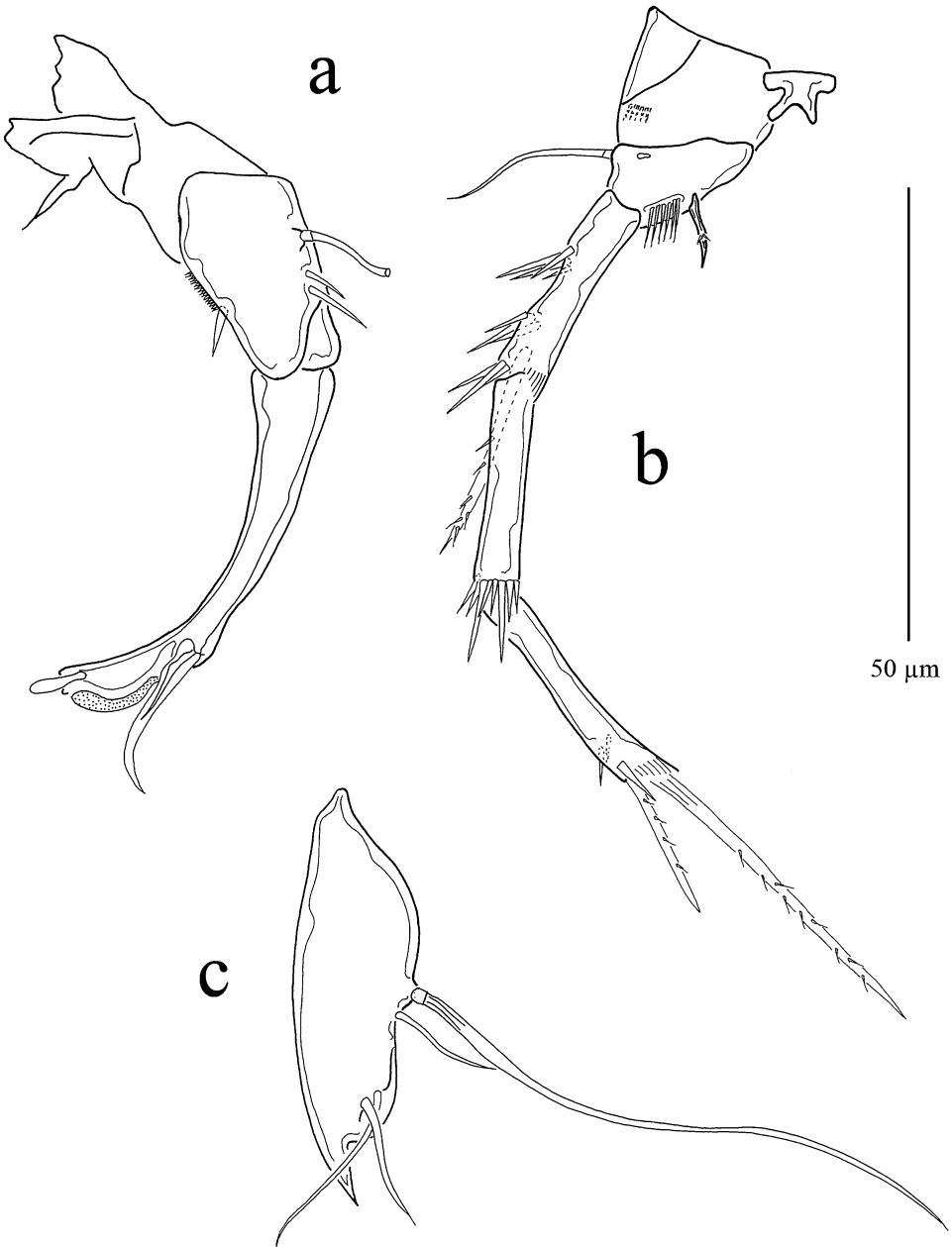


Fig. 8. *Noodtcaris tapajosensis* (Noodt, 1963) n. gen., n. comb., male: a, P3; b, P4; c, P5.

exp-1, as long as exp-3, inserted on anterior surface of segment near outer distal corner; exp-2 without armature, with row of distal spinules of unequal sizes at distal margin; exp-3 with row of spinules anterior to outer spine, and inner hyaline

frill, 1 unipinnate apical spine and 1 bipinnate apical setae, outer spine shorter than inner seta; enp small, spiniform, with very small spinules at distal third, slightly curved outwards.

P5 (fig. 8c) large, salient in lateral view, intercoxal sclerite not observed. Armature different than described by Noodt (1972), with proximal outer basal seta, one small seta near the basal seta and 2 setae inserted on distal half, almost midlength between the proximal outer seta and distal spiniform process.

Female unknown.

DISCUSSION

Relationships of the new genera

Colombocaris is considered as a new genus of the family Parastenocarididae based on the combination of the following characters: (1) male A1 (of coiled type) armed with 4 setae on the second segment, whereas other species of the family usually have 6 setae on this segment (e.g., Schminke, 2009; Ranga Reddy et al., 2016). An exception to this occurs within *Remaneicaris*, which bears 5 setae on the second male A1 segment (Corgosinho et al., 2007); (2) Integumental window on ur-2 strongly reduced; (3) P2 with slender 1-segmented enp carrying at its tip a long naked seta and 3 small spinules; (4) P3-exp with short apophysis and curved tiny apical seta fused to the segment, long and thin thumb with inner median process, and no enp; (5) P4 with basis not bearing spinules between insertions of exp and enp, long enp of P4 leaf-like (in lateral view) and lacking ornamentation; (6) P5 with no trace of intercoxal sclerite, bilobate, with inner lobe extending backwards like a long tongue, outer margin bearing 4 outer setae inserted proximally; and (7) furca dorsally inflated, with an inner distal corner extended as a spinose process, and setae I-III and VII inserted opposite to each other at the distal third.

Males of *Colombocaris* n. gen. reveal to be close to *Noodtcaris* n. gen., sharing the 8-segmented A1, of coiled type; enp P2 shorter than exp-1; P3-exp long, slightly curved inwards; P4-enp shorter or of about the same length as P4 exp-1, thin and unornamented, curved outwards with forceps-like tips (except for *N. tapajosensis* n. gen., n. comb. with short and spiniform enp); P4 exp-2 about the same length of P4 exp-3 (in *Noodtcaris* n. gen. also of the same length of P4 exp-1 or longer); P5 well developed, elongated, reaching beyond the middle of the ur-2, with 4 setae inserted along the outer margin; furcal setae I-III and VII inserted at distal third, opposite to each other. Male of *Colombocaris* n. gen. differs from male of *Noodtcaris* n. gen. particularly by the shape of P5, the structure and ornamentation of P2 to P4, and the armature of the second A1 segment.

Both genera can be considered as belonging to the subfamily Fontinalicaridinae Schminke, 2010. The four species constituting *Noodtcaris* n. gen. were already included in this subfamily by Schminke (2010). Except for the ornamentation of basis and coxa of P4 and the position of lateral and dorsal setae of the caudal rami, *Colombocaris* n. gen. conforms to the distinctive features given by Schminke (2010) for males: antennule of coiled type, morphology of apophysis and thumb of exp P3, and large P5, extending beyond P5-bearing somite.

The *Parastenocaris columbiensis*-group had been established by Noodt (1972) to accommodate the Colombian species *Parastenocaris columbiensis*, *P. kubitzkii* and *P. roettgeri*. According to this author, the inclusion of *P. tapajosensis* within this group was pending confirmation, as well as the description of the female. We, however, propose placing the species of the *P. columbiensis*-group plus *P. tapajosensis* into the new genus *Noodtcaris* n. gen.

The monophyletic condition of the *Parastenocaris columbiensis*-group was briefly addressed by Noodt (1972) and Corgosinho et al. (2012b). Corgosinho et al. (2012b) argued that the group could be placed between the genera *Potamocaris*/*Forficatocaris* and the remaining Neotropical Fontinalicaridinae. According to these authors, this hypothesis is supported by the long and rectangular shape of the basis of the male P3 in *P. columbiensis*, *P. kubitzkii* and *P. tapajosensis*, similar to that of *Brasilibathynellocaris*, *Siolicaris* and *Iticocaris itica*. It is also supported by the structure of the enp of the P4 in *P. columbiensis*, *P. kubitzkii* and *P. roettgeri*, closely resembling that of some *Potamocaris* species. Our new finds raise difficulties in supporting this hypothesis without a proper phylogenetic analysis. *Potamocaris* and *Forficatocaris* seem to be closely related to the African species *Parastenocaris fossoris* Fryer, 1956 and *P. crassicaudis* Chappuis, 1955. They share with them the modified spinule on the enp of male P1, and a male P4-enp curved outwards against an inner row of spinules on the male P4 exp-1, the latter being a character we consider as present in the ground pattern of the monophyletic group *Forficatocaris*/*Potamocaris*. These characters are not found in the original descriptions of Chappuis (1955) and Fryer (1956). However, Fischer (1998, unpublished thesis) extensively sampled the shores of Lake Malawi, finding and redescribing both species. Corgosinho has studied this material (curated by T. Glatzel, Carl von Ossietzky University of Oldenburg, Oldenburg, Germany), confirming the presence of these structures. Additionally, a recent phylogenetic analysis based on several new species of *Forficatocaris* and *Potamocaris* collected during intensive sampling surveys in Brazil (Corgosinho et al., data not shown) revealed that *Potamocaris* is a derived group within the *Forficatocaris*/*Potamocaris* monophylum. Therefore, any similarity of the male P4 enp of the *P. columbiensis*-group with *Potamocaris* must be considered a convergence. Corgosinho, Previattelli and Falavigna da Rocha (data not shown) identified the *Forficatocaris* P4

enp of males, which is courved outwards within *Forficatocaris*, as a basal character for the *Forficatocaris/Potamocaris* monophylum. Within *Potamocaris* some species have an enp slightly courved outwards, this character appearing at the basis of this genus, and almost straight in the derived species. The straight male P4 enp, superficially resembling those of the derived *Potamocaris* species occur in some species of the *Parastenocaris columbiensis*-group. As discussed above, the *Parastenocaris columbiensis*-group does not share synapomorphies with *Forficatocaris/Potamocaris*.

Schminke (2010) recognised two subfamilies within Parastenocarididae, Parastenocaridinae and Fontinalicaridinae. He placed all the then known 258 nominal species within them, after thoroughly checking their original accounts, and also consulting the unpublished data of Ahnert (1994) and Corgosinho (2007) (Ranga Reddy et al., 2014). According to Karanovic & Cooper (2011), this system is “overly simplistic”, and Schminke (2010) failed to define the two proposed subfamilies by a clear set of morphological synapomorphies (Corgosinho et al., 2012a). However, Corgosinho et al. (2012a) and Ranga Reddy et al. (2014) consider the Fontinalicaridinae a monophyletic taxon based on the two following synapomorphies: enp of female P3 lacking a terminal seta (appearing as a relatively short element with a rounded apex), and the roundish shape of the female genital field. Another distinctive but plesiomorphic character is the male antennule of the coiled type.

These three characters warrant some considerations: (1) enp of female P3: the female of *C. isabellae* n. gen., n. sp. is unknown. Among the species of *Noodtcaris* n. gen., there is no endopodite on P3 of females of *N. columbiensis* n. gen., n. comb., *N. kubitzkii* n. gen., n. comb. and *N. roettgeri* n. gen., n. comb.; the female of *N. tapajosensis* n. gen., n. comb. is also unknown (hereafter referred to as *N. columbiensis*, *N. kubitzkii*, *N. roettgeri* and *N. tapajosensis*). This character can be considered as synapomorphic, but cannot be used because not all females of both genera are known; (2) female genital field: Noodt (1972) did not describe the genital field for the species which he included within the *P. columbiensis*-group. Unfortunately, the females are unknown for *Colombocaris isabellae* n. gen., n. sp. (hereafter referred to as *C. isabellae*) and *Noodtcaris tapajosensis*, so that the genital field cannot be used here either to justify the inclusion of these two species within the Fontinalicaridinae; (3) the coiled type male antennules: this character is present in the species assigned to the Fontinalicaridinae (in the subfamily Parastenocaridinae, it is present only in *Remaneicaris*). A A1 coiled-type typical of the Fontinalicaridinae is described for *Colombocaris isabellae* and *Noodtcaris tapajosensis*, but it is not mentioned or figured by Noodt (1972) in his description of *N. columbiensis*, *N. kubitzkii* and *N. roettgeri*. Considering this is a plesiomorphic character within the Parastenocarididae, it cannot be used

to support the inclusion of these 5 species within the Fontinalicaridinae. The alternative pocketknife-like A1 morphology is considered a synapomorphy for the Parastenocaridinae (Ranga Reddy et al., 2014).

Species of *Noodtcaris* n. gen. can be included within the Fontinalicaridinae based on the following characters described by Schminke (2010), which we consider synapomorphic at less inclusive taxonomic levels within this subfamily: (a) in case there are spinules on the basis of male P4, they always are located between enp and exp; (b) P5 of male and female are predominantly large, triangular or trapezoidal plates with a spiniform distal inner corner.

Noodtcaris columbiensis, *N. kubitzkii* and *N. roettgeri* have both the characters mentioned above. In *N. tapajosensis* the presence of a row of fine spinules between the exp and the enp of the male P4 is clearly visible, and the male P5 is strongly enlarged, agreeing with character “b” (see later comments on characters M and N).

The inclusion of *Colombocaris* n. gen. within the Fontinalicaridinae is only possible by establishing synapomorphies shared between this genus and other Fontinalicaridinae genera. Hence, supporting synapomorphic characters are: the morphology of the male P4, which is similar to the condition observed for *Noodtcaris* n. gen. (except for the absence of spinules between enp and exp); the large male P5, a synapomorphy for the Fontinalicaridinae (Ranga Reddy et al., 2014) (independently appearing within certain Parastenocaridinae genera such as *Kinneccaris* and *Monodicaris*), and the insertion of lateral setae at the distal third or at the distal rim of the furca, opposite to the dorsal seta — this character convergently appears as a synapomorphy at different levels of taxonomic resolution, i.e. at the ground pattern of the Parastenocaridinae, and in the Fontinalicaridinae at least within the *Forficatocaris/Potamocaris*- and the *Noodtcaris/Colombocaris*-lineages.

Once the genera *Noodtcaris* n. gen. and *Colombocaris* n. gen. are included within the Fontinalicaridinae, we focus our discussion of character distribution and variability on those species and genera included by Schminke (2010) within this subfamily, with special attention to the Neotropical members of the subfamily.

The position of the lateral and dorsal setae of the furca of the 5 species treated in this contribution differs from Schminke’s (2010) description of the topology of the same setae as being present in the ground pattern of Fontinalicaridinae. He mentioned that these setae are inserted at a distance from one another, the lateral ones being inserted proximally and the dorsal one being inserted distally within the Fontinalicaridinae. Within *Colombocaris* n. gen. and *Noodtcaris* n. gen. the lateral and dorsal seta are inserted at the same level at the distal third of the furca, a character considered synapomorphic for the Parastenocaridinae (Corgosinho et al., 2008; Ranga Reddy et al., 2014). In the Neotropical region, the insertion of the lateral and dorsal setae at the same level also appears in the

two Fontinalicaridinae genera *Potamocaris* and *Forficatocaris*. In *Potamocaris* all setae are inserted at the very distal rim of the furca, in *Forficatocaris* lateral and dorsal setae are inserted at the same level on the distal third or the distal half of the furca. Within other Neotropical Fontinalicaridinae, there is a gap between the proximally inserted dorsal seta and the distally inserted lateral setae. In *Noodtcaris* n. gen. and *Colombocaris* n. gen. the lateral setae and the dorsal seta are inserted proximally on the distal third. In the Fontinalicaridinae *Parastenocaris bolbodes* Kiefer, 1968 from the Tapajós River (Brazil), a species from which only the female is known, the lateral and dorsal setae are at the same level, and they insert at the distal half of the furca. However, the absence of the male makes it impossible to define its relation to *Potamocaris*, *Forficatocaris*, *Noodtcaris* n. gen., *Colombocaris* n. gen. These setae are also inserted at the same level of the furca in species of the genus *Remaneicaris* (Parastenocaridinae), the insertion being located from the distal third to the distal quarter. The exceptions are *R. staheli* Menzel, 1916 and *R. euniceae* Corgosinho & Martínez Arbizu, 2005. Hence, here we assume that this character has convergently evolved within the Parastenocarididae, appearing as a convergent synapomorphy for the Parastenocaridinae and within the Fontinalicaridinae at uncertain levels of taxonomic resolution. Within the Neotropical Fontinalicaridinae, the genera *Murunducaris*, *Brasilibathynellocaris*, *Itiocaris*, *Siolicaris* and the species *Parastenocaris santaremensis* Noodt, 1963 have the typical furcal armature of the Fontinalicaridinae.

The diagnostic characters proposed by Noodt (1972) for the *P. columbiensis*-group are listed in table I.

Character A is too general and of unclear phylogenetic value. Characters B-G and J-K are plesiomorphic and widely distributed within the family Parastenocarididae. A clear one-segmented enp of the male P3 is characteristic of *Remaneicaris* only. All other males of Parastenocarididae have lost this enp (Corgosinho & Martínez Arbizu, 2005) or have it transformed into a small seta or a modified one. A female P4 slim, tapering distally is a character present in the ground pattern of the family. The remaining characters (H, I, L, M and N) hold putative synapomorphic value at different levels of taxonomic inclusiveness.

Character H (female P3-enp completely absent) is probably synapomorphic for the *P. columbiensis*-group, convergently evolving within other Neotropical Fontinalicaridinae genera and species such as *Siolicaris* and *Potamocaris*. As the female is unknown for *Colombocaris* n. gen. and *N. tapajosensis*, it is impossible to state without a proper phylogenetic analysis and character optimization if it is synapomorphic for a clade formed by *Colombocaris* n. gen., *Noodtcaris* n. gen. and *Potamocaris*, reverting to the plesiomorphic condition within *Forficatocaris*, or if it evolved independently at least within both *Noodtcaris* n. gen. and *Potamocaris*. Corgosinho et al. (2012b) revised the genus *Siolicaris* and concluded that within

TABLE I

Morphological characters as listed by Noodt (1972), present (+) or absent (–) in the species of *Noodtcaris* n. gen. and *Colombocaris* n. gen.

Character	<i>Noodtcaris</i>				<i>Colombocaris isabellae</i>
	<i>columbiensis</i>	<i>kubitzkii</i>	<i>roettgeri</i>	<i>tapajosensis</i>	
A Body of intermediate size	+	+	+	+	+
B Integumental windows, if present, only dorsally distributed	+	+	+	+	+
C Anal segment occasionally with weak ventral ornamentation	–	+	–	–	–
D Furca slim, outer setae distally inserted	+	+	+	+	–
E P1 without sexual dimorphism	+	+	+	?	?
F Enp of P2 at most with weak sexual dimorphism	+	+	+	?	?
G Outer spine of exp-2 of P3 (female) and of exp-3 of P4 (female, male) completely distal	+	+	+	+ male ? female	+ male ? female
H Female P3 enp completely absent	+	+	+	?	?
I Exp of male P3 slim, with curved inner margin and mostly with an apophysis with a hyaline element ^a	+	+	+	+	–
J Enp P3 of male very slight or absent ^b	+	+	+	+	+
K Female enp of P4 slim, tapering distally	+	+	+	?	?
L Enp of male P4 directed inwards, curved outwards, frequently with conspicuous distal rim and noticeable marginal structure	+	+	+	–	+
M Basis of male P4 with ornamentation between enp and exp	–	+	+	+	–
N P5 similar in both sexes, enlarged, triangular, close-fitting to the body with strong end tip, with four outer setae, and in male with weak ornamentation on the inner margin	+	+	+	?	?

Lettering according to text.

^a Apophysis corresponds to the inner apical armament of exp.

^b Question mark added by Noodt (1972) on page 111.

this genus the P3 enp of the female is reduced to a spinule or absent. New data from Corgosinho, Previattelli, and Falavigna da Rocha (unpublished) show that this is a derived character within this genus, with a female enp of the Fontinalicaridinae type appearing in new species from Central Brazil.

Character I is weakly defined. We consider it as a synapomorphy for *Noodtcaris* n. gen. when defined as follows: P3-exp long and slim, slightly curved inwards,

without distal ornamentation on the outer margin, apophysis much longer than wide, with distal seta incorporated to the segment or transformed into a hyaline spine, thumb shorter or as long as apophysis. The absence of outer or only distal ornamentation on the exp of male P3 also occurs in *Brasilibathynellocaris*, *Iticocaris*, *Siolicaris*, *Parastenocaris santaremensis* and *P. staheli* Menzel, 1916 within the Neotropical region. *Murunducaris* exhibits a proximal row of spinules and a distal ornamentation composed of one or two spinules, absent only in *M. dactyloides* (Kiefer, 1967). A distal ornamentation is also described for species of *Potamocaris* and *Forficatocaris*, hence supporting our assumption that the absence of distal outer ornamentation on the male P3 exp is a synapomorphy for the genus *Noodtcaris* n. gen. Outside the Neotropical region, a distal ornamentation on the outer margin of the male P3 exp is also absent in the genus *Fontinalicaris* and *Proserpinicaris* (partim). Other species of unclear phylogenetic position within the Fontinalicaridinae, such as *Parastenocaris nigerianus* Chappuis, 1959, *P. jeanninei* Dumont, 1981, *P. kimmi* Dumont, 1981, *P. fossoris* Fryer, 1956, *P. crassicaudis* Chappuis, 1955 and *P. conimbrigensis* Noodt & Galhano, 1969, also have this character. However, two features do not support any hypothesis of close relationship between *Noodtcaris* n. gen. with the genera and species just mentioned above: the ornamentation of the basis of male P4 which, when present, is represented by a single spinule, and the distribution of setae on the furca, with a gap between the lateral setae and the dorsal one.

Character L as described by Noodt (1972) occurs in *Colombocaris* n. gen. and *Noodtcaris* n. gen.; it is absent in *N. tapajosensis*. Except for the latter species, the enp is long and unornamented, curved outwards with tips almost touching each other like a forceps between the legs. A strongly modified exp curved outwards and almost connecting to each other in the middle of the rami is present within *Forficatocaris*, also appearing in many basal species of *Potamocaris* (Martínez Arbizu, pers. commun.; Corgosinho et al., data not shown). We consider this kind of transformation also as a synapomorphy for *Potamocaris* and *Forficatocaris*, independently supporting *Noodtcaris* n. gen. and *Colombocaris* n. gen. Male P4 enp turned outwards and curved also appears within *Brasilibathynellocaris*, in *B. brasilibathynellae* (Jakobi & Loyola e Silva, 1962) and *B. paranaensis* (Jakobi, 1972). Whether it is present in the ground pattern of this genus is a matter of discussion (Corgosinho et al., 2010). Potentially, there is a trend for this kind of transformation in *Murunducaris juneae* Reid, 1994 and *M. loyolai* Corgosinho et al., 2008. In these species the enp of P4 bends proximally, and the enp lamina points to the inner margin. The whole endopodite structure and ornamentation, together with other morphological discrepancies, do not support a close relationship of *Murunducaris* and *Brasilibathynellocaris* with

the genera proposed here and preclude the enp transformation among these genera as homology.

For character M, within the monophyletic group formed by *Colombocaris* n. gen. and *Noodtcaris* n. gen., only *Colombocaris isabellae* lacks ornamentation on the basis of male P4, an autapomorphy for this genus. A row of fine spinules between the exp and the enp of male P4 is present in some species of *Forficatocaris* and *Potamocaris*. The ornamentation of the basis of male P4 between the exp and the enp is practically absent in the remaining Neotropical genera of Fontinalicaridinae such as *Siolicaris*, *Iticocaris* and *Brasilibathynellocaris*. When present, for example in certain species of the genus *Murunducaris*, the ornamentation is represented by a single long spinule or setule. A single spinule between the enp and the exp of male P4 is also present in other Fontinalicaridinae genera such as *Proserpinicaris* (partim) and *Fontinalicaris*, and in some African species of unclear phylogenetic position within this subfamily, such as *Parastenocaris fossoris*, *P. crassicaudis* and *P. kimi*. Two long spinules are present in this region in *Dussartstenocaris bisetosa* Ranga Reddy et al., 2016. To our knowledge, a row of fine spinules as ornamentation between the exp and enp of male P4 occurs only within *Noodtcaris* n. gen., *Forficatocaris* and *Potamocaris*. Nonetheless, as mentioned above, *Forficatocaris* and *Potamocaris* would be closer to *Parastenocaris fossoris* and *P. crassicaudis* than to *Noodtcaris* n. gen. Hence this character would be convergent between *Noodtcaris* n. gen. and the aforementioned genera.

Character N is synapomorphic for the Fontinalicaridinae (Ranga Reddy et al., 2014). In *Colombocaris isabellae* the P5, although modified in this species, superficially fits the character “b” (see above) described by Schminke (2010), being an enlarged limb and reaching beyond the middle of the next urosomite. It also lacks an intercoxal sclerite as a result of its fusion to the somite as shown in *Colombocaris* n. gen. The lack of an intercoxal sclerite on P5 appears convergently within the Parastenocaridinae at least in *Remaneicaris*, *Indocaris*, *Himalayacaris* and *Asiacaris*. To date we have not observed the loss of the P5 intercoxal sclerite in other Fontinalicaridinae except in *Colombocaris* n. gen. Importantly, within the Neotropical Fontinalicaridinae, the male P5 is modified in species of *Forficatocaris*, *Potamocaris* and *Murunducaris*. Within these genera the typical Fontinalicaridinae P5 is present in the females only, although the P5 of the males is large. However, the condition found within *Murunducaris* is not homologous to that described for *Potamocaris*, *Forficatocaris* and *Colombocaris* n. gen. *Murunducaris* seems to be closely related to *P. santaremensis*, with which it shares a hypertrophied P5 intercoxal sclerite with a median process and probably a hypertrophied distal spine on the P5 (which makes the limb so large). In contrast, in *Potamocaris* and *Forficatocaris* the large limb size is conferred by the whole P5 plate which suffers hypertrophy, although a distal exopodal

seta is transformed in *Potamocaris* males, and the proximal-most exopodal seta is transformed in both sexes of *Forficatocaris*. These transformations are not homologous to the condition in *C. isabellae*. In this species all setae are of normal size, proximally inserted, and the distal lobe probably homologous to the typical distal spiniform process. Unfortunately, the female of *Colombocaris isabellae* is unknown, making impossible to discuss possible dimorphism in *Colombocaris* n. gen. Nonetheless, we can assume that the potential for hypertrophy of the male P5 is only a Fontinalicaridinae character. A large P5 has been described for both sexes of the Parastenocaridinae genera *Kinnecaris* and *Monodicaris*. No dimorphic and hypertrophic male P5 is known in these genera.

Other characters with phylogenetic value

Based on the discussion above, *Noodtcaris* n. gen. is supported by the three following characters which are considered synapomorphic (table II):

(O) P3 exp long and slim, slightly curved inwards, without distal ornamentation on the outer margin (see discussion on character I above), (P) P3 exp apophysis completely or partially hyaline, and (Q) elongation of exp-2 and exp-3 of the male P4, reaching the same size of exp-1 or being larger than exp-1.

Character Q is unique within the family Parastenocarididae. The plesiomorphic condition is the exp-1 being larger than each of the following segments. An exception occurs within *Brasilibathynellocaris* and *Forficatocaris*. In these genera, exp-1 is shorter than exp-3 in response to a modification of the exp-1 in males, probably as an adaptation to grasping, involving nonhomologous modifications and structures in these genera. In *Noodtcaris* n. gen., however, exp-1 is normally sized. In the Colombian species *N. roettgeri* and *N. columbiensis*, exp-1 and exp-2 are of the same size, whereas exp-3 is slightly longer than each of the previous segments. In *N. kubitzkii*, exp-1 and exp-3 are of the same size and larger than exp-2. Finally, in *N. tapajosensis* the length of the exopodites increases distally, with exp-1 being slightly smaller than exp-2, which is smaller than exp-3.

An interesting character in the exp 1 of male P2 is evident in *N. tapajosensis*. In this species the outer spine is very long, 1.75 times as long as exp-1 and about as long as exp-2 and exp-3 together. According to Corgosinho et al. (2010), the size of the outer spine of P2 exp-1 is another very distinctive character for the genus *Brasilibathynellocaris*. In all member species of *Brasilibathynellocaris* this spine is longer than usually seen in other parastenocaridids, although not as long as in *N. tapajosensis*. Despite this character, not a single synapomorphy indicates a close relationship between the genus *Noodtcaris* n. gen. and *Brasilibathynellocaris*. In *N. tapajosensis* the outer spine of the male P4 exp-1 is longer.

The genus *Colombocaris* n. gen. is well supported by the following characters which we consider autapomorphic for this genus (table II):

TABLE II

Morphological characters with phylogenetic value within males of the different species of *Noodtcaris* n. gen. and *Colombocaris* n. gen.

Character	<i>Noodtcaris</i>				<i>Colombocaris isabellae</i>
	<i>columbiensis</i>	<i>kubitzkii</i>	<i>roettgeri</i>	<i>tapajosensis</i>	
O P3 exp long and slim, slightly curved inwards, outer margin without distal ornamentation on outer margin	+	+	+	+	—
P P3 exp apophysis completely or partially hyaline	+	+	+	+	—
Q P4 elongation of exp-2 and exp-3, reaching the same size of exp-1 or being larger than exp-1	+	+	+	+	—
R P2 end almost as long as the first exp	—	—	—	—	+
S P3 exp with short apophysis bearing a distal spinule incorporated to the segment	—	—	—	—	+
T P3 thumb longer than apophysis	—	—	—	—	+
U P4 basis without ornamentation	+	—	—	—	+
V P5 bilobed with all setae proximally inserted	—	—	—	—	+
W Furca with dorsal protrusion and inner distal corner extended into a spinose process	—	—	—	—	+
X Ur-2 dorsal integumental window very reduced in size	?	—	?	?	+

Lettering according to text.

(R) The enp of P2 is almost as long as the first exp; (S) the male P3 exp has a short apophysis bearing a distal spinule which is therefore incorporated to the segment; (T) the thumb is longer than the apophysis; (U) the basis of male P4 lacks ornamentation; (V) the male P5 is bilobed with all setae proximally inserted; (W) the furca has a dorsal protrusion and the inner distal corner is extended into a spinose process; and (X) the dorsal integumental window of ur-2 is very reduced in size. Additionally, as a plesiomorphic diagnostic character we can mention the outer margin of male P3 exp being ornamented with spinules along its length, and the inner margin with a proximal hump.

It is not possible to determine if the enp of P2 (character F, table I) is dimorphic for *C. isabellae*, although dimorphism of the enp of the P2 — with this structure appearing stronger, or longer, or more ornamented in the male — is well documented for the Fontinalicaridinae. According to Corgosinho et al. (2008), all species of *Murunducaris* have a more or less pronounced dimorphism in the enp of the P2 of males. This condition is more developed in *M. juneae*,

M. loyolai and *M. noodti* Corgosinho et al., 2008, appearing in *M. juneae* as a foliaceous structure. In *M. dactyloides* it is less conspicuous. A stronger P2 enp is also evident, for example, in species of *Brasilibathynellocaris*, *Itiocaris itica* (Noodt, 1962), *P. santaremensis*, *P. fossoris*, *P. crassicaudis* (Corgosinho, pers. obs.) and in the species close to *Fontinalicaris fontinalis* (Schnitter & Chappuis, 1915), e.g., *Fontinalicaris hispanica* (Martínez Arbizu, 1997). With the exception of *Brasilibathynellocaris brasilibathynellae* and *B. paranaensis*, in none of these genera and species is the enp as long or almost as long as exp-1. Other species of South American parastenocaridids, such as *Siolicaris jakobii* (Noodt, 1963), *S. siolii* (Noodt, 1963) (Corgosinho, pers. obs.) and species belonging to the genera *Potamocaris* and *Forficatocaris* (except *F. shadeni* Reid, 1982), do not have this character; rather, when dimorphism is verified, it involves only minor differences in small ornamentation. Dimorphic P2 enp also seems to be present in the *P. columbiensis*-group of Noodt (1972), but this is difficult to evaluate and this character needs to be reinvestigated. For character R, a male P2 enp as long or almost as long as the first exp occurs in *C. isabellae*, *Brasilibathynellocaris brasilibathynellae* and *B. paranaensis*, being dimorphic in the last two species. The evidence here points to a convergent evolution of the dimorphism of P2 enp within the Fontinalicaridinae.

Considering characters S and T, a clear autapomorphy for *Colombocaris* n. gen. is indicated by the exp of the male P3: a short apophysis, quadrate, almost as long as wide, with incorporate, but conspicuous distal seta and a thumb longer than apophysis. The closest genus *Noodtcaris* has an apophysis longer than wide, whereby the distal spine, in many cases, is not fused to the apophysis, this being considered a plesiomorphic condition for this subfamily (Ranga Reddy et al., 2014). In *Noodtcaris* n. gen. the thumb is at most slightly longer than the apophysis. The apophysis is short and robust in some *Siolicaris* such as *S. sioli* and *S. sandhya* (Ranga Reddy, 2001), and the thumb is much longer within this genus. Nonetheless, in these species the apophysis is already longer than wide. Outside of the Neotropical region, to our knowledge, a short apophysis co-occurring with a longer thumb is present only in *Dussartstenocaris bisetosa* (to some extent also *Dussartstenocaris idioxenos* Karanovic & Cooper, 2011) and *Parastenocaris* (*Siolicaris species inquirenda*) *xyrophora* Noodt & Galhano, 1969. These species and *Siolicaris* are clearly not closely related to *Colombocaris* n. gen. as evidenced by the enp of male P4 and the arrangement of the furcal armature.

Character U occurs only in *Colombocaris* n. gen. As discussed above for character M, a fine row of spinules at the basis between the exp and the enp of male P4 is present within *Noodtcaris* n. gen. (except *N. columbiensis*), also occurring in some species of *Forficatocaris* and *Potamocaris*.

Character V is unique within the Parastenocarididae. Something closer to a bilobed male P5 can be found in *Parastenocaris matopoica* Wells, 1965 and *P. fossoris* (Corgosinho, pers. obs.). In these species, however, a closer observation does not support homology. In *C. isabellae* the proximal lobe develops as the result of an invagination of the outer margin; the distal process loses the distal spiniform morphology, probably due to hypertrophic growth in this region, and all setae are inserted proximally on the outer margin. In contrast, in *P. fossoris* (pers. obs.) and probably also in *P. matopoica*, the lobe is formed between the inner spiniform process and a hyperthrophied outer spine apparently fused to the P5 distal margin, conferring to the limb a long and pointed tip. A completely different bilobed male P5 was described for *P. xyrophora* (see Noodt & Galhano, 1969). In this species the lobe is positioned between the exp seta I and the exp seta II. The P5 has a rounded inner margin and the setae are arranged distally.

A male with a dorsal protrusion of the furca (character W) is considered unique to *C. isabellae*. A modified furca occurs in males of *Forficatocaris*, but was not reported in other Fontinalicarididae. We are unable to determine whether this is a dimorphic character, with a normal condition or even a much more modified version in the female. What can be stated here, however, is that the transformation of the furca, with leaf-shaped or bulbous form, normally occurs in females.

The phylogenetic importance of integumental windows (character X) has only recently received some attention. Corgosinho et al. (2007) used the distribution and position of this structure to address the phylogeny of *Remaneicaris*. Schminke (2009) discussed the lateral position of the integumental windows in *Monodicaris* to support a close relationship of this genus with *Kinnecaris*, and the absence of integumental windows was described for *D. idioxenos* by Karanovic & Cooper (2011). The first researchers who studied the family, however, attached little importance to this character. Even Noodt in his series of publications on the family (Noodt, 1955, 1962, 1963, 1965, 1972; Noodt & Galhano, 1969) neglected these structures. Hence, not much information can be extracted from the literature. The recent study of Neotropical Parastenocarididae and the comparison of data with new and old descriptions when the habitus was described, lead us to the following conclusion. Within Neotropical Fontinalicaridinae, the integumental windows are present dorsally in all urosomites in *Murunducaris*, *Brasilibathynellocaris*, *Iticocaris*, *Potamocaris* and *Forficatocaris*. *Parastenocaris santaremensis* exhibits an integumental window at least on the last urosomite before the furca. Only *Potamocaris* and *Forficatocaris* have relatively large, mostly rectangular dorsal integumental windows which cover, as a belt from side to side, the dorsal margin of each urosomite. In *Murunducaris* and *Brasilibathynellocaris* the windows are relatively small, oval, and do not cover the whole dorsal margin. Our observation of Noodt's material containing *Siolicaris* and *P. santaremensis* does not shed much

light on the issue because this material has been dissected and the urosomites are lost. Nonetheless, the original descriptions, in which the last urosomites are depicted, enable some discussion. The dorsal window of the last urosomite of *Iticocaris* and *P. santaremensis* (see Noodt, 1962, 1963) is of the same type found in *Murunducaris* and *Brasilibathynellocaris* (see Corgosinho, 2008, 2010). The redescription of *I. itica* by Corgosinho et al. (2012) indicates that the condition found in *Murunducaris* and *Brasilibathynellocaris* also occurs in *Iticocaris*. No integumental window is described for *Siolicaris* by Noodt (1963), but Corgosinho et al. (2012) illustrate a small dorsal window in the last urosomite of *S. jakobi* (Noodt, 1963). Its absence in the last urosomite before the furca is described for *N. tapajosensis*, *N. columbiensis*, *N. kubitzkii* (for which Noodt describes a dorsal integumental window on urosomite 3 similar to those of *Potamocaris* and *Forficatocaris*) and *N. roettgeri* (see Noodt, 1963, 1972), which could be a synapomorphy for this genus. The low detail in the description of *P. staheli* precludes any conclusion. The complete absence of integumental windows is described, for example, for *D. idioxenos* by Karanovic & Cooper (2011). The condition which we describe for *C. isabellae* is unique inside the Fontinalicaridinae and probably unique in comparison with other species within the family Parastenocarididae. In *C. isabellae* the windows on urosomites three to five are dorsal and similar in shape and size to those in *Potamocaris* and *Forficatocaris*. However, the dorsal integumental window of urosomite-2 is much smaller, a character hitherto found only in this genus.

Colombocaris isabellae was collected in submerged mosses of a high Andean lake. Only two other species of the family in South America, *Parastenocaris surinamensis* Menzel, 1921 and *Parastenocaris staheli* Menzel, 1916, are known from epigeal habitats and were collected in mosses in Suriname. *P. surinamensis* should be considered as *species inquirenda* (Wells, 2007) due to its incomplete description based on a single male originated from a dry sample (Menzel, 1916); Schminke (2010) did not include it within any of the subfamilies of Parastenocarididae. This species clearly differs from *C. isabellae*. *Parastenocaris surinamensis* has longer furca, being as long as the anal somite (0.7 times as long as the anal somite in *C. isabellae*), and P5 consists of an acute plate with lateral knobs armed with setae (bilobate plate in *Colombocaris* n. gen.). The main differences to the male of *P. staheli* are the P5 formed by an acute plate whose inner margin is ornamented with spinules (naked and bilobed in *C. isabellae*) and the male exp P3, which is smooth along the outer margin in *P. staheli* (ornamented in *C. isabellae*). The 2-segmented enp of P4 in *P. staheli* should be considered as an error in the description because no Parastenocarididae has 2-segmented enps on P2 to P4 (Martínez Arbizu & Moura, 1994; Corgosinho et al., 2007).

The phylogenetic position of the new genera within the Fontinalicaridinae is difficult to address. It remains unclear whether the Neotropical Fontinalicaridinae constitutes a monophyletic group and how closely other genera and groups of species outside the Neotropical zone are related to them.

KEY FOR THE IDENTIFICATION OF SPECIES OF THE GENERA *COLOMBOCARIS* AND *NOODTCARIS*

Males

1. P5 consisting of bilobate plate, inner lobe transformed into large tongue-like process *C. isabellae*
– P5 consisting of triangular or semi-oval plate, with acute posterior tip 2
2. P5 consisting of semi-oval plate *N. tapajosensis*
– P5 consisting of triangular plate 3
3. P3 without endopod. Exopod, outer margin with 5 proximal spinules *N. kubitzkii*
– P3 with endopod, represented by 1 spinule. Exopod, outer margin without spinules 4
4. P4 basis with row of hairs on distal margin between endopod and exopod. Endopod with distinctly separated apical section. P5, basal margin slightly larger than outer margin *N. roettgeri*
– P4 basis without row of hairs on distal margin between endopod and exopod. Endopod with fused apical section. P5, basal margin shorter than 0.5 times outer margin *N. colombiensis*

Females (females of *C. isabellae* and *C. tapajosensis* are unknown)

1. P5 long and narrow, inner margin more than 2 times as long as basal margin *N. colombiensis*
– P5 short and broad, inner margin less than 2 times as long as basal margin 2
2. P1 endopod, first segment reaching 1/2 the length of second segment of exopod *N. kubitzkii*
– P1 endopod, first segment reaching 3/4 the length of third segment of exopod *N. roettgeri*

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